ABSTRACT

Title of Dissertation: SPATIAL CONTRAST SENSITIVITY OF BIRDS

Mimi M. Ghim, Doctor of Philosophy, 2003

Dissertation Directed By: Professor William Hodos
Department of Psychology

Contrast sensitivity (CS) is the ability of the observer to discriminate between adjacent stimuli on the basis of their differences in relative luminosity (contrast) rather than their absolute luminances. Prior to this study, birds had been thought to have low contrast detection thresholds relative to mammals and fishes. This was a surprising phenomenon because birds had been traditionally attributed with superior vision. In addition, the low CS of birds could not be explained by retinal or optical factors, or secondary stimulus characteristics. Unfortunately, avian contrast sensitivity functions (CSFs) were sparse in the literature, so it was unknown whether low contrast sensitivity was a general phenomenon in birds. This study measured CS in six species of birds sampled across different taxa and different ecological backgrounds in order to answer this very question. The species chosen for this experiment were American kestrels (*Falco sparverius*), Barn owls (*Tyto alba*), Japanese quail (*Coturnix coturnix japonica*), White Carneaux Pigeons (*Columba livia*), Starlings

(*Sturnus vulgaris*), and Red-bellied woodpeckers (*Melanerpes carolinus*). CSFs were obtained from these birds using the pattern electroretinogram (PERG), and compared with CSFs from the literature.

The quail and pigeon data obtained in this experiment fit well with existing CS data for these species. The kestrel data were not similar to kestrel data in the literature; however the data in the literature were collected from a single subject. All of the birds studied had contrast sensitivities that were consistent with their retinal or optical morphologies relative to other birds (in species for which such data exists) and seem well suited for their natural environments. In addition, all of these birds exhibited low CS relative to humans and most mammals, which suggests that low CS is a general phenomenon of birds. Explanations for this avian low CS phenomenon include a possible trade-off between contrast mechanisms and UV mechanisms in cone systems, and lateral inhibitory mechanisms that are perhaps categorically different from mammals. Lateral inhibition affects contrast gain, and has been shown to differ according to ganglion cell types, which in turn will differ in vertebrate species.

SPATIAL CONTRAST SENSITIVITY OF BIRDS

by

Mimi M. Ghim

Dissertation submitted to the Faculty of the Graduate School of the
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Advisory Committee:
    Professor William Hodos, Chair
    Professor Catherine Carr
    Professor Robert Dooling
    Professor Cynthia Moss
    Dr. Vittorio Porciatti
    Professor David Yager

DEDICATION

To Smoosh.

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CHAPTER 1: INTRODUCTION

Survival in the visual environment depends on the ability to use the properties of light to find food, select a mate, avoid predators, and care for young. Among these properties are (1) the wavelength of light, (2) the intensity of light, (3) relative light intensity or contrast, and (4) the spatial and temporal distributions of the first three properties. One of the factors in the evolutionary success of birds in terms of their large numbers of species and the wide range of environments that they inhabit, has been their exploitation of these properties of the visual world. For example, birds have at least three, and often four or more cone photo-pigments, which in combination with colored oil-droplets that act as additional wavelength filters, act to create many more spectral sensitivity maxima (Bowmaker, 1977; Chen and Goldsmith, 1986). These pigments and oil-droplets give birds richer color vision than could ever be experienced by humans with their three cone photopigments and no oil-droplets. Birds are even capable of utilizing the ultra-violet portion of light, as demonstrated in behavioral studies using pigeons (Emmerton, 1983; Remy and Emmerton, 1989; Wright, 1972) and passerines (Bennett and Cuthill, 1994; Bennett et al., 1997; Smith, Greenwood, and Bennett, 2002).

Birds also possess superior acuity, which is the ability to resolve tiny objects or fine detail. Hawks and eagles are especially notorious for having acuities that far outstrip human acuity (Fox, Lehmkuhle, and Westendorf, 1976; Reymond, 1985; Schlaer, 1971). Acuity is only one narrow aspect of spatial vision, however, and it is of interest to obtain a more complete representation of spatial vision from such visually endowed species. Contrast sensitivity testing offers a broader measure of spatial vision, which includes in its measure an indication of visual acuity as well as the ability to see larger objects of varying contrasts within the environment. The research proposed here will investigate the spatial vision of several species of birds using contrast sensitivity.

CONTRAST SENSITIVITY

Contrast sensitivity (CS) is the ability of the observer to discriminate between adjacent stimuli, usually the light and dark bars of a grating, on the basis of their differences in relative luminosity (contrast) rather than their absolute luminances (Wandell, 1995). The observer's capacity to detect differences in contrast is dependent upon the periodicity (spatial frequency) of the grating pattern. The functional relationship between sensitivity to contrast (the reciprocal of the contrast threshold) and spatial frequency is known as the spatial contrast sensitivity function (CSF). The CSF has become a common indicator of the ability of the visual system to process spatial-frequency information in both humans (De Valois and De Valois, 1990; Regan, 1991) and animals (Uhlrich, Essock, and Lehmkuhle, 1981). The CSF typically is obtained by presenting a subject with a series of gratings, usually sinusoidal, of varying contrasts between the dark and light bars. The mathematical definition of contrast typically used for gratings is the Michelson contrast, or

$$(L_{max} - L_{min}) / (L_{max} + L_{min}) \tag{1}$$

where L_{max} is the luminance of the brighter bar and L_{min} is the luminance intensity of the darker bar. A psychophysical method can then be used to determine the threshold contrast that the subject requires to detect each grating. When plotted, the reciprocals of several of these thresholds generally have the form of an inverted U, with a shallower slope on the low-frequency limb and a steeper slope on the high-frequency limb. The intercept of the high-frequency limb with the abscissa, which represents 100% contrast, corresponds to measurements of visual acuity, such as those measured with square-wave gratings, or the conventional Snellen acuity chart of the ophthalmologist's office. An example of a human CSF is shown in Figure 1.

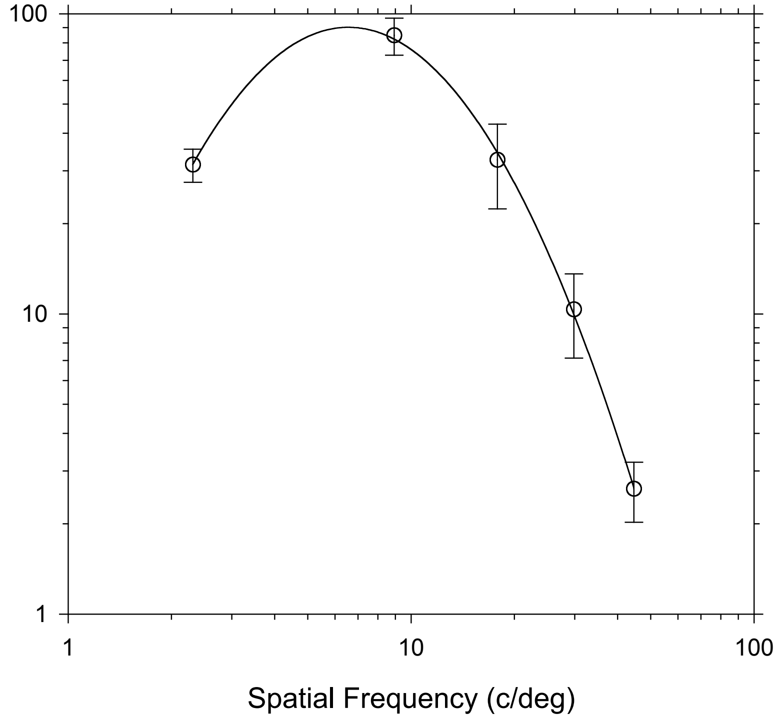

Figure 1: Human behavioral-CSF obtained from Ghim (1997). Data are the average from three normal subjects, aged between 22 and 27 years. Error bars are standard errors.

NEURAL DETERMINANTS OF THE CSF:

Contrast sensitivity at low spatial frequencies often is attributed to neural factors. An optimal grating stimulus will have a periodicity that stimulates only the excitatory portion of a center-surround receptive field. Thus, low spatial frequency attenuation frequently is attributed to lateral inhibition when the inhibitory portion of the same receptive field is activated. Irvin et al. (1993) measured the relationship between a receptive field's center and its surround in primates (bush babies), as the ratio of their relative strengths

$$K \times \pi \times R^2 \tag{2}$$

(where K is sensitivity as calculated to fit a difference of Gaussians (DOG) profile, and R is radius measured in degrees of visual angle). These authors found a close correspondence between the ratio of surround strength to center strength and low spatial frequency roll-off. As this ratio increased, the roll-off became progressively greater, making the CSF more narrowly band-pass; i.e. as surround gets bigger, its overall strength increases, and sensitivity at low spatial frequencies decreases. Surround / center ratios differentiate retinal ganglion cell classes as well. Irvin et al. (1993) also report a lower average surround / center strength for M cells, a type of ganglion cell that projects to the magnocellular layers of the lateral geniculate nucleus (LGN) of the thalamus, as well as some M cells with a surround sensitivity of zero. On the other hand, all P cells, ganglion cells that project to the parvocellular layers of the LGN, had some surround sensitivity. Different species of vertebrates have populations of ganglion cells that differ in some characteristics; for example cats have X-, Y-, and W- cells and birds have predominantly W- cell ganglion cells. These differences may result in corresponding changes in CSF bandwidth across species.

Neural factors also play a role at high spatial frequencies. One would expect the neural limit of visual acuity (high spatial frequency vision at high contrast) to be determined by the packing density of photoreceptors as well as the optical properties of the eye. The calculated limit of resolution based on photoreceptor density alone is referred to as the Nyquist limit, which roughly predicts the contrast sensitivities at high spatial frequencies (Dacey, 1993; Lynch et al., 1992; Pak and Cleveland, 1991; Troilo, Howland, and Judge, 1993). Also, in the primate fovea, where a single cone will most often provide the input to the center of a single ganglion cell receptive field (RF), visual acuity is very well predicted by ganglion cell RF center sizes (R=0.96) (Irvin et al., 1993). The surround / center strength ratio (see previous paragraph) is not a good indicator of contrast sensitivity at high spatial frequencies because the contribution of surrounds is negligible in this range (Irvin et al., 1993).

OPTICAL DETERMINANTS OF THE CSF:

Optical variables also determine high spatial frequency characteristics (high frequency roll-off). Optical modulation transfer functions (MTF), which measure the spatial filtering properties of the optics (cornea, lens, and photoreceptor, outer-segment diameter for photon catch), show high spatial frequency attenuation that closely mimics the high spatial frequency limb of the CSF in the same eye of humans (Losada, Navarro, and Santamaria, 1993). In addition, decrements at mid- and high-spatial frequencies due to reduced target luminance, aging, or other factors are largely attributed to degradation in optical quality in humans (Elliott, 1987; Losada et. al., 1993).

Sources of optical degradation are defocus caused by refractive errors of the eye (myopia and hyperopia) due to mismatches between refractive power of the optical media and axial length, and such related factors such as diffraction, optical aberrations, and pupil size (Campbell and Green, 1965; Losada et al., 1993). Photoreceptor optics, specifically sampling, aperture, and the Stiles-Crawford effect, as well as quantal fluctuations contribute to the slope and intercept of the high frequency limb as well (Losada et al., 1993). Pupil size can be a considerable source of optical degradation. Campbell and Green (1965) found that changing the focus or increasing pupil size would degrade the CSF, but preferentially at higher spatial frequencies. The increase in the influence of spherical aberration with increasingly larger pupillary areas (Pflibsen, et al., 1988; West, 1988) can be quite substantial. Campbell (1995) applied photorefractive methods to determine that spherical aberration is sizable enough to cause refractive errors of approximately ±1.3D.

What one may conclude from this is that both the optics and the neural system are important for determining CS at high spatial frequencies. Campbell and Green (1965) attempted to separate the optical and neural contributions to the CSF by measuring only the neural response to stimuli to compare with the response from the whole visual system. They were able to do this by using coherent light sources to by-pass the optics of the eye. Focused in the plane of the pupil near the nodal points of the eye, the light beams illuminated a patch on the retina, creating interference fringes where they overlapped. Interference fringes are luminance maxima and minima caused by the wave fronts aligning in-phase and out-of-phase, respectively. This effectively created a sinusoidal grating directly on the retina, for which the beam intensities modulated contrast, and the physical separation of the two coherent sources determined the SF. The researchers concluded that with the optimal pupil diameter, the optics contributed one-third of the high-SF, CS-attenuation, while the neural system was responsible for the remaining attenuation.

MODELS TO PREDICT THE MAXIMUM HEIGHT OF A CSF:

The height of a CSF, or maximum CS, is of importance for the research proposed here because the current literature on avian CS indicates that maximum CS is relatively low in birds (Hirsch, 1982; Hodos et al., 1997; Lee, Holden, and Djamgoz, 1997; Reymond and Wolfe, 1981). Neither physiological characteristics nor models are able to fully predict maximum CS, however. The models are limited in their application by varying degrees. Koenderink & van Doorn (1978) proposed one of the first models, which predicted CS to grating patterns of all SFs, at any eccentricity. The parameters that they deemed to be relevant include SF, stimulus contrast or modulation depth, stimulus size (target area; see below), retinal eccentricity, and retinal illuminance to the degree that it affects luminous flux. The most important parameters, however, were found to be the number of stimulated ganglion cells and the transfer function of the average ganglion cell. The transfer function that they used was a rudimentary go/no-go paradigm, the simplicity of which led to tractable, mathematical calculations. The researchers contended that a more realistic transfer function would have resulted in better predictions by the model. The number of stimulated ganglion cells, on the other hand, was approximated in a density function

$$\mu(\varepsilon,s)=(2P/\pi * 1/s^3) \tag{3}$$

of which the integral denotes the number of units with diameters in the range (**s,s+ds**) in an area **dr** at eccentricity ε. The overlap factor, **P**, is the ganglion cell density multiplied by the mean receptive field area, which is independent of eccentricity. The overlap factor is simply a proportionality constant in the density equation, which is expected to differ for different species. The researchers fit their model to human data, and found **P** to be slightly greater than 13, while Fischer (1973) found a **P** of 35 for the cat. Once proportionality constants are determined in a given species, this model could be applied to predict maximum CS.

Virsu and Rovamo (1979) proposed another model in which CS increases as a power function

$$CS=K(AF^2)^n \tag{4}$$

of the cortical area stimulated by a grating. In this equation, **A** is stimulus area,

F is SF, and **n** and **K** are constants. This model corroborated their behavioral finding that, when the retinal area over which the stimulus projected was increased in the periphery to keep the cortical representation constant, a given grating yielded the same CS independent of retinal eccentricity. This model is also limited in its application because of its reliance on constants. For example, while the determinants of **K** were theorized to be the optical attenuation of contrast in the eye and the sampling limitations of receptive fields, there is still the task of determining **K**, as it would most likely be different from the **K** found for humans, on which this model was fitted. In addition, the constant **n** is only obtained from mathematical fitting, and it is unclear whether this constant would be the same for different species. Specifically, this model cannot be easily applied to find the maximal CS in species other than humans without further experimentation.

The Virsu and Rovamo model does not necessarily contradict Koenderink and van Doorn's model, in that the cortical representation of a given stimulus is proportional to the square root of RF density of retinal ganglion cells being activated (Rovamo and Virsu, 1979). In an earlier study, however, Koenderink et al. (1978) found that CS is proportional to the square root of the number of stimulated ganglion cells. Cortical representation is inversely proportional to ganglion cell diameter (*s*), a primary component of the density function used by Koenderink and van Doorn, and since ganglion cell diameter is related to CS in an inverted power function, the two models may be equated with a constant.

EFFECTS OF STIMULUS PARAMETERS ON THE CSF:

Number of Cycles

While the neural and optical configuration of a species will largely determine the CSF, to the point at which individual differences in CS within a species are very small,[1] experimental conditions between studies will significantly modify the function. For example, the number of cycles that are displayed in a stimulus has been shown to determine CS (Savoy and McCann, 1975; Hoekstra, van der Goot, van den Brink, and Bilsen, 1974) and acuity (Anderson, Evans, and Thibos, 1996) for targets containing six or less cycles. Savoy and McCann, and Anderson et al. found the largest effect at or below 3 cycles, with weaker effects closer to 6 cycles. Thus, there is great value in comparing different CSFs obtained from the same laboratory, using the same set of methodological parameters.

Target Luminance and Retinal Illuminance

The luminance of the stimulus (target luminance) is also an important variable. In humans, reducing target luminance attenuates acuity, CS, and peak spatial frequency (Bilotta and Powers, 1991; De Valois, Morgan, and Snodderly, 1974; Ghim, 1997; Jacobs, 1977; Pasternak and Merigan, 1981; Sloane, Owsley, and Jackson, 1988). Reducing target luminance will also reduce retinal illuminance according to the formula

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[1] Age-related deficits in CS do not appear in white carneaux pigeons living in captivity, until they are approximately 9 to 10 years old (Hodos et al., in prep). Since the average lifespan of a wild pigeon is only 3 to 4 breeding seasons, it will be assumed that any wild-caught birds that appear robust will also have normal CS.

$$\mathrm{Td} = \mathrm{L} \times \mathrm{P} \tag{5}$$

where Td is retinal illuminance in Trolands, L is target luminance, and P is pupillary area. When retinal illumination is being measured in an animal with a different axial length than in humans (24.14 mm), however, a correction factor based on the ratio of the squares of the posterior nodal distances of the human eye and the animal eye should be used (Berkeley, 1976). This scaling factor (S) is mathematically represented by

$$(\mathrm{PND}_h)^2 / (\mathrm{PND}_a)^2 \tag{6}$$

where PND_h is the posterior nodal distance of the human, and PND_a is the posterior nodal distance of the animal. The correction factor is incorporated into the calculation of retinal illuminance as such:

$$\mathrm{Td} = \mathrm{L} \times \mathrm{P} \times \mathrm{S}. \tag{7}$$

Because a given target luminance and pupillary area will produce less retinal illuminance in an eye larger than a human's, and greater retinal illuminance in a smaller eye, this correction factor is necessary for comparative studies.

Retinal Illuminance Affects Contrast Gain

A mechanistic explanation for the effects of retinal illuminance may be found in contrast gain experiments (Purpura, Kaplan, and Shapley, 1988; Purpura et al., 1990; Kaplan, Lee, and Shapley, 1990; Shapley and Enroth-Cugell, 1984). Contrast gain is a measure of an individual cell's sensitivity to contrast, and is loosely estimated as the slope of the linear portion of the cell's contrast response function (response of cell in impulses per second or amplitude as a function of percent contrast). More specifically, contrast gain is defined as the product of the gain (impulses per quantum) of the receptive field (RF) center mechanism and the average luminous flux (quanta per second) effectively absorbed in the center (Shapley and Enroth-Cugell, 1984). The luminous flux is dependent on the area of RF center mechanism and the level of retinal illumination. Therefore, as retinal illumination decreases, luminous flux will decrease, reducing contrast gain. Conversely, contrast gain increases with retinal illuminance, as shown in macaque ganglion cells (Purpura et al.,1990). At sufficiently low luminances, photon noise, the statistical fluctuations in the number of photons reaching individual photoreceptors, will become too great for the underlying ganglion cells to reliably determine intensity differences (Hecht, Shlaer, and Pirenne, 1942; Donner, Copenhagen, and Reuter, 1990; Reymond and Wolfe, 1981). Contrast gain is but one example of the dependence of the neural response on light intensity.

Small RFs will be more susceptible to photon noise at low luminances than larger diameter RFs, because of their smaller levels of luminous flux. This inequality may partially explain why the magnitude of these sensitivity decrements at reduced target luminance differ according to the spatial frequency of the stimulus, with the greatest decrements at mid- and high-spatial frequencies. The end result of reducing the luminance level, which in effect reduces retinal illuminance, is to affect the ability to detect fine detail to a greater extent than the ability to detect coarse detail. This causes a negative shift in peak spatial frequency. In addition, since acuity is dependent on the fineness of the photoreceptor mosaic, photon noise as a function of photoreceptor diameter may be the underlying cause for the apparent trade-off between contrast sensitivity and spatial resolution at low luminances, as suggested by Reymond and Wolfe (1981).

Luminance Affects Receptive Fields

Furthermore, luminance decrements have been shown to alter the relative strengths of a receptive field's center and surround in cats. This same relationship may exist in pigeons, quail, and other avian species. Barlow, Fitzhugh, and Kuffler (1957) report the disappearance of the antagonistic surround of retinal receptive fields in cats, while Enroth-Cugell and Lennie (1975) demonstrated only diminished sensitivity. These alterations in organization occur even at the level of the lateral geniculate nucleus (LGN) of the thalamus (Kaplan, Marcus, and So, 1979) with a sufficiently large reduction in luminance (4 log units). In addition to the reduction in the surround response, Kaplan also reports increases in the size of receptive field centers recorded from both retinal ganglion cells and LGN cells. A similar alteration also occurs in cat cortex. Bisti et al. (1977) report reorganization of RFs similar to that found in the LGN by Kaplan et al. (1979). Therefore at low luminances, the cat visual system has the ability to act as a low SF filter at several different levels of the CNS.

Stimulus Area

A third stimulus variable that affects CS is grating area, or the size of the area over which the grating stimulus is presented. Rovamo, Luntinen, and

Näsänen (1993) and Luntinen, Rovamo, and Näsänen (1995) report that at a given retinal illuminance, increasing grating area will increase CS when the grating area is smaller than a critical value. In this target range, CS is proportional to the square root of area. For grating areas larger than the critical area, the increase saturates and CS becomes independent of area. Critical area is dependent on spatial frequency (SF), however, increasing with decreasing SF (critical area for 4 c/deg = 1.92, for 1 c/deg = 28.1, for 0.5 c/deg = 80-100, for 0.25 c/deg = 224 deg^2). Even at spatial frequencies at which two targets are below the critical area, the smaller target will still have lower contrast sensitivity because contrast sensitivity is proportional to the square root of area as explained above. Campbell and Robson (1968), and Koenderink and Van Doorn (1978) also demonstrated the effect of target size. Campbell and Robson's human data show much higher contrast sensitivity at low spatial frequencies attained solely by increasing field size.

Target areas differ greatly in the CS literature. They range from small areas that are clearly below the critical area for some portions of the CSF, to large areas that are well above the critical area. Examples include 3.14 deg^2 for macaques (De Valois et al., 1974), 9.29 deg^2 for squirrel monkeys (Merigan, 1976), 4.50 deg^2 for a falcon (Hirsch, 1982), 3.60 deg^2 for an eagle (Reymond and Wolfe, 1981), 46.56 deg^2 for behavioral pigeons (Ghim, 1997), and 467.6 deg^2 for Japanese quail (Ghim et al., in progress). CSFs in the literature would be further comparable if they were obtained with the same target area.

CHAPTER 2: COMPARATIVE LITERATURE ON CONTRAST SENSITIVITY

OVERVIEW:

The CS literature contain examples of CS functions that have been obtained from humans (Campbell and Green, 1965; De Valois et al., 1974; Elliott, 1987; Sloane, Owsley, & Jackson, 1988), macaques (De Valois et al., 1974), squirrel monkeys (Merigan, 1976), owl monkeys (Jacobs, 1977), bush babies (Langston, Casagrande, and Fox, 1986; Bonds et al., 1987), cats (Bisti and Maffei, 1974: Blake et al., 1974; Pasternak and Merigan, 1981; Aiken and Loop, 1990), dogs (Aiken and Loop, 1990), rats (Birch and Jacobs, 1979; Silveira, L. C. L., Heywood, C. A., and Cowey, A., 1987; Legg, 1984; Keller et al., 2000), ground squirrels (Jacobs et al., 1980), tree squirrels (Jacobs, Birch, and Blakeslee, 1982), tree shrews (Petry, Fox, and Casagrande, 1984), opossums (Silveira, Picanco-Diniz, and Oswaldo-Cruz, 1982), rabbits (Pak, 1984; Kulikowski, 1978), goldfish (Bilotta and Powers, 1991; Northmore and Dvorak, 1979), sunfish (Celenza, 1994), quail (Lee, Holden, and Djamgoz, 1997), pigeons (Hodos et al., 2002; Nye, 1968), an eagle (Reymond and Wolfe, 1981), and a kestrel (Hirsch, 1982). These functions encompass both electrophysiological and behavioral data. One may observe from compilations of these functions (see Figure 2 and Figure 3) that all of them have the same characteristic shape.

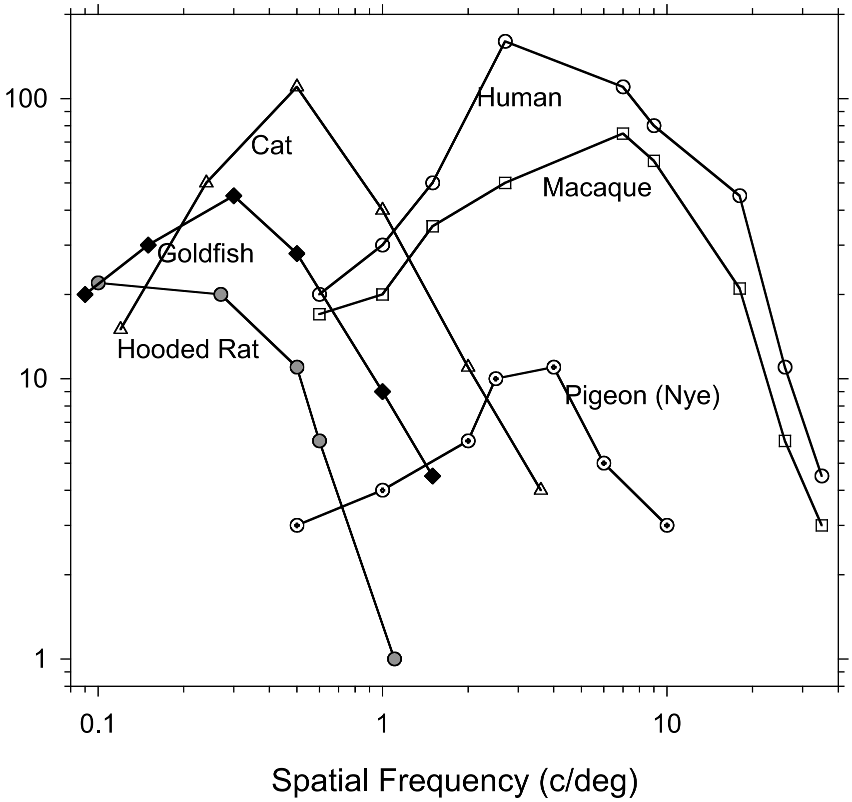

Figure 2: Behavioral-CSFs obtained from Uhlrich, Essock, and Lehmkuhle (1981). Their CSFs for albino rat, squirrel monkey, and owl monkey have been omitted for clarity. The hooded rats possibly do not show a low spatial frequency fall-off due to technical limitations at that time in presenting sufficiently low spatial frequencies; i.e., a target display capable of presenting three complete cycles of a stimulus with frequencies below 0.1 c/deg would have to have subtended at least 30 degrees of visual angle.

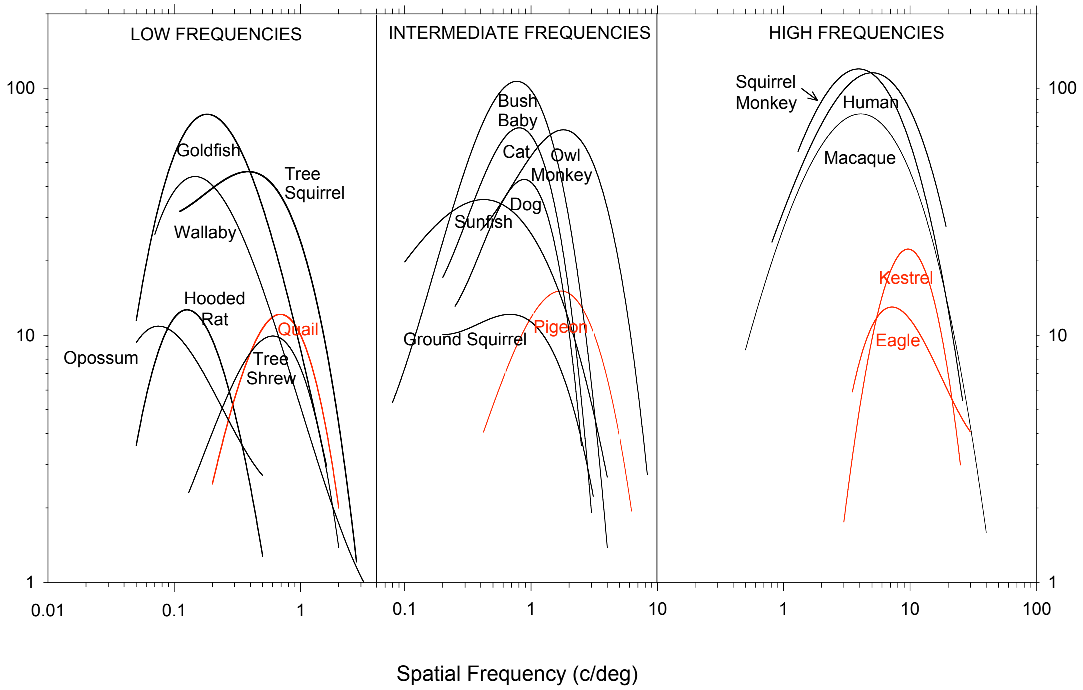

Figure 3: Behavioral-CSFs obtained from Hodos et al. (1997). Additional behavioral-CSFs as well as electrophysiological-CSFs have been included. This was the most complete collection of comparative CSFs available prior to this study. The figure has been divided into three panels, in which CSFs have been grouped according to similarity of band-pass frequencies. Avian functions have been plotted in red.

AVIAN CSF:

Half-Height Bandwidth

Among the high-frequency species, the avian functions have much narrower band-pass characteristics than that of humans, having sharper slopes on both low- and high-spatial frequency limbs. The greater low frequency roll-off of the birds could be a reflection of their different ganglion cell populations and the differences in RF properties between birds and humans. As discussed above

(*Neural Determinants of the CSF*), the ratio of receptive field surround strength to center strength (surround strength / center strength) differ for different categories of retinal ganglion cells, which may determine the extent of low SF roll-off. A larger roll-off, in turn, will lead to a narrower band-pass CSF.

Location of the CSF on the SF-Axis and Physiology

Each bird species' unique physiology and anatomy also contribute to the position of the high SF limb on the comparative graphs. For example, pigeons have been reported to have a cone packing density of 160,000 / mm^2 (Hodos, Miller, and Fite, 1991a) and a ganglion cell density of 40,000 to 41,000 / mm^2 in the area dorsalis (Binggeli and Paule, 1969; Hayes and Holden, 1983). Pigeon cones and ganglion cells are packed less densely than those of humans, which have a cone density of 205,000 / mm^2 and a ganglion cell density of 410,000 / mm^2 (Curcio and Allen, 1990)[2]. In addition, pigeon receptive fields are quite large, the smallest measuring close to 2 degrees (Hughes and Pearlman, 1974), especially when compared to primate (rhesus monkey) receptive fields, which subtend as little as 0.01 degrees (smallest midget RF) in the fovea (De Monasterio and Gouras, 1975). If one assumes, based on information processing theory[3], that the pigeon's optics would not provide appreciably better resolution than the capability of its neural system, one could expect the

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[2] This ganglion cell density includes those ganglion cells that are laterally displaced from the foveal center. Extent of lateral displacement was estimated on data from monkey retina.

[3] Barlow (1961) and Attneave (1954) provide an alternative viewpoint to the often-debated dichotomy of neural versus optical determination. They pose an information processing theory that suggests that the resolution provided by the retina does not exceed the resolution limit imposed by the optics simply because there is no need.

pigeons to perform much worse than humans at high SFs based on these neural data alone. The pigeons' high spatial frequency limb and acuity is in fact positioned at relatively lower spatial frequencies (resulting in a lower peak SF) when this comparison is made. Quail, on the other hand, have a cone density of 25,000 / mm^2 (Budnik et al., 1984), a ganglion cell density of approximately 35,000 / mm^2 (Budnik et al., 1984; Ikushima, Watanabe, and Ito, 1986), and receptive fields measuring 1.3 degrees (Uchiyama and Barlow, 1994) in area dorsalis. These data would predict a high spatial frequency limb and acuity that is shifted even farther leftward than that of the pigeons, as is shown in Figure 2 and Figure 3.

Eagles and kestrels have approximately similar densities of cones and ganglion cells. Eagles have a cone density of 520,000 / mm^2 (Reymond, 1985) while kestrels have a cone density of 297,000 / mm^2 (Fite and Rosenfield-Wessels, 1975). Also, eagle[4] ganglion cell density has been counted as 62,000 / mm^2 in both nasal and temporal fovea and the kestrel ganglion cell density numbers 65,000 / mm^2 in the nasal fovea, and 45,000 /mm^2 in the temporal fovea (Inzunza et al., 1991). Their enormous difference in body size and corresponding eye size, however, produce differing visual abilities. Eagle eyes have a central axial length of 34.7 mm (Reymond, 1985), while the kestrel axial length is merely 12.7 mm (Rochon-Duvigneaud, 1943), which create large differences in cone and ganglion cell densities between these two species when

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[4] Species is *Buteo fuscenses australis.* Ganglion cell data are not available for *Aquila audax*, the species used in Reymond and Wolfe's (1981) behavioral study, depicted in Figure 3.

the densities are calculated per square degree of visual angle rather than square millimeters. The ganglion cell density of the eagle in square degrees (2,415 / deg^2) could account for their poorer contrast ability as compared to kestrels, which have a higher density by this measure (947 to 1,367 / deg^2). The superior acuity of the eagle, however, may be explained by their deep foveal pit that may act as a telephoto lens (Snyder and Miller, 1978).

The neural physiologies of the species in Figure 3, as well as for the subjects in this experiment, are provided in Table 1 to the extent that they were available in the literature.

Table 1: Retinal Cell Densities of Mammalian Species

	Cone Density (per mm^2)	Ganglion Cell Density (per mm^2)
Bush baby (*Galago crassicaudatus*)	8,500 (Wikler and Rakic, 1990)	unknown
Cat (*Felis catus*)	26,000 (Berkeley, 1976)	6,000 (Binggeli and Paule, 1969)
Dog (*Canus lupus familiaris*)	10,000 (Koch and Rubin, 1972)	14,400, but as little as 6,400 in small dogs (Peichl, 1992)
Ground squirrel (*Spermophilus beecheyi*)	49,550 (Kryger et al., 1998)	24,000 (Long and Fisher, 1983)
Hooded rat (*Rattus norvegicus*)	unknown	6,500 (Fukuda, 1977)
Human (*Homo sapien*)	205,000 (Curcio and Allen, 1990)	410,000 (Curcio and Allen, 1990)
Opossum (*Didelphis marsupialis aurita*)	3,000 (Ahnelt, Hokoc, and Rohlich, 1995)	2,900 (Hokoc and Oswaldo-Cruz, 1979)
Owl monkey (*Aotus trivirgatus*)	7,000 (Wikler and Rakic, 1990)	15,000 (Silveira et al., 1993)
Rabbit (*Oryctolagus cuniculus*)	unknown	6,035 (Oyster et al., 1987)

Macaque (*Macaca nemestrina* & *fascicularis*)	210,500 for *M. Nemestrina* (Curcio, 1991); 100,400 for *M. fascicularis* (Perry and Cowey, 1985)	33,000 for *M. mulatta* (Perry and Cowey, 1985)
Squirrel monkey (*Saimiri sciureus*)	105,000 (Rolls and Cowey, 1970)	exact number unknown, but estimated >6,000 (Stone and Johnston, 1981)
Tree shrew (*Tupaia belangeri*)	36,000 (Muller and Peichl, 1989)	20,000 (Petry, Fox, & Casagrande, 1984)
Tree squirrel (*Sciurus niger*)	unknown	25,000 for *Sciurus griseus* (Hughes, 1977)
Tamar wallaby (*Macropus eugenii*)	18,500 (Hemmi and Grunert, 1999)	5,600 (Tancred 1981; Wong, Wye-Dvorak, and Henry, 1986)

Table 2: Retinal Cell Densities of Fishes

	Cone Density (per mm^2)	Ganglion Cell Density (per mm2)
Goldfish (*Carassius auratus*)	12,000 (Hester, 1968)	6,500 in *Carassius carassius* (Koch & Reuter, 1978)
Sunfish (*Lepomis macrochirus*)	35,714 (Northmore, personal communications)	unknown

Table 3: Retinal Cell Densities of Avian Species

	Cone Density (per mm^2)	Ganglion Cell Density (per mm2)
Barn owl (*Tyto alba*)	unknown	12,500 (Wathey and Pettigrew, 1989)
Eagle (*Aquila audax*)	290,000-550,000 (Reymond, 1985)	62,000 in both areas of *Buteo fuscenses australis* (Inzunza et al., 1991)

Japanese quail (*Coturnix coturnix japonica*)	25,000 (Budnik et al., 1984)	35,600 area centralis (Ikushima, 1986); 36,500 area dorsalis (Budnik et al., 1984)
Kestrel (*Falco sparverius*)	297,000 (Fite and Rosefield-Wessels, 1975)	65,000 in fovea; 45,000 in temporal fovea (Inzunza et al., 1991)
Pigeon (*Columba livia*)	160,000 (Binggeli and Paule, 1969)	42,000 area centralis; 36,000 area dorsalis (Binggeli and Paule, 1969)
Starling (*Sturnus vulgaris*)	unknown[5]	unknown
Woodpecker (*Melanerpes carolinus*)	unknown	unknown

Low Contrast Sensitivity

The most notable feature of Figure 2 and Figure 3 is that these birds exhibit low maximum contrast sensitivities as compared to the mammals, which suggests that poor contrast detection may be a common feature of avian vision. There does not seem, however, to be any neural or optical explanation for this phenomenon. In the same meta-analysis that produced Figure 3, Hodos et al. (1997) investigated the relationship between CS and the various stimulus parameters (target luminance, retinal illuminance, target area, bar length); optical variables (posterior nodal distance, pupil area); and retinal variables (cone-photoreceptor density, ganglion-cell density, cone to ganglion-cell convergence) among these animals. While many of these variables had high

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[5] Although cell counts and densities are not known for this species, much is known about photoreceptor types and relative proportions in different regions of the retina. Accurate counts and densities are difficult to obtain relative to obtaining percentages using spectrophotometry and epifluorescent light microscopy on the visual pigments that are unique to reptilian and avian cone photoreceptors. For a review on existing data on starling photoreceptors, see Hart (2001).

correlations to peak SF and maximum CS, no variable accounted for the difference in maximum CS between the avians as a group, and the mammals and fishes as another group. This was a startling phenomenon for a class of vertebrate animals that traditionally has been viewed as having remarkably good acuity and color vision, often having better vision, in these respects, than humans (Fox et al., 1976; Reymond, 1985; Schlaer, 1971).

RESEARCH OBJECTIVE:

Figure 3 also shows that at the time of the Hodos et al finding (1997), CSFs had been reported for only four species of birds, compared to the multitude of mammals that had been studied. In addition, the eagle function (Reymond and Wolfe, 1981) and the kestrel function (Hirsch, 1982) are each comprised of data from a single subject only. This paucity of data is rather surprising considering the substantial literature that exists on the optics, anatomy, physiology, and histochemistry of the eye, the retina, and the central visual system of birds (Karten, 1969; Karten et al., 1973; Shimizu, Cox, and Karten, 1995; Hodos and Erichsen, 1990; Holden, 1980; Bagnoli, 1984; Wang, Jiang, and Frost, 1993), including a number of studies that have been carried out on their visual acuity (Hodos and Leibowitz, 1976; Hodos, et al., 1991a; Gaffney and Hodos, 2003; Güntürkün and Hahmann, 1994; Hahmann and Güntürkün, 1993; Schmid and Wildsoet, 1998; Porciatti, et al., 1991; Hirsch, 1982; Reymond and Wolfe, 1981; Reymond, 1987; Martin and Gordon, 1974; Fite, 1973; Fite and Rosenfield-Wessels, 1975; Fox, et al., 1976; Dabrowska, 1975; Blough, 1971;1973).

CS functions from a broader cross-section of the Class Aves would provide a more complete and perhaps different picture of visual capabilities of birds. As visual adaptations are most likely based on adaptations to the environment, rather than on taxonomy, investigative species were chosen for their diversity of ecological habitats. This is especially true in the case of Passeriformes, as there are almost as many species within this Order as there are in the other Orders combined. Since a great deal of diversity is found in avian visual morphology, specialized for various econiches, it would not be surprising to find avian species that had contrast sensitivities currently considered to be in the mammalian range.

In this study, I attempted to obtain avian CSFs from species additional to, and including some, for which these functions already exist in the literature. These species have adapted to different types of environments. In addition, they represent different taxonomic Orders. This experiment aimed to resolve the question of whether low CS is a general avian phenomenon or whether it is merely typical of the small sample of species already studied. Observed low contrast sensitivity in these additional species would provide stronger evidence that the maximal-CS difference between birds and mammals was not due to sampling error. In addition, this study provided CS functions of species that had been previously untested.

The method selected to obtain these CSFs was the pattern electroretinogram (PERG), which has the advantage over non-electrophysiological methods of relatively swift procurement. This allowed the testing of many more species than a more traditional method would have been capable of.

CHAPTER 3: BEHAVIORAL METHOD OF COLLECTING THE CSF

Behavioral testing to obtain CSFs is the most common method used. Behaviorally obtained CSFs exist for all of the four avian species tested thus far, as well as for the majority of mammals in Figure 3. Behavioral testing involves training subjects to respond to visual stimuli (periodic waveform gratings) using operant schedules of reinforcement. The psychophysical response is then typically measured using the forced-choice method, in which the animal is reinforced for making the response corresponding to the “correct” stimulus. Various methods have been used to obtain thresholds, including the method of constant stimuli, method of limits, random presentation of stimulus values, and combinations of the above. Each of these methods has its unique disadvantages. The method of constant stimuli requires a large number of presentations of a fixed set of stimuli to obtain an ogival psychometric function. This requires prior knowledge of the approximate threshold and still requires a large number of trials. The method of limits requires ascending or descending presentations of stimuli, and the averaging of the two resulting thresholds, or the repeated presentation of stimuli in a large number of trials (the block method). Random presentations may not be as accurate on easy discriminations (Blough, 1971), and often commits the experimenter to a range of stimulus values that is later found to be inappropriate or insufficient. Currently, thresholds are generally obtained by tracking or staircase methods. In this method, stimuli values either ascend or descend in regular steps, similar to the method of limits, until an approximate threshold is found. Then the threshold is titrated by presenting small sweeps of stimuli values in very small increments only around the threshold value. These psychophysical techniques are widely used in visual psychophysics, and have been used to obtain all of the existing avian behavioral-CSFs.

A considerable disadvantage of animal psychophysics in general is the length of time required to obtain data. In addition to training the animal to perform the discrimination task, which can take a considerable length of time, psychophysical measures are not accurate until the asymptote of the learning curve has been reached. CS thresholds are particularly sensitive to training. In pigeons, stable CS threshold measures cannot be obtained prior to a minimum of four months of training (Ghim, Thesis, 1997). Training effects in behavioral-CSFs have been found even in humans, with the largest improvements in threshold at low spatial frequencies (Masson et al., 1994; Higgins et al., 1988; and Long & Penn, 1987). The length of this training appears to be substantial, as seen when comparing human data from De Valois et al. (1974) with human data from Ghim (1997), in which the De Valois et al. subjects received several months of practice to maximize performance compared to Ghim's subjects (all other conditions such as target luminance and target area being equal). De Valois et al. consequently noted large training improvements in CS especially in the low- and mid- SF range.

Behavioral testing of CSF has been in long practice, with many modifications and controls to ensure reliable, consistent measures. However, due to time constraints and the ease of procurement of CS across many species, electrophysiological methods were used in this experiment to collect all CSFs.

CHAPTER 4: ELECTROPHYSIOLOGICAL METHOD OF COLLECTING THE CSF — THE PATTERN ELECTRORETINOGRAM

OVERVIEW:

There are many different ways to measure contrast sensitivities, based on the location within the CNS (for example retina, optic nerve, optic tectum, or visual wulst), and whether the recordings are being made from single or multi-units. Complete CSFs are only obtained from multi-unit recordings, however; CSF recordings obtained from the retina are categorically pattern electroretinograms or PERGs (to distinguish them from other types of electroretinograms (flash ERG), and the multi-unit recording obtained from deeper levels of the CNS are categorically visual evoked potentials (VEPs). VEPs and PERGs have been used to obtain complete CSFs in a variety of animals (Peachey and Seiple, 1987; Bonds et al., 1987; Pak, 1984; Kulikowski, 1978; Jacobs et al., 1980; Pasternak and Merigan, 1981; Silveira et al., 1982; Silveira et al., 1987; Hemmi and Mark, 1998; and Porciatti et al., 2002), including birds (Porciatti, et al., 1991; Hodos, et al., 2001; Lee, et al., 1997). However, complete avian electrophysiological CSFs exist only for pigeons and quail, which, due to the rarity of avian CSFs, must be compared to behavioral measures of CSF from one kestrel and one eagle.

VEP and PERG contrast thresholds are similar (Porciatti, et al., 1991), which is to be expected since contrast is thought to be processed early in visual processing (chapter 1). In addition, the PERG is far less invasive, which made this method far more attractive for use in this study.

The pattern electroretinogram (PERG) can be a useful alternative to behavioral testing of a number of visual functions. It is less time-consuming and thus more efficient, therefore enabling data collection from a large number and variety of species in a reasonable time period. Furthermore, an electrophysiological method eliminates training effects that are typically seen in behavioral CS testing (chapter 3). Contrast thresholds have already been extrapolated from the amplitude of PERG recordings in a few species: pigeon (Hodos et al., 2002), quail (Lee et al., 1997), and human (Peachey and Seiple, 1987). PERG estimates of CS are also reasonably reliable, in those within-subjects results are quite reproducible (see Figure 4).

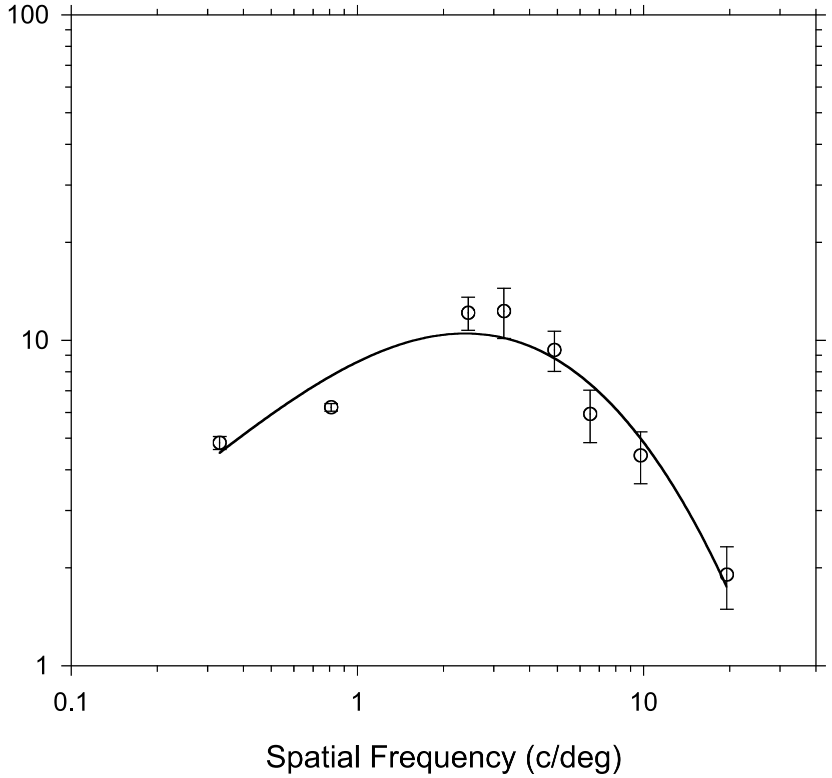

Figure 4: Data from a single kestrel based on observations from three separate recording sessions at each SF, except at 3.25 and 19.53 c/deg, for which only two observations each were obtained. Note the small error bars, which are standard errors.

The PERG has two components, a pattern-contrast response and a local luminance-change response (Odom, Maida, and Dawson, 1982/83). Local luminance-change responses increase with decreasing spatial frequency (until some critical frequency) and increasing contrast and/or mean luminance (Spekreijse and van der Tweel, 1972). Thus, some human optic atrophy patients show a PERG response to high contrast, low spatial frequency stimuli while low contrast, high spatial frequency stimuli fail to produce a response (Dawson et al., 1982).

TEMPORAL MODULATION:

Because the PERG depends upon local luminance changes, a phase reversal of a contrast pattern is required to generate a response. The rate of modulation often used for humans and non-human primates is 7.5 or 8.0 Hz, which is equivalent to 15 to 16 reversals per second (Plant, Hess, and Thomas, 1986; Salgarello et al., 1999; Viswanathan, Frishman, and Robson, 2000). This rate should produce optimal response amplitudes over other rates of modulation, as it is the peak temporal-frequency in the human temporal-modulation function determined electrophysiologically (Hess et al., 1986; Plant et al., 1986; Porciatti et al., 1992; Regan, 1966; Simon, 1992). Animal studies also have found the peak frequency to be in this range of temporal modulation: 8.0 Hz for cats (Maffei and Fiorentini, 1982; Sieving and Steinberg, 1987), 7.7 Hz for quail CS (Lee et al., 1997), 8.3 Hz for pigeon acuity (Porciatti et al., 1991), and 7.5 Hz for pigeon CS (Hodos et al., 2002). In the pigeon and quail studies, the temporal modulation selected was based on parameters that had previously yielded optimal PERG-responses (Bagnoli et al., 1984; Porciatti and Hodos, unpublished data). 7.5 Hz modulation will be used in this experiment, with the assumption that all of the birds being studied will have the peak of their temporal-modulation function in the 7.5 to 8 Hz range.

NEURONAL SOURCE OF PERG SIGNAL:

While the PERG is thought to originate from ganglion cells in mammals, the avian PERG may originate from a different group of retinal cells. In cats (Maffei and Fiorentini, 1981), humans (Dawson, Maida, and Rubin, 1982; May, et al., 1982), and rats (Berardi et al., 1990), trans-section or atrophy of the optic nerve leading to degeneration of ganglion cells eliminates the PERG response. In such cases, the flash ERG, which originates from outer and inner nuclear layers, remains intact. In pigeons, however, ganglion cell atrophy due to sectioning of the optic nerve does not result in a decrement of the PERG (Bagnoli et al., 1984; Blondeau et al., 1987), which suggests that the avian PERG may not be produced by ganglion cells. Bipolar cells have been suggested as a possible candidate for pigeon-PERG generation because of the band-pass spatial tuning that would be inherent to their center-surround antagonism (Holden, 1982). In addition, Holden (1982) has shown that the intraretinal PERG and the intraretinal b-wave of the flash ERG, which is produced in the inner nuclear layer, behave similarly, reaching maximal amplitude at the same retinal depth and reversing polarity over the same range of depths. In a pharmacological study, however, Porciatti et al. (1987) demonstrated the preservation of the PERG after the abolition of the b-wave first with DL alpha amino adipic acid (DL alpha AA), then with 2-amino-4 phosphonobutyric acid (APB). While a specific class of cell has not yet been identified as the pigeon PERG generator, it is probable based on existing data that similar to ganglion cells in mammals (Odom, Maida, and Dawson, 1982/83), a mechanism or class of cell exists in the pigeon, which has spatial and temporal tuning characteristics as well as contrast thresholds that approximate behavioral ranges and thresholds.

INTERPRETATIONS OF THE PERG METHOD:

Differences between PERG-generated and behaviorally-generated CSFs

An obvious distinction between behavioral and PERG CSFs is that behavioral contrast sensitivities typically are generated by 0-Hz stimuli, whereas PERG studies require a temporally modulated pattern. Behavioral-CSFs of pigeons are little affected by temporal modulation, as seen in Figure 5 which compares 0 Hz and 8 Hz data (Hodos et al., 2002). The two CSFs exhibit similar maximal CS. The two functions differ somewhat in peak spatial frequency; the 0-Hz curve peaks at 1.0 c/deg, whereas the 8-Hz curve peaks at 0.85 c/deg. At the low spatial-frequency end, the 8-Hz curve shows a slight flattening, but not as pronounced as that reported by Blake and Camisa (1977) in cats, or by Robson (1966) in humans. Figure 6 shows a comparison of 8 Hz behavioral data to 7.5 Hz PERG data, taken from the same study. While the CSFs in this figure are not identical, the differences are not so large as to suggest that they were obtained from unrelated species (differences in CS below a CS of 10 are magnified due to the logarithmic nature of the ordinate scale). One can reasonably conclude from these figures that 7.5 Hz PERG data is a rough approximation to 0 Hz behavioral data.

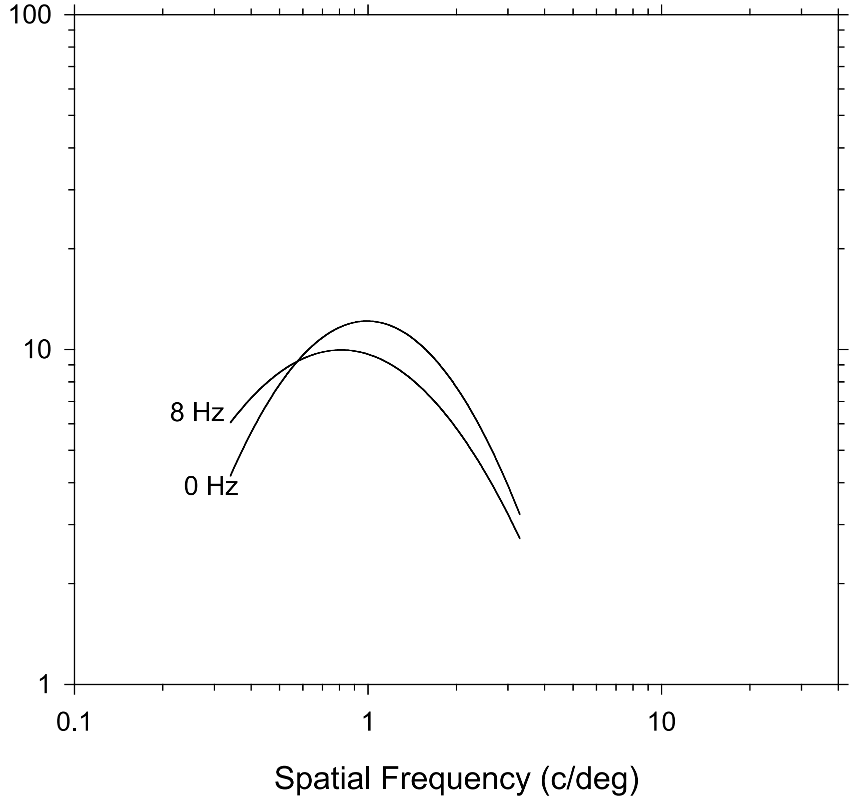

Figure 5: Comparison of behavioral-CSFs using stationary and temporally modulated gratings. Data are from Hodos et al. (2001).

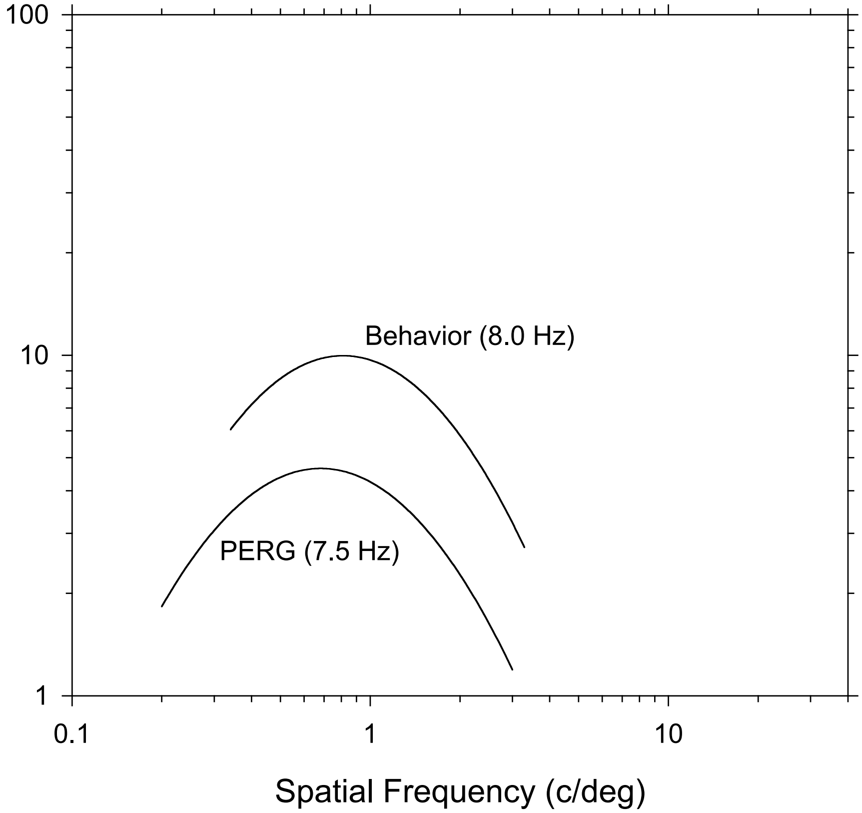

Figure 6: Comparison of behavioral and PERG measures of CS. Data are from Hodos et al. (2001).

Peachy and Seiple (1987), the only research investigators who have compared PERG and behavioral-CSFs in the same human subjects, found approximately the same relationship between PERG-CS and behavioral-CS. In their comparison, however, the behavioral and PERG stimuli had the same temporal modulation (5.0 Hz). This further confirms that temporal modulation has at most a moderate effect in pigeons, and that the 7.5 Hz PERG and the 0 Hz behavioral comparison can be made in pigeons with this difference in mind. Finally, in a study of behavioral, temporal modulation in pigeons, Hodos et al.

(2003) showed that their temporal CS functions are flat up to 16 Hz; i.e. contrast thresholds obtained with temporally modulated stimuli exhibit little change at temporal rates below 16 Hz.

Another consideration when collecting PERG data is that in birds like pigeons and quail that have two areas of high ganglion-cell density in each retina, electrophysiological measures are made with the stimulus image centered on the fovea area or the area centralis, while behavioral measures are usually made with the dorsal-temporal area. The area centralis is aligned with the central optical axis, and is associated with panoramic vision and distance viewing, while the area dorsalis is more temporal, and because of lateral placement of the eye on the head, is used for binocular vision and seeing near objects. The best evidence for this is that the area centralis is emmetropic, while the area dorsalis, which receives from the lower, frontal visual field, is myopic (Fitzke et al., 1985; Hayes et al., 1987; Hodos and Erichsen, 1990; Hodos et al., 1985). Ganglion cell density is also higher in the area centralis. In the pigeon, for example, ganglion cell density is reported at 42,000 / mm^2 versus 36,000 / mm^2 in the area dorsalis (Binggeli and Paule, 1969), which corresponds with a higher measured behavioral acuity. Behavioral acuity of the frontal field can reach 18-20 c/deg (Hodos et al., 1991a), while the behavioral acuity of the lateral field, although reports have been variable (Bloch and Martinoya, 1982; Uhlrich, Blough, and Blough, 1982), is only 14-16 c/deg (Hahmann and Güntürkün, 1993) under optimal conditions. This difference of 2 c/deg, however, is rather small. There is currently no reason to believe that the magnitude of the difference in CS from these two viewing areas will be measurably different.

Similarities between PERG-generated and behaviorally-generated CSFs

The two studies that have compared PERG and behavioral methods of obtaining CSF in the same subjects, all other conditions being equal (or nearly so), found that CSFs were nearly identical in shape and bandwidth (Hodos et al., 2001; Peachey and Seiple, 1987). The only difference found was that the PERG function appeared to be moderately downshifted across all SFs. This difference can be taken into account when making such comparisons in these two species. It is not known whether all other species will exhibit this same difference between these two methods. For example, several studies have shown that contrast thresholds obtained from VEPs are nearly indistinguishable from contrast thresholds obtained behaviorally, also tested on the same subjects (rabbit-Kulikowski, 1978; ground squirrel-Jacobs et al., 1980; and cat-Pasternak and Merigan, 1981). In addition, any differences between PERG-CSFs and behavioral-CSFs may not be appreciably different from CSFs obtained from different laboratories using the same method (for example, when comparing the behavioral-CSF from one laboratory to the behavioral-CSF from another). These variances could also invert the relationship between electrophysiological and behavioral methods. As an example, the VEP-CSF obtained by Silveira et al. (1987) has a higher maximum CS than the behavioral-CSF obtained by Legg (1984), despite the larger target area in the behavioral study. One may conclude from this that there is a reasonable possibility that the PERG-CSFs obtained in this experiment will be very similar to behavioral-CSFs, or at least could be compared.

The CS literature is comprised of CSFs obtained using all three of these methods: VEP, PERG, behavioral. However the data are still sparse in that a given species often has a CSF obtained from only one of these methods. If any comprehensive comparisons between species are to be made, small differences between the methods of measure must be accepted.

CHAPTER 5: OBJECTIVES AND PROCEDURES

OBJECTIVES:

The purpose of this experiment is to obtain CS functions using the pattern electroretinogram (PERG) in several selected species of birds that represented different Orders and a variety of visual adaptations. This study is compelling for two broad reasons. It is not known whether low CS is a general phenomenon among birds, and some of the existing avian data are questionable due to statistical unreliability or contradiction with other existing data. The proposed research will attempt to provide solutions to these questions and contradictions. The rationale behind the specific questions being posed by this research is outlined below.

Experimental Questions:

(1) *Do birds in general have low CS?*

- Because of the paucity of CS functions in avian species, additional species need to be tested in order to determine the generality of the low CS phenomenon.
- Because of the diversity of adaptations to the visual environment among birds, there is a need for additional data that represent a broader cross-section of the Class Aves.

(2) *What are the CSFs of kestrels, woodpeckers, barn owls, and other individual species of birds?*

- Birds for which CS data already exist, such as the kestrel, are often based on a single subject. This experiment will provide additional data on this species that may corroborate previous findings. The kestrel in particular also has conflicting behavioral acuity measures. The only published measures of visual acuity are from Hirsch (1982), who reports approximately 40 c/deg, and from Fox, Lehmkuhle, and Westendorf (1976), who report 160 c/deg. Both studies were based on an N of one. A recent study by (Hodos, Gaffney, and Potocki, 2001; and Gaffney and Hodos, 2003) using nine kestrels to obtain PERG measures of visual acuity support Hirsch's data, which are also consistent with the kestrels' Nyquist limit. The extrapolated acuity of 30.1 c/deg for the kestrels in this experiment is thus far consistent with the acuity of 25.3 c/deg obtained by Hodos et al.

METHODS

Procedure:

Subjects

Subjects were three white carneaux pigeons, three Japanese quail, four barn owls, three American kestrels, six starlings, and one red-bellied woodpecker (Table 4). The white carneaux pigeons and Japanese quail were domesticated strains, housed in separate vivaria at the University of Maryland at College Park. The barn owls and American kestrels were non-domesticated strains that were housed in colonies at the University of Maryland or the

Patuxent Wildlife Research Center. The starlings and red-bellied woodpecker were wild-caught (see Appendix B) for the purpose of this experiment and euthanized with an overdose of anesthetic at the end of the experiment. All animals were approved for use and were treated humanely under IACUC protocol R-00-60 at the University of Maryland, College Park. State Permit / License SCO-31348 and Federal Permit / License MB038451-0 were obtained for the capture and use of the wild animals.

Table 4: Subject species used in this research.

Common Name	**Species Name**	**Order**
American kestrel	*Falco sparvarius*	Ciconiiformes Falconiformes
barn owl	*Tyto alba*	Strigiformes
budgerigar (attempted--no data)	*Melopsittacus undulatus*	Psittaciformes
common starling	*Sturnus vulgaris*	Passeriformes
ring-billed gull (attempted--no data)	*Larus delawarensis*	Charadriiformes
Japanese quail	*Coturnix coturnix japonica*	Galliformes
red-bellied woodpecker	*Melanerpes carolinus*	Piciformes
white carneaux pigeon	*Columba livia*	Columbiformes

All taxonomic data are from Sibley and Ahlquist (1990), except for the classification of the American kestrel as a Falconiformes (Wetmore, 1960).

Pharmacological Treatments

The animals were anesthetized with Isoflurane, an Isoflurane and Ketamine combination, or Chloral Hydrate (see Appendix C for a detailed discussion of avian anesthesia techniques and practices used in this research). The choice of anesthetic protocol used reflects the method that was safest and most effective for the given species. If Isoflurane was used, its concentration was adjusted to effect, and was typically 4% to induce and 0.25-2.25% during data collection. The Isoflurane was delivered in an oxygen (725 ml/m) and nitrous oxide (350 ml/m) mixture. Concentration and flow rates were controlled with a Vetroson, small animal, anesthetic machine, which was set-up as an open (non re-breathing) system. Small amounts of Ketamine (usually 20 mg/kg – see Appendix C for specifics) were sometimes used in conjunction with Isoflurane. Chloral Hydrate (20%) was often used as the sole anesthetic in certain species, which was delivered in the pectoral muscles. Dosages differed for each species, ranging from 280-520 mg/kg (Appendix C).

Vecuronium bromide[6] (1 mg/mL), a synthetic curariform agent obtained from Organon Laboratories, was then used as a cycloplegic agent to control fluctuating accommodation (see Appendix D) during recording in all species but the owl. The topical curariform was ineffective as either a cycloplegic or a

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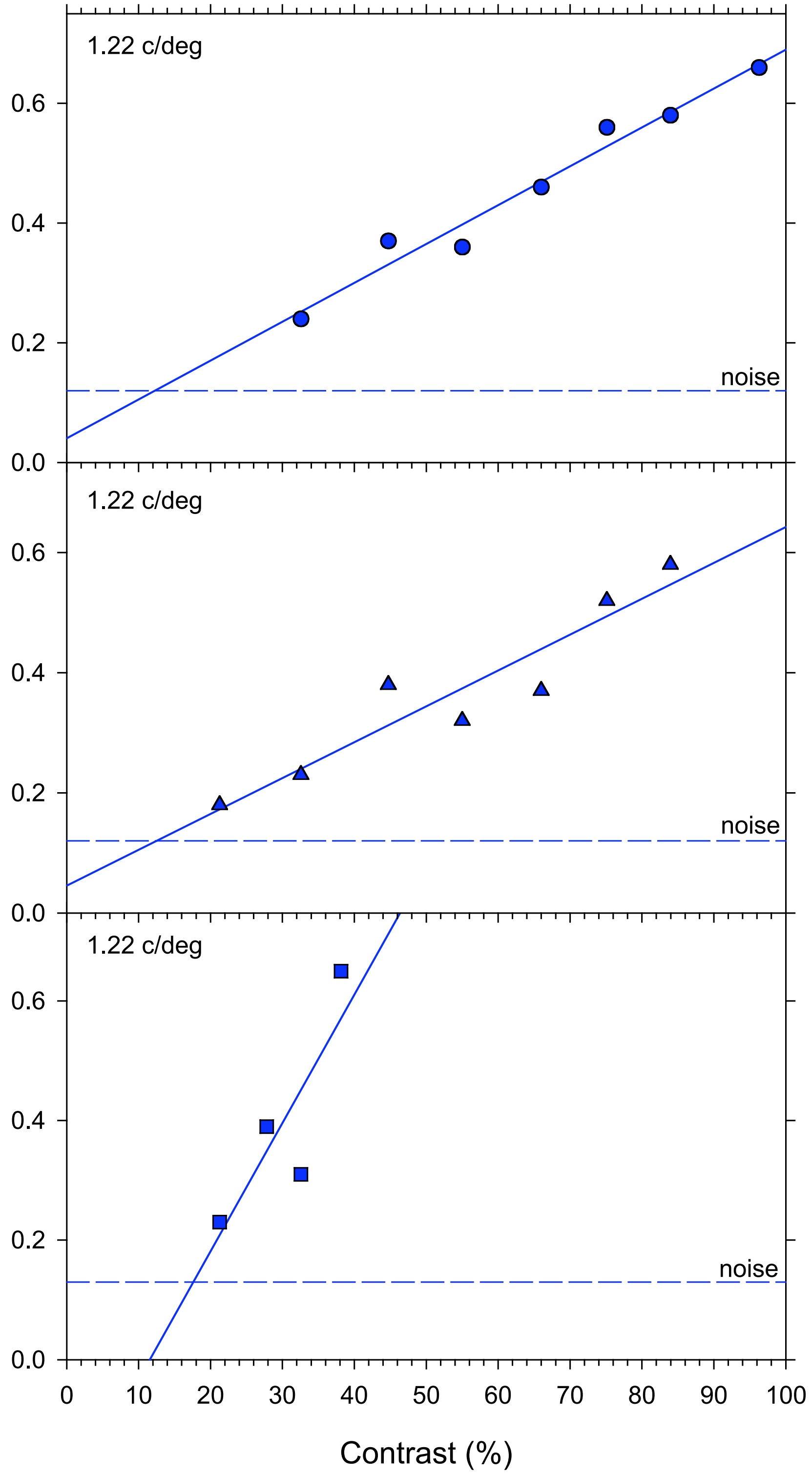
[6] Because of the slow rate of absorption through the cornea, and because excess amounts will enter the body through the oral-nasal cavity, the solution was administered at a rate of 1 drop per 30 sec. The size of the drops was adjusted for the size of the animal, thus different species received differing volumes of Vecuronium Bromide. Volumes ranged between 0.01 and 0.20 cc. Previous refractive measures from this laboratory showed that the time course and frequency of administration of the drops were more effective for attaining cycloplegia than total volumes of administration.

mydriatic in the owls, which suggests either of two possibilities. (1) The muscles that control these processes have a substantial proportion of smooth muscle, as in mammals, and are not striated as it is assumed to be in all avian species (Walls, 1942), or (2) the application method is ineffective for this species. A Medline search revealed no references on cycloplegia, mydriasis, or ciliary muscles for owls, however the empirical evidence suggests that both explanations may correct. Professor Christopher Murphy at the School of Raptor Ophthalmology, University of Wisconsin, Madison, suggested (personal communication) that the topical application is ineffective because the unusually large anterior chamber of the owl eye results in dilution of the cycloplegic by the large amount of aqueous humor. This is corroborated by the striking and immediate effectiveness of direct intracameral injections of d-tubocurarine, in his experience. On the other hand, Porciatti, Fontanesi, and Bagnoli (1989) were able to induce cycloplegia on little owls (*Athene noctua*) via cyclopentolate hydrochloride, a topical antimuscarinic that acts on smooth muscles. Taken together, these data suggest that owls have some combination of smooth and striated fibers. In any event, without cycloplegia, the owl recordings were nonetheless stable, yielding relatively consistent thresholds (Figure 7) both within and between sessions for an individual owl. In addition, the trial lens rarely changed for an individual owl, either between or within sessions, which further confirms the stability of the refractive state. An optometric trial lens was placed in front of the eye during recording to correct for the viewing distance and to compensate for any refractive errors (Gaffney and Hodos, 2003). Finally, Walls (1942) states that the range of accommodation for owls is at the most only half that of the pigeon.

Figure 7: Contrast-response functions obtained at the same SF, from owl O53, in a single session (5/14/03). Thresholds are as follows (top to bottom): 12.58, 12.57, and 17.36% contrast. These are 7.95, 7.96, and 5.76 CS, respectively.


1.22 c/deg
0.0
0.2
0.4
0.6
noise
1.22 c/deg
0.0
0.2
0.4
0.6
noise
1.22 c/deg
0.0
0.2
0.4
0.6
noise
0
10
20
30
40
50
60
70
80
90
100
Contrast (%)

Streak retinoscopy on an anesthetized owl revealed a modest 0.6 to 0.7 Diopter accommodative fluctuation over a four-hour period (see Appendix D), which is the longest duration of an actual recording session. Since these birds do not show any fluctuations of accommodation that would be of concern, and since these animals were borrowed from a different laboratory, it was deemed an unnecessary risk to attempt cycloplegia with the uncustomary pharmacological agents and techniques described above. Thus, owls were not subjected to cycloplegia in this study.

For all other species than owls, approximately 0.01 ml (for the smallest animal) to 0.3 ml (for the largest animal) volumes were administered topically at a dosage of 1.0-mg Vecuronium bromide per 1.0-ml saline, in 1.0 drop (0.001 ml) per 30-sec increments.[7]

PERG Procedure

After anesthesia, the animals were lightly restrained in a cloth wrap to prevent occasional movement, and then placed in stereotaxic ear bars with the center of the pupil of one eye aligned with the center of the stimulus display. In this orientation, the fovea was within the retinal image of the stimulus display. Body temperature was maintained by isothermal pads from Braintree Scientific, Incorporated.

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[7] A concern in using a curariform is that several varieties cause a reduction in blood pressure. Blockade of sympathetic ganglia and ganglionic transmission in the adrenal medulla, as well as excitation of histamine release, contribute to the hypotensive response. Vecuronium bromide, however, does not block ganglia or vagal neuroeffector junctions and does not release histamine (Volle, 1990). As a result, this agent is not believed to affect choroidal blood flow.

A 0.5-mm platinum electrode was inserted through the eyelid, and after approximately 5 mm (depending on the size of the animal's eye), exited the eyelid (Figure 8). The portion of the electrode that remained under the eyelid made contact with the cornea to record the pattern ERG. The electrodes were sterile and smooth, passed easily through the lids and produced no abrasion or irritation to the cornea. A reference electrode was similarly placed on the other eye, and a ground electrode was inserted under the skin on the head.

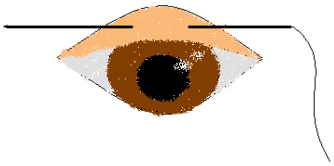

Figure 8: Schematic of the electrode on the corneal surface, held in place by the eyelid.

Optometric trial lenses of various powers were placed less than 2 cm in front of the eye prior to recording contrast-response functions to correct for the 62 cm viewing distance and to compensate for any refractive errors. The lens that resulted in the highest acuity during the refraction test was placed in position during the measurements of contrast-response functions. The refractive state was determined from the power of the lens that resulted in the highest acuity minus the 1.6 D correction for the distance from the cornea to the monitor (Appendix D). An example of a refractive plot used to determine the power of this "best" lens is provided in Figure 9. Cycloplegia prior to the refraction test and the use of a lens during data collection are necessary to ensure that the stimulus is in focus on the photoreceptive layer of the retina, because refractive errors and fluctuating accommodation while recording PERGs severely reduce PERG amplitudes. This was observed in chickens and pigeons in our laboratory, and has in addition been documented in primates (Siegel, Marx, Bodis-Wollner, and Podos, 1986).

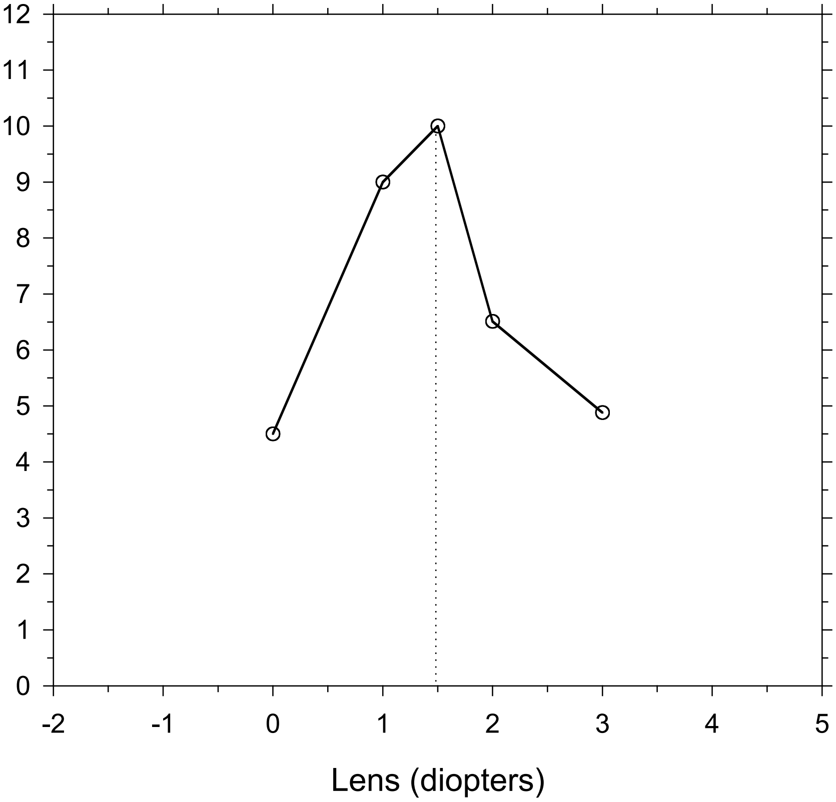

Figure 9: Acuity as a function of trial-lens power in front of the eye. These data are from a quail obtained in a single session. Each refractive plot such as the one shown isolates one peak. The lens power at this peak is used for the duration of the session.

Stimuli

The stimuli were sets of sine-wave gratings presented in sequentially ascending Michelson contrast (referred to hereafter as “sweeps”) at a particular spatial frequency, with a mean luminance of 94 cd/m^2, generated by an Enfant™ 4010 Visual Stimulator/Electrophysiological Assessment System from the NeuroScientific Corp., Farmingdale, NY. The display was a 38.26 (horizontal) by 29.21 (vertical) cm, monochrome, gamma corrected 1024 line, CRT computer monitor, located 62 cm from the corneal surface of the animal, subtending 34.3 by 26.51 degrees of visual angle. The lower limit of contrast display by the equipment was 1.83%; the upper limit was 96.28%. The Enfant™ is also a data acquisition program, and is capable of offline processing of regressions, Fourier transformations, signal filtering and other analytical techniques.

The gratings were phase reversed (alternation of light and dark bars) at a rate of 7.5 Hz (cycles/sec). Each contrast grating was presented for 17 reversals before the next contrast grating in the sweep was presented. There were 9 contrast steps in a sweep, and a total of forty to fifty sweeps or 6,360 to 7,950 reversals that were averaged in a contrast-response graph. The duration of forty sweeps was 6 minutes, 48 seconds, and the duration of 50 sweeps was 8 minutes, 30 seconds.

The contrast of the grating stimuli were calibrated frequently during the course of the study by measuring the luminance of the bars on the display monitor with a Minolta Luminance Meter (calibrated against a standard traceable to the National Institute of Standards and Technology), and comparing the calculated, Michelson contrast with the nominal contrast indicated by the software. Each contrast depth that was used was measured in this manner and subsequently plotted in the contrast-response curves.

PERG Analysis

The response is a periodic, sinusoidal waveform (e.g., Figure 13) that follows the pattern of the local luminance change. The signals were recorded through an amplifier with a gain of 10,000 and filtering of 0.5-100 Hz. Discrete Fourier transforms were performed on the signal to determine second harmonic response amplitudes (7.5 Hz yields 15 reversals of contrast per second). Second harmonic amplitudes collected during 40 sweeps of contrast gratings were averaged in a data file, calibrated for contrast (described below), and then displayed on a contrast-response graph for a single spatial frequency.

Contrast thresholds were obtained by applying a linear regression to the linear portion of the contrast-response functions near the visual approximation of threshold. Thresholds were then extrapolated as the intercepts of these regressions with the noise level that was recorded during that particular sweep[8]. In addition, the corresponding phase lag and phase lag variance of the response were collected at each contrast level.

Mean phase lag (mean response latency) was relatively consistent with increasing contrast. Phase lag variance also decreases with increasing levels of

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[8] Due to fluctuating noise levels, in a small percentage of cases (5%) noise was exceedingly low and the contrast-response function generated an un-interpretable threshold (i.e., the y-intercept was a negative number or was close to zero yielding an anomalously high CS). In this small set of sweeps, the mean noise for the entire session was calculated and used to obtain threshold.

contrast. Phase lag variance reliably exceeds ±180º at contrast levels that are at or below threshold. For an example, note that the phase lag variance increases as the threshold is approached, and the increase of variance to greater than ±180º at 0% contrast (Figure 10 and Figure 11). A threshold can be approximated using phase lag and phase lag variation alone. Sudden changes of phase lag slope combined with a marked increase in phase lag variance are consistent indicators of the vicinity of the threshold. Thresholds visually approximated from phase lag and phase lag variation data are consistently similar to thresholds obtained from linear extrapolation of contrast-response data. Therefore, phase lag data were always used as an independent measure to verify extrapolated thresholds and also as a criterion to distinguish signal from noise when applying linear regressions. Only those amplitudes that showed a corresponding phase lag variation of less than ±90 degrees were included in the linear regression. Thus, each threshold estimate by linear extrapolation had an independent measure of threshold from the phase lag data.

There are many alternate methods of determining absolute thresholds. Among these are the visual detection method, in which the threshold is approximated as the lowest intensity at which a response is visually detected (Boettcher, et al., 1993), setting the threshold as a pre-determined criterion value below the lowest intensity that elicited a measurable response (Walsh, McGee, and Javel, 1986), and defining threshold as the lowest intensity producing a response amplitude 1 SD above the mean noise level (Brittan-

Powell, 2002). Since visual contrast thresholds are nearly always obtained by extrapolation of linear regressions to either noise or baseline (0 μV), this method was chosen for this experiment for ease of comparison with the literature. The phase lag data provided a reliable check on the accuracy of these thresholds.

Upon extrapolation of contrast thresholds, the reciprocals of these thresholds were calculated and plotted as contrast sensitivities. A polynomial regression was fit to each CS data set to more clearly delineate the function. Although the well-known double exponential function first employed by Blakemore and Campbell (1969), and Campbell, Carpenter, and Levinson (1969) could have been used, it was not a good fit for all of the CSFs presented in Figure 3. Another approach commonly taken by comparative researchers is to fit a function by visual approximation (tree shrew – Petry, Fox, and Casagrande, 1984; wallaby – Hemmi and Mark, 1998; squirrel monkey – Merigan, 1976; owl monkey – Jacobs, 1977; cat – Pasternak, Merigan, and Movshon, 1981). A third possibility is to simply present the data without fitting a function. Fitting a function seemed useful, however, in order to graphically represent multiple CSFs (in this case from 6 different species) in a single graph for comparison, especially since I could not assume from prior experience that all of the individuals within a species could be tested at exactly the same spatial frequencies so that data can be averaged. Therefore, in light of the first two possible approaches, a least-squares approach for fitting a CSF was the best compromise. Polynomial regressions fit the CS data very well without exception.

CHAPTER 6: RESULTS

Figure 10 and Figure 11 show typical contrast-response functions from two starlings. These figures also show the corresponding phase lag and variances obtained for each contrast level, used to determine whether the amplitude generated was signal or noise. Note that phase lag is relatively consistent, in addition to having small variances that increase as the contrast level diminishes to threshold. Phase lag at 0% contrast (luminance-matched blank) always has maximum variance, which supports our use of the response (in μV) at this contrast level as a measure of noise, represented in the top graph of each figure as the horizontal reference line marked as noise.

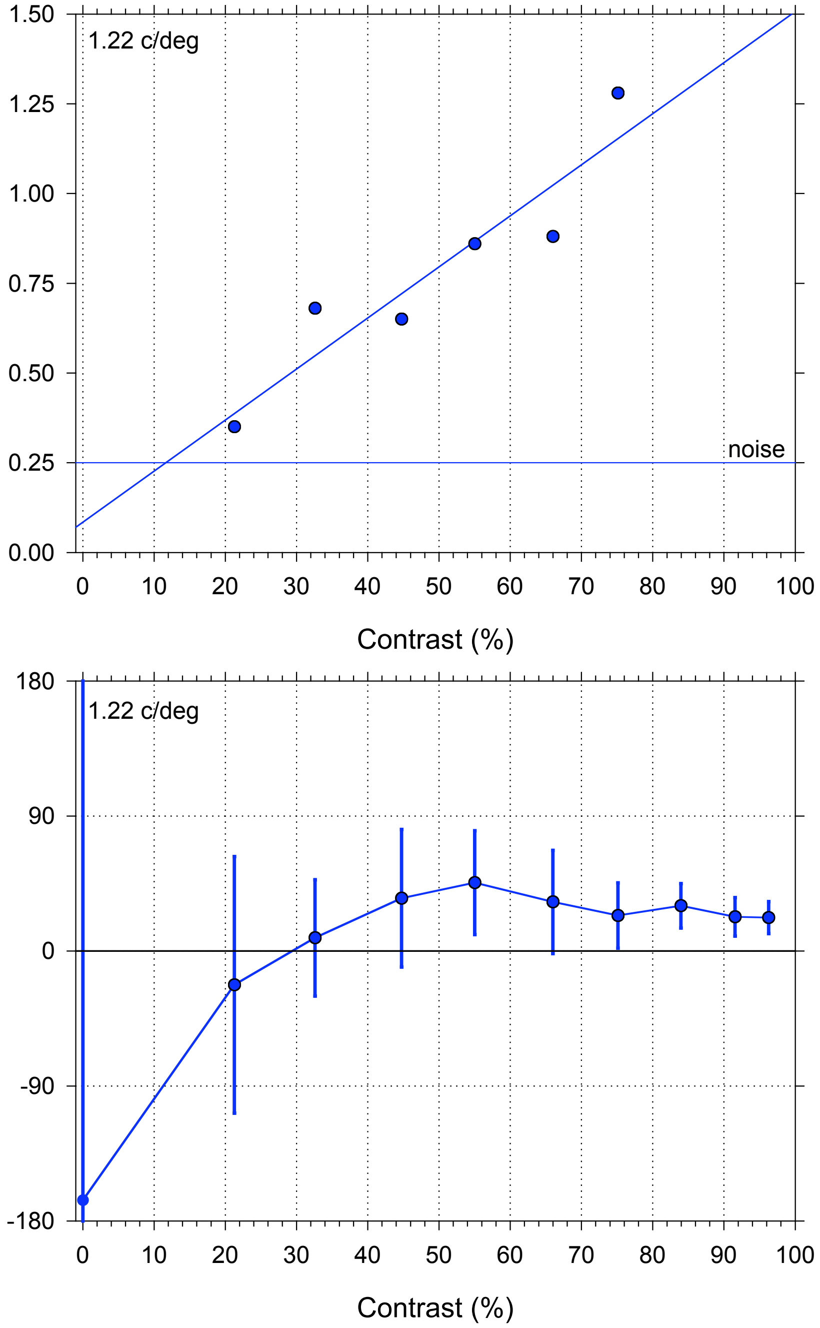

Figure 10: Sample contrast-response function (top) with corresponding phase lag and phase variance (bottom), obtained from starling SV13.

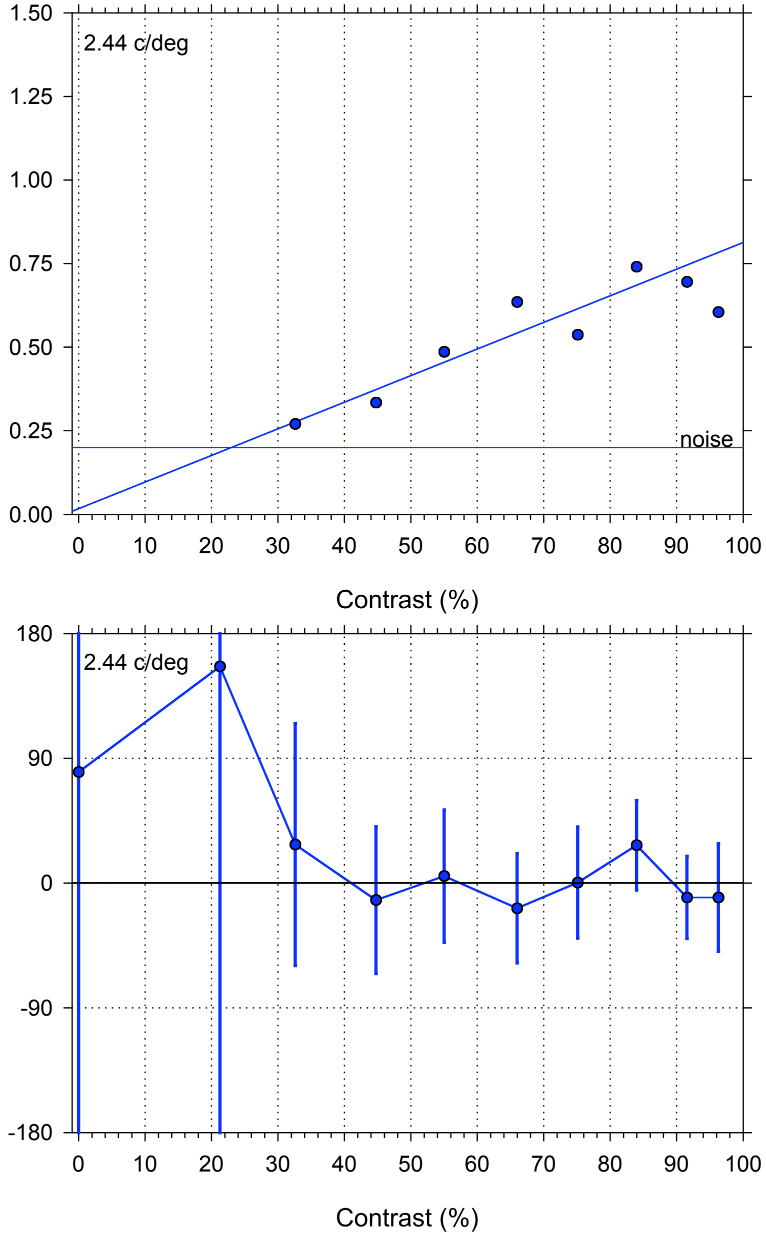

Figure 11: Another example of a contrast-response function (top) with corresponding phase lag and phase variance (bottom), obtained from starling SV19. Data points in the saturation portion of the CRF were not included in the linear regression. In addition, the PERG amplitude (at 21% contrast) that had a phase lag similar to noise was not included in the regression (not shown as it was treated as noise).

The mean session noise was obtained for threshold extrapolation for some sessions. Figure 12 provides an example of noise fluctuation through the duration of a recording session, as well as an example of how a mean session-noise level was attained.

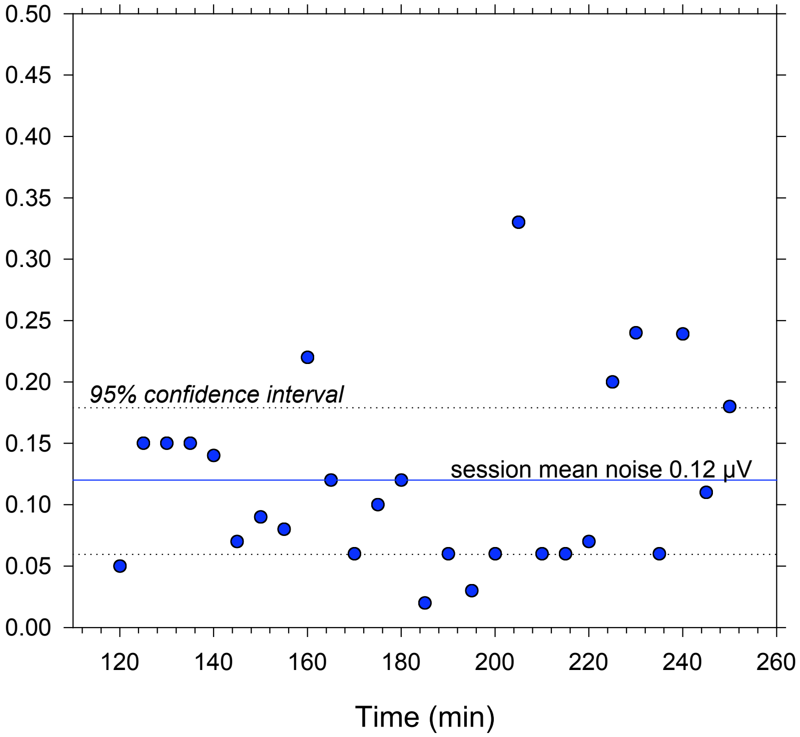

Figure 12: Noise fluctuations are represented by solid symbols. The solid horizontal reference line is mean session noise.

All avian CSFs obtained in this experiment had low maximum contrast sensitivities compared to mammalian functions. Sample periodic, response waveforms, sample contrast-response functions, and CS data for each species are provided below.

PIGEONS

Figure 13 shows sample response waveforms at a single spatial frequency obtained from one pigeon, one session. The typical pattern is of amplitude reduction with diminishing contrast. At contrasts below threshold, waveforms were indistinguishable from noise. These waveforms are all more or less in-phase. The second harmonic amplitudes of waveforms such as these were used to generate contrast-response functions, shown in Figure 14. The contrast-response functions shown here are a small, but representative sample of the total obtained for this species. The great majority of pigeon contrast-response functions were decidedly linear with narrow 95% confidence limits. These and other contrast-response functions were used to extrapolate contrast thresholds, from which CSFs were constructed.

Pigeon CSFs are shown in Figure 15. CS data for each individual subject are shown in Figure 15a-c. The variation in the CS data (Figure 15d) can be accounted for by age-related changes quite beautifully. Pigeons peak in developmental maturity at two to three years, breed until five- or six-years of age, do not show age-related acuity deficits until eight- to nine-years (Hodos, et al., 1991a), and continue to live in captivity until about 21-years. Pigeons in captivity have been documented to live to 30-years (Altman and Dittman, 1974), but this has not been observed in our colony. The eight-year-old pigeon in Figure 15 shows reduced sensitivity at all SFs compared to the seven-year-old (ages shown in the legend). A more pronounced decrement at high SFs suggests optical changes related to aging. The two-year-old pigeon shows a robust CSF compared to either of the two older birds. The slight negative shift in peak SF, however, indicates a slightly immature visual system that has not quite peaked in visual functioning (Hodos, et al., 1991a). The average acuity was 17.17 c/deg, the average maximum CS was 7.98, and the average peak SF was 1.29 c/deg.

The best azimuth for recording was found to be 75 degrees and the best elevation was found to be 30 degrees. The lens typically used for recording was a +2.5 Diopter lens (ranging from +1.5 to +3.0 Diopters), which suggests that these pigeons were hyperopic in the lateral field.

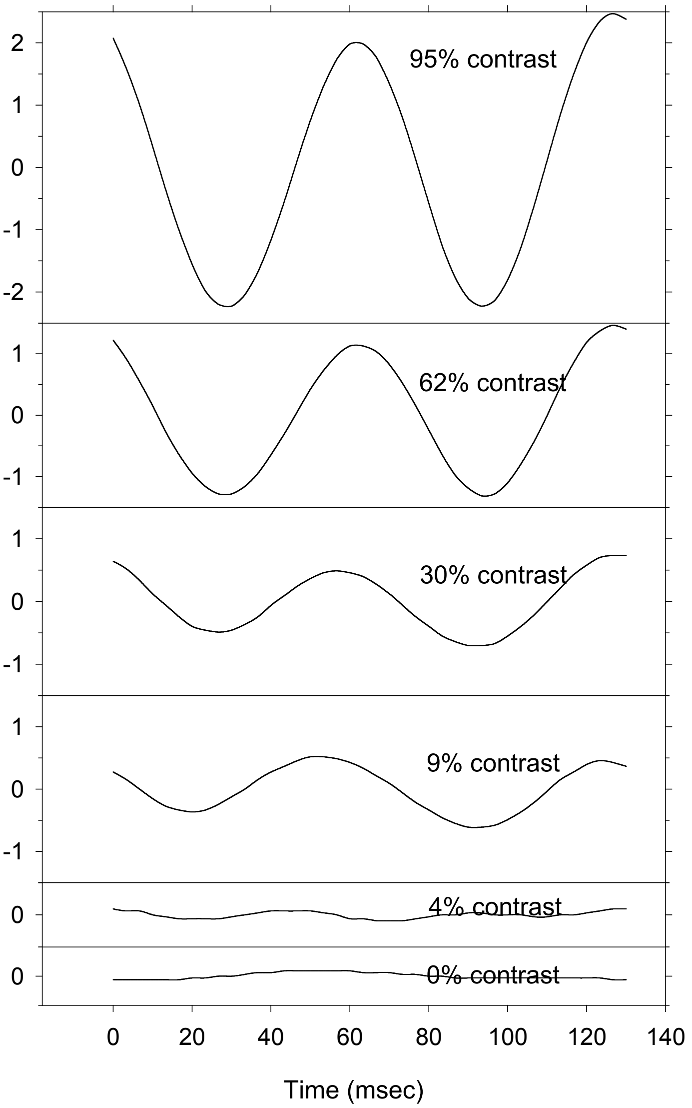

Figure 13: Sample response waveforms of a pigeon. These represent the raw signal that has been low-pass filtered at 26-Hz, which serves to filter 60-Hz and other noise and smooth the waveform. Note the reduction in amplitudes as contrast decreases.

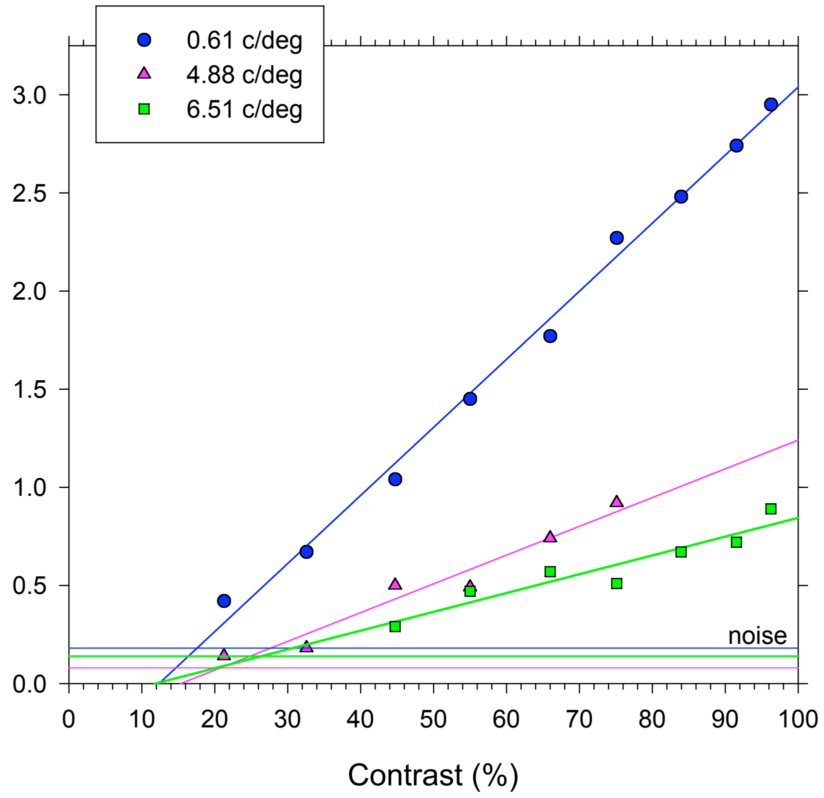

Figure 14: Sample contrast-response functions obtained from pigeon E4585. These were obtained in a single session.

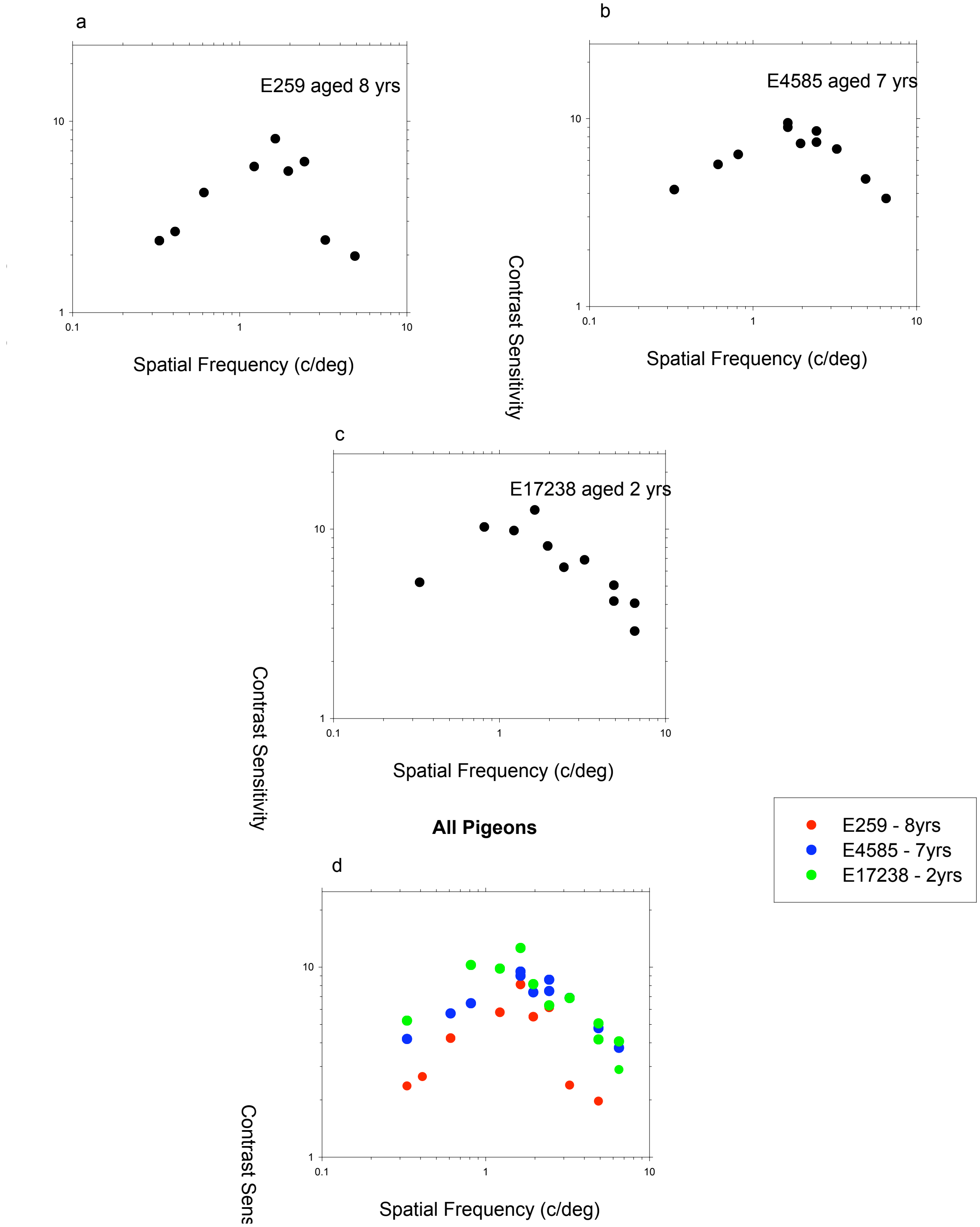

Figure 15: Pigeon data. Subjects were E259, E4585, and E17238. Sexes were not known. Functions in graph d were obtained by applying polynomial regressions to that individual's CS data in graphs a, b, or c.

KESTRELS

Sample kestrel PERG waveforms are shown in Figure 16. These waveforms also show the characteristic in-phase amplitudes that diminish with diminishing contrast. The waveform at 4% contrast is indistinguishable from noise (0% contrast), indicating that threshold is between 4% and 10% contrast at this spatial frequency.

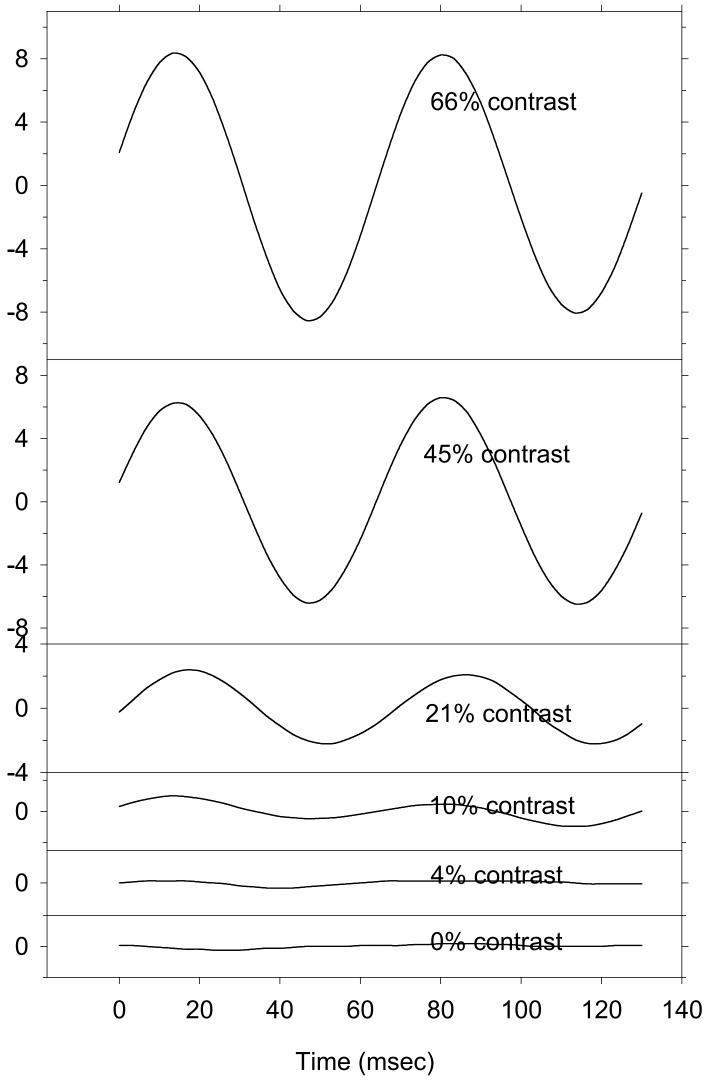

Figure 16: Sample response waveforms of a kestrel.

Figure 17 shows sample contrast-response functions from a different kestrel. Similar to all of the subjects in this experiment, these contrast-response functions are linear. An example of within session reliability is provided in Figure 18. Similar tests of reliability were conducted in several sessions with several species.

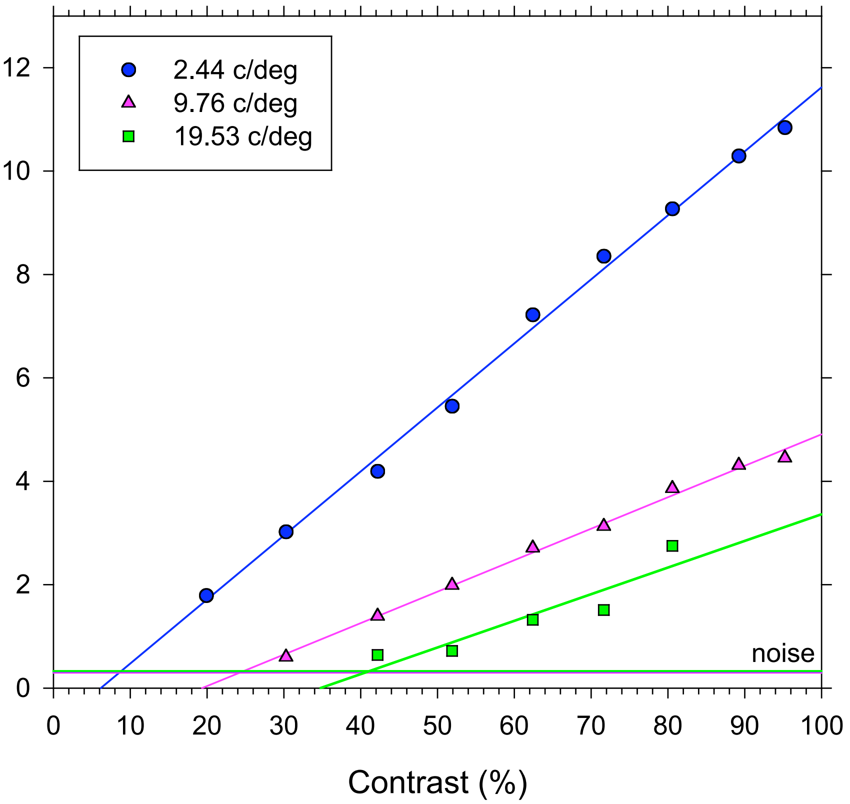

Figure 17: Sample contrast-response functions from kestrel K049. Note the strong linearity of the functions, which is typical in contrast-modulated PERGs.

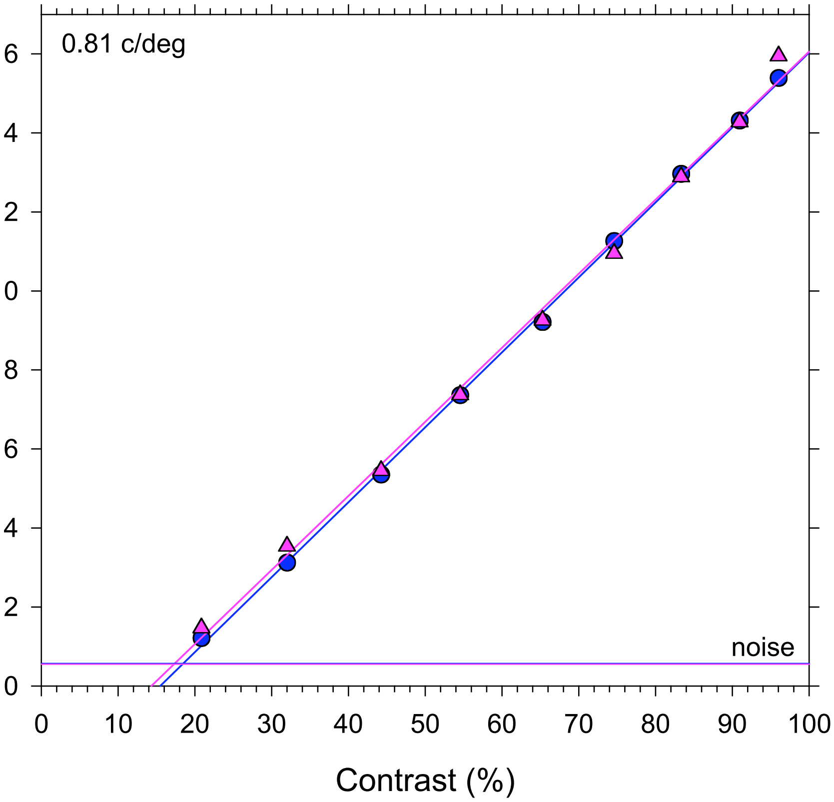

Figure 18: Sample contrast-response functions from one kestrel, obtained in a single recording session. This is another example of reliability within a session. Both functions were obtained at 0.81 c/deg, but three hours apart. The amplitudes are nearly identical, as can be seen by the overlapping functions. The extrapolated thresholds are also virtually identical. The difference in the two noise levels is 0.02 μV.

Kestrel CSFs are shown in Figure 19. CS data for each individual subject are shown in Figure 19a-c. The ages of the kestrels are indicated in the legend, as age effects on acuity and CS are well documented (Hodos et al., 1991b; Elliot, 1987; Sloane, Owsley, and Jackson, 1988; Owsley, Sekuler, and Siemsen, 1983). Since there were not enough subjects to determine whether there was an effect due to sex, that information is provided only in the figure legends. The kestrels show similar CSFs, however, with an average acuity of 30.10 c/deg, average maximum CS of 10.72, and average peak SF of 2.09 c/deg.

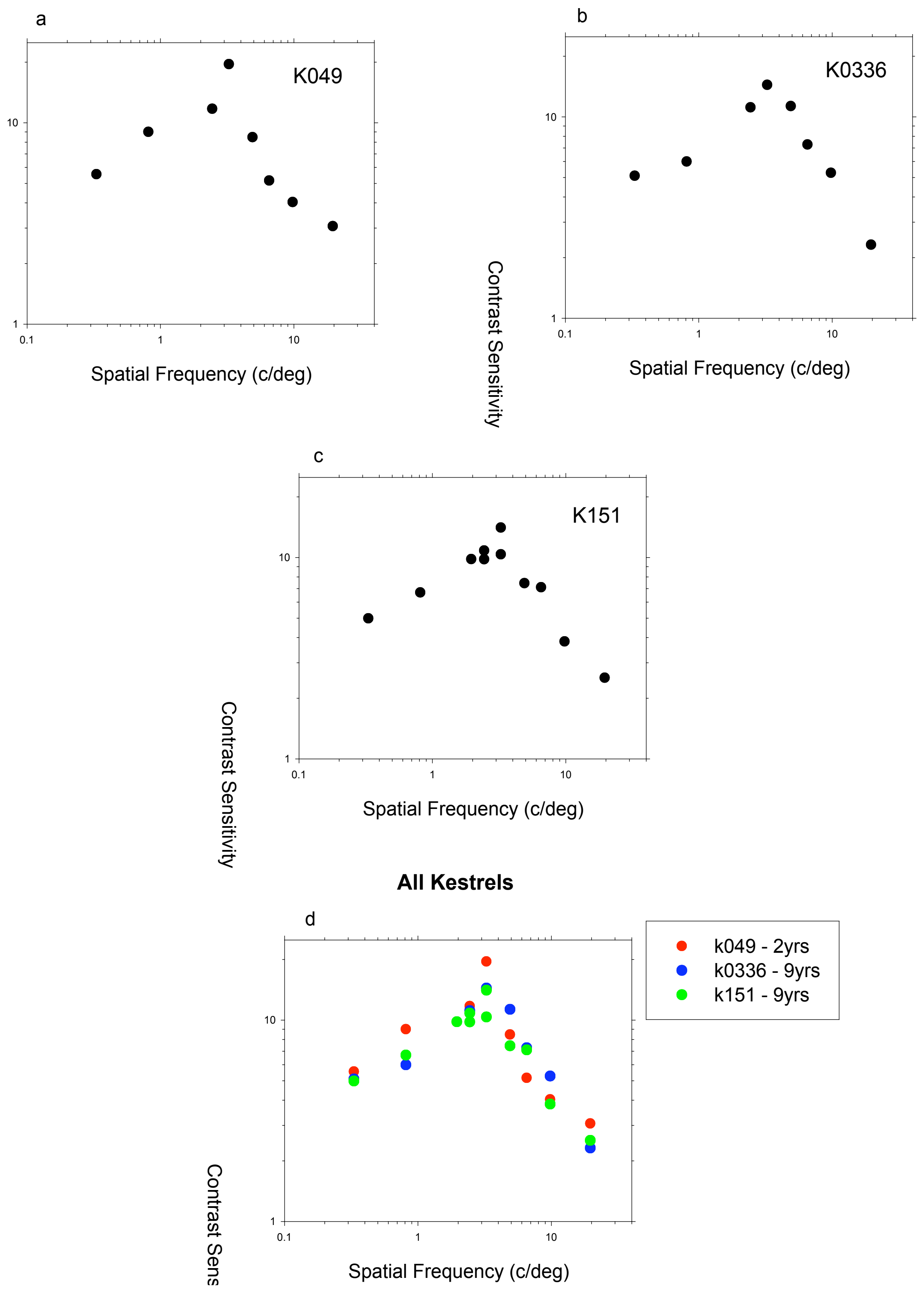

Figure 19: Kestrel CS data. Subjects were K049 (female), K0336 (male), and K151 (female). The ages of the subjects are shown in the figure legend.

The best recording parameters for kestrels were found to be at an azimuth of 55-degrees and an elevation of 30-degrees. The best corrective lens was +1.5 Diopters, which indicates that the refractive state of the animals was emmetropia.

WOODPECKER

Data from only one woodpecker could be obtained, although nine were captured and eight were recorded from. Due to logistical difficulties in maintaining these birds in a colony at the University of Maryland, sample PERG waveforms could not be attained on this subject. The contrast-response functions from which the CS data were obtained are shown in Figure 20. The woodpecker’s CSF is shown in Figure 21. The CSF indicates an average acuity of 2.29 c/deg, a maximum CS of 6.72, and a peak SF of 0.81 c/deg. The recording was obtained at an azimuth of 65 deg and an elevation of 40 deg, using a +0.0 Diopter lens. This woodpecker function is speculative, in that data were recorded from an N of one. In addition, the age and sex of the subject was unknown as this species was wild-caught.

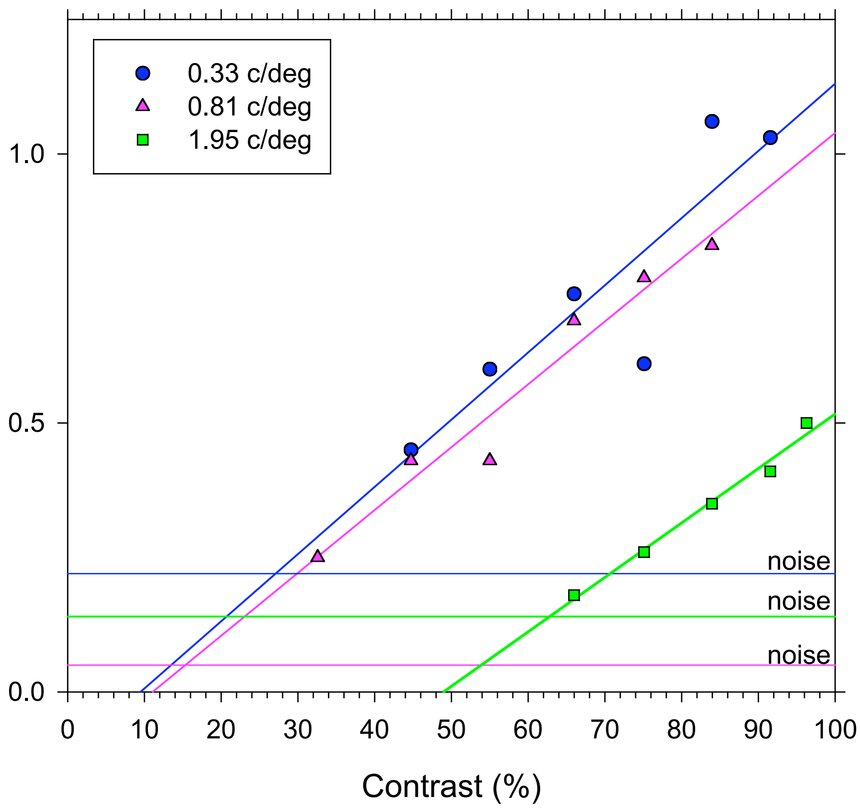

Figure 20: Contrast-response functions from the woodpecker. All three of these CRFs were used to determine this species' CSF.

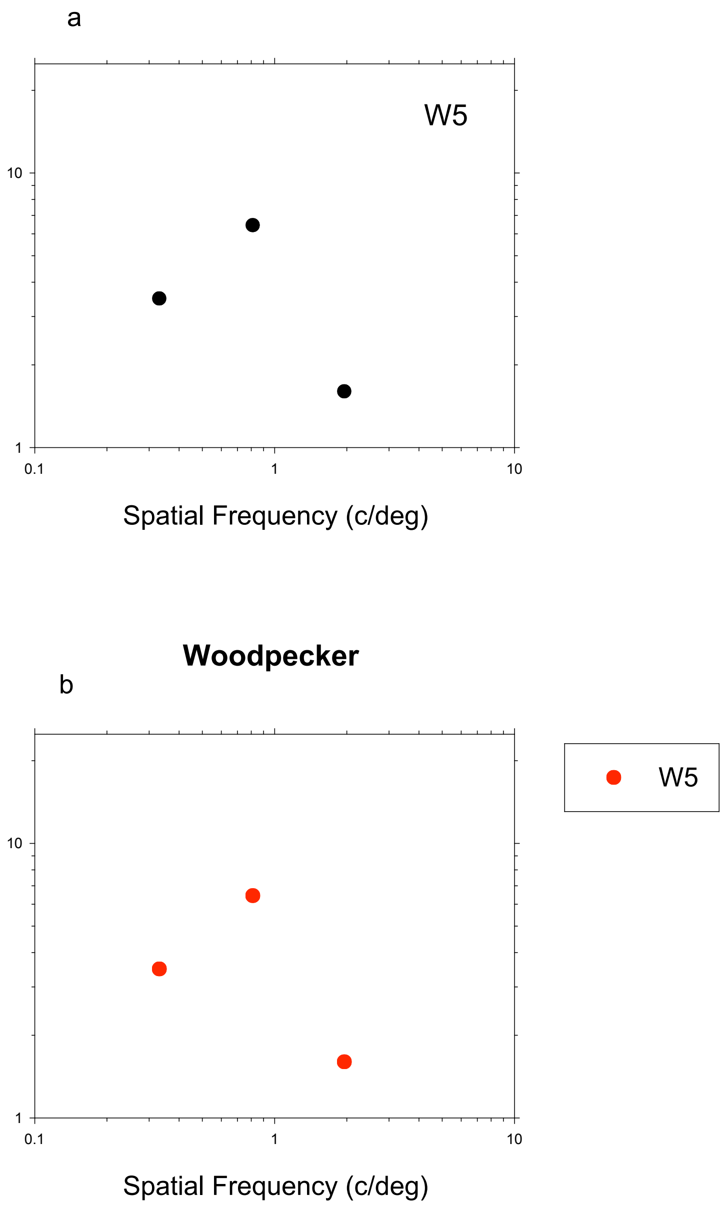

Figure 21: Woodpecker CS data. Age and sex of subject W5 were not known.

QUAIL

Sample quail PERG waveforms are provided in Figure 22. Noise (0% contrast) appears more erratic than the noise from the kestrel waveforms, but this is largely due to the expanded scaling on the Y-axis due to the smaller overall amplitudes obtained from quail. Quail sessions were, however, noisier than pigeon sessions, perhaps due to larger amounts of exposed surface area of electrodes due to the smaller eye of the quail, or perhaps due to higher biological noise. These noise fluctuations appeared random, however, as they are largely out-of-phase.

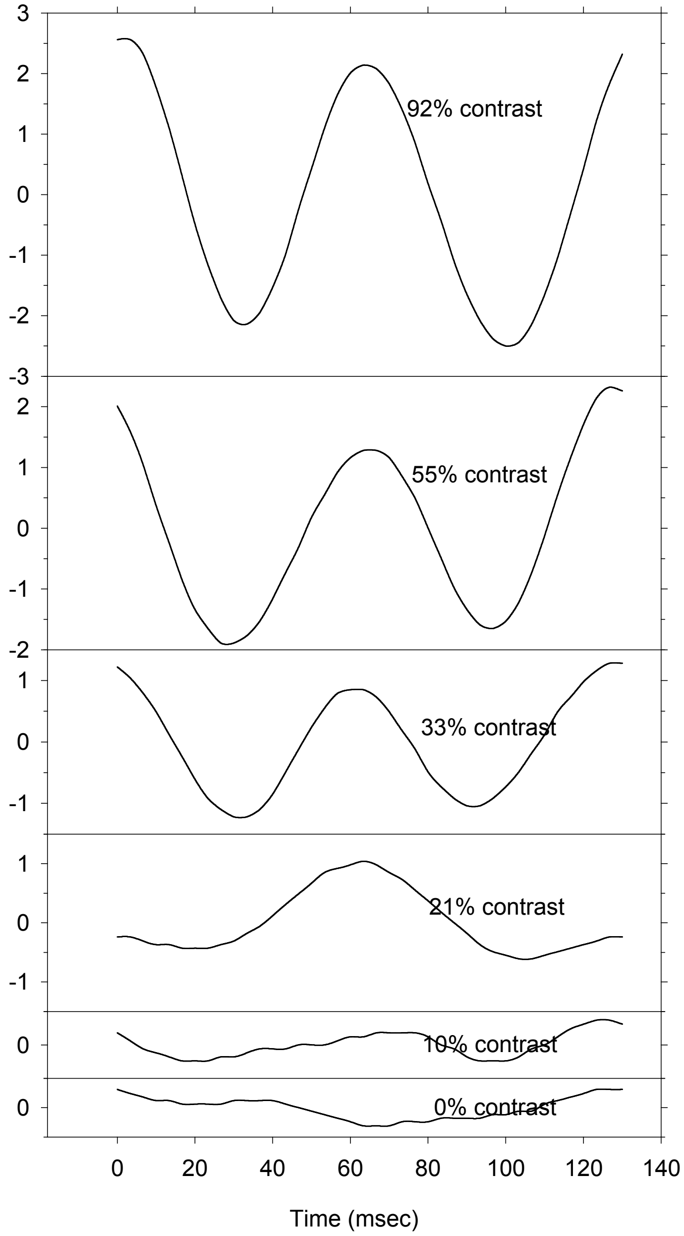

Figure 22: Sample contrast waveforms of a quail.

Sample contrast-response functions for this species are provided in Figure 23. These also are remarkably consistent, linear functions. CS data for all quail are shown in Figure 24d; individual data are shown in Figure 24a-c. Functions are again extremely consistent. The subjects were all males, received in the same shipment from the breeder, and were the same age at the time of shipment, with only slight differences in age at recording due to the date of recording. Peak maturity for quail, in stark contrast to pigeons, is about 6 to 7 months, breeding ending a little after one year of age, and lifespan not expected to exceed two years. Due to this short lifespan, some of the variation in CSFs may be attributed to age, in particular the inferior function of the nine-month-old quail compared to the six- and seven-month-old quail. The average acuity was 6.38 c/deg, the maximum CS was 9.85, and the peak SF was 1.03 c/deg.

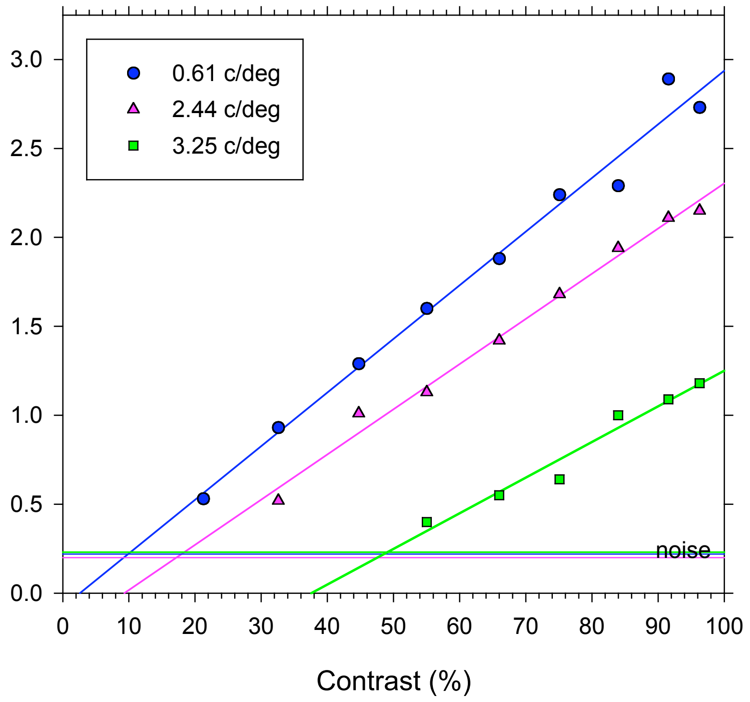

Figure 23: Sample contrast-response functions from quail Q11.

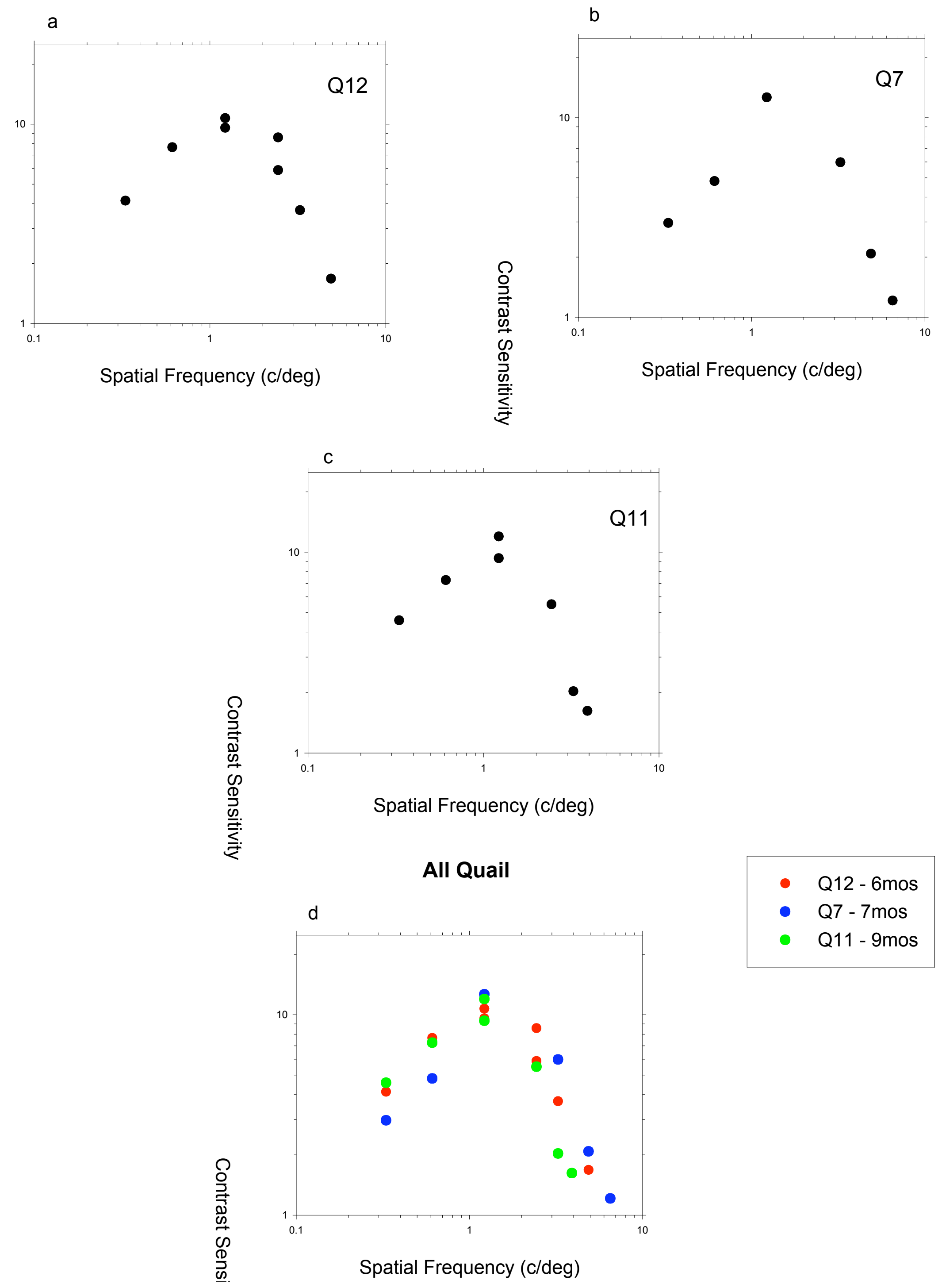

Figure 24: Quail CS data. Subjects were Q12, Q7, and Q11. All three subjects were males.

The best recording parameters found for quail were 75 deg azimuth and 45 deg elevation. The best lens ranged from +1.5 to +2.0 Diopters.

STARLINGS

Starling waveforms are shown in Figure 25. Slightly higher response latencies are observed in these waveforms than for other species, as shown by the phase shifts with progressively lower contrast. In all other respects, these waveforms look very similar to those shown for other species. These waveforms crudely estimate the threshold between 21 and 10% contrast. At 10% contrast, the signal is indistinguishable from noise.

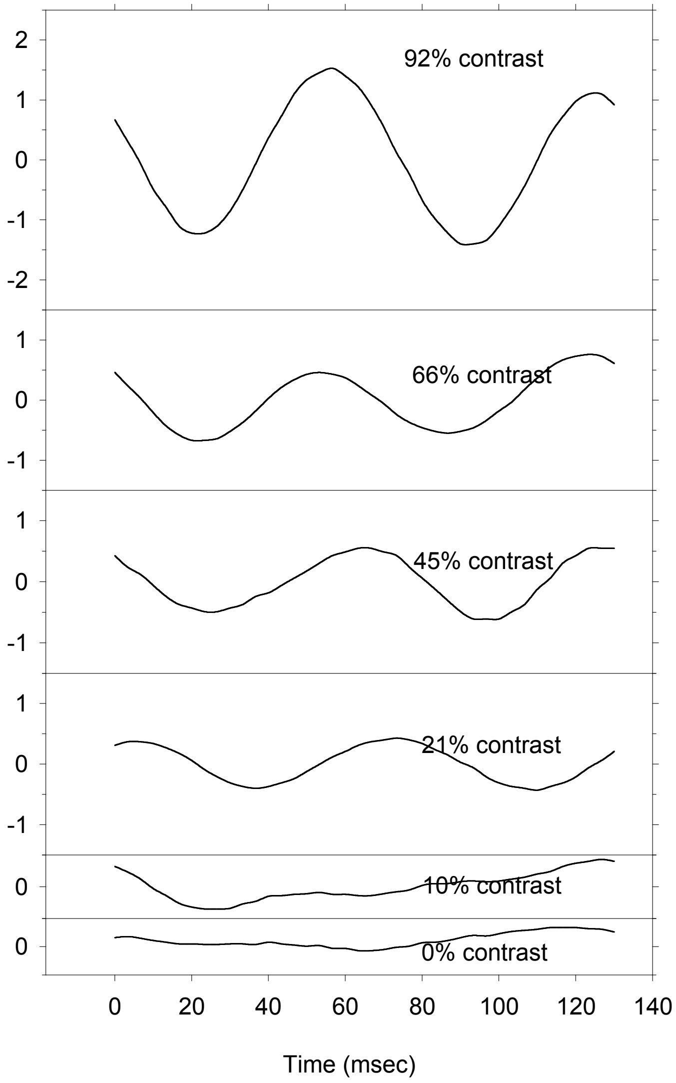

Figure 25: Sample response waveforms from starling SV23.

Sample starling contrast-response functions are depicted in Figure 26. Response amplitudes are reasonably linear with contrast; the contrast-response function with only three amplitudes is unambiguously linear upon visual inspection. In addition, all three extrapolated threshold contrasts were not very different from the contrasts that elicited the weakest, measurable responses.

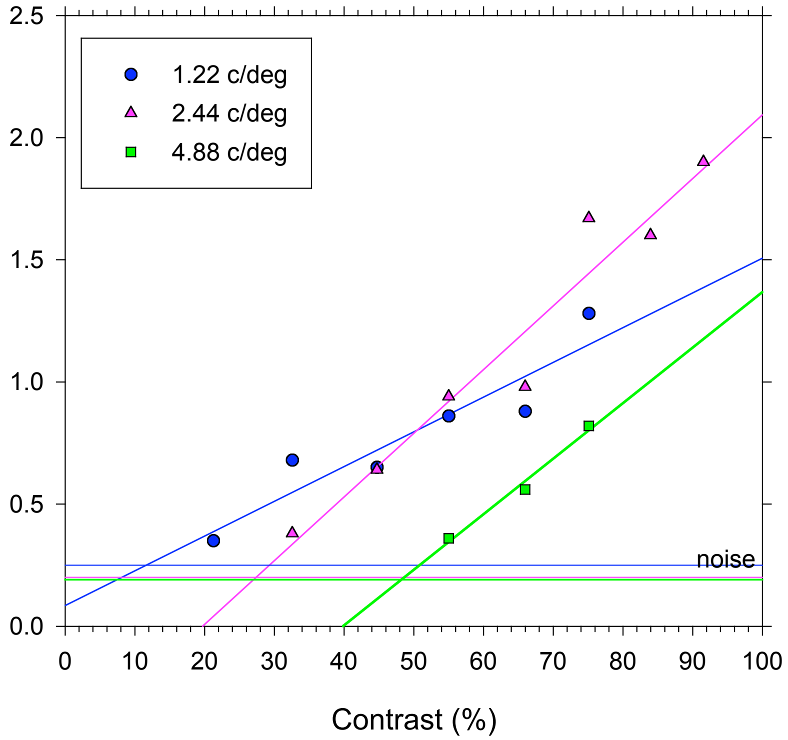

Figure 26: Sample contrast-response functions from starling SV13.These functions were not obtained in the same session because these birds had to have abbreviated sessions to reduce fatalities.

CS data from all starlings are shown in Figure 27; individual data are shown in Figure 27a-d. The composite function in Figure 27d are all of the data points from three starlings (not sv14, sv13, or sv21, which are already represented in the figure), bringing the total number of starlings from which data were obtained to six. Their data were combined in one graph due to the paucity of data from any one of the birds, due to extremely abbreviated recording sessions (due to high metabolism and high fatality rate of this species, see Appendix C), yet their data fit the other starling data very well as can be seen by the conformity of the CSF formed by this composite data with the other starling CSFs.

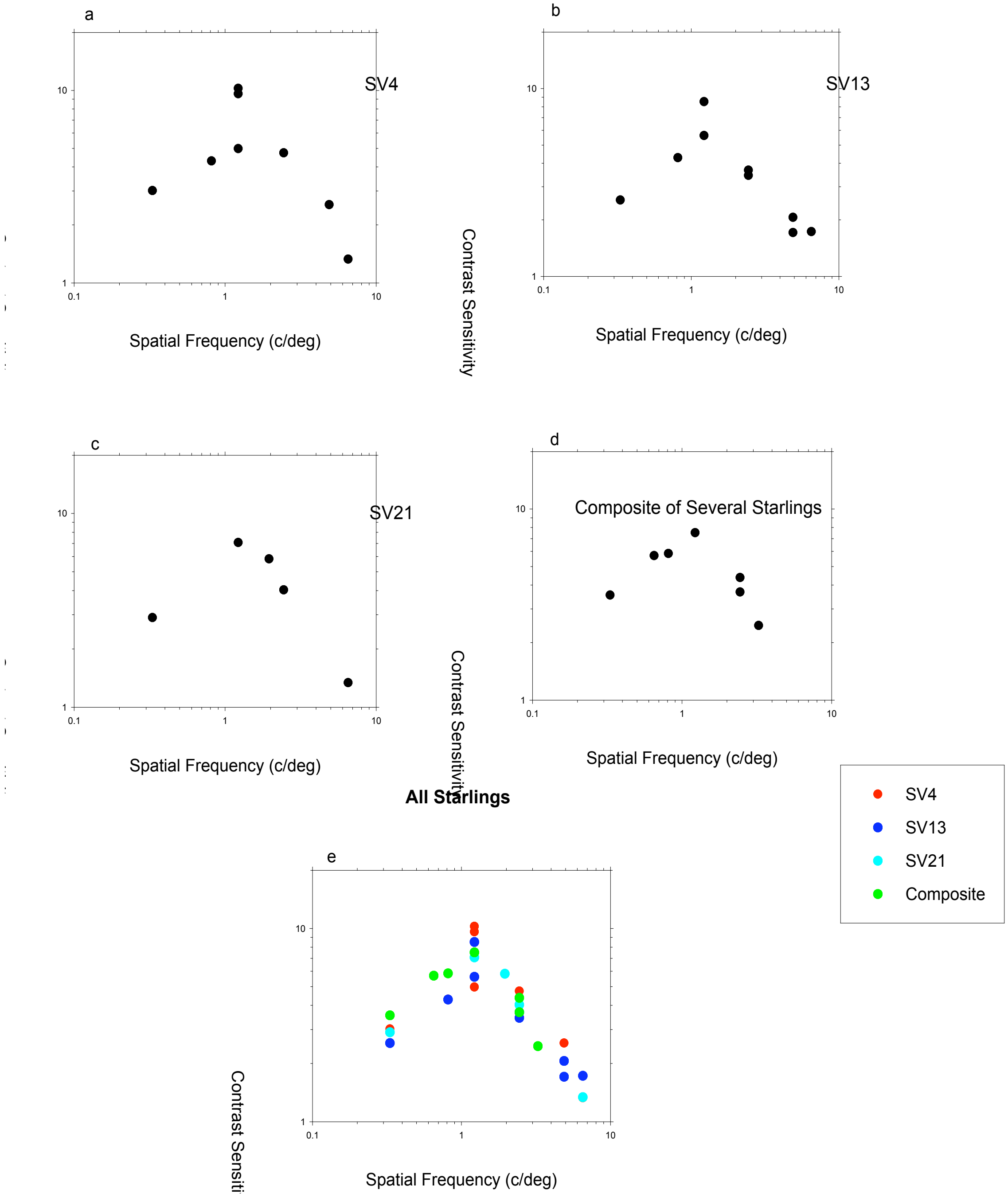

Figure 27: Starling CS data. Subjects in graphs a, b, and c were SV4, SV13, and SV21. Subjects in graph d were SV12, SV14, and SV19.

The average acuity was 7.56 c/deg, the maximum CS was 6.18, and the peak SF was 1.11 c/deg. As members of this species were wild-caught as well, ages and sexes were unknown or unconfirmed. Sexes were determined by identifying outward physical characteristics (Ball, personal communication). However this can be confirmed only by necropsy. In addition, juveniles of this species were not used, as they are easily identifiable.

The azimuth of recordings was 65 deg; the elevation was 30 deg. The best corrective lens ranged from +1.5 to +2.5 Diopters.

OWLS

Owl sample PERG waveforms are shown Figure 28. The noise waveform in this species appears to fluctuate like that of the quail. Similar to the quail, this is mostly due to scaling. The owls exhibited the lowest response amplitudes and signal-to-noise ratios of all of the species in this experiment, with the exception of the budgerigar. (The owl may have experienced the opposite problem as the small budgerigar, in that the large eye of the owl may have diluted the retinal signal reaching the corneal electrodes). Therefore, the Y-axis is greatly expanded (physical distance on printed page is larger per unit voltage), magnifying any fluctuations. At 10% contrast, however, it is apparent that no measurable response to the stimuli is present. At 21% contrast, a noticeable deterioration of the signal is seen. These waveforms together suggest a threshold between 10% and 21% contrast for this individual at the spatial frequency tested.

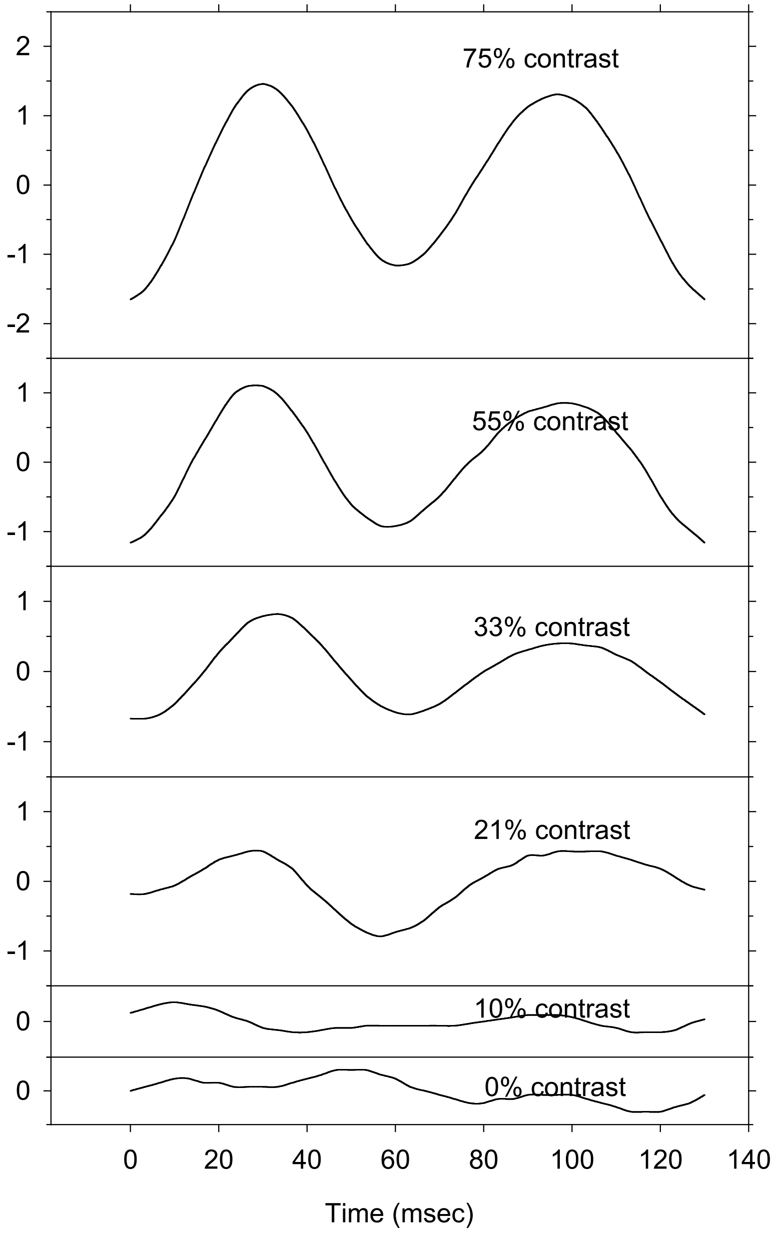

Figure 28: Sample response waveforms from owl O68.

Sample contrast-response functions, from which the actual thresholds were extrapolated, are shown in Figure 29. These are also strongly linear, barring two aberrant data points.

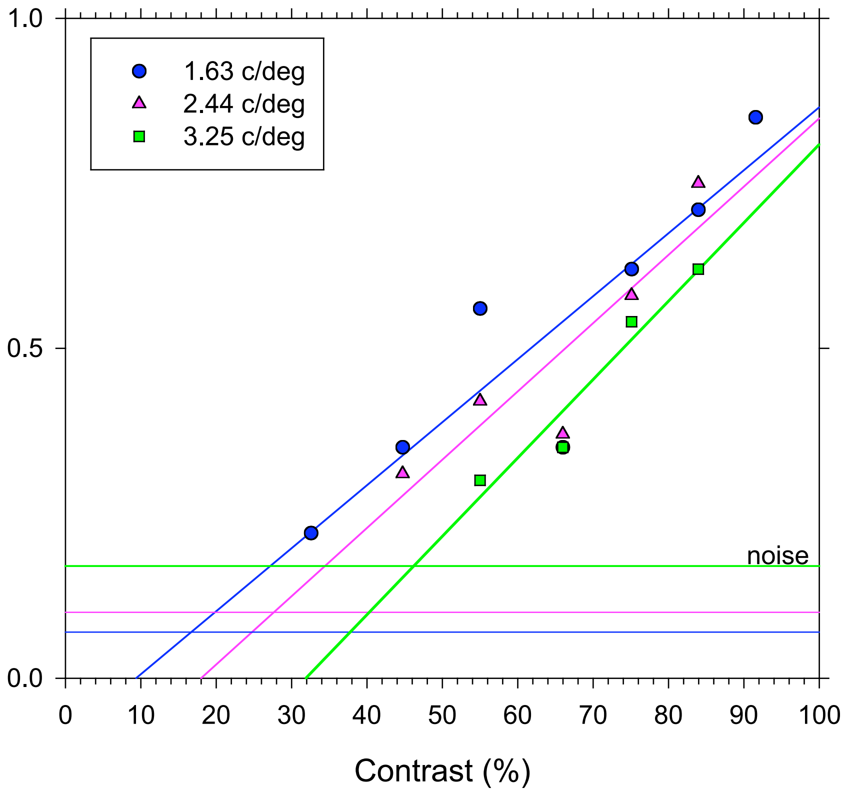

Figure 29: Sample contrast-response functions from owl O22. These psychometric functions were not obtained in the same session because these birds had to have somewhat abbreviated session lengths in order to maintain reliability of recorded data.

CS data are shown in Figure 30; individual data are shown as well. Owl average maximum CS is 6.04, their average acuity is 6.98 c/deg, and their average peak-SF is 1.08 c/deg.

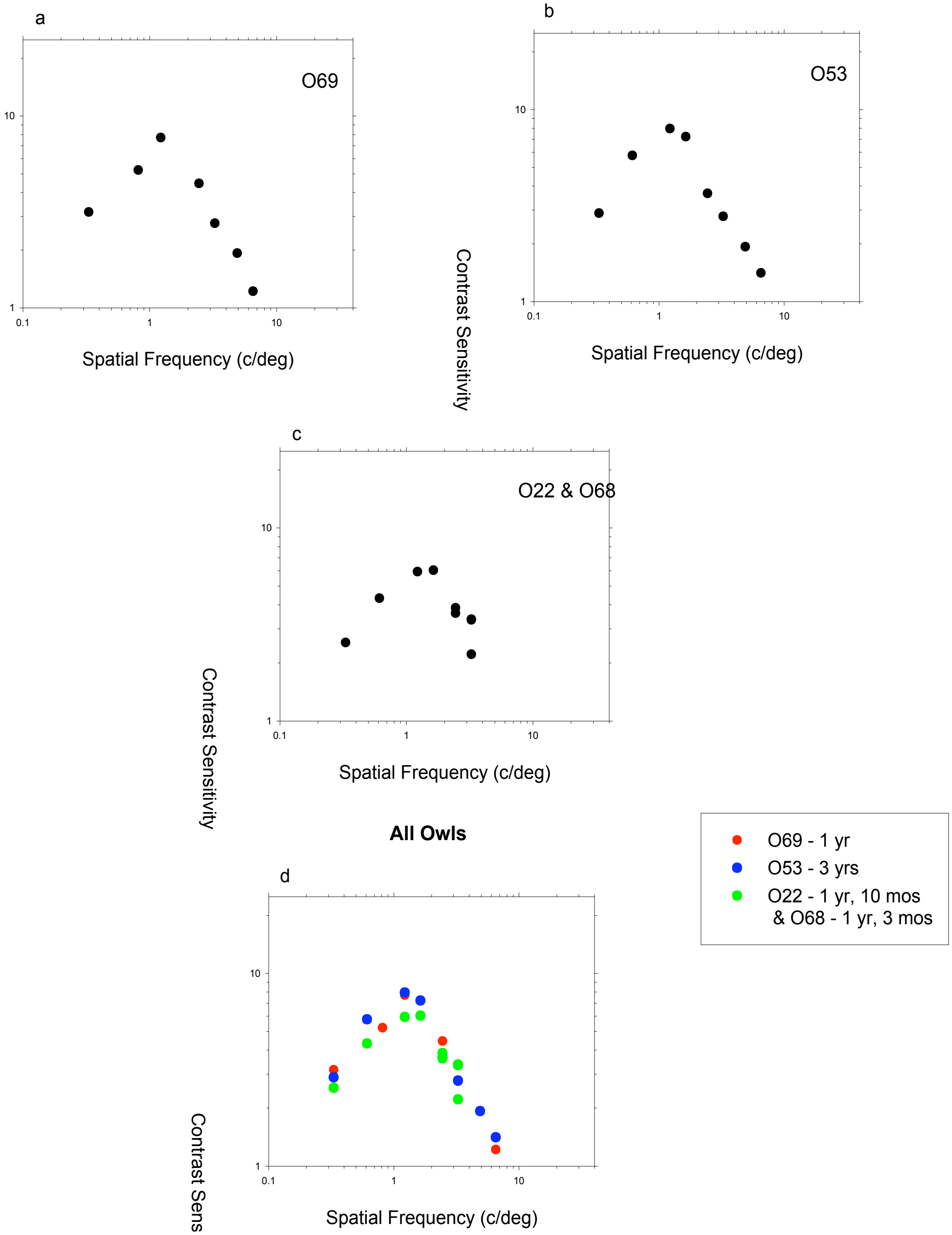

Figure 30: Owl CS data. Subjects were O69 (male), O53 (female), O22 (female) and O68 (male).

The best azimuth for owls was 15 deg and the best elevation was 30 deg. Although the best corrective lens remained nearly constant for an individual owl within and between sessions (applies to all species except the woodpecker, as they could not be tested for consistency between sessions), the best lens ranged from +1.0 to +2.0 Diopters between individuals.

CHAPTER 7: DISCUSSION

AVIAN CSFS

A composite graph of all of the avian data is shown in Figure 31 for ease of comparison. As may be seen in the figure, all of the avian CSFs are low in maximum CS, although there seems to be a diverse range of acuities and half-height bandwidth. Kestrels, with their wide bandwidth and high acuity, are no exception to the general avian pattern of low CS. CSF data from barn owls, common starlings, or woodpeckers have not been reported previously. The starling and barn owl data are nearly identical in every facet. They also show remarkable similarity to quails in bandwidth.

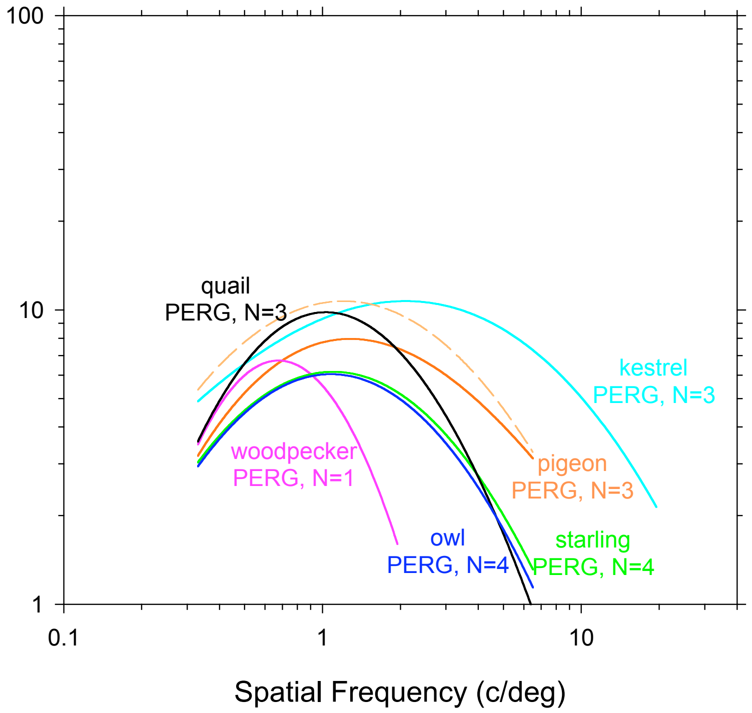

Figure 31: PERG-CSFs of all six species. Each function was generated by applying a single polynomial regression to all existing conspecific data shown in the previous figures. Light, dashed CSF is from E17238 (2 yrs old), which was provided to allow an age-based comparison to young adult birds in this study and in the literature. All analyses and interpretations, however, were made using the CSF from all three pigeons.

Comparison to the Literature

Pigeons

There are no previously reported PERG-CSFs for pigeons in the literature. However, the estimated acuity of the pigeons in this experiment (17.17 c/deg) match closely with PERG derived acuity in the literature (18 c/deg) (Porciatti et al., 1991). Comparison to the behavioral CSFs in the literature also shows reasonable similarity (Hodos et al., 2002; Nye, 1968). The average maximum

CS from behavioral functions is approximately 13, while the maximum CS of the pigeons in this study was 7.98. This is a reasonable approximation based on a study of differences between CS measures obtained with PERG and behavioral methods in this species (Hodos et al., 2001). The peak SF obtained in this study lies between the peak SFs obtained in the two behavioral studies. The small discrepancies between these behavioral functions are probably due to differences in stimulus presentation variables between the laboratories, such as target area and target luminance, discussed earlier in the Introduction.

American Kestrel

The kestrel CSF underestimates the behavioral CSFs in the literature, as depicted in Figure 31 (Hirsch, 1982), but in the aspect of high-SF cut-off, is nearly identical to the kestrel acuity of 29 c/deg from Gaffney and Hodos (2003), which they obtained using PERGs. Aside from the aforementioned phenomenon that the PERG-CSF can underestimate the behavioral-CSF[9], there is the important consideration that the CSFs in the literature (one obtained at 0.0 Hz modulation, the other obtained at 0.25 Hz) were obtained from the same kestrel (N=1). The possibility of a low N anomaly is even greater when one considers the unusual attenuation of the low SF-limb of the CSF obtained from stationary gratings (0.0 Hz). This results in an extreme right-shifted low-SF cut-off that would be unique among any mammal, bird, or fish found in the

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[9] The kestrel high-SF cut-off obtained in this experiment is a reasonable match to the acuity obtained by Hirsch. When the PERG high-SF cut-off is adjusted for the 37-40% difference typically found between PERG acuity and behavioral acuity (Hodos, et al., 2002; Peachey and Seiple, 1987), the adjusted acuity of 41.24 c/deg is functionally identical to Hirsch's acuity of 40.0 c/deg.

literature or found in this study (34). The eagle function, obtained by Reymond and Wolfe (1981), is also right-shifted, although to a far lesser extreme than for the kestrel. In the case of the kestrel, this high, low-frequency cut-off (in addition to a modest acuity) creates a correspondingly exceptional, narrow bandwidth (Figure 32 and Figure 33). Both the behavioral eagle and kestrel CSFs were collected using extremely small target areas when measured in degrees of visual angle squared. As reported in the introduction, small target areas depress CS at low SFs. The target areas used in the acquisition of the behavioral kestrel (4.5 deg^2) and eagle (3.6 deg^2) functions were the smallest found in the CS literature, with the exception of the target area used by DeValois et al. (1974) on humans and macaques (3.14 deg^2). In addition, these target areas are well below critical area, where such effects on the CS are expected to be seen, and are significantly smaller than the target area of 909 deg^2 that was used in this experiment.

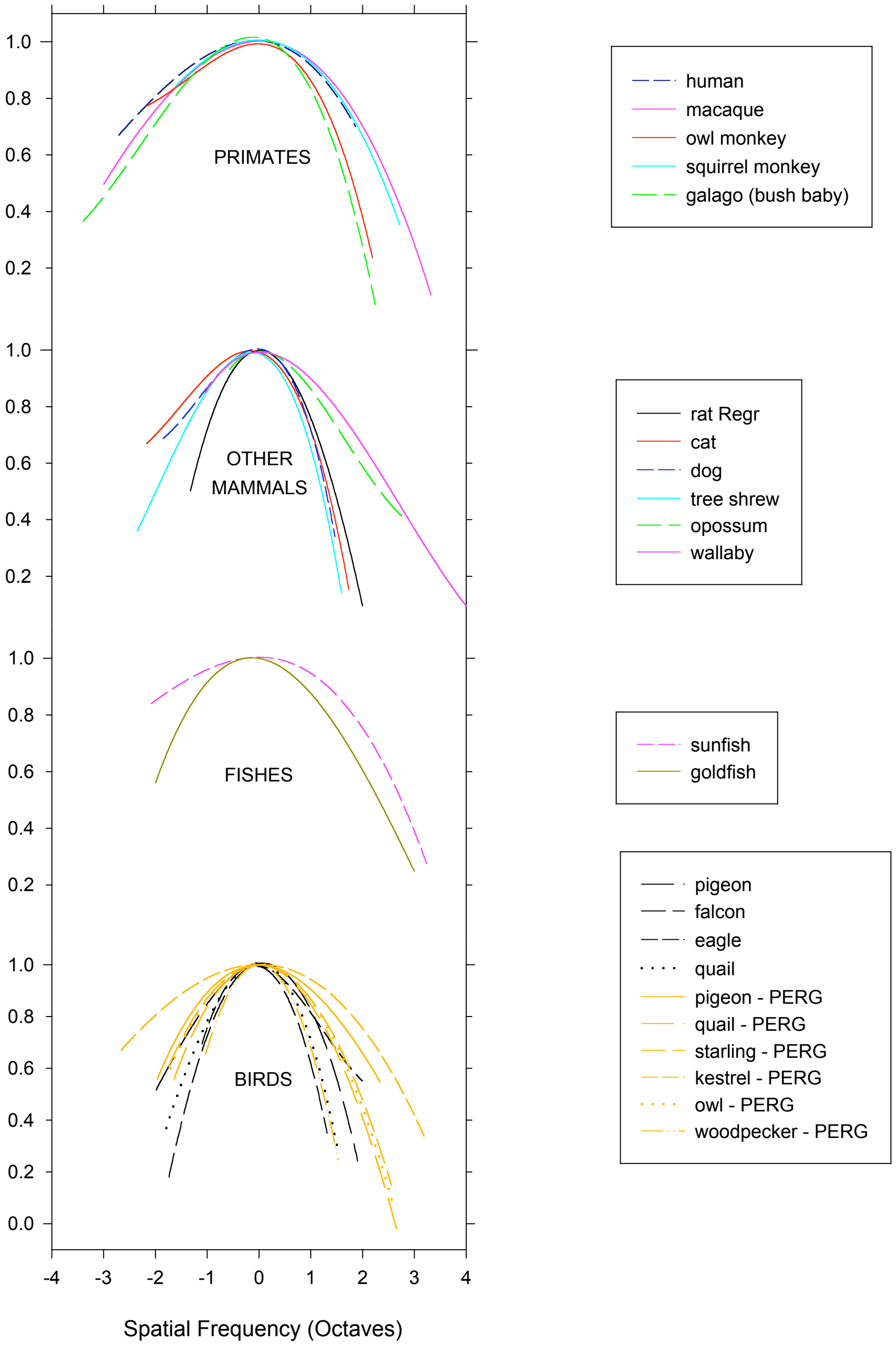

Figure 32: Comparison of CSF bandwidths, grouped taxonomically. CS magnitudes have been normalized and centered on a SF-axis converted to octaves for ease of comparison. The bandwidths of the avian CSFs obtained in this experiment are monochromatic (gold), for ease of differentiation from previously obtained avian bandwidths.

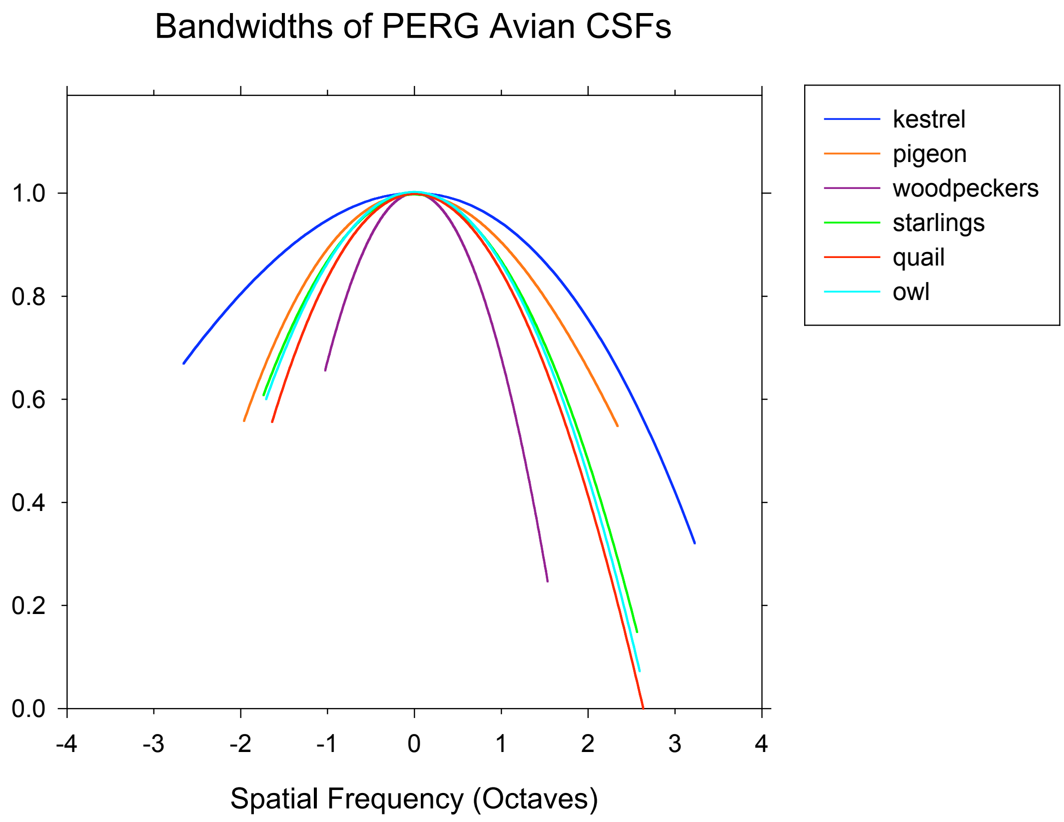

Figure 33: Avian bandwidths obtained in this experiment.

Hirsh's kestrel CSF obtained from a temporally modulated display (also behavioral, obtained from a single subject as mentioned above) is a better match to the CSF obtained in this report, in respect to half-height bandwidth and low-SF sensitivity. The low-SF limb from the function obtained with 0.25 Hz temporal modulation extends to much lower SFs than the function from the 0.0 Hz gratings. Hirsch's 0.25 Hz CSF, however, was obtained with the same, small target area used to obtain the 0.0 Hz CSF. One might speculate that the same animal tested with sufficiently large target area would have yielded a CSF with a more gradual low-SF roll-off, as is typical in other animals.

Reasons for the discrepancy of the maximum height of the 0.25 Hz CSF with the maximum CS obtained in this study, on the other hand, is not as obvious. The maximum CS reported by Hirsh for temporally modulated gratings is much higher than that reported for stationary gratings. The maximum sensitivity is surprising for a bird, rivaling that of humans and primates. Such a dramatic rise in CS with temporal modulation is also unique, as temporal modulation characteristically results in equivalent or reduced maximum CS[10] in cats (Blake and Camisa, 1977), humans (Robson, 1966; Watson and Nachmias, 1977; Yang and Makous, 1994; Masson et al., 1994), and pigeons (Hodos et al., 2003). This unusual finding may be the result of some perceptual or attentional effect that this exceptionally low rate of modulation (0.25 Hz = one reversal every 2 secs!) imposed. Since such low rates of temporal modulation are not used elsewhere in the human or animal literature, there is nothing with which to compare Hirsch's 0.25 Hz data. Ethological implications of this will be discussed under Ethological Considerations, below.

Woodpecker

The woodpecker function is speculative, in that data were recorded from only a single subject, due to the extreme difficulties in maintaining these birds in captivity. There are no other woodpecker data with which to compare these data. In addition, retinal cell densities have not been previously obtained in this

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[10] Temporal modulation improves contrast sensitivity only at low SFs. This results in altered half-height bandwidth and general appearance of the CSF, without affecting maximum CS, except in a deleterious manner at progressively higher temporal modulation rates.

species, rendering any speculative estimates of acuity or maximum CS impossible.

Quail

The quail data are in agreement with previous electrophysiological reports on acuity (Lee et al., 1997). Peak SF cannot be compared to Lee et al.'s PERG data, however, because her CSFs for young adult quail do not exhibit a low-SF roll-off. Rather, the low-SF limb of her CSF continues to ascend linearly with decreasing SF, after what appears to be the beginning of a peak. This is a pattern that is not seen in any animal tested thus far, including birds, and does not match the pattern obtained both behaviorally by Hodos (unpublished data) and electrophysiologically in this experiment. When the data from this experiment are compared to data obtained by Hodos (behavioral quail CSF in Figure 31), however, a close approximation of shape, maximum CS, and bandwidth are seen. The PERG-CSF obtained here is slightly shifted to higher SFs, which at mid- to high-SFs may be accounted for by the use of younger birds in this study. The quail in this study were between 6 and 9 months of age, which is the age at which they are at the peak of their visual acuity (Hodos et al., 1991b). The higher sensitivity of behavioral quail at low SFs is perhaps due to the underestimation of the CSF by PERG methods that is seen in humans (Peachey and Seiple, 1987) and pigeons (Hodos et al., 2001).

Starlings

Starling CSFs have not been previously reported. While much is known about the optics, eye movements, and relative photoreceptor proportions in these birds (Martin, 1986; Hart, 2001), retinal cell density data are lacking. Thus, similar to the red-bellied woodpecker, speculative estimates of acuity and maximum CS for this species is not possible.

Barn Owls

Previous CS data on only one other species of owl exists (little owl, *Athene noctua*) (Porciatti, et al., 1989). These data, however, were collected at only a single spatial frequency. Since a complete CSF was not obtained for the little owl, a detailed comparison is not possible. The estimated acuity obtained in this experiment for barn owls (6.98 c/deg), however, is very close to the theorized acuity of 8.4 c/deg reported by Wathey and Pettigrew (1989), which they estimated from retinal ganglion cell density (12,500/mm^2) in this species. Ganglion cell density can also be used to project estimated maximum CS, using the meta-analysis used by Hodos et al. (1997), as described in the Introduction. Using the density count of 12,500/mm^2, projected maximum CS is approximately 5, which is very similar to the obtained maximum CS of 6.04.

Ethological Considerations

Pigeons

In the wild state, rock pigeons, from which all current pigeon strains are descended, habit rocky seacoasts or inland in gorges, river valleys, caves, desert oases, and more commonly, human cities. Their diet consists of grains, legumes, various weeds, some invertebrates such as moth larvae and pupae, snails and slugs (del Hoyo, 1994). As they are ground feeders, food items need only be resolved in their binocular field. Based on the average height of a pigeon (pupil height of 20 cm) (Hodos and Erichsen, 1990) and their measured acuity, food items need only be 1 mm for detection (0.029 deg of visual angle). Thus, acuity seems sufficient for foraging in this species, which among the daily activities of the pigeon would require the highest degree of resolution. Although this species has low CS, objects are detected against their background probably with the aid of their superior color vision, motion detection, and UV sensitive systems (Romeskie, 1976; Hodos et al., 2001; Bennett and Cuthill, 1994).

Kestrels

There are seventeen subspecies of kestrels, distributed widely over the entire US, Mexico, Central America, and most of Canada (Smallwood and Bird, 2002). Kestrels inhabit mostly open areas covered by short ground vegetation. Some males habit areas that are densely vegetated, however hunting is restricted to small open patches within the dense vegetation. Their diet consists of arthropods (especially grasshoppers) and small vertebrates (mostly voles, mice, and small passerines) (Smallwood and Bird, 2002). Both the estimated acuity obtained in this study and the behavioral acuity from Hirsch are much lower than the behavioral acuity of 160 c/deg reported by Fox et al. (1976). In an analysis of prey size and hunting distance, Gaffney and Hodos (2003) concluded that an acuity of 160 c/deg in the kestrel would far exceed the needs of these birds in the wild. In an analysis based solely on their measured acuity of 29 c/deg (which is nearly identical to the acuity of 30.1 c/deg obtained in this experiment), Gaffney and Hodos determined that kestrel prey are within detection parameters. Furthermore, the optical and retinal configuration of the kestrel does not support Fox et al.'s findings. Gaffney and Hodos point out that kestrels have a posterior nodal distance (PND) that is only 40% of that of the wedge-tailed eagle (Aquila audax), yet according to Fox et al., the kestrel acuity is superior[11]. A longer PND will result in a larger retinal image size, and hence higher acuity. This is further enhanced in the wedge-tailed eagle by a denser packing of photoreceptors (Table 3), which results in higher resolution. Finally, there may have been a methodological flaw in Fox et al.'s measurement. As no control was used to ensure that the stimulus was hidden from view as soon as the kestrel left the observation perch, it is highly probable that the viewing distance was not maintained; i.e. stimulus remained in view, as the kestrel left the observation perch and approached the stimulus to register its discrimination choice. A closer viewing distance would result in larger stimuli and therefore an artificially high acuity. Hirsh, on the other hand, maintained viewing distance, and as such her acuity data are more credible than Fox et al.'s.

Hirsch's narrow bandwidth, however, is also highly questionable on ethological grounds. If her estimate of bandwidth is actually correct, one must consider the following absurd implication of the extremely sharp low frequency

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[11] Comparison is to behavioral acuity of the wedge-tailed eagle.

roll off of kestrel data; namely, that Hirsh's narrow CSF implies that these birds could detect a high contrast mouse (high SF) at a far distance, but would not detect a high contrast elephant (low SF) at the same distance. A more likely possibility is that the very small target area that was used was insufficient to elicit a measurable response at low SFs. Another possibility is that kestrel visual behavior is heavily dependent on motion. Prey motion has been found to be a better predictor of predatory response from kestrels, than prey size or color (Smallwood, 1989; Sarno and Gubanich, 1995). This may in part explain the unusual pattern of significantly diminished CS to stationary gratings relative to 0.25 Hz gratings found by Hirsch (1982). In other words, the CSF from 0.0 Hz stimuli may have produced inferior results for either attentional or perceptual reasons because the stimuli were not as perceptually salient to the kestrel.

Furthermore, American kestrels may compensate for less than stellar achromatic contrast sensitivity by depending on their UV vision, an aspect of vision that humans and most mammals lack. For example, these birds have demonstrated the ability to detect and localize voles by the ultraviolet reflections from their urine trails (Viitala, et al., 1995).

Woodpeckers

The range of the red-bellied woodpecker is widespread in the East and Southeast, as far north as Massachusetts and as far West as the wooded portions of the Great Plains. Red-bellied woodpeckers prefer humid forests dominated by pines or hardwoods or a mixture of both, but in the Northeast US are predominantly found in pure deciduous forests. Some sources recognize subspecies of the red-bellied woodpecker (Burleigh and Lowery, 1944; Koelz, 1954), which may explain some of these habitat differences. Their diet consists of fruit (which they frequently eat while hanging upside-down), mast (acorns and nuts), seeds, sap, and arboreal arthropods, which they forage; they are also known to take small or young vertebrate prey as well (Shackelford, Brown, and Connor, 2000). Although these woodpeckers are reported to seldom excavate wood for insects, these foraging habits differ depending on season, sex, and geographical location (some of these probably due to food availability). In Maryland, for example, where these birds were captured for study in this experiment, these birds were found to spend 7.4% of their foraging time in excavating their prey, and 26.5% of their time in probing the surface of bark. The remainder of their foraging time was spent on fruits and nuts (Shackelford et al., 2000). In Minnesota, this species spends 26.3% of their foraging time excavating, and 62.4% of their time probing (Shackelford et al., 2000). In addition, these birds are also highly adapted for excavation and probing. A red-bellied woodpecker's tongue is highly muscular and cylindrical, pointed, and barbed at the tip, aiding in extraction of prey from crevices. The tongue is also long, extending more than 3 inches beyond the tip of the bill, and is in addition highly maneuverable. Their tongue is better suited for probing and extraction from bark than other woodpeckers studied (Shackelford et al., 2000).

Although this species was chosen for this experiment due to its forested habitat, which lends an environment of lower contrast stimuli than that of diurnal raptors or granivorous birds, red-bellied woodpeckers may have the least reliance on vision among the species studied. As the woodpecker's live prey is very close to the end of its bill, and is often not visible, this species therefore may not require high acuity to detect and capture their prey. This may explain the extremely low, estimated acuity obtained in this experiment. The movement afforded by live prey may in addition preclude the need for high spatial ability. Fruits and nuts, which comprise the remainder of this species' diet, may further be detected using UV vision, which, although not yet studied in this species, is commonly considered a general characteristic of avian vision (Bennett and Cuthill, 1994).

An examination of other aspects of this species' ecology lends further evidence that red-bellied woodpeckers may not rely as heavily on vision as other diurnal birds. Courtship displays, both male and female, appear to be entirely auditory, consisting of tapping (light drumming), calls, and drumming (bill rapidly strikes a hard surface that has good resonance, for example dead or hollow trees, metal light fixtures) (Shackelford et al., 2000). However, UV reflectance from red-bellied woodpecker plumage and mate selection thereupon has not yet been tested. In addition, the response to predators is to hide on the opposite side of trunks or limbs and remain still and quiet, rather than to fly to safety. In the event that capture is imminent, the response is not to evade by flying between branches or around trees, but rather to dive erratically into low dense vegetation (Shackelford et al., 2000).

Quail

Japanese quail primarily habit grasslands, marshes, cultivated fields, and pastures. Their flight is slow, usually brief, and is usually seen only when flushed (Wild Bird Society of Japan, 1982). As they prefer dense, low vegetation, the level of contrast sensitivity that they exhibit is not surprising. In addition, this environment does not necessitate far-distance viewing, which requires high acuity.

Japanese quail feed on seeds of grasses, weeds, grain, and also some invertebrates such as beetles, ants, earwigs, grasshoppers, spiders, worms, and mollusks. Since the dimensions of the smallest of these foraged items are not known, as well as the frequency at which these items are foraged, it is difficult to speculate whether the acuity of these animals is sufficient for successful foraging. However, the smaller items comprising the diet of quail relative to that of pigeons do not belie the mediocre acuity obtained for quail. Quail are considerably smaller than pigeons, bringing their eyes much closer to the ground. This will effectively increase the visual angle that an object subtends. Moreover, this species is well noted for their ability to detect UV, and in addition have been shown to use UV wavelengths to enhance detection of chromaticity differences (Smith, Greenwood, and Bennett, 2002). It is likely that UV sensitivity is used by quail to aid in detection of food items.

Starlings

Starlings are distributed nearly over all of continental North America, prominently found around cities and towns where supplemental food and shelter are available. North American starlings seem to avoid large expanses of undisturbed non-grassland native habitats such as forests and deserts. There is significant geographic variation in body mass, feather mass, wing length, culmen length, and tarsus length. Genetic variation, however, is virtually nil, due to the introduction on this continent from a single population (*Sturnus vulgaris vulgaris*) and subsequent rapid expansion. They migrate mostly during daylight, using the sun and learned landmarks.

Starling diet consists mostly of invertebrates (arboreal included), which are preferred, comprising 44 to 97% of their diet depending on the season. Most of this type of foraging is spent in open areas with short vegetation such as fields and lawns. Head and bill musculature are well adapted to foraging in the soil. The bill is inserted in soil and then opened, whereupon the area between the bills is visually inspected for live prey. With such close vision, similar to the case of quail, even small prey subtends a large visual angle. Also included in the diet are some fruits and berries, grains, and seeds. A significant portion of their diet (depending on the season) could also include man-made sustenance, such as garbage and livestock feed. However, as these are found in large quantities, are densely localized, and are consistently found in the same areas, they provide a reliable source of food that does not have to be resolved in fine spatial detail to be foraged. For foraging purposes, the moderate acuity of the starling seems to be in excess of their needs.

These species are considered generalists, however, with a wide repertoire of visual displays for communication, mating, or establishing and maintaining territories, a wide range of diet, wide distribution over most habitats, and highly developed vocal abilities consisting of many calls, and eight classes of songs

(Cabe, 1993). Their moderate acuity and moderate CS would seem to support this view of a generalist.

In addition, this species is able to detect ultraviolet wavelengths, which has been shown to aid in migration in other avian species, could possibly aid in foraging, and most likely plays a strong role in sexual selection. For example, in sexual selection, mate preference in female starlings is significantly influenced by degree of ultraviolet reflectance from male plumage (Bennett et al., 1997).

Owls

Barn owls occupy all of Central America and all but some of the northern-most regions of the US. There are 35 generally recognized subspecies, and they are generally non-migratory. Barn owls need cavities and crevices to roost and nest in, such as found in trees, cliffs, caves, riverbanks, church steeples, barn lofts, hay stacks, and nest boxes. Aside from these perquisites, barn owls do not need forests. These owls may predominantly be found in rural forest edges or agricultural areas, especially as clearing forested lands for agriculture has apparently allowed these birds to expand their range in several areas. Unfortunately, changing agricultural practices such as lessened availability of open farm structures for nesting and roosting, and better pest control, have provided insufficient densities of prey.

Barn owl diet consists of small mammals, primarily rodents, and of rodents, primarily voles (*Microtus*) and deer mice (*Peromyscus*). They hunt mostly at night, one hour after sunset to about one hour before sunrise, at low altitudes (1.5-4.5 m) above the ground in open habitats, and sometimes hunt from perches. Prey is detected by both excellent low-light vision (Dice, 1945; Marti, 1974) and hearing (Payne, 1971; Konishi, 1973). Adaptations of owl eyes to nocturnal environments include large tubular eyes with large pupils and highly curved corneas and lenses (Martin, Gordon, and Cadle, 1975). This in addition to a high density of ganglion cells explains the respectable CS and acuity of barn owls in this experiment, equivalent to other diurnal birds.

In another nocturnal species, the owl monkey (Aotus trivirgatus), visual acuity was inferior to diurnal humans at photopic light levels. However, in scotopic conditions, the acuity of the nocturnal owl monkey was far superior to that of humans because of the steeper rate of decline at these dim luminances in humans (Jacobs, 1977). It would be interesting to test barn owls in a variety of luminance levels, to determine how CS might change.

The little owl (*Athene noctua*), for which Porciatti et al. (1989) has obtained CS at one SF, is crepuscular. Thus this species probably relies more heavily on vision in low contrast situations. In addition, this species does not appear to be able to supplement vision with the hearing and superior auditory localization like the barn owl possesses. The single data point that Porciatti et al., obtained was higher than would be expected from my barn own data. There may be a parallel here to the unexpectedly high maximum CS of the nocturnal owl monkey.

AVES COMPARED TO MAMMALIA

None of the birds measured in this study has a CSF that can rival that of humans, primates, and some other mammals. This includes even kestrels, which are considered to have superior visual abilities, exemplified as high acuities in the range of humans. The compiled avian CSFs are shown with all other existing CSFs for mammals and fishes in Figure 34. Figure 34 shows that all of the CSFs measured here are within the range of all the previously reported avian CSFs (Hodos et al., 1997). This is a somewhat surprising finding considering the diversity of ecological backgrounds and the corresponding adaptations represented by our subjects. While further testing of a wider range of avian taxa and phyletic branches might reveal greater levels of maximum contrast, the data of the present sample would seem to indicate that low maximum contrast sensitivity is a fundamental characteristic of avian vision.

In all other aspects, however, avian CSFs appear to be comparable to mammals'. This study shows bandwidths that are similar in both mean and variability between birds and mammals (Figure 32). In addition, acuities and peak SFs for the different species of birds encompass a range that reflects the diversity of ecological adaptations and is as broad as that of mammals (34). Finally, avian CSF studies in the literature suggest that with the exception of maximum contrast sensitivity, contrast functioning operates similarly in birds and mammals, as determined by CSF responses to luminance changes (pigeon, Ghim, Master's Thesis, 1997) and CSF responses to temporal modulation (pigeon, Hodos, et al., 2003).

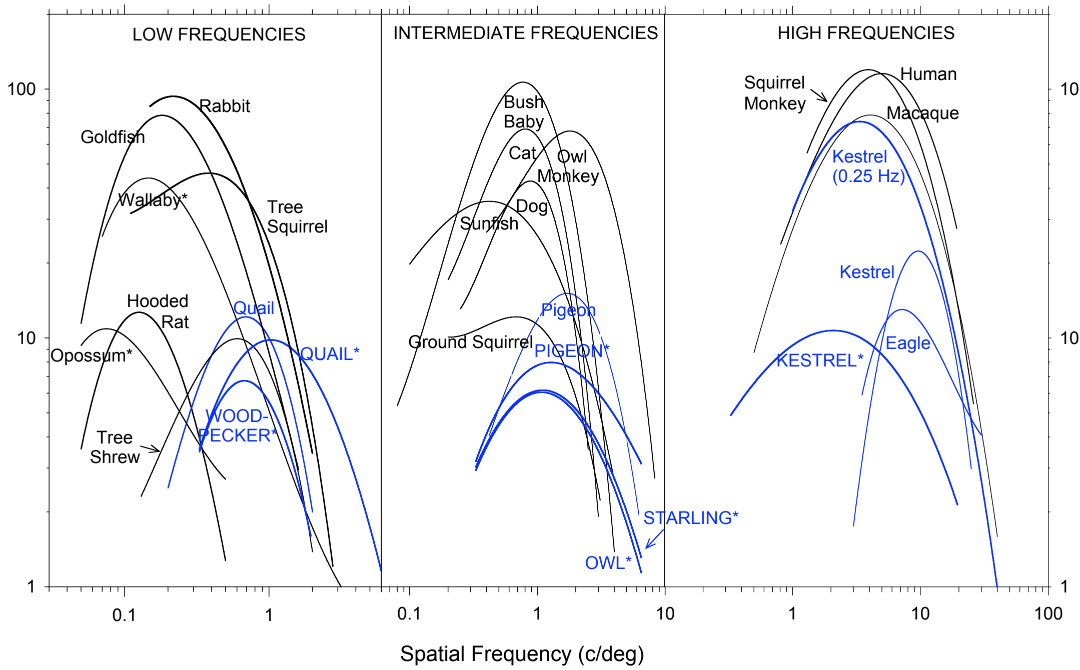

Figure 34: This is a comprehensive collection of species from which a complete CSF has been measured[12]. The CSFs collected in this study are labeled in ALL CAPS. All non-avian CSFs are monochrome for ease of comparison to avian CSFs, shown in blue. Curves for species that are asterisked were derived from electrophysiological data. All other curves are based on behavioral data.

The Low Peak Contrast Sensitivity of Birds

The precise cause of the low contrast phenomenon in birds is baffling. While contrast functioning appears similar in birds and mammals, there are

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[12] Aside from the CSFs collected in this experiment, the CSFs depicted are from the following sources: Human and Macaque – DeValois and Morgan (1974); Bush baby – Langston et al. (1986); Cat – Pasternak & Merigan (1981); Dog – Aiken & Loop (1990); Rat – Legg (1984); Opossum – Silveira et al. (1982); Ground squirrel – Jacobs et al (1980); Owl monkey – Jacobs (1977); Rabbit – Pak (1984); Squirrel monkey – Merigan (1976); Tree shrew – Petry et al (1984); Tree squirrel – Jacobs (1982); Wallaby – Hemmi & Mark (1998); Sunfish – Cenlenza (1994); Quail – Hodos (unpublished data); Pigeon – Ghim (1997); Kestrel – Hirsch (1982); and Eagle – Reymond (1985). Mouse CSF was obtained by Porciatti et al. (2002), but is not depicted here for clarity.

differences in the details of the mechanism. For example, in pigeons at least, contrast responses are not generated by retinal ganglion cells, as measured by the PERG (Bagnoli, et al., 1984; Blondeau, et al., 1987), whereas in mammals, properties of the ganglion cells are thought to shape the contrast response (Purpura et al., 1988; Purpura et al., 1990; Kaplan et al., 1990; Shapely and Enroth-Cugell, 1984). Furthermore, ganglion cell atrophy in mammals has been shown to eliminate the PERG response (Berardi et al., 1990; Maffei and Fiorentini, 1981; Dawson, Maida, and Rubin, 1982; May, et al., 1982). Single unit responses to contrast, however, show similarities between pigeons and highly contrast sensitive mammals such as cats and primates (Jassik-Gerschenfeld and Hardy, 1979). It is unknown at this time whether other avian species would also show effects similar to those reported from pigeons or to the results reported from mammals.

The low CS of birds may be imposed by one or more trade-offs. Reymond and Wolfe (1981) suggest that the lower avian maximum contrast sensitivity may represent a trade-off between contrast sensitivity and acuity based on retinal cell receptive field sizes and photon noise (Shapley and Enroth-Cugell, 1984; Hecht, Shlaer, and Pirenne, 1942; Donner, Copenhagen, and Reuter, 1990). Unfortunately, no one has as yet actually tested this hypothesis in birds.

Another possible trade-off is the specialized retinas of birds for ultraviolet vision and the subsequent compromise of contrast sensitivity. UV vision has been confirmed in at least 29 species of birds, spanning a diverse range of taxonomies and ecological habitats, and is thought to be a general property of birds, although it may be absent in some nocturnal species (Bennett and Cuthill, 1994; Cuthill et al., 2000). Birds have a cone receptor type (the double cone) that appears to be dedicated to this function (Bennett and Cuthill, 1994). In addition, pigments within these cones that are maximally sensitivity in the UV range have been isolated for many species of birds. Behaviorally, birds appear to be as sensitive, if not more sensitive, to UV wavelengths as are humans to any wavelength in their visible spectrum. In addition, birds can discriminate between various UV wavelengths. UV detection is thought to serve navigational, foraging, and sexual selection functions[13].

Interestingly, rats have also been shown to be UV sensitive (Jacobs, Neitz, and Deegan, 1991). This may explain their low CS, in direct contrast to the high maximum CS of rabbits (34). It remains to be seen whether rabbits are UV sensitive, as mammals are generally considered to be UV insensitive (Bennett and Cuthill, 1994).

Fish are also considered to be UV sensitive, however, this has only been implicated in trout and goldfish (Douglas, 1989; Chen and Stark, 1994). UV sensitivity is not known for sunfish (34). Peculiarly, fish UV sensitivity (including goldfish) is evident only in juvenile specimens (measured behaviorally) (Chen

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[13] Navigation: birds have been shown to orient to the sun during navigational flights using plane polarization of light, which occurs predominantly at short wavelengths (UV wavelengths). Foraging: numerous fruits, waxy coatings on seeds, and moths and butterflies have been shown to absorb or strongly reflect UV wavelengths relative to the background. These items comprise a significant proportion of avian diets. Sexual selection: over 47 species of birds have been shown to have UV reflectant plumage. Female mate preference has been shown to be dependent on the presence of UV reflectant plumage on males in zebra finches and starlings (Bennett et al., 1997). Many of the avian species that have been shown to have this plumage, have also been shown to be sensitive to UV, although it remains to be seen whether this is a correlation of 1 when the data set is more complete.

and Stark, 1994), and not in adult specimens (measured both behaviorally and electrophysiologically) (Fratzer, Dörr, and Neumeyer, 1994; Chen and Stark, 1994), which may explain the CS data for goldfish. A behavioral study in which contrast increment thresholds (difference thresholds) were measured for each cone type in goldfish showed that contrast increment thresholds of UV sensitive cones were five times larger than those for other cones[14] (Hawryshyn, 1991). It is highly probably that similar results could be obtained in birds on the principle of evolutionary conservation.

A possible mechanism for reduced contrast sensitivity in UV cones is that there is a reduction in lateral inhibition, which may in turn reduce the contrast gain of the receiving retinal cells. In other words, when one retinal area is stimulated, the inhibition or dampening of adjacent retinal areas may be weakened, reducing the ability to enhance contrast edges. This same reduction in contrast gain could perhaps be achieved through some inherent property of the double-cone morphology of the UV sensitive cones, such as increased innervation of receiving bipolar cells and the consequent dilution of inhibitory signals from the surrounding single cones.

In conclusion, this experiment has served to greatly expand the CS literature on birds. In addition, the CS data from these subjects seem to support the general phenomenon of low CS in birds. Avian contrast sensitivities generally appear to be low compared to those of humans, primates (with the exception of

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[14] Individual cone mechanisms were isolated by bleaching or chromatic adaptation of other cone types with visual stimuli.

the tree shrew), and some mammals. Avian maximum CSs are about equivalent to that of some rodents and marsupials, animals that are not considered to be vision specialists, and that have correspondingly low acuities and narrow bandwidths. Furthermore, the CSs of these birds seem well-suited for their environment. Finally, current data on cone receptor mechanisms in fish as well as the general pattern of CS and UV vision across all species suggest that avian low CS is due to a trade-off for UV vision. The UV sensitive cone type in birds, as well as the visual pigments involved in UV detection, which play such a vital role in the ecology and behavior of birds, may preserve the spatial resolution of images at the cost of contrast enhancement. UV detection in combination with superior color vision and in some cases superior acuity, may be sufficient for successful survival in the visual domain.

APPENDIX A—FLICKER MASKING

All recent experiments that have obtained CSFs from birds, whether behaviorally or electrophysiologically, have used CRT monitors or oscilloscopes with a 60 (in the U.S. and Canada) or 50 Hz (in many other countries) flicker to display stimuli. The 50-60 Hz flicker rate is of particular concern if one considers that this is detectable by most if not all birds. Chickens (Nuboer, Coemans, and Vos, 1992) and pigeons (Hendricks, 1966; and Powell, 1967) have been shown to detect flicker up to about 105-120 Hz, which is their critical flicker fusion (CFF) threshold, beyond which flickering appears to fuse (as described in humans) into an unvarying field.

However, Nye (1968) used photographic displays of contrast gratings, which did not flicker, to obtain CSFs. Of the four different strains of pigeon that he tested, his homing pigeon and white carneaux pigeon yielded CSFs that were reasonably similar to white carneaux and homing pigeon data obtained behaviorally in our laboratory. The bandwidth of his white carneaux CSF, however, was slightly wider than those reported from this laboratory, but it is uncertain whether this was due to his non-flickering stimuli or to his lower psychometric response criterion of approximately 60% rather than the 75% response criterion typically used.

PERG CSFs obtained from birds in the current experiment have been compared to CSFs in the literature that have also been obtained from flickering CRT displays; therefore any effect of flicker, assuming that flicker will affect all of these studies in the same manner, should be factored out. With respect to comparisons of CSFs obtained at 7.5 Hz with those obtained from unmodulated gratings (0 Hz), however, the following points should be considered.

(1) In humans, uniform flicker affects CSFs of 0-Hz gratings only to a limited extent. Breitmeyer, Levi, and Harwerth (1981) found that a 6-Hz flicker was deleterious to the CSF at low spatial frequencies (see Figure D1), with very little effect on maximum CS (approximately a 0.2 log unit difference). Avian CSFs obtained with 0-Hz gratings also should be little affected by flicker. Of primary concern is the maximal CS of the avian functions, which even with the 0.2 log unit adjustment, will still not be within the range of mammals. Breitmeyer et al. found a larger masking effect, however, on temporally modulated gratings. This poses a potential problem when gathering PERG data from birds because of the grating phase reversal necessary to generate a response. However, Breitmeyer et al.'s stimulus modulation rate was also 6 Hz (matching their masking flicker rate), which may have produced much larger interaction effects than would a 60-Hz flicker on a 7.5-Hz stimuli, as would be used in the current experiment.

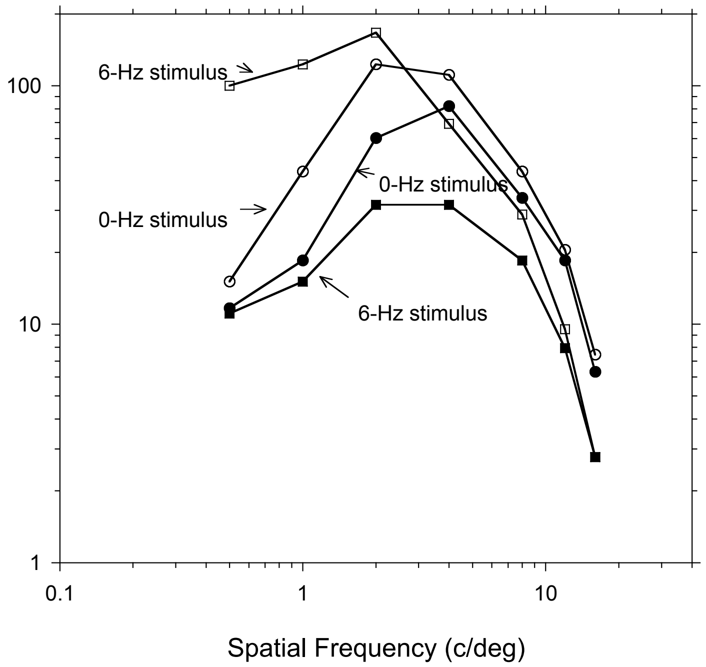

Figure A1: Flicker masking of CS, from Breitmeyer, Levi, & Harwerth (1981). Open symbols represent CSFs obtained with a steady background; closed symbols represent CSFs obtained with a 6-Hz, flickering background. The type of stimulus used is indicated on the plots.

(2) In addition, Peachy and Seiple's (1987) human data show a difference in maximum contrast sensitivities between PERG and behavioral methods that are nearly identical to the difference found by Hodos et al. (2001) in the same comparison in pigeons. Since humans cannot detect 60-Hz flicker as it is above their CFF, it is probably the case that there was no masking effect due to flicker on either of their CSFs (where zero masking effect on both is the same as identical masking effect on both).

Taken together, these observations suggest that flicker-masking effects are not likely to introduce a serious artifact in comparing PERG-derived CS functions in birds with those obtained from mammals. If there were an effect, avian temporal frequency functions would most likely exhibit erratic data points rather than the smooth slopes that are observed in pigeons (Hodos et al., 2003).

APPENDIX B—TRAPPING BIRDS

Each wild species requires a unique method of trapping. Trapping involves devising a suitable trap that will not harm the animal. The trap must be placed in an appropriate location and at an appropriate season of the year.

WOODPECKERS

The first step in trapping woodpeckers is to identify the type of forest that they dwell in: flicker and red-bellied woodpeckers primarily habit deciduous forests, and hairy woodpeckers are specialized for dwelling in conifer forests. Next, appropriate bait must be found. Since woodpeckers' primary diet consists of insects, suet is effective bait. In order to maximize trapping efficiency, suet should be placed in the trapping location several weeks prior to attempted captures. This should be done in winter, since the birds' normal food is plentiful the rest of the year. In addition, the cold weather will ensure that the suet will not melt and drip into the ground.

After one to two weeks, the suet should be found by the birds. The suet can be monitored on a daily basis by looking for marks left in the suet by birds as well as by diminishing quantities of the suet. To ensure that the suet is not eaten by squirrels, it should be placed on a smooth, non-wooden pole, and not be within reach of any nearby tree branches from which squirrels can jump.

Six meter, 36 mm mesh mist nets were used to capture the woodpeckers for this study. Mesh size is measured as the diagonal length of a typical hole in the net when it is stretched in the plane of the measurement.

On the morning a capture is desired, the nets should be unfurled from their posts. The nets should form a V around the suet post, approximately level with the suet (Bub, 1978, p 140). The open end of the V should face the direction from which you think that the woodpeckers will be arriving to reach the suet. The trapper should remain hidden, or be monitoring the other trapping sites that have been set up. A trap should be monitored every 10 to 15 minutes, or less in severely cold or windy weather, as most of the birds caught will be chickadees and other small species that will get severely tangled in the net and potentially die from hypothermia unless they are released quickly. The nets will get especially full a day before the arrival of a cold weather front. Note that mist nets would be largely ineffective out of the cover of trees on a sunny day, most likely due to greatly improved visibility. Mist nets must be closed (furled) when unmonitored.

Once a woodpecker is captured and untangled from the nets, it should be placed in a small, soft sack and transported immediately to the vivarium. Woodpeckers like to cling to vertical objects; if left in a cage without a confining sack, they would thrash and damage themselves.

STARLINGS

Starlings are ubiquitous. However, no starlings were ever caught in the mist nets used to capture woodpeckers, even though these mist nets were the appropriate size and gauge. In addition, they are omnivorous and are commonly seen eating insects, worms, French fries, bread, seeds, and even meat. The difficulties in capturing starlings arise in trying to find a place where they like to land and feed on a consistent basis. Once such a location has been found (a particular field, a parking garage, a farm, a landfill), traps can be set up. The largest local concentrations of starlings were found at a USDA dairy farm (Laurel, MD), where all of the successful starling captures took place.

Two types of traps were successfully used to capture starlings in this study: a Potter’s trap and a ladder trap (Bub, 1978, pp 89-92). While mist nets can also be used, this requires the cooperation of several assistants, and the trapping must be done in an enclosed area such as a barn. There are also constraints on ladder trap use, as these generally have to be large to be effective, and there are certain locations where a large trap such as this would not be appropriate: i.e. cannot be left unattended, should not be observed by the public as this usually causes alarm and some hostility, and is difficult to transport. Moreover, feral birds in general are wary, and starlings were no exception, being very jittery near the traps and reluctant to enter to get the bait. Ladder traps have an advantage over Potter’s traps in that once the starlings acclimate to the trap in their normal environment, the ladder trap seems less enclosed. Ladder traps can trap dozens of starlings in a very short period of time, especially when trapping in winter when starlings tend to form extremely large flocks and are desperate for food and non-frozen water.

The bait used was calf feed, which is primarily a mixture of ground corn and protein. Starlings preferred this over any other type of bait, with the exception of mealworms which are not practical to use as bait in winter. The bait was scattered around the traps to get their attention, as well as inside the traps. When the weather was extremely cold (below freezing), starlings exhibited what can only be described as a sort of “feeding frenzy,” when they would swarm over the bait so densely that they would climb over each other and the ground around the trap was not visible. In this sort of weather, a Potter’s trap was extremely effective as they would ignore the confines of the trap and boldly venture inside to get the bait. Once the ground thawed, however, starlings would exhibit extreme wariness and would not venture inside the traps. Some starlings would be able to reach some of the bait inside the Potter’s trap, thereby springing the trap, but would not venture far enough inside the trap to allow capture. On mild winter mornings, starlings would not exhibit “feeding frenzy.”

Once captured, starlings can be transported in small carrying cages. They can be transported in a dark car trunk. Capturing more than one starling, and placing the carrying cages next to each other visibly reduced their stress behaviors.

SEAGULLS

Seagulls typically habit in coastal areas. Unfortunately, permission to trap on private and / or public beaches was not attainable. In addition, as my seagulls could not be housed due to limitations imposed by the campus IACUC, it was deemed impossible to trap a seagull in the morning then drive four hours back to the University to do a same-day recording. Moreover, the traps used to catch waterfowl such as seagulls are quite large, usually in the form of either drive nets (15-17 m long) or modified versions of fyke nets (10 x 8 x 4 m minimum, but as large as 100 x 30 x 12 m) (Bub, 1978, pp75-81). These are usually set up for the entire duration of a trapping season, making them the ideal solution for a University field station. The University of Maryland, however, does not have such a field station.

During winter months, many seagulls come further inland, to landfills where food is more easily attained and plentiful. Permission to attain seagulls was obtained at two landfills, the Prince George's County Landfill and the Millersville Landfill and Resource Recovery Facility. The recommended method for capturing seagulls at landfills is to bury oneself up to the neck in a large pile of trash, camouflage one's head with a paper bag with holes cut for the eyes, then grab a seagull by the legs when one comes near (Bub, 1978, pp 239-241). A critical key for success using this method is to grab slowly; sudden movements cause seagulls to fly in fright, and when it comes to a race of speed, the seagull will always win.

Due to the political nature of modern US landfills, however, this method was rejected by landfill managers, even upon submission of legal hold-harmless and indemnifying statements. At both landfills, permission to use the site for capture was granted contingent upon accompaniment by landfill staff, use of safety equipment such as safety vests, hard hats and steel-toed, steel-shanked boots, and finally the avoidance of active trash piles where trash was being compacted, which unfortunately was where most of the seagulls were feeding.

The first trap that was attempted was a ladder trap. Birds were wary of this trap and were not interested in going near it for the most part. A few starlings flew inside, but no seagull perched at the top near the opening, and no seagull jumped into the trap. Most seagulls actively avoided the trap.

Many different types of bait were tried, some of which did not seem to elicit interest from the seagulls. Unsuccessful bait are as follows: fresh fish, canned mackerel, and the calf feed that was used for the starlings. Bait which seemed to generate a large amount of interest by the seagulls were French fries, bread, and hot dogs. When using the latter types of bait, the seagulls formed a tight ring around the ladder trap. However none crossed what appeared to be an invisible line that measured approximately 0.5 m around the perimeter of the trap. When hand-feeding with the bait was attempted, to ensure that they were interested in the bait, the seagulls would get as close as approximately six feet, and fought each other for the bait[15]. Once the trap was removed, the seagulls swarmed over the food that had been around the trap, but refused to step over the marks in the dirt where the trap had been sitting.

As the seagulls hungrily approached the trap only from the ground, the ladder trap was then modified into a stationary funnel trap (Bub, 1978, p63, 66-74), and the bait was placed as a trail into the funnel, as well as inside the trap. The floor of the trap was removed and thus the ground served as the floor. The

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[15] Several assistants, at one time or another, attempted to fling themselves toward a seagull in a desperate attempt to catch one manually, however, none were caught.

portion of the trap frame at the funnel opening, which might be perceived as a threshold, was also removed. However, the seagulls maintained their wariness and did not enter the trap. Following these unsuccessful attempts, the sides of the funnel trap were made less visible, by replacing the existing chicken wire with aviary wire. In addition, the trap was both visually camouflaged as well as scent camouflaged; modest amounts of trash were placed near the trap, and dirt and bait were rubbed over all surfaces (seagulls have large olfactory bulbs compared to other birds). It was deemed from empirical and anecdotal evidence that seagulls are extremely wary of walking under a cover or under objects that protrude from the ground. Hans Bub reports that while camouflage is usually not necessary when most capturing birds, Corvids and gulls are extremely suspicious (Bub, 1978, p37).

A canon net would probably have resulted in successful captures; however, the canon gun is extremely expensive (over $3,000) and the loading of the net is potentially very dangerous. The net is projected out of the canon gun at extremely high velocity, would open far into the air, and catch whatever is underneath it due to the large size of the net. This was not practical at a landfill with their safety restrictions. In addition, should the edges of the net hit a bird during its projectile course, which was highly probable, it would surely kill the bird, which was not covered under my Federal or State Scientific Collection Permits.

A six ft diameter, circular casting net, used in fishing, was tried next as a substitute for the canon net. An assistant and I practiced the throwing technique until we could throw the net proficiently; i.e., it should open in the air and stay open until it hits the ground uniformly. In practical employment of this technique, we were not successful in landing the net over a seagull, even when the seagull was 2-3 m away. It quickly became evident that this method was too slow and the net was too small. A larger net would have been more unwieldy and impractical for use; therefore this method is not recommended for capturing seagulls.

A semi-elevated trap was tried next. First, a simple box or fall trap (Bub, 1978, p46) was tried. In this method, a box is elevated on one side by a stick that has a string attached to it. The bait is visible to the seagulls under the box. Theoretically, the box is manually collapsed onto the seagull by the trapper, by removing the support away from the box with the use of the string when the seagull positions itself to retrieve the bait. This was predictably unsuccessful.

The next elevated trap was a 21 by 21 foot net suspended on five, 10 ft conduit poles impaled vertically into the ground. The net was fine, black polyurethane with a large mesh to eliminate glare and minimize visibility, weighted around the edges with lead fishing tackle. The net was held at the tops of the poles by pegs inserted through the poles. The pegs were designed to be removed from a distance with a manual trigger, which would cause the net to fall quickly (due to the weights) onto any seagull that was underneath. The bait was on the ground, underneath this tent-like canopy. As the net was far above the ground, not very visible, and there were no sides to this trap with the exception of the poles, it was hoped that the seagulls would not deem it threatening. Unfortunately, this trap was also unsuccessful as no seagull ventured under the net.

Finally, as it was observed that seagulls regularly stood on top of the garbage at the landfills, and would even stand on top of the 21 by 21 ft net described above as it was being disassembled, I concluded that only a ground trap would be effective. A bal-chatri raptor trap (Bub, 1978, pp 195-196) was modified for a flat, 0.75 by 0.75 m surface, and placed on the ground. Pieces of hot dog buns were sprinkled on top, along with some garbage in order to camouflage the trap. Many seagulls began feeding on the trap within 10 mins. While feeding, their feet and legs became tangled in the coils and loops, made with transparent fishing wire. The researchers then charged the birds on the trap from their hidden surveillance area approximately 20 m away, which caused the seagulls to panic and attempt to flee, which further tightened the loops. This method consistently resulted in successful seagull captures only until the end of the winter season.

Once captured using the modified bal-chatri trap, the seagulls were transported in a cat carrying-cage in a cool, dark car trunk. Based on trial and error, transport similar to woodpeckers is not recommended for this species, as these birds may be particularly prone to overheat or become overly stressed, which in my experience has led to fatality.

APPENDIX C—ANESTHESIA IN BIRDS

In general, inhalant Isoflurane has been touted as the safest anesthetic (Ludders, 2001; Abou-Madi, 2001; Curro, 1998) or the anesthetic of choice (chap 24 in Avian Anesthesia book; Ritchie, 1991) for birds. Consequently, Isoflurane was initially used for all species, except for owls (last species – I knew better by this time), in an attempt to keep methods identical throughout the experiment for ease of comparison between species. It was discovered during the course of this experiment that Isoflurane had a high mortality rate among certain species. Table 5 provides mortality rates for Isoflurane and other anesthetics used in our laboratory for electrophysiological recordings.

Table 5: Anesthetic mortalities

				Pigeons			Quail			Kestrels			Owls			Woodpecks			Budgies			Seagulls			Starlings		
Anesthetic	**Total Attempts**	**Mortality (N)**	**Mortality (%)**	Attempts	Mortality (N)	Mortality (%)	Attempts	Mortality (N)	Mortality (%)	Attempts	Mortality (N)	Mortality (%)	Attempts	Mortality (N)	Mortality (%)	Attempts	Mortality (N)	Mortality (%)	Attempts	Mortality (N)	Mortality (%)	Attempts	Mortality (N)	Mortality (%)	Attempts	Mortality (N)	Mortality (%)
Ketaset / Xylazine	65	3	5	8	0	0	50	3	6	N/A			N/A			N/A			N/A			N/A			N/A		
Chloral Hydrate	484	15	3	157	5	3	65	4	6	202	3	1	25	0	0	N/A			N/A			N/A			32	3	9
Isoflurane Related	79	11	14	9	0	0	16	2	13	16	2	13	N/A			7	0	0	5	1	20	4	1	25	21	5	24
Chloral Hydrate & Pentobarb	6	0	0	N/A			N/A			N/A			N/A			N/A			N/A			N/A			N/A		

These fatalities occurred regardless of low Isoflurane doses, fine adjustment of flow rate (oxygen delivery) and dose during a recording to accommodate fluctuations in the animals' breathing rate and depth of anesthesia, and careful monitoring of the animal. Further precautions included using a non-rebreathing circuit, because they offer minimum resistance to ventilation, and the mixture of small amounts of nitrous oxide to utilize intrapulmonary chemoreceptors that stimulate respiration (Ludders, 2001; Heard, 2000). There are several potential reasons why I suffered these high mortality rates.

- Feral animals react quite differently to conventional anesthetics than do domesticated species such as pigeons and quail, often requiring much higher doses of anesthetic. This makes the threshold between sufficient anesthesia and death exceedingly small. This problem was compounded by my inability to house some of the wild-caught species, due to limitations imposed by the campus IACUC. This left me no choice but to try to record from some species (woodpeckers, and initially seagulls and starlings) on the same day that they were caught. With no time to acclimate to captivity, these animals had extremely high stress levels. High stress is implicated in many fatalities, due to stress-induced cardiac arrhythmias, hypertension, and hyperthermia (Heard, 2000; Muir and Hubbell, 1995). In order to both reduce stress levels and to further reduce already low doses of Isoflurane used, initial and supplemental injections of ketaset were administered on many of the wild-caught animals. As Ketamine administration did not appear to bring mortality rates down to an acceptable level, Isoflurane related procedures were pooled into one statistic in Table 5.

- Small birds, especially Passerines, have higher metabolisms (Sedgwick, Pokras, and Kaufman, 1991; Abou-Madi, 2001). This presents several problems when using any anesthetic for a long procedure, such as dehydration, loss of metabolites, blood sugar, and vascular volume, and hypo-oxygenation, any of which could result in shock and death (personal communication with Ted Mashima, associate director of Veterinary Medicine, University of Maryland, a diplomate of The American College of Zoological Medicine, and co-author of Exotic Animal Formulary, 2001). Isoflurane is not a good choice of anesthetic if hypoventilation and apnea are concerns, as Isoflurane has been shown to have a dose-dependent hypoventilatory effect in birds, and some avian species (for example the African grey parrot) are particularly susceptible to this effect (Ludders, 2001; Goelz, Hahn, and Kelley, 1990; Abou-Madi, 2001; Curro, 1998).

Used for long durations, Isoflurane adds additional complications of hypothermia due to delivery of cold gases to the animal's core, which cannot be compensated by heating the animal externally. Heating the gas line can be achieved with additional expensive equipment, however, this would not compensate for the drying effects of the gas flow, nor did there seem to be any guarantees either from personal communications or in the literature that this would effectively reduce fatalities. Moreover, a lab-constructed system for heating the gas line was not attempted due to the potential danger of exploding gases, necessity of rigid control of temperatures, and potential interference with the electrophysiological signal when using electronic heat sources. Large extensions in the length of the gas line / delivery tube would also affect consistency of gas delivery due to altered air flow / resistance.

- As described above, the long duration of the recording sessions was not conducive to the use of Isoflurane. A typical procedure consisted of 60-90 mins of prep under anesthesia, followed by 2.5 to 3 hours of recording, still under anesthesia. This prep could not be shortened due to the nature of Vecuronium Bromide application, which alone took 30 mins. Glenn Olsen, chief veterinarian at the Patuxent Wildlife Research Center and the co-editor of Manual of Avian Medicine (2000) strongly recommended (also in personal communication) that any procedure using birds be restricted to less than two hours under anesthesia, even with controlled ventilation. Isoflurane, even though it is widely used in avian surgeries, is not used in procedures requiring long periods of anesthesia[16]. All anesthetics, including injectable anesthetics, depress respiratory functions due to the relaxation of avian respiratory muscles. Birds do not have a muscular diaphragm like mammals

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[16] The duration of a long procedure is not defined in the clinical literature. However, Ted Mashima and Glenn Olsen both estimate that a long procedure is one that extends beyond 90 mins. In addition, a typical surgery is rarely over 2 hours. In the event that a prolonged procedure is needed, the clinical literature unconditionally advises ventilatory support (Curro, 1998;) among other maintenance issues such as fluid replacement. Most clinicians and researchers are more conservative, advising intubated ventilatory support for any procedure that lasts more than 10 or 30 minutes (Sinn, 1994; Ritchie,1991; Muir and Hubbell, 1995), or even for any Isoflurane procedure regardless of length (Ludders, 2001; Abou-Madi, 2001). Assisted or controlled ventilation is accomplished either manually or mechanically. Manual ventilation would require that a person be in the recording chamber with the bird, which may interfere with the recording. Mechanical ventilation is usually only effective with endotracheal intubation. Intubation, however, is not recommended for birds under 100 g (budgerigars, starlings, woodpeckers) because the smallest tubes (catheter-sized) are often too large. It is extremely easy to induce tracheal trauma on a small bird. In addition, such narrow tubes have very high resistance to gas flow, and furthermore will easily become plugged with mucous or blood (Curro, 1998).

and must rely on active cervical, thoracic, and abdominal muscles for respiration. Therefore, any depression of muscle function via anesthesia will negatively affect ventilation (Ludders, 2001). Inhalant anesthetics such as Isoflurane further depress respiration to a level that is much more severe than what is observed in mammals (Abou-Madi, 2001), partly due to hypothermia, induced by the length of a procedure (Ritchie, 1991). Further contraindications of Isoflurane in birds, as found in the literature, are apnea (two species of owls, Redig, 1998), cardiac arrhythmias (chickens, Greenlees, et al., 1990), and dose-dependent cardiopulmonary depression (most species, Heard, 2000) most likely due to peripheral vasodilation (Ludders, 2001). Due to these unique avian concerns, the duration of the experimental procedure and selection of anesthetic is critical to the success of the experiment.

Starlings are a perfect example of a small Passerine that did not respond well to Isoflurane. Their mortality rate under Isoflurane was among the highest of all the species studied in this experiment (Table 5).

Raptors appear to be an exception to these and other effects of anesthetics in general. For example, ketaset is widely used on birds as an effective anesthetic; however, ketaset is ineffective in producing general anesthesia in Cooper's and sharpshinned hawks (also ineffective on great horned and snowy owls, and waterfowl). Great caution should be used to anesthetize a particular species of raptor, however, since there are often conflicting recommendations in the literature on the anesthetic of choice. Moreover, raptors (with a few exceptions including the bald eagle) have been found to respond very well to inhalants such as Isoflurane both in the veterinary journals (Redig, 1998) and empirically in our laboratory, possibly due to lower metabolisms. (Metabolism does not seem to be the sole factor for Isoflurane-related fatalities, for example, when one compares the effects of Isoflurane on quail and woodpeckers, both of which will be discussed below). Raptors can even sustain prolonged anesthetic periods when Isoflurane is used (Redig, 1998). The kestrels in this study received Isoflurane. As seen from Table 6, however, injectable anesthetics (Chloral Hydrate) have also been safely used on them in our laboratory.

In general, owls (Strigiformes) also respond well to inhalants according to the literature, much like other raptors[17] (Reddig, 1998). However, since owls had previously been safely recorded from using Chloral Hydrate (injectable) in this laboratory, and since the safety of the owls were of primary concern as they were borrowed from another laboratory (Catherine Carr, University of Maryland), Chloral Hydrate and not Isoflurane was used on the owls in this experiment.

In addition, the two anesthetics chloral hydrate and Isoflurane do not appear to differ in their effects on the PERG. Furthermore, chloral hydrate has been used in other PERG studies (Blakeslee and Jacobs, 1987; Porciatti et al., 1991; Porciatti, Fontanesi, and Bagnoli, 1989).

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[17] Great horned and snowy owls, unlike other raptors, have episodes of apnea under Isoflurane (Redig, 1998). This is another example of species-specific tolerances to anesthetics even within a similar grouping of animals.

Another example of species-specific safety of anesthetics was observed in red-bellied woodpeckers. The woodpeckers used in this study were extremely stable under Isoflurane, in spite of their small size. These same woodpeckers were used to obtain auditory data in another laboratory (Robert Dooling and Bernard Lohr, University of Maryland), some prior and some proceeding my data collection, but were administered ketamine hydrochloride and diazepam in the auditory experiments. The mortality rate under ketamine and diazepam was higher than the mortality rate under Isoflurane (11% versus 0%). In addition, the efficacy of the different anesthetics was quite large. Table 6 shows the dose of Isoflurane used to achieve the desired plane of anesthesia, which was quite small compared to the recommended dose for birds in general (1.5 to 2.0% maintenance, Heard, 2000; 0.5 to 2.5% maintenance, Muir and Hubbell, 1995; 1.0 to 1.5% maintenance, Ritchie, 1991; 2.5 to 3.0% maintenance for raptors, Redig, 1998), and compared to the doses used for the other birds in this study. The dose of ketaset and diazepam used by the auditory researchers, on the other hand, was necessarily quite large (150 mg/kg ketamine and 6 mg/kg diazepam) compared to doses used on other small birds in that laboratory, such as budgerigars (50 mg/kg ketamine and 2 mg/kg diazepam).

Quail were another exception. The quail were on average more than twice the body weight of starlings (average weight 70 g) and woodpeckers (average weight 80 g), having an average weight of 170 g. In addition, as they are not in the Passeriformes Order, it was expected that they would respond well to Isoflurane. Unfortunately, most quail consistently produced copious amounts of visible mucous that accumulated in their oral cavity, which blocked their tracheas. This necessitated aborting many recording sessions to prevent death from suffocation. Removal of this mucous was only an extremely short-term solution, as this mucous would be continuously produced. This is apparently a common ventilatory problem with inhalant anesthetics that is caused by the accumulation of blood and fluids in the air sacs with subsequent migration to the lungs. In addition, the drying effects of the inspired cold, dry gases, the mucous becomes thick and tenacious (Ludders, 2001). Please see Table 5 for the mortality rate for quail under Isoflurane. For problematic species such as these (quail and starlings), Chloral Hydrate was used as the anesthetic under which data were collected.

Table 6 provides the anesthetics and their doses that were used on the various species used in this laboratory, including the species that were used in this experiment.

Table 6: Anesthetic dosages

Species	Chloral Hydrate	Isoflurane	Ketamine & Isoflurane
Pigeons	390-400 mg/kg. No supplements necessary.	Induction 4.0-5.0%; maintenance 1.9-2.2%; oxygen flow _ L/m; NO_2 flow is none to 3/8 L/m.	N/A
Quail	410-460 mg/kg. No supplements necessary.	N/A	Ketamine: 20 mg/kg. Isoflurane: Induction 3.5-4.0%; maintenance 1.0-2.0%; oxygen flow 1 L/m; NO_2 flow 1/8 L/m.
Kestrels	325-350 mg/kg. No supplements necessary.	Induction 3.0-4.0%; maintenance 1.7-2.5%; oxygen flow _ L/m; NO_2 flow 3/8 L/m.	N/A

Species	Chloral Hydrate	Isoflurane	Ketamine & Isoflurane
Owls	280-360 mg/kg. No supplements necessary.	N/A	N/A
Woodpeckers	N/A	Induction 1.0-3.0%; maintenance 0.2-0.5%; oxygen flow _ to 1 L/m; NO_2 flow 1/8 L/m.	Ketamine: 20 mg/kg. Isoflurane: Induction 1.0-3.0%; maintenance 0.2-1.0%; oxygen flow _ to 1 L/m; NO_2 flow 1/8 L/m.
Budgerigars	N/A	Induction 3.5%; maintenance 1.2-2.2%; oxygen flow _ L/m; NO_2 flow 3/8 L/m.	N/A
Seagulls	N/A	N/A	Ketamine: 13 mg/kg. Isoflurane: Induction 5.0%; maintenance 1.5-2.5%; oxygen flow _ L/m; NO_2 flow 3/8 L/m.
Starlings	440-520 mg/kg. _ of initial dose for 1st supplement after 50 mins; zero to _ initial dose for 2nd supplement one hr after 1st supplement; 3rd supplement is fatal.	Induction 4.0%; maintenance 0.7-1.5%; oxygen flow _ to 1 L/m; NO_2 flow 1/8 L/m.	Ketamine: 20 mg/kg. Isoflurane: Induction 4.0%; maintenance 0.5-1.0%; oxygen flow _ to 1 L/m; NO_2 flow 1/8 L/m.

Dosages provided in this table were the dosages used in this experiment. These dosages provide a light to medium depth of anesthesia, as defined by Abou-Madi (2001). Ranges given are an indication of individual tolerances.

APPENDIX D—OPTICAL ACCOMMODATION AND REFRACTIVE STATES

As objects get closer to the eye, the focal length of the eye needs to change in order for the image to remain in focus. The distance at which the focal length begins to change is the far point of accommodation. The mammalian and avian eyes change focal length by changing the curvature of the lens, known as accommodation. This is accomplished by the coordination of ciliary muscles (either striated in birds or smooth in mammals) attached to the lens. While some animals use other methods of accommodation, such as anterior-posterior positioning of the lens (fish and some species of waterfowl, such as diving birds) or corneal accommodation (chickens), there were no data to suggest that the species studied in this experiment accommodated by means other than changes in lenticular curvature. The distance at which the image is still in focus, with the lens maximally curved, is the near point of accommodation.

Refractive state is the degree to which light bends as it passes through the eye's optics. If the eye is emmetropic, it means that when accommodation is relaxed, the far point is at infinity and the near point is at the focal length of the eye. In ametropia, two other refractive states occur: myopia (near-sightedness), the condition in which the image is focused anterior to the plane of the retina, and hyperopia (far-sightedness), in which the image is focused posterior to the plane of the retina.

While refractive states of various avian species were not the data of interest in this experiment, it was necessarily obtained as a by-product of the process of assuring that the retinal image of the grating display was in focus at the photoreceptor plane of the retina. A summary of the refractive states of the various individual birds for which CSFs were obtained in this study are provided in Table 7. In general, the table shows that individual birds were emmetropic or slightly hyperopic, with the exception of the woodpecker. The average refractive state of these birds combined is emmetropia.

Table 7: Refractive states and best lens for individual subjects

Species	Subject	Net Refraction*
American kestrel	K049	-0.1
	K0336	-0.1
	K150	-0.1
Barn owl	O69	-0.1
	O53	-0.6 to +0.4
	O68	-0.1
	O22	-0.6 to +0.4
Pigeon	E4585	+1.4
	E17238	-0.1
	E259	+0.15
Japanese quail	Q12	+0.4
	Q7	-0.1
	Q11	-0.1
Starling	SV14	+0.9
	SV13	+0.9
	SV21	+0.4
	SV19	+0.4
	SV12	+0.4
Red-Bellied Woodpecker	W5	-1.6
Average		+0.03

***The animal's refractive state was obtained by subtracting +1.6 D, which was required to correct for the viewing distance, from the final lens power.**

In general, when an animal is anesthetized, accommodative state fluctuates. This has important negative implications for PERGs as the focal plane of the retinal image can drift during the course of the session resulting in defocus and the consequent loss of the high spatial frequency content of the stimulus. For this reason, cycloplegics, which are pharmacological agents that stabilize accommodation at the far point by paralyzing ciliary muscles are always used.

A series of ophthalmic trial lenses are then placed in front of the active eye, one at a time, to determine which lens produces the best thresholds. This lens is then used to collect the CS data. This method is precisely analogous to what occurs in an optometrist's or ophthalmologist's office when the refractionist inserts various lenses in front of the patient's eyes in order to determine which one results in the sharpest vision.

Refractive state can be measured by streak retinoscopy. In this method, the refractionist uses an optical device known as a streak retinoscope. This device places a bar of light across the subject's pupil. An assistant holds a trial lens in front of the eye. The refractionist rotates the retinoscope in a shallow right-to-left, left-to-right arc and observes whether the reflection from the eye is “with” (in the same direction as the rotation) or “against” (in the opposite direction of the rotation.) “With” movement indicates a myopic refraction and “against” movement indicates a hyperopic refraction. When the correct lens is found, the pupil floods with light and no “with” or “against” movement is seen. The assistant then reports the optical power of the lens to the refractionist who records the data.

A weakness of streak retinoscopy for small eyes derives from the fact that the optics of the instrument assumes an axial length of the eye of 25 mm, which is the human axial length. Shorter axial lengths result in hypermetropic readings (Glickstein and Millodot, 1970) and require a correction factor.

Streak retinoscopy was used on owls in this study to verify that there was little or no accommodation in this species. This was accomplished by performing a retinoscopic refraction on a barn owl every 15 mins over a four-hour period, which is long enough to include the maximum session length. The results indicated that once the Glickstein and Millodot correction factor for the shorter axial length of the owl was applied, the owl's refractive state remained within ±0.35 D for this period of time, which indicates no serious shift in refractive state due to accommodation.

APPENDIX E—NOTES ON THE EFFECTS OF VARIOUS THRESHOLD ESTIMATION METHODS ON THE DATA AND ITS RELIABILITY:

I. ALTERNATIVE CONTRAST THRESHOLD ESTIMATION AND RELIABILITY

The linear regressions applied to contrast-response functions typically were a good fit to the data. All of the amplitudes used to calculate the linear regression were within the 95% confidence interval of the regression line. While this occasionally excluded the use of some amplitudes at very high contrast due to either a sharp increase in amplitudes or a saturation of the response (both result in a change in slope), the majority of contrast-response functions exhibited linearity over the entire range of contrasts presented; in these cases all amplitudes were used to calculate the regression. Furthermore, there did not appear to be any consistent patterns regarding saturation at high contrasts. Calculated in this manner, the R squared values of these regressions ranged from 0.6842 to 0.9985. The mean R squared value was 0.9203, the median R squared value was 0.9554, and the mode was 0.9947, all of which indicate an exceptionally good fit to the data. These very high R squared values also indicate that a linear model, rather than a logarithmic, exponential, or other model, was the appropriate model to use to extrapolate thresholds.

Another measure of reliability of the threshold is the consistency of the threshold between and within sessions. Unlike contrast-response slopes, overall amplitudes, or even latencies, the thresholds were consistent within individuals, regardless of whether measures were repeated within or between sessions. The consistency of thresholds between sessions was remarkable considering changes in factors such as electrode positioning and depth of anesthesia between sessions; these factors are thought to affect response amplitudes, noise, and contrast gain. Examples of such consistency exist for all species studied except for the woodpecker, and are shown in Table 8. While the within session repeated data points have been shown in the figures in Results, some of these points were not apparent in the figures because the repeated measures were too close together to be resolved. Some between session repeated measures are being shown here for the first time. As these were primarily control sessions, and / or incomplete CSFs were obtained, these were not included in the Results or any analyses.

Table 8: Reliability Within and Between Sessions

Species	Subject	SF (c/deg)	Contrast Threshold in same session	Contrast Threshold in different sessions
Kestrel	K151	2.44	9.23	
		2.44	10.20	
		3.25	9.64	
		3.25	7.10	
	K0336	0.33	19.61	18.87
		0.81	16.67	16.37
		0.81		15.27
		2.44	8.96	9.68

		9.76	18.94	19.31
Owl	O68	3.25	29.94	
		3.25	29.67	
	O22	2.44	25.91	
		2.44	27.62	
	O53	1.22	12.58	
		1.22	12.56	
		1.22	17.36*	
Pigeon	E259	1.63	12.35	12.64*
		1.95	18.25*	20.83
	E4585	0.33	23.87	24.15
		0.33		18.32*
		0.61	17.54	23.58
		1.63	10.54	
		1.63	11.11*	
		1.95		16.39
		1.95	13.57*	15.55*
		2.44	11.66*	
		2.44	13.35*	
		3.25	14.51*	14.33
		4.88	20.96*	23.15
		4.88		26.60
	E17328	4.88	19.80*	
		4.88	24.04	
		4.88	21.93*	
		6.51	24.63	

		6.51	34.60	
Quail	Q12	0.33	40.65	31.75
		0.33		30.03*
		0.33		24.21
		1.22	9.33	
		1.22	10.43*	
		2.44	11.66	
		2.44	17.01*	
	Q11	1.22	8.35	
		1.22	10.72*	
Starling	SV4	1.22	9.76	
		1.22	10.42	
	SV13	1.22	11.75	
		1.22	17.79	
		2.44	28.99	
		2.44	27.17	
		4.88	58.48	
		4.88	48.54	

Thresholds were even consistent when using different contrast gratings; for example, nine contrast gratings ranging from 20 to 95% contrast, in gradations of approximately 10% contrast, yielded thresholds similar to nine contrast gratings ranging from 5 to 45% contrast, in gradations of approximately 5% contrast. Thresholds obtained from sweeps of these lower contrast gratings have been combined into Table 8, denoted with asterisks.

Furthermore, changes in both response latency and response latency variance served as a crude check and second measure of threshold in all (100%) threshold extrapolations using a linear regression fit to the data, as discussed in Methods.

Another check of threshold can be obtained from analyzing the filtered response waveforms. While these have been obtained for only one subject from each species category (with the exception of the woodpecker, as explained in Results), all of the waveforms collected show that the response becomes indistinguishable from the response to noise around the threshold obtained from extrapolation of the linear regression fit to the data. As this yields an even cruder threshold estimate than using either response latency and latency variation or extrapolation of linear regressions, this was only used as a rough check on the accuracy of the threshold.

As a final measure of reliability, jackknife statistics (Broemeling and Wolfe, 1993) were employed on the thresholds. The jackknife method makes use of the regression techniques that have already been used for obtaining the threshold. First, the extrapolation using the linear regression is performed in the normal way as described in the Methods. Then, the linear regression is recalculated with one response amplitude eliminated, after which a new threshold is extrapolated. The linear regression is calculated yet again with the missing amplitude replaced and a different amplitude removed. The threshold is recalculated in this manner until all amplitudes have been eliminated once. This is a statistical resampling procedure that, as applied to these thresholds, shows the possible variability of threshold induced by each of the response amplitudes used in the linear regression.

Thresholds from one kestrel, one owl, one pigeon, one quail, two starlings, and one woodpecker were analyzed using the jackknife procedure. In all of these cases, the original thresholds obtained with all of the amplitudes included fell within the peak bin of the middle of the jackknife distribution. Figure E1 shows an example of such a histogram for a pigeon. Because of differences in variability, the same bin width could not be used for all subjects analyzed with this method. For all of these subjects, however, a bin width of 0.5% or 1.0% contrast was satisfactory. Moreover, the original thresholds were well within the 95% confidence interval of the mean. This is further confirmation that the thresholds reported in this experiment were not statistical outliers, nor were they affected greatly by the position of any individual data point.

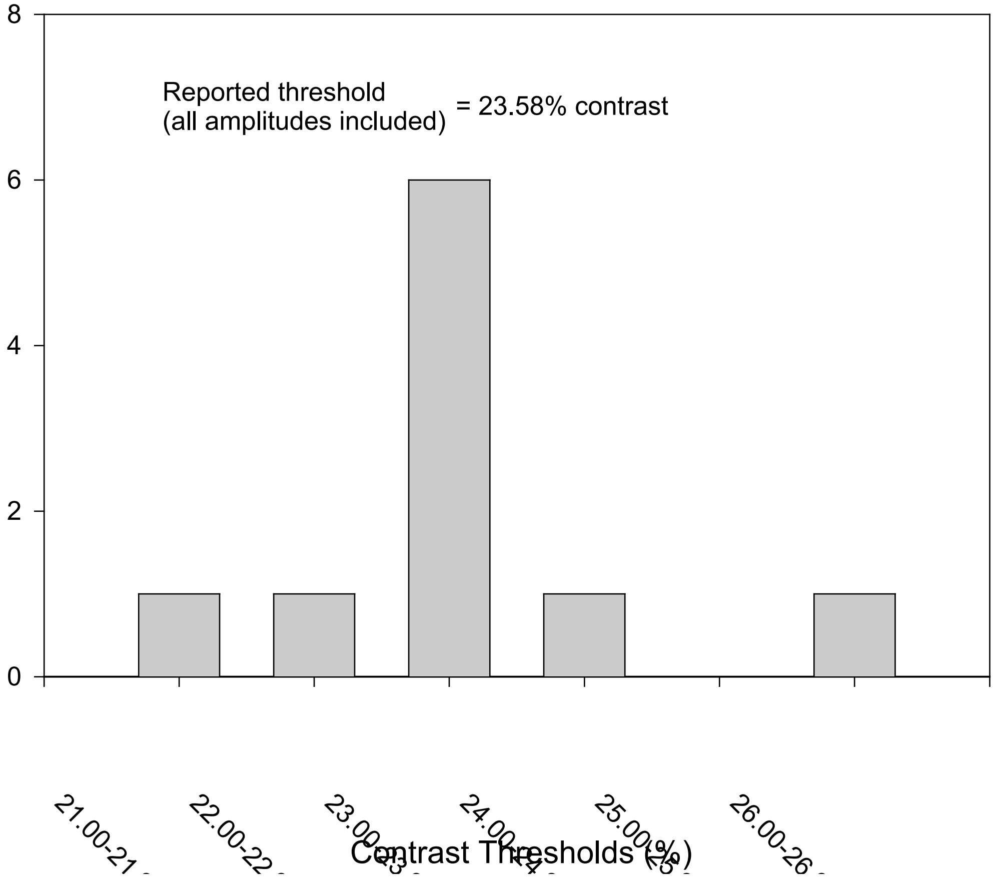

Figure E1: Frequency histogram for jackknife distribution of contrast thresholds.

II. CRITERION-RESPONSE ANALYSIS OF CONTRAST SENSITIVITY

While the linear extrapolation method of determining threshold is widely used in the literature and is deemed to be accurate as employed in this experiment, an alternative approach is to determine the shape of the CSF using different response criteria. This method circumvents the problem of arbitrarily setting just one response criterion (usually either noise or zero volts) as the threshold criterion. A particular advantage of this method is that it allows suprathreshold comparisons.

The criterion response method has been used in visual and auditory physiology (Chafee and Hampson, 1924; Riggs, Berry, and Wayner, 1949; Dooling and Walsh, 1976; Boynton, 1979) to generate iso-potential curves. The iso-potential contrast sensitivity curves generated from the contrast-response functions in this experiment are shown in Figures E2 through E7. The reciprocal of the contrast at each response criterion has been obtained in order to show these iso-potential curves as CSFs. In general, the CSFs flatten and / or progressively degenerate at high amplitudes. The CSFs at low amplitudes approximate the shape of the CSF at threshold.

When comparing these iso-potential CSFs to behavioral CSFs, as shown for the quail and the pigeon, an additional dimension of comparison is provided by the additional physiological CSFs. For quail, the behavioral CSF, obtained from Figure 34, matches the shape of the low amplitude iso-potential CSFs very well, but is displaced on the x-axis. For pigeons, the behavioral CSF, also obtained from Figure 34, is located in approximately the same region as the iso-potential CSFs on the x-axis, but is narrower in bandwidth. Closer approximations between behavioral and iso-potential CSFs are expected for measures in the same subjects. While the pigeon iso-potential curves do not provide a perfect fit to the pigeon behavioral data, these sets of curves provide a good basis of comparison for future behavioral CSFs as well as physiological CSFs obtained from extrapolation to zero volts or different criteria, measured in the species studied here.

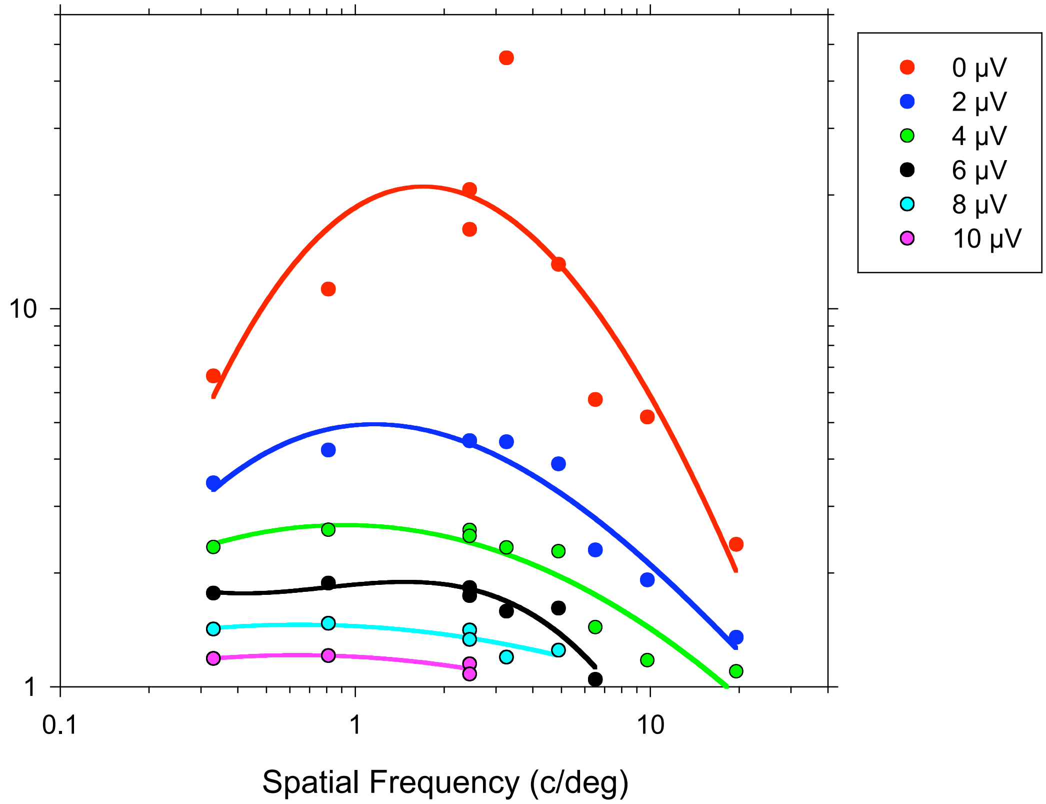

Figure E2: Iso-potential CSFs for kestrel K049.

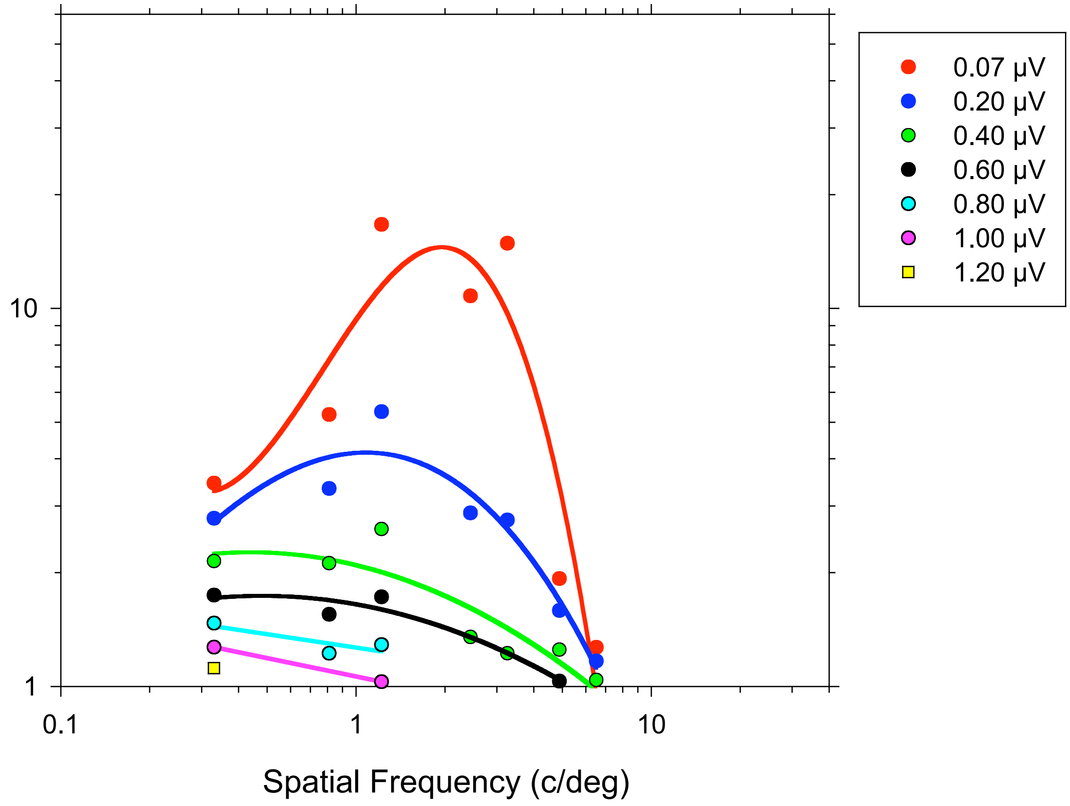

Figure E3: Iso-potential CSFs for owl O69.

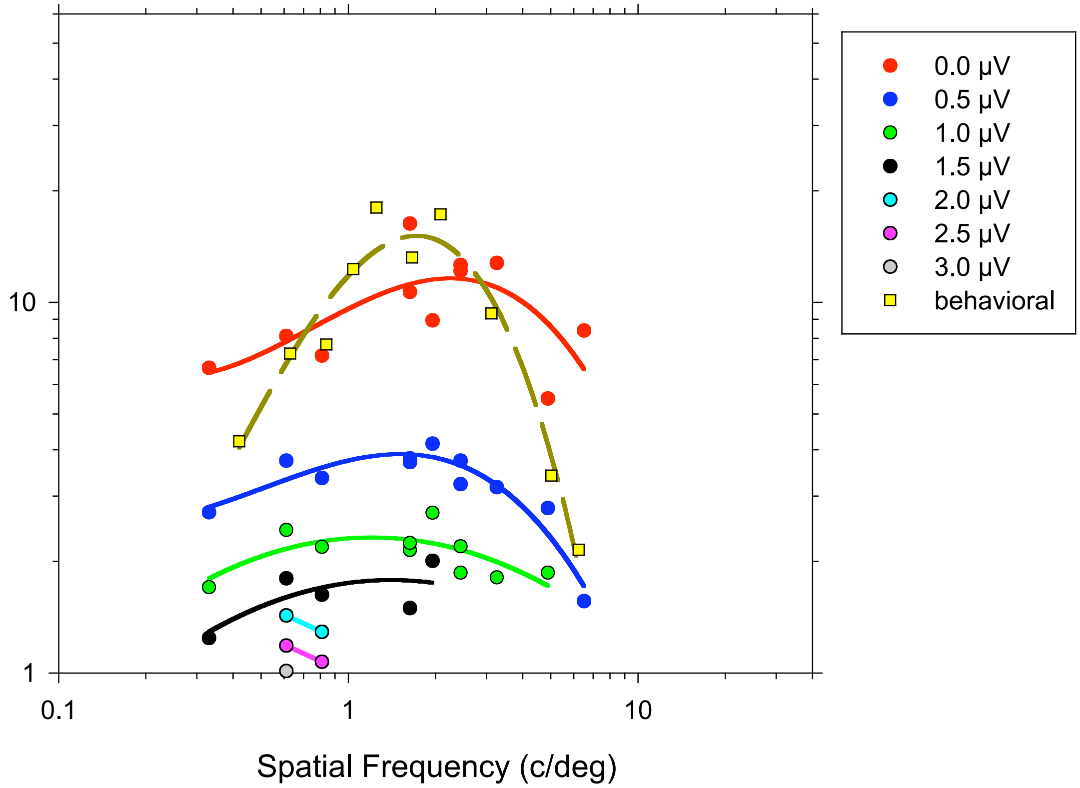

Figure E4: Iso-potential CSFs for pigeon E4585. Behavioral CSF is shown by dashed function.

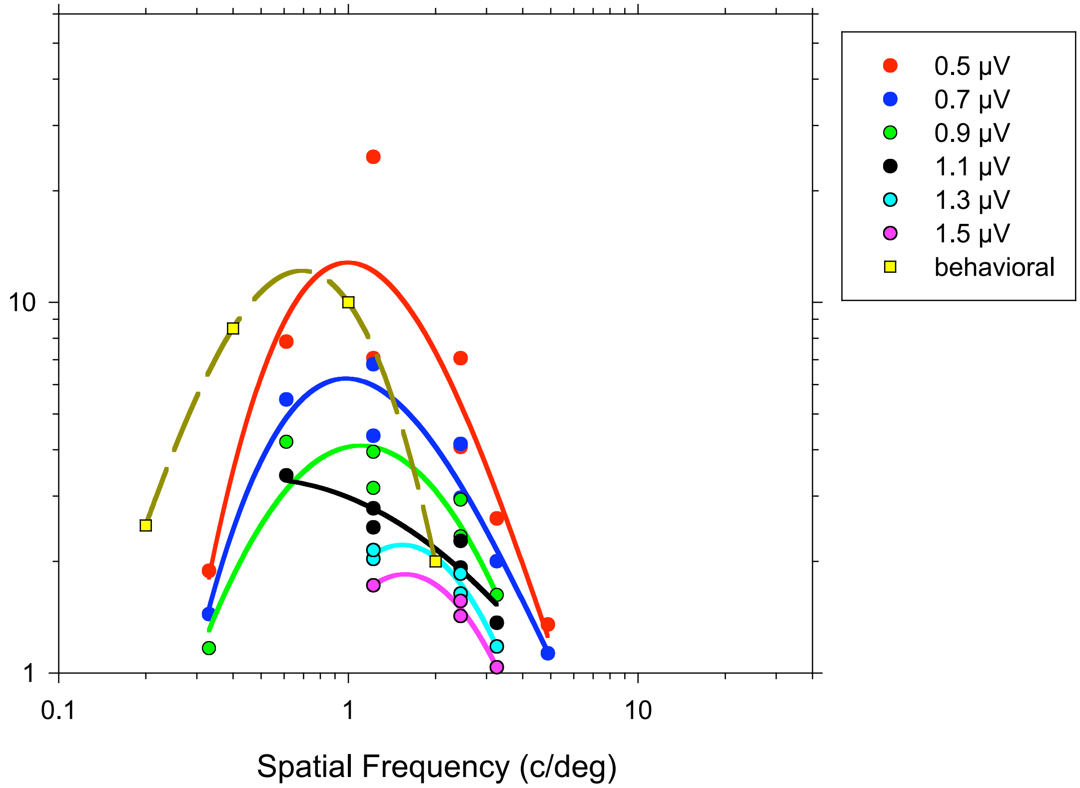

Figure E5: Iso-potential CSFs for quail Q12. Behavioral CSF is shown by dashed function.

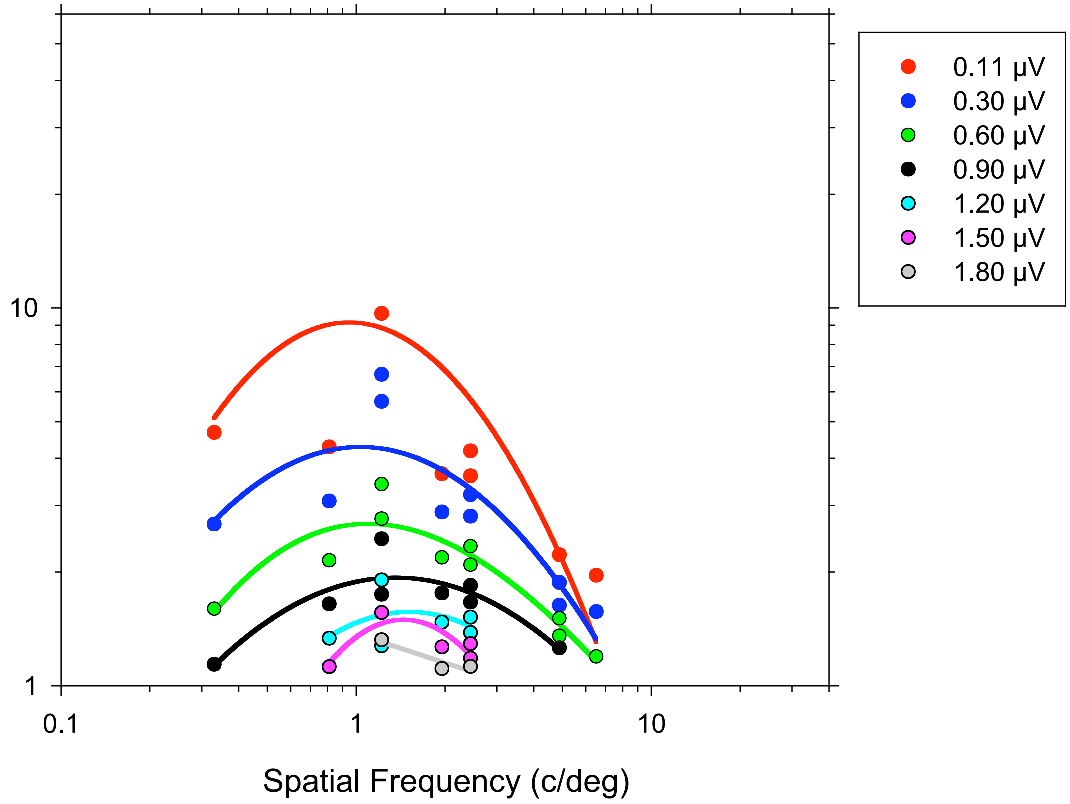

Figure E6: Iso-potential CSFs for starling SV13.

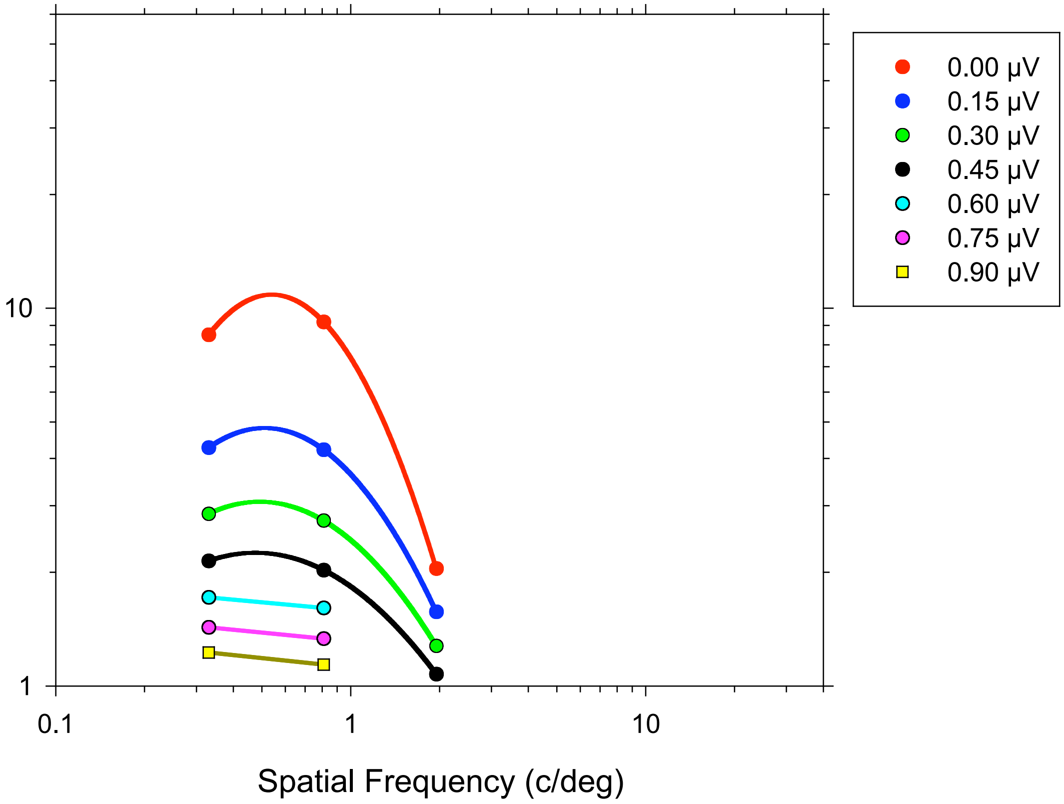

Figure E7: Iso-potential CSFs for woodpecker W05.

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