

Spatial contrast sensitivity and grating acuity of barn owls

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The eyes of barn owls (*Tyto alba pratincola*) display very little aberrations, and have thus excellent optical quality. In a series of behavioral experiments, we tested whether this presumably beneficial feature is also reflected at a perceptual level in this species. As fundamental indicators for visual performance, the spatial contrast sensitivity function (CSF) and grating acuity were measured in two barn owls with psychophysical techniques. Stimulus luminance was 2.7 cd/m². The CSF found here renders the typical band-limited, inverted U-shaped function, with a low maximum contrast sensitivity of 8–19 at a spatial frequency of 1 cyc/deg. Grating acuity was estimated from the CSF high frequency cut-off and yielded 3.0–3.7 cyc/deg. In a second experiment, in which contrast was held constant and spatial frequency was varied, grating acuity was measured directly (2.6–4.0 cyc/deg). These results put barn owls at the very low end of the visual acuity spectrum of birds, and demonstrate that visual resolution and sensitivity cannot be predicted by optical considerations alone.

Keywords: spatial vision, contrast sensitivity, detection/discrimination, visual acuity, animal vision, barn owl

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Introduction

Barn owls are nocturnal predators which have evolved specific sensory and morphological adaptations to a life in dim light conditions. They are particularly renowned for outstanding sound localization capabilities (Payne, 1971; Wagner, Brill, Kempter, & Carr, 2005) and ultra-silent flight (Bachmann et al., 2007; Graham, 1934). Photoretinoscopy and, most recently, wavefront measurements of barn owl eyes demonstrated that they are equipped with high-quality optics (Harmening, Vobig, Walter, & Wagner, 2007b; Schaeffel & Wagner, 1996). In particular, the amount of higher order aberrations in barn owl eyes is only one third of what is found in human eyes (Howland, 2002). This finding suggests paramount spatial vision performance in barn owls, since retinal image quality is shown to be extremely clear, theoretically granting a resolution equal to or higher than that of man (Harmening et al., 2007b). However, retinal ganglion cell density was found to be comparably low, yielding a limiting Nyquist frequency that is by an order of magnitude lower than that calculated from human retinal

organization (Wathey & Pettigrew, 1989). Similar values for a theoretical grating acuity can be deduced from PERG measurements (Ghim & Hodos, 2006).

While higher processing stages of visual perception in barn owls have been detailed in diverse approaches (Harmening, Göbbels, & Wagner, 2007a; Nieder & Wagner, 1999; Ohayon, Harmening, Wagner, & Rivlin, 2008; van der Willigen, Frost, & Wagner, 1998, 2002), there is so far no account made to study the basics of spatial vision on a behavioral level in these birds. We here present for the first time a measure of both the contrast sensitivity function (CSF) and grating acuity of barn owls in a set of psychophysical experiments. If measured behaviorally, the CSF incorporates visual functions of both physical (i.e. the visual transfer function of the eye) and physiological nature (i.e. visual processing in the nervous system) (Cornsweet, 1970; Graham, 1972; Westheimer, 1972). The CSF may therefore be regarded as one of the fundamental functional descriptions of a visual system, and is a direct measure of the perceptual high-level process of seeing. The CSF together with a measure of grating acuity are finally used to test whether the spatial vision thresholds of barn owls match the excellent optics of their eyes.

Materials and methods

Subjects

Experimental animals were two male adult American barn owls (*Tyto alba pratincola*, subjects SL, PT), taken from the institute's breeding stock. The birds were hand-raised and tame. During the phase of experiments, body weight was maintained at about 90% of their free feeding weight. Water was given ad libitum, food (chick meat) was given only in the experimental booth via a food dispenser or as a reward directly after the experiment. Training and experiments took place on 5 days per week. The owls were fed in their aviary when no experiment took place. Care and treatment of the subjects was carried out in accordance with the guidelines for animal experimentation as approved by local authorities (Landespräsidium für Natur, Umwelt und Verbraucherschutz Nordrhein Westfalen, Recklinghausen, Germany), and complied with the "NIH Guide for the use and care of laboratory animals."

Experimental setup and stimuli

All experiments were conducted in a sound and light proof chamber (1.5 m × 2 m × 2.5 m), with no light source other than the stimulus display. The owls were sitting on a wooden perch in front of two response keys

that were symmetrically placed left and right to an automated food dispenser. The head was unrestrained and, upon the onset of a trial, oriented fronto-parallel relative to the stimulus display. Viewing distance was measured by observing the owl's stereotypical pose under infrared illumination, and equaled 85 cm, making one pixel subtend 1.044 arcmin of visual angle (Figure 1). Visual stimulus generation was controlled by custom written software (ANSI-C with the Open-GL utility kit GLUT), running on an Apple G5 workstation with a 8-bit graphics board (NVIDIA GeForce 6800 GPU), and digitally output on a 23" Apple Cinema Display (at its native resolution, 1920 × 1200 pixel).

Two kinds of stimuli were used throughout this study. One was a Gaussian filtered sinusoidal grating, often called Gabor patch (hereafter referred to as Gabor). The other stimulus was a sinusoidal grating, which was, except for the Gaussian filter, identical to the Gabor (hereafter referred to as Sinusoid). The stimuli could appear at two discrete axes of orientation, i.e. the sinusoidal function propagated either in 0° or 90° direction relative to the coordinate system of the display (horizontal or vertical orientation, respectively, see Figure 1).

The standard deviation of the Gaussian of the Gabor was held constant at 0.48. The phase of the sinusoidal function was altered trial by-trial randomly in a 180° interval (not in training sessions). The stimuli, 12.2 degree of visual angle in diameter, were shown centered on the screen when a trial was initiated. The rest of the display was filled with a

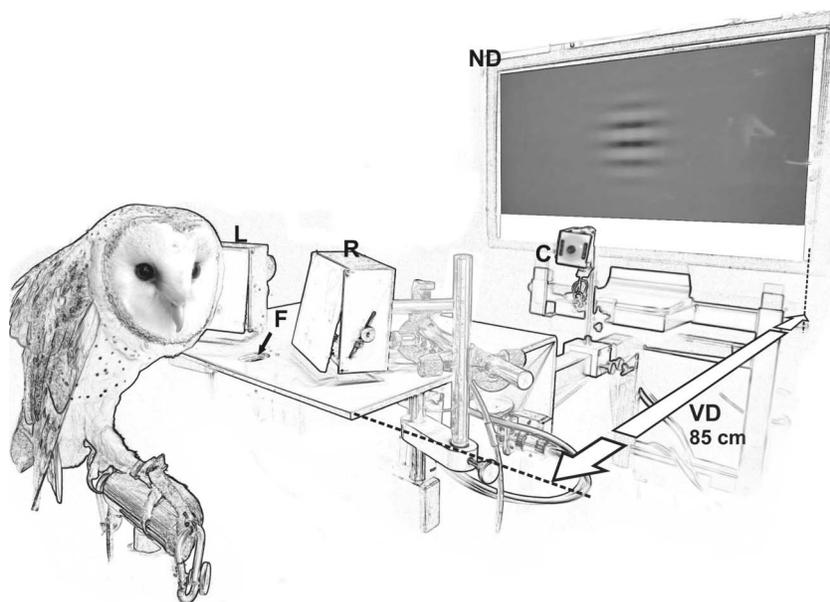


Figure 1. A sketch of the experimental booth, showing the relevant parts of the experimental setup. The barn owl was sitting on a wooden perch fixed in front of an automated feeder, which delivered small pieces of meat upon correct responses (F). The two response keys (L,R), corresponding to the two stimulus configurations, were in easy reach of the owl's beak. Viewing distance (VD) was 85 cm. The computer display was covered with a linear neutral density filter (ND) to reduce glare. This picture shows the situation when the horizontal oriented Gabor patch was presented. A small IR-camera (C) monitored the owl's gaze, which in case of a fronto-parallel orientation triggered trial progress. Note that except for the light originating from the display the room was completely dark under experimental conditions.

uniform gray surface. The background was black when the Sinusoid was presented. The whole screen was covered with a large sheet of linear neutral density filter (Lee Filters, UK) that lowered overall luminance by approximately one log unit, producing a mean luminance of 2.74 cd/m², equally distributed within the stimulus area. The filter was removed for grating acuity experiments with one animal only (mean luminance: 30 cd/m²). Stimulus contrast was controlled by modification of the amplitude of the sinusoidal function and was measured at viewing distance in a pre-experimental calibration sequence with a luminance meter (LS-100, Konica Minolta). Our display system was able to reliably produce stimulus contrasts ranging from 0.99 to 0.01, whereby aliasing artifacts could be excluded due to psychophysical tests with a human observer. Contrast is defined throughout this study according to the Michelson-formula (1):

$$C_M = \frac{lum_{max} - lum_{min}}{lum_{max} + lum_{min}}. \quad (1)$$

The choice of spatial frequencies used in the training sessions and experiments followed observations from pilot testing and earlier studies with the same subjects and setup (Harmening et al., 2007a).

Psychophysical procedures

A small, flashing fixation target was shown in the center of the display between trials to attract the owls' gaze and to support correct orientation. When the subject oriented its gaze toward the screen, a trial was initiated and the stimulus was shown. After stimulus onset the owls had to peck one of the two response keys, corresponding to either a horizontal (right key) or vertical (left key) orientation of the grating. The right-left/horizontal-vertical association was used for both animals. Horizontal or vertical gratings were presented in a pseudo-random order, i.e. no more than three repetitions of one of the two alternatives were presented consecutively. The owls were rewarded after every correct response, false responses were not punished. The time course was self-paced to allow an exact observation of the stimulus. Whenever the owls made large head movements and stopped fixating the display, a trial was aborted. Possible accommodation during experiments was not monitored.

Both owls were extensively trained to discriminate the two different orientations correctly before experiments began. Because the animals were involved in psychophysical two-alternative forced choice (2-AFC) tasks before (Harmening et al., 2007a), the orientation discrimination task could be progressively introduced as transfer tests in training sessions. During this training phase the stimulus contrast, its spatial frequency, and the phase position of the sinusoid was held constant (contrast: 0.99, spatial frequency: 0.61 cyc/deg, phase: 90°). When owls reached significant performance in the task (i.e. performance was higher than 85% correct), the experimental phase began.

Prior to contrast sensitivity experiments, several control experiments were conducted (684 trials). First, the pseudo-random design of the trial sequence was altered to allow up to 7 repetitions of one alternative consecutively. This control intended to rule out strategy learning in the subjects, making them, at low stimulus intensities, guessing better than chance level. Second, to exclude learning of stimulus feature other than orientation, stimuli with (a) random phase (0–180°) and (b) random spatial frequencies drawn from a predefined interval (1.5–0.5 cyc/deg) were rendered at maximum contrast. In all control sessions, the owls responded more than 85% of the time correctly.

Typically, a single experimental session consisted of about 30 to 50 trials. Each session was conducted at a single spatial frequency, or, in grating acuity experiments, at a single contrast level. A simple staircase procedure was employed: stimulus intensity progression within a session followed an up-down transformed rule. That is, stimulus intensity (i.e. contrast in the CSF experiments, and spatial frequency of the grating in grating acuity experiments) was decreased after two consecutive correct responses and was increased after every false response. In this way, converging to stimulus intensities at which the animal responded 70.7% of the time correctly, the choice of stimulus intensities presented to the animal lay near the threshold. To prevent fatigue and frustration of the owl at low stimulus intensities, bonus trials at high intensities were given from time to time. Spatial frequencies used in CSF experiments ranged from 0.4 to 2.4 cyc/deg, and, thus, covered about 2.6 octaves. To avoid systematic impact of learning processes, spatial frequencies across CSF experiments were applied in a non-systematic order.

For further analysis, the results of two consecutive experimental sessions at each spatial frequency were combined to build the basis of psychophysical raw data. This was done by re-calculating the performance level at each stimulus intensity from the pooled data of both runs. The psychophysical raw data was further combined across two or more experimental days (see Figure 2 for an example). Due to the adaptive staircase, this procedure increased the number of trials presented below the targeted threshold, and, thus, increased the validity of subsequent curve fitting. Furthermore, the combination balanced out inconsistencies in animal performance that sometimes occurred on different testing days. Note that it did not necessarily produce an average threshold of the individual runs.

Data analysis

For all spatial frequencies, the combined behavioral performance, i.e. the percentage of correct responses, was plotted as a function of stimulus intensity. With a

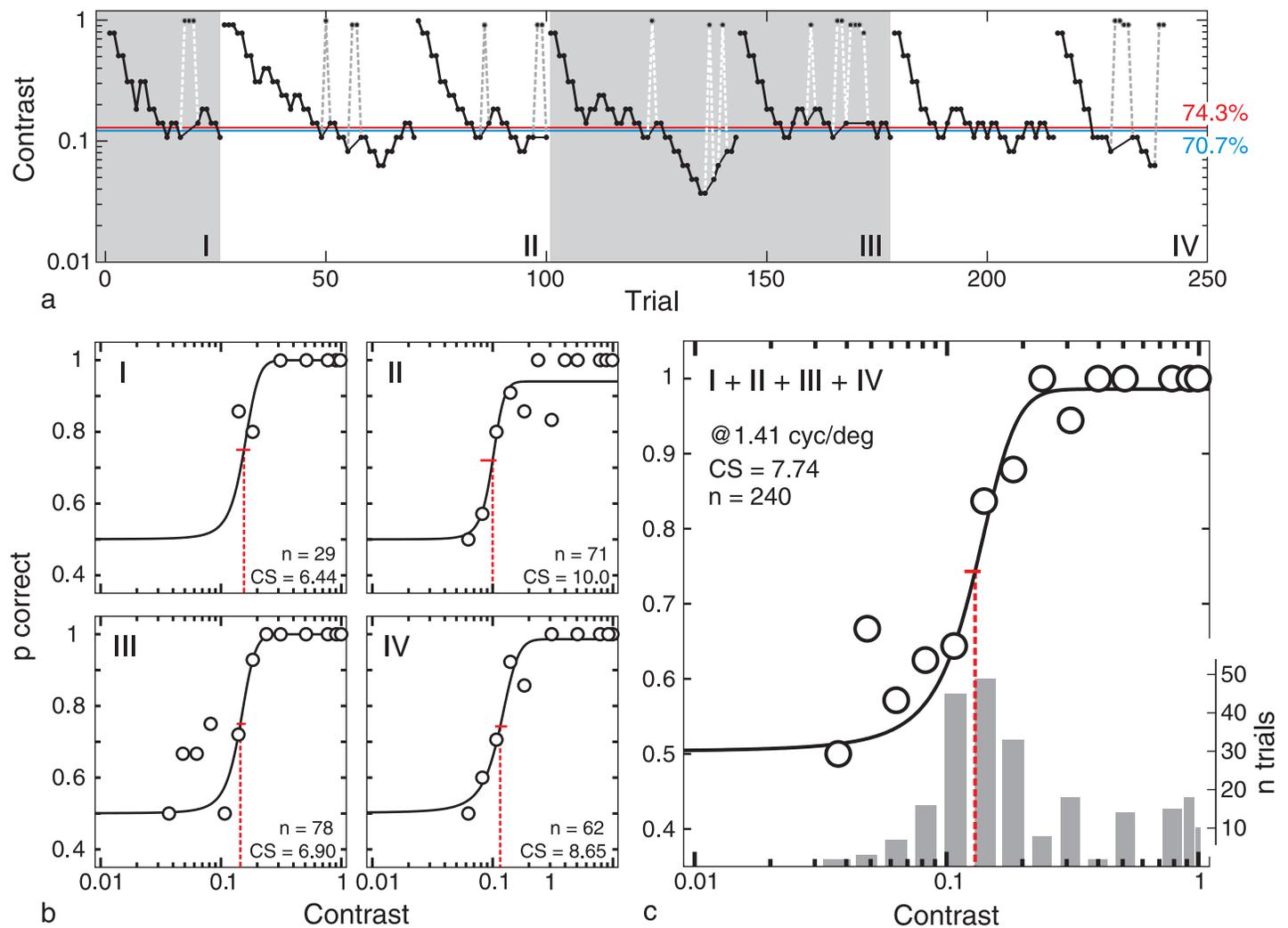


Figure 2. The method of data pooling used throughout this study. In this example, results from owl PT in the contrast sensitivity experiment (@ 1.41 cyc/deg) are shown. In (a) individual staircase runs from four experimental days (I–IV) are plotted. Dashed lines represent high intensity bonus trials. The two horizontal lines correspond to the threshold level calculated from the combined data (compare (c), 74.3% correct), and the theoretical convergence level of the 2down-1up method (70.7% correct), respectively. Note that many trials were conducted in close proximity of the threshold. In (b) results from each day (I–IV) were combined and expressed as psychometric functions. The ratio of correct responses is denoted on the y-axis. Contrast threshold and, inversely, contrast sensitivity (CS) were calculated from fitting a logistic psychometric function to the data, and were defined at the inflection point of that function. The small horizontal bar is the 95% confidence interval at threshold level. N is total trial number. In (c) the results of the four days are combined by re-calculating the performance at each contrast level for the pooled data from (b). The distribution of number of trials across stimulus intensities is given in the bar plot at the bottom.

parametric bootstrap method described by Wichmann and Hill (2001a) used in the Matlab function `pfit`, a logistic function $\Psi(x)$ was fitted to the data points, generating a complete psychometric function (2).

$$\Psi(x) = \gamma + (1 - \gamma - \lambda) \cdot \frac{1}{1 + e^{\frac{\alpha - x}{\beta}}}, \quad (2)$$

where $\Psi(x)$ is behavioral performance at stimulus intensity x , α and β are the fit parameters. Threshold was

defined as the stimulus intensity on the psychometric function half-way between lower (γ) and upper (λ) asymptote, at the inflection point of that function. γ was numerically fixed at 0.5, reflecting the 2-AFC design of the experiment. λ was corrected to account for lapses (false responses) the owl frequently showed at high stimulus intensities (lapse-rate interval {0,0.2}). The parametric bootstrap method (re-sampling $n = 1000$) was also used to obtain an estimate of the 95% confidence level of each individual threshold (Wichmann & Hill,

2001b). Contrast sensitivity was expressed as the inverse of the Michelson contrast at threshold level.

A double exponential function (3) was fitted to the sensitivity normalized data by a method of least squares. This four-parameter function was found to provide a good fit to the CSF of several species (Uhlrich, Essock, & Lehmkuhle, 1981).

$$S(\nu) = 100(K_1e^{-2\pi a\nu} - K_2e^{-2\pi b\nu}), \tag{3}$$

where $S(\nu)$ is contrast sensitivity at spatial frequency ν . Grating acuity was derived computationally from an extrapolation of the CSF beyond the high frequencies tested ($\max\{S(\nu) = 1\}$). Additionally, grating acuity was measured directly in a way similar to the method described above: at maximum contrast ($c_M = 0.99$) spatial frequency was altered according to the transformed up-down rule. A psychometrical function was then fitted to the behavioral discrimination performance at the different levels of spatial frequency. The grating acuity threshold was defined as the spatial frequency at the inflection point of the corresponding psychometric function. Confidence intervals were calculated as stated above.

Results

Contrast sensitivity

Contrast sensitivity was expressed as the inverse of the stimulus contrast at which discrimination performance was at threshold level (compare Table 1 and Figure 4). A maximum contrast sensitivity (CS) of 19.6 (confidence interval (CI): 17.9–23.2) was found in subject SL at a spatial frequency (SF) of 1 cyc/deg with the Gabor

stimulus. This value corresponds to a Michelson contrast of 0.051. A similar value could be found with the Sinusoid (18.7, CI: 17.0–20.8). Sensitivity values decreased monotonically with both higher and lower SFs. At the highest SF tested with the Gabor (2.2 cyc/deg) sensitivity dropped to 2.2 (CI: 2.0–3.0), and to 2.6 (CI: 2.3–3.7) at 2.4 cyc/deg with the Sinusoid. The lowest SF tested with SL (0.4 and 0.5 cyc/deg, respectively), yielded sensitivity values of 2.7 (CI: 2.2–3.3) for the Gabor, and 4.2 (CI: 3.8–4.7) for the Sinusoid. Generally, the results from the two stimulus configurations in SL were very similar. In owl PT, highest sensitivity appeared at the same SF as in SL, but with decreased magnitude (CS: 8.1, CI: 7.3–9.2), corresponding to a Michelson contrast of 0.124. The same observation, a reduction of absolute sensitivity to about one half of the values found in SL, holds for all spatial frequencies tested. The terminal SFs (0.5 and 2.0 cyc/deg, respectively) yielded sensitivity values of 2.6 (CI: 2.4–2.7) and 3.7 (CI: 3.3–4.4).

Grating acuity

Grating acuity was measured at the highest contrast possible to be displayed ($c_M = 0.99$), and was defined as the SF of the sinusoidal function at which discrimination performance was at threshold level. In addition to discrimination, a detection paradigm was applied in experiments with the Sinusoid. Here, gratings were presented in horizontal configuration only, while the null-stimulus was a uniform gray surface with identical mean luminance (depicted as a small inset in Figure 3a). Measured with the Gabor, owl SL displayed a grating acuity of 3.95 cyc/deg (CI: 3.82–4.12 cyc/deg). In detection experiments grating acuity was 3.43 cyc/deg (CI: 3.22–3.78 cyc/deg). Discrimination performance with the Sinusoid yielded a grating acuity of 3.23 cyc/deg

SL(G)					SL(S)					PT(S)				
SF	CS	CI	n	p.thr	SF	CS	CI	n	p.thr	SF	CS	CI	n	p.thr
2.2	2.2	2.0–3.0	146	.702	2.4	2.6	2.3–3.7	84	.701	2.0	3.7	3.3–4.4	295	.671
2.0	10.1	9.3–11.4	340	.729	2.0	7.0	6.3–7.9	139	.732	1.7	5.0	4.6–5.6	170	.730
1.5	14.9	13.0–16.7	188	.726	1.5	10.4	9.6–12.7	81	.737	1.4	7.7	7.1–8.5	240	.742
1.2	16.0	15.1–17.2	290	.693	1.0	18.7	17.0–20.8	222	.732	1.0	8.1	7.3–9.2	290	.712
1.0	19.6	17.9–23.2	263	.721	0.8	8.7	8.0–9.5	363	.726	0.8	5.4	5.1–6.0	236	.740
0.9	15.6	14.3–17.2	176	.750	0.5	4.2	3.8–4.7	282	.730	0.6	4.5	4.3–4.9	185	.750
0.8	8.7	7.7–10.0	198	.737						0.5	2.6	2.4–2.7	389	.744
0.6	5.3	4.3–6.8	432	.702										
0.5	3.5	3.1–4.5	171	.718										
0.4	2.7	2.2–3.3	201	.711										

Table 1. Results from contrast sensitivity experiments across subjects (PT, SL) and conditions (G: Gabor, S: Sinusoid). Contrast sensitivity (CS) values at all spatial frequencies (SF [cyc/deg]) are given, together with the 95% confidence interval borders (CI), the number of trials (n), and the performance level at which threshold was defined (p.thr).

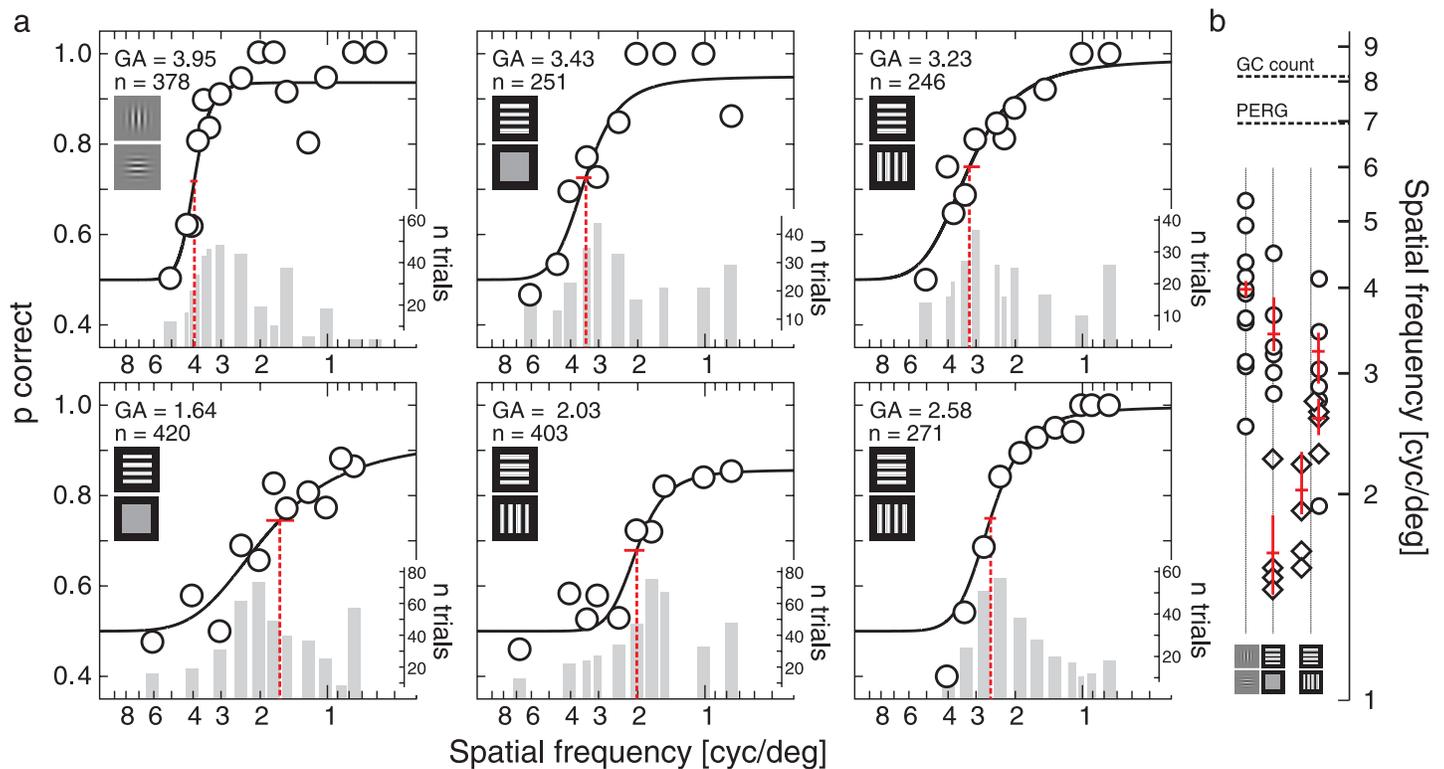


Figure 3. Results from grating acuity (GA) experiments. (a) Top row: measurements in owl SL, bottom row: owl PT. The ratio of correct responses is plotted against spatial frequency (SF). The circles denote discrimination performance at a given SF. The solid line is the logistic fit to the data, the small horizontal bar is the 95% confidence interval (CI) at threshold. The majority of trials were conducted around threshold level (see bar plot at the bottom of each panel, denoting trial numbers (n) per stimulus intensity). The small inset on the left part of each panel denotes experimental condition: Gabor and Sinusoid stimuli, detection and discrimination tasks. (b) Comparison of individual runs across animals and conditions. Circles are results from owl SL, diamond markers denote results from owl PT. The vertical bars are the CIs, the smaller horizontal bar is the threshold from (a). As a reference, the dotted lines represent earlier results from pattern electroretinogram (PERG) measurements (Ghim & Hodos, 2006), and ganglion cell (GC) count (Watney & Pettigrew, 1989).

(CI: 2.90–3.44 cyc/deg). With this animal only, we performed grating acuity experiments in 1476 trials at a ten-fold higher mean stimulus luminance (30 cd/m^2), and the threshold was marginally lower (4.07 cyc/deg, CI: 3.95–4.18 cyc/deg). Owl PT performed grating acuity experiments with the Sinusoid only. In detection experiments grating acuity was the lowest reported, and yielded 1.64 cyc/deg (CI: 1.41–1.87 cyc/deg). Grating acuity was measured twice in the discrimination task, as a test and re-test control. In the first measurement, grating acuity was 2.03 cyc/deg (CI: 1.88–2.33 cyc/deg). In the re-test, grating acuity was 2.58 cyc/deg (CI: 2.44–2.76). The results of the individual experimental runs were all higher in later measurements. Thresholds were (in chronological order): 1.51, 1.06, 1.45, 1.56, 2.25 cyc/deg in detection experiments, and 1.65, 1.56, 1.89, 2.21, 2.29, 2.61, 2.66, 2.73 cyc/deg in discrimination experiments. See Figure 3b for results of all individual staircase runs and also for a comparison of grating acuity results across animals and conditions with reference to earlier electrophysiological and anatomical estimates (result from higher luminance level not shown in figure).

Contrast sensitivity function

Contrast sensitivity values derived from the combined experimental sessions were plotted against spatial frequency on a double logarithmic scale (see Figure 4). Sensitivity values increased strictly monotonic from low spatial frequencies up to intermediate spatial frequencies, where sensitivity was maximal at 19.6, 18.7, and 8.1 at 1.01 cyc/deg for owl SL(Gabor), owl SL(Sinusoid), and owl PT(Sinusoid), respectively. Consistently, going further to higher spatial frequencies, sensitivity decreased strictly monotonic in both animals.

According to Equation (3), our best fit for the pooled data of both owls for both the Gabor and the Sinusoid was found for the following parameters: $K_1 = 1.4989$, $K_2 = 1.5230$, $\alpha = 0.2630$, $\beta = 0.2691$ (normalization factor: 19.61). Peak sensitivity derived from this function was 12.58 at a spatial frequency of 1.01 cyc/deg. The width of the CSF was measured in octaves as the distance between the spatial frequency on either side of the peak frequency at which sensitivity declined by a factor of two. Thus, width at half amplitude was

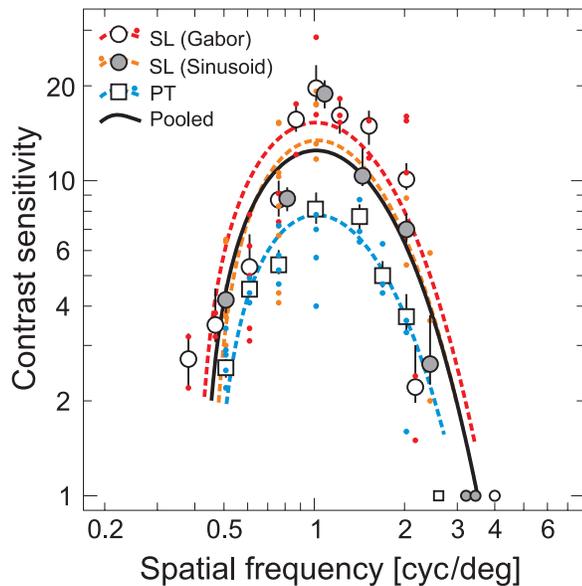


Figure 4. The behavioral contrast sensitivity function of barn owls. Contrast sensitivity was defined as the inverse of contrast threshold and was plotted against spatial frequency. The different markers represent the two animals and conditions (legend). The vertical bars are the 95% confidence intervals calculated from the combined psychometric functions. Small dots are results from individual runs. Sensitivity values were fitted to a double exponential function, plotted as dashed lines for the different conditions, and as solid line for pooled data. Results from grating acuity experiments are plotted for reference as well (bottom right).

1.88 octaves (0.55–2.02 cyc/deg). The high frequency cutoff, $\max\{S(\nu) = 1\}$, was 3.51 cyc/deg. The according values were calculated for individual results, and are shown as their corresponding function in Figure 4.

Discussion

The data presented here are the first measure of the behavioral spatial contrast sensitivity function and grating acuity in the visual system of barn owls. A mean maximum contrast sensitivity of around 12 was found at a spatial frequency of 1 cyc/deg. Sensitivity declined rapidly for spatial frequencies lower than 0.8 cyc/deg and higher than 2 cyc/deg. Width at half amplitude was rather narrow, with a mean of 1.8 octaves. Grating acuity as derived from the high-frequency cut-off of the CSF was between 3.0 and 3.7 cyc/deg. Furthermore, grating acuity was reported independently in a second behavioral experiment. Here, grating acuity values between 2.6 and 4.0 cyc/deg were found. These results constitute a pronounced optics-acuity disagreement in these animals, because calculations based solely on the optics of their

eyes predict resolution capabilities that are at least an order of magnitude better than the behavioral acuity reported here.

Methodological considerations

A detailed ROC analysis combining data from both animals across experimental conditions revealed no significant or systematic response bias towards one of the two alternative stimulus orientations. Similar to our results, a lack of an orientation anisotropy for the principal orientations (horizontal/vertical) was reported from CSF measurements in human and cat subjects (Bisti & Maffei, 1974; Campbell, Kulikowski, & Levinson, 1966).

Based on the results of the control experiments, we conclude that the owls were able to incorporate a concept of the orientation discrimination task. In transfer trials, with gratings of spatial frequencies that were never used in the training sessions before, the owls showed similar performance as in the training sessions. This was also the case when the grating was presented with random phase configuration. Moreover, the responses to the stimulus showed robustness against a change in inter-trial alternative choice to a quite large extent. While in training trials no more than three repetitions of one alternative occurred consecutively, this was changed to a maximum of 7 possible consecutive repetitions in the control sessions. Again, performance did not drop significantly, although this change might have increased fatigue and frustration in the owl. We conclude from this, that the applied psychophysical method and stimuli produced a stable behavioral response in the animals.

In one animal (PT), learning processes might have had influences on grating acuity estimates. That is, during the course of experiments, thresholds generally improved. A look at the corresponding psychometric functions of a test and re-test (Figure 3) reveals that baseline performance at high intensities differ to a large extent (85% correct, and 99% correct, respectively). As a consequence, grating acuity in this animal is reported as the performance displayed in the (chronologically) last experiment (2.58 cyc/deg).

Significance of the results

For validation, our results can be compared to at least two studies, in which contrast sensitivity and grating acuity of barn owls was measured and computed electrophysiologically and anatomically, respectively (Figure 5). In the electrophysiological study, the authors measured contrast sensitivity in 4 barn owls with the pattern electroretinogram (Ghim & Hodos, 2006). Combined peak sensitivity of about 6 was found at a spatial frequency of 1.1 cyc/deg (Figure 5). In this study, grating acuity (6.98 cyc/deg) was computed based on extrapolation

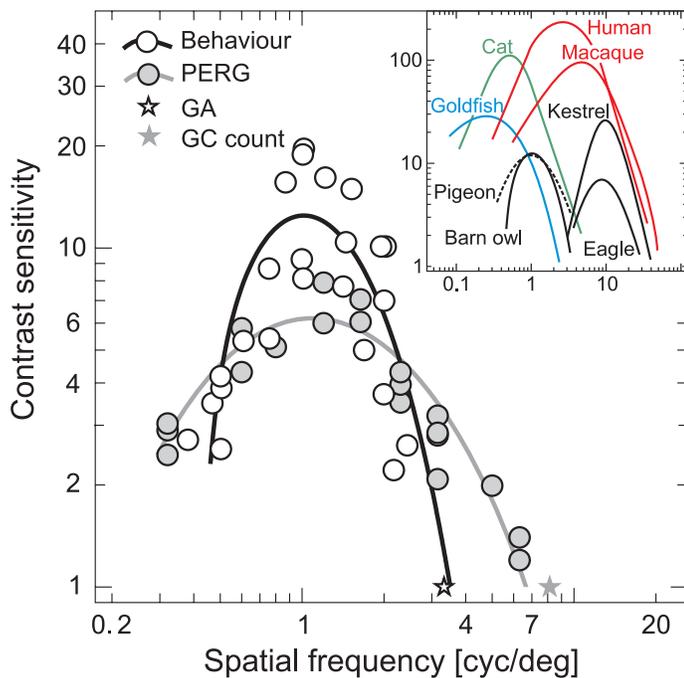


Figure 5. Comparative view on contrast sensitivity and grating acuity of barn owls and other animals. Open markers and black solid line are the contrast sensitivity values and CSF found in the present study. Filled markers and gray solid line are a re-plot of the barn owl CSF found by Ghim and Hodos (2006) with the pattern electroretinogram (PERG). Mean grating acuity (GA) found in our study is shown as open star, a gray star marks the grating acuity estimate based on ganglion-cell count by Wathey and Pettigrew (1989). The inset at the top right compares CSFs across several species. These plots are re-drawings of either mean or representative results. References are: human (Berkley, 1976), macaque (De Valois, Morgan, & Snodderly, 1974), cat (Bisti & Maffei, 1974), goldfish (Northmore & Dvorak, 1979), kestrel (Hirsch, 1982), eagle (Reymond & Wolfe, 1981), and pigeon (Hodos et al., 2002).

of the CSF beyond the measured high spatial frequencies, similar as in the present study. While the spatial frequency at which sensitivity peaks is in good accordance with our results (1 cyc/deg), data with respect to maximum sensitivity values, bandwidth, and high frequency cut-off are at variance with the present results. This might be due to the different methodological approach: the PERG method is known to produce about 40% differences in peak sensitivity when compared to behavioral data in the same subject (Hodos, Ghim, Potocki, Fields, & Storm, 2002; Peachey & Seiple, 1987). Bandwidth and grating acuity differences might be due to different luminance values used for visual stimulation. In the PERG study, mean luminance of the display was 94 cd/m². Our experiments were conducted at intermediate light levels (2.7 cd/m²), a more than 30 fold reduction of mean luminance. In human, primate, and cat subjects it has been shown that a reduction of stimulus luminance affects

the CSF, and, therefore, grating acuity estimates to a large extent (Bisti & Maffei, 1974; Blake, Cool, & Crawford, 1974; De Valois & Morgan, 1974; Jacobs, 1977; Patel, 1966).

In an anatomical study, the retinal ganglion cell density was used as the basis for a grating acuity estimation. A maximum ganglion cell density of 11000–12500/mm² was reported at the area centralis, and, thus, a grating acuity of 7.9–8.4 cyc/deg was calculated by application of the Shannon sampling theorem and an assumptive retinal magnification factor of 0.15 mm/deg (Wathey & Pettigrew, 1989). While the geometry of barn owl eyes is described in detail (Schaeffel & Wagner, 1996), it remains unclear how many of the ganglion cells in area centralis are involved in spatial acuity tasks. Moreover, considering the topography of ganglion cell density in the retina of barn owls, displaying a horizontal streak of lower cell density (5000–8000/mm²), behavioral acuity values lower than the theorized 8 cyc/deg become reasonable (Wathey & Pettigrew, 1989).

Inter-species comparison

How do the results presented here compare to data from other birds and animals? A rather qualitative answer is given with the inset of Figure 5. Common with all birds that have been tested so far, barn owls display a relatively low maximum sensitivity (below 20). Bird maximum contrast sensitivity has so far never exceeded 30, or expressed as Michelson contrast, 0.03. Given that birds are generally regarded as highly reliant on visual information, this finding is surprising and still unsolved as to which mechanisms are responsible for this relatively low sensitivity (Hodos, Ghim, Miller, Sternheim, & Currie, 1997). The barn owl behavioral CSF is narrower than any other CSF, which might be simply explained by the illumination conditions used in our experiments. On the other hand, it might reflect the presence of only few, narrowly tuned spatial frequency channels (Irvin, Casagrande, & Norton, 1993). A comparison with PERG results in which bandwidth is clearly increased (Ghim & Hodos, 2006) would then dictate the origin of this effect to be strictly post-retinal. While small bandwidth and low contrast sensitivity are all common among bird CSFs, the location of the CSF on the spatial frequency axis differ among species. This is easily explained by the individual maximum acuity the birds exhibit. While the eagle and kestrel, both equipped with high resolution capabilities (70–140 cyc/deg), have CSFs with maximum sensitivity at a spatial frequency of around 10 cyc/deg, the pigeon and barn owl's maximum sensitivities are shifted towards lower spatial frequencies, lying somewhere around 1 cyc/deg. Consistently, these two species have maximum resolutions (pigeon: 6 cyc/deg, barn owl: 3.3 cyc/deg) that are essentially lower than those of the two raptorial species.

Interestingly, especially in the light of the excellent optical quality of barn owl eyes, the behavioral results from grating acuity experiments reported in our study (2.6–4.0 cyc/deg) put barn owls at the very low end of the acuity spectrum of birds that were tested at similar luminances. Other owls, like little owls (6 cyc/deg) (Porciatti, Fontanesi, & Bagnoli, 1989), great horned owls (6–7.5 cyc/deg) (Fite, 1973), and tawny owls (8 cyc/deg) (Martin & Gordon, 1974), have slightly higher maximum resolutions. Generally, compared to other raptorial birds, owls lie on the lower end of the acuity spectrum, possibly because their hunting success is less reliant upon vision than this is the case for diurnal raptors. Known behavioral acuity values in raptors span from extraordinary high

values in wedge tailed eagles (140 cyc/deg) (Reymond, 1985; Schlaer, 1972), to manlike values of around 70 cyc/deg in Australian brown falcons (73 cyc/deg) (Reymond, 1987) or American kestrels (about 50 cyc/deg) (Hirsch, 1982). Superb acuities of 160 cyc/deg in an American kestrel (Fox, Lehmkuhle, & Westendorf, 1976) have been questioned due to an about 3 fold lower anatomical resolution (46 cyc/deg) (Dvorak, Mark, & Reymond, 1983), and were re-tested in an electrophysiological study (39.7–71.4 cyc/deg) (Gaffney & Hodos, 2003). Grating acuity of some other non-raptorial birds have been measured, either electrophysiologically or behaviorally, and the results place them somewhere between owls and eagles on the acuity scale. Among those are for example

Species name	Acuity [cyc/deg]	@luminance [cd/m ²]	Reference
Barn owl (<i>Tyto alba pratincola</i>)	2.6–4.0/4.1	2.7/30	Harmening, present study
Little owl (<i>Athene noctua</i>)	6 ^a	200	Porciatti et al. (1989)
European robin (<i>Erithacus rubeculus</i>)	6/6	1.53/19.1	Donner (1951)
Great Horned Owl (<i>Bubo virginianus</i>)	6–7.5	80	Fite (1973)
Reed bunting (<i>Emberiza schoeniclus</i>)	2.17/7.8	1.53/19.1	Donner (1951)
Domestic chick (<i>Gallus gallus domesticus</i>)	4.2–6.4/7.7–8.6	3.5/65	DeMello, Foster, and Temple (1992), Schmid and Wildsoet (1998)
Yellowhammer (<i>Emberiza citrinella</i>)	2.17/9.7	1.53/19.1	Donner (1951)
Tawny owl (<i>Strix aluco</i>)	8.8/12/8–11.1	5/50.5/160	Martin and Gordon (1974)
Pigeon (<i>Columba livia</i>)	3/6/12/18	0.85/3.2/32/317	Hodos et al. (1976)
Blue Jay (<i>Cyanocitta cristata</i>)	15–19 ^b	–	Fite and Rosenfield-Wessels (1975)
Peafowl (<i>Pavo cristatus</i>)	20.6 ^b	–	Hart (2002)
Skylark (<i>Aulada arvensis</i>)	22.5/11.4	1.53/19.1	Donner (1951)
Fieldfare (<i>Turdus pilaris</i>)	22.5/15.9	1.53/19.1	Donner (1951)
Blackbird (<i>Turdus merula</i>)	22.5/22.5	1.53/19.1	Donner (1951)
Chaffinch (<i>Fringilla coelebs</i>)	22.5/22.5	1.53/19.1	Donner (1951)
Sacred kingfisher (<i>Halcyon sancta</i>)	26 ^b	–	Moroney and Pettigrew (1987)
Rook (<i>Corvus frugilegus</i>)	29.5/29.5	9.5/60	Dabrowska (1975)
Jackdaw (<i>Corvus monedula</i>)	13.0–23.7/29.5–33.3	9.5/60	Dabrowska (1975)
Magpie (<i>Pica pica</i>)	23.7–29.5/29.5–33.3	9.5/60	Dabrowska (1975)
Laughing kookaburra (<i>Dalco gigas</i>)	41 ^b	–	Moroney and Pettigrew (1987)
American kestrel (<i>Falco sparverius</i>)	54/100/160	3.5/35/350	Fox et al. (1976)
American kestrel (<i>Falco sparverius</i>)	46 ^b /39.7–71.4 ^a	–/93	Dvorak et al. (1983), Gaffney and Hodos (2003)
Australian brown falcon (<i>Falco berigora</i>)	52/73	2/2000	Reymond (1987)
African serpent eagle (<i>Dryotriorchus spectabilis</i>)	120 ^c	–	Schlaer (1972)
Wedge tailed eagle (<i>Aquila audax</i>)	30–40 ^d /58/138	2/20/2000	Reymond (1985), Reymond and Wolfe (1981)
Goldfish (<i>Carassius auratus</i>)	1.4–2.2	5	Northmore and Dvorak (1979)
Galago (<i>Galago crassicaudatus</i>)	2.6–4.3	22	Langston et al. (1986)
Cat (<i>Felis catus</i>)	5.0 ^d	2	Bisti and Maffei (1974)
Macaque (<i>Macaca nemestrina/fascicularis</i>)	31/46	1.7/17	De Valois and Morgan (1974)
Human (<i>Homo sapiens</i>)	35/50	1.7/17	De Valois and Morgan (1974)

Table 2. An overview of visual acuity thresholds across bird species, ordered by the maximum acuity exhibited. Where possible, results that were obtained at similar luminances as used in our experiments are shown. A few non-avian species are given for comparison. Note: Grating acuity estimated by: ^aelectroretinogram, ^bganglion cell count, ^coptics, ^dCSF.

some passerine birds (2.2–22.5 cyc/deg) (Donner, 1951), domestic chicks (7.7–8.6 cyc/deg) (Schmid & Wildsoet, 1998), Blue Jays (15–19 cyc/deg) (Fite & Rosenfield-Wessels, 1975), pigeons (18 cyc/deg) (Hodos, Leibowitz, & Bonbright, 1976), rooks (29.5 cyc/deg), and magpies (29.5–33 cyc/deg) (Dabrowska, 1975) (compare Table 2 for an elaborated list of visual acuity in birds).

The optics-acuity disagreement

The grating acuity of the two barn owls tested here is of a magnitude comparable to results found in cats (5.0 cyc/deg) (Bisti & Maffei, 1974) and galagos (2.6–4.3 cyc/deg) (Langston, Casagrande, & Fox, 1986), a prosimian primate. This observation across animal species of such divergent phylogenetic origins supports the speculation that their common nocturnal lifestyle is the most important ecological factor setting the limits of spatial vision in these animals (Warrant, 2004). What remains rather surprising in this respect is why barn owls display such remarkably high-quality optics while visual acuity is poor. In fact, our results suggest that spatial vision in barn owls is among the worst ever recorded in a bird, and optical quality is among the best ever measured in any vertebrate eye (Harmening et al., 2007b). The former finding, albeit known from other owl species, contrasts the commonly accepted superb visual capabilities in birds of prey. Put together, both findings constitute a remarkable optics-acuity disagreement in the barn owl visual system. A similar discrepancy was observed in a wavefront study of cat eyes (Huxlin, Yoon, Nagy, Porter, & Williams, 2004).

In contrast, it is well established that the anatomical and behavioral resolution of humans and other high-acuity animals like for example the wedge-tailed eagle match the optical transfer characteristics of their eyes very well (Campbell & Green, 1965; Reymond, 1985). A match in optics and acuity may be a reasonable design feature, because an undersampling of the retinal image through a coarser sensory array would impose visible moiré patterns onto the perceived image (Barlow, 1981; Williams, 1985). Also, other interference effects come into play which may ultimately degrade spatial vision (Coletta, Williams, & Tiana, 1990). Whether barn owls perceive interference patterns due to retinal undersampling is unclear. However, if this would actually be the case, their resolution capacity could have shifted beyond the limits set by the photoreceptor lattice, which would be then visible in our grating acuity experiments (Thibos, Walsh, & Cheney, 1987). This was not observed. We suggest that the presence of low higher-order aberrations (HOA) is a beneficial feature also for low-acuity animals who are active at mesopic or scotopic luminance conditions, because HOA are known to produce visual deteriorations such like glare, halos, ghost images, and general blurring, which are probably disadvantageous regardless of the visual resolution its bearer exhibits. It

would be interesting to study aberration properties in a larger set of species, to maybe discover that low HOA is a common optical design feature across animals that share relatively low visual acuity and a crepuscular/nocturnal lifestyle.

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