Night vision in barn owls: Visual acuity and contrast sensitivity under dark adaptation

Julius Orlowski

Department of Zoology and Animal Physiology, Rheinisch-Westfaelische Technische Hochschule Aachen University, Aachen, Germany

Wolf Harmening

Department of Zoology and Animal Physiology, Rheinisch-Westfaelische Technische Hochschule Aachen University, Aachen, Germany
Present address: School of Optometry, University of California, Berkeley, CA, USA

Hermann Wagner

Department of Zoology and Animal Physiology, Rheinisch-Westfaelische Technische Hochschule Aachen University, Aachen, Germany

Barn owls are effective nocturnal predators. We tested their visual performance at low light levels and determined visual acuity and contrast sensitivity of three barn owls by their behavior at stimulus luminances ranging from photopic to fully scotopic levels (23.5 to 1.5×10^{-6}). Contrast sensitivity and visual acuity decreased only slightly from photopic to scotopic conditions. Peak grating acuity was at mesopic (4×10^{-2} cd/m^2) conditions. Barn owls retained a quarter of their maximal acuity when luminance decreased by 5.5 log units. We argue that the visual system of barn owls is designed to yield as much visual acuity under low light conditions as possible, thereby sacrificing resolution at photopic conditions.

Keywords: scotopic vision, avian vision, absolute sensitivity, detection, discrimination, grating acuity, psychophysics, spatial vision

Introduction

Barn owls (*Tyto alba*) are crepuscular and nocturnal birds of prey that hunt small vertebrates. Barn owls display various adaptations to be effective under low light conditions. They are renowned for outstanding sound localization capabilities (Payne, 1971; Takahashi, 2010) and for silent flight due to a specific feather design (Bachmann et al., 2007). Equally remarkable are the owls' large, frontally oriented eyes, which are the basis of the barn owls' stereovision system (van der Willigen, 2011). Despite large differences in neural organization, higher levels of visual perception in barn owls generally show striking similarities to those of humans, as has been demonstrated in studies of perceptual completion (Nieder & Wagner, 1999), disparity sensitivity (van der Willigen, Harmening, Vossen, & Wagner, 2010), and visual search (Harmening, Orlowski, Ben-Shahar, & Wagner, 2011).

Like many other nocturnal animals, barn owls are believed to have a visual system capable of exploiting their dim surroundings by maximizing sensitivity to small amounts of light by sacrificing fine spatial resolution (Martin, 1986; Warrant, 2004). Barn owls have a rod-dominated retina that lacks an anatomically visible fovea (Fite & Rosenfield-Wessels, 1975; Oehme, 1961). Their fovea displays only a weakly developed horizontal streak of higher ganglion cell density (Wathey & Pettigrew, 1989). The owls' tubular shaped eye has a length of 17.5 mm and an f-number of 1.13. These anatomical features allow for bright retinal images (Schaeffel & Wagner, 1996). The retinal organization in barn owls is indeed typical for night active birds (Jones, Pierce, & Ward, 2007). At high light levels acuity and contrast sensitivity are comparably poor in the owl (Ghim & Hodos, 2006; Harmening, Nikolay, Orlowski, & Wagner, 2009). This is consistent with the retinal sampling limit inferred from ganglion cell density (Wathey & Pettigrew, 1989). The low acuity is in stark contrast to the optical quality of barn owl

eyes, which was found to be exceptionally good (Harmening, Vobig, Walter, & Wagner, 2007). High quality optics like those of barn owls are usually conjunct with high-resolution visual systems, as in humans or diurnal raptors (Liang & Williams, 1997; Reymond, 1985). On the other hand, eyes with low aberration produce less deterioration, such as glare, halos, and general blur, and increase image contrast when only little light is available (Huxlin, Yoon, Nagy, Porter, & Williams, 2004). Retinal image quality may thus benefit from good optics also at low spatial frequencies, but it is unclear how much this affects the barn owls' perceptual capabilities, especially at the light levels they usually encounter.

Here, we set out to measure spatial performance of barn owls under low light conditions in a series of behavioral experiments. We determine visual acuity and contrast sensitivity in three animals under photic and mesopic to low scotopic light conditions.

Methods

Animal subjects

Three barn owls, *Tyto alba pratincola* (subjects SL, PT, YA), taken from the breeding colony of the Department of Zoology at RWTH Aachen University were used for the experiments. All animals were hand-raised and tame. Experiments were conducted under a permit issued by the Landespräsidium für Natur, Umwelt und Verbraucherschutz Nordrhein Westfalen, Recklinghausen, Germany. During the experiments the owl's body weight was kept at about 90% of their free-feeding weight. They were rewarded with single slices of chick meat during experiments and were fed with additional chick meat after an experimental session to maintain body weight irrespective of behavioral performance. The owls participated in experiments 5–6 days a week, approximately 1.5 hours a day, and were fed in their aviaries when no experiment was conducted. No attempt was made to reverse their nocturnal cycle.

Experimental setup, procedures, and data analysis

The general experimental setup, operant conditioning of the owls, and behavioral procedures have been described earlier (Harmening et al., 2009). We describe only pertinent details briefly here. All experiments were carried out in a light- and soundproof booth. Using sinusoidal gratings with either horizontal or vertical orientation as stimuli, barn owls performed a two-alternative forced choice orientation discrimination task at various levels of stimulus luminance. The birds were trained to press one of two buttons corresponding to the stimulus orientation. Correct responses were rewarded with chick meat delivered by an automated food dispenser. Stimuli were presented on a computer display that was masked by black cardboard, leaving only a central portion visible to the subjects. In this way, background light leakage was minimized, and stimulus luminance could be easily controlled by introducing sheets of neutral density filters (LEE Filters, Colorfilter type 211, 0.9 ND [LEE Filters Worldwide, Andover, Hampshire, UK]) in front of the unmasked screen. The average stimulus luminance produced by the unfiltered screen was measured with a luminance meter (Konica Minolta LS-100 [Konica Minolta Optics, Inc., Tokyo, Japan]) across a circular aperture of 1° of visual angle, and yielded 23.5 cd/m^2. While this measurement incorporates the standard human spectral sensitivity, it has to be noted that the owls' luminosity function is nearly identical to that of humans in the visible part of the spectrum (Bowmaker & Martin, 1978; Martin, 1977). Stimulus luminance was decreased by a premeasured set of filter sheets, each of the individual sheets reducing luminance by a factor of ~ 8. Ten stimulus luminance levels were used in the experiments, according to the number of filters applied. The luminance levels were 0 (23.5 cd/m^2), 1 (3.0 cd/m^2), 2 (3.8×10^{-1} cd/m^2), 3 (4.8×10^{-2} cd/m^2), 4 (6.0×10^{-3} cd/m^2), 5 (7.5×10^{-4} cd/m^2), 6 (9.3×10^{-5} cd/m^2), 7 (1.2×10^{-5} cd/m^2), 8 (1.5×10^{-6} cd/m^2), and 9 (1.82×10^{-7} cd/m^2). Maximum stimulus contrast was 0.99. Throughout this study, contrast is defined according to the Michelson-formula $C_M = (L_{Max} - L_{Min})/(L_{Max} + L_{Min})$ Proper stimulus luminance control was validated psychophysically with two human subjects, confirming earlier results of human grating acuity under dark adaptation (Pirenne & Denton, 1952; Shlaer, 1937).

Two separate experiments were conducted with the owls, measuring grating acuity and contrast sensitivity. Prior to all experiments, the barn owls were dark adapted for approximately 25 minutes. A single daily experimental session comprised 30–50 trials, corresponding roughly to 1 hour of continuous testing. In Experiment 1, for luminance levels 0–6 at least 450 trials per owl and luminance condition were conducted. At level 7 only around 250 trials were conducted, because owls were difficult to motivate to conduct the experiment consistently at very low luminance levels. In Experiment 2, 150–200 trials per owl and luminance-frequency configuration were conducted. Experiments were carried out sequentially from the highest to the lowest luminance condition. After experiments at the lowest luminance condition had been completed, control experiments at higher luminance levels were
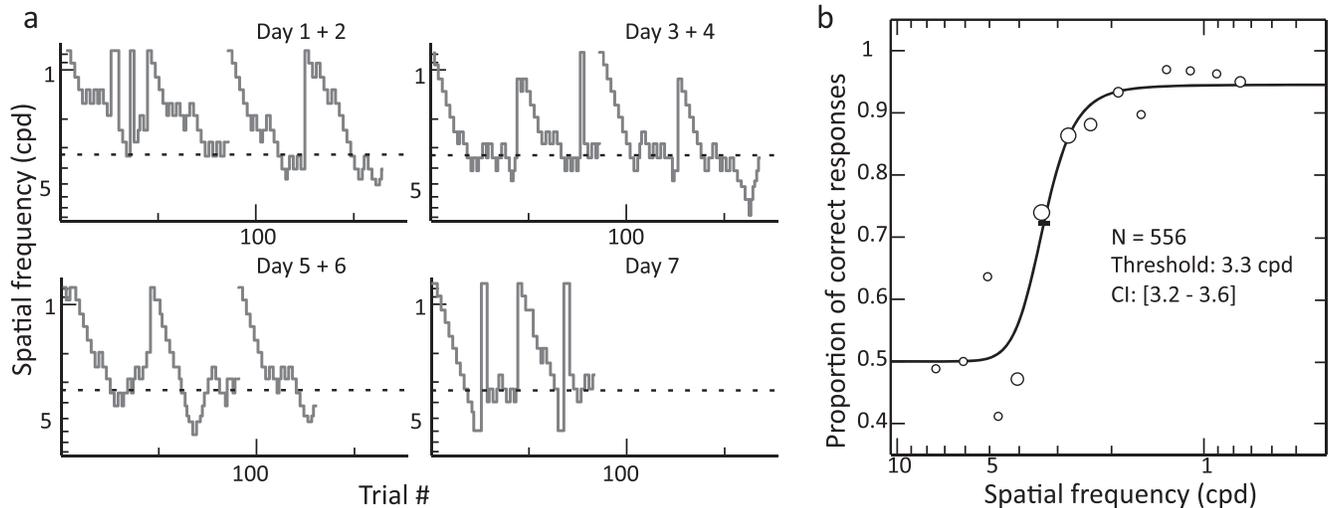
Figure 1. Behavioral threshold estimation. (a) A two-down, one-up adaptive staircase procedure was employed to place stimulus intensities tested near the perceptual threshold. Shown here are the exemplary sessions recorded on seven different days in one animal for a single experimental condition in Experiment 1 (grating acuity). High intensity trials were introduced to prevent fatigue and to keep animal motivation on a high level. (b) Data from a was pooled and the proportion of correct responses for each stimulus intensity was plotted as a function of spatial frequency (circles). A four parameter logistic function was fitted to the data (Harmening et al., 2009). The threshold was defined as the *x*-value at the inflection point of that function. A confidence interval was calculated from 400 simulated runs of statistical resampling (horizontal bar). Dot size represents number of trials per intensity.

repeated to verify that no further learning occurred. To reach threshold, an adaptive two-down, one-up staircase procedure was employed (Levitt, 1971). High stimulus intensities were introduced from time to time to ensure good animal motivation (Figure 1a). Frequency of response curves were constructed and analyzed using parametric bootstrapping software (Wichmann & Hill, 2001). Data that were recorded on separate days were pooled to arrive at a single frequency of response curve and threshold for each condition (Figure 1b).

For Experiment 1, grating acuity was determined at nine different luminance levels (levels 0–8, as already described), ranging from photopic to fully scotopic illumination. During a single experimental session, spatial frequency was varied according to the staircase, while stimulus contrast and luminance was held constant. Contrast was held at maximum (0.99). In Experiment 2, contrast sensitivity was determined at three intermediate stimulus luminances, levels 1, 3, and 6 (3 to 9.3×10^{-5} cd/m^2). For each luminance level, thresholds were measured for four grating spatial frequencies ranging from 0.3 to 2 cycles/degree (cpd). During a single session, the grating's frequency and luminance was kept constant while contrast was varied following the staircase. Contrast sensitivity was defined as the inverse of the Michelson contrast at threshold performance.

At the lowest light levels used, the barn owls did no longer discriminate the grating orientations correctly. This happened at light level 8 (1.5×10^{-6} cd/m^2) for

two owls and at level 9 (1.82×10^{-7}) for the other owl. While they showed clear behavioral responses at stimulus onset they stopped pressing the buttons consistently, and if they did their discrimination performance was at chance level. Among those responses were re-orientation of the head towards the stimulus, prolonged fixation of the stimulus, intermittent peering head movements, forward inclination of the body, and finally button presses, or attempts thereof.

Results

Each owl performed in about 100 experimental sessions of 30–50 trials. Approximately 65 of these were grating acuity experiments and 35 were contrast sensitivity experiments. Each single experiment was conducted using a two-down, one-up staircase procedure (Figure 1a). The raw data of all sessions at the same stimulus condition were summed. Grating acuity data consisted of about 400 trials for each light level yielding a total of at least 4,000 trials per owl (SL: 6,386, PT: 4,097, YA: 5,592). Contrast data consisted of nearly 200 trials for each of the 12 (3 × 4) light level–acuity combinations resulting in more than 2,000 trials per owl (SL: 2,252, PT: 2,523, YA: 2,996). Frequency of response curves were fitted to the combined data pool to yield a single threshold at each condition (Figure 1b).
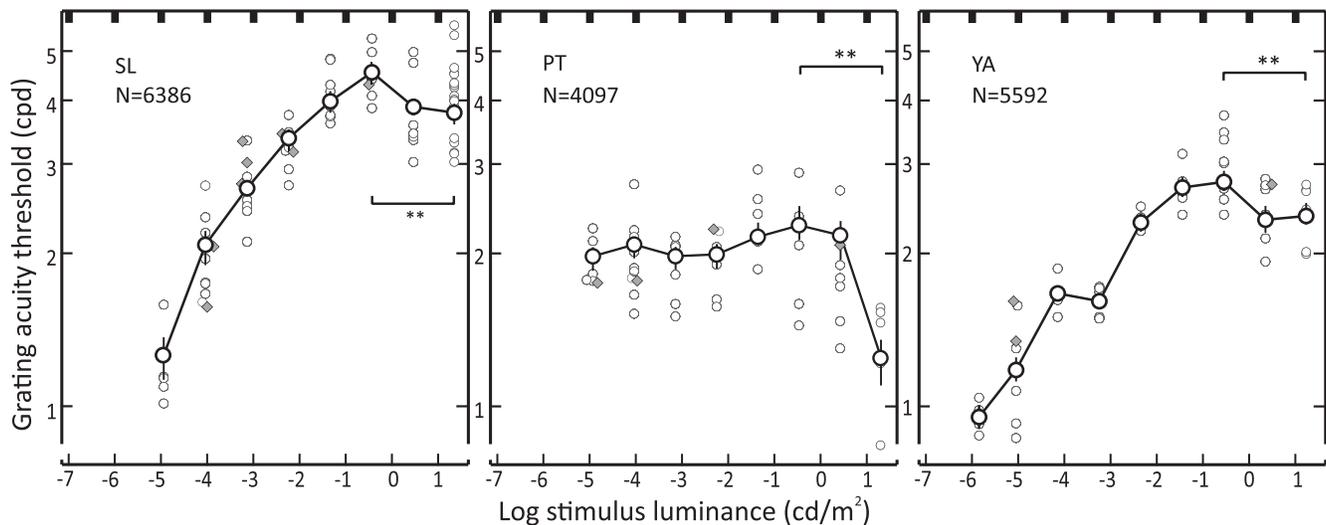
Figure 2. Behavioral grating acuity thresholds as a function of stimulus luminance for three barn owls (subjects SL, PT, and YA). Large circles are thresholds extracted from the frequency of response curves constructed from combined data of individual experimental sessions (smaller circles). Error bars are the 95% confidence intervals (see text). Gray rhombs represent results from control experiments carried out intermittently to exclude possible learning between experiments. Note the significant drop in performance with increasing light levels above 1 cd/m^2 (**$p \leq 0.01$).

Grating acuity

Grating acuity thresholds were determined at eight different luminance levels in two owls, and nine levels in another owl (Figure 2). All owls displayed an acuity peak in mesopic conditions at ~ 0.1 cd/m^2. Maximum acuity was 4.5 cpd for owl SL, 2.8 cpd for YA, and 2.3 cpd for PT, values comparable to those found in an earlier study with the same subjects (Harmening et al., 2009). Acuity declined toward photopic and scotopic conditions, which was most pronounced in subjects SL and YA. In both animals acuity decreased from their peak acuity to their lowest measurable threshold by a factor of approximately 3 (SL: 4.5–1.3 cpd, YA: 2.8–1.0 cpd). Towards photopic luminance levels, acuity decreased only slightly but significantly for all three owls ($p \leq 0.01$). At photopic and mesopic conditions, owl SL constantly outperformed YA by a factor of approximately 1.5. At scotopic conditions this difference decreased. Owl PT's acuity luminance curve looks different from those of the two other birds. Acuity decreased to nearly half the maximal acuity at photopic light levels, but the acuity decrement towards scotopic conditions was small (2.3–2.0 cpd). With the exclusion of light level 1, owl PT's acuity at photopic to mesopic lighting (levels 2–5) was similar to that of owl YA, but PT's acuity was higher at lower light levels. At light level 8 owl PT's acuity was the highest of all three owls. While owl YA displayed the lowest acuity at scotopic light levels (levels 6–9) it was the only owl that responded reliably at the lowest light level tested (1.5 × 10^{-6} cd/m^2). The other owls still reacted to the stimulus onset but did not discriminate the grating

orientations with enough fidelity for proper threshold estimation. Control experiments conducted after the data acquisition for Experiment 1 did not yield significantly different thresholds ($p \geq 0.05$, compare Figure 2).

Contrast sensitivity

Contrast sensitivity was measured at three different light levels for three owls. When contrast sensitivity was plotted against spatial frequency, all functions showed an inverted U-shape (Figure 3). Contrast sensitivity functions (CSFs) of the three barn owls at photopic conditions (3 cd/m^2) were similar to those reported earlier (Harmening et al., 2009). That is, contrast sensitivity of the three owls was highest at 1 cpd and decreased towards higher and lower spatial frequencies. For owl SL the maximum was 18.9, which decreased to 3.4 at 0.3 cpd and 7.0 at 2.0 cpd. Owl PT's CSF was similar in shape, but its individual contrast sensitivity values were only half as large, while YA's CSF was nearly identical to SL's with only a lower peak contrast sensitivity of 13.0. When stimulus luminance was lowered, the CSF maxima shifted toward lower spatial frequencies and maximum sensitivity values decreased. In photopic conditions, the maximum occurred at around 1 cpd and the mean contrast sensitivity across owls was 11.7. The spatial frequency dropped to 0.5 cpd for mesopic and scotopic conditions, respectively. Maximum contrast sensitivity was 8.1 at mesopic and 4.0 at scotopic conditions. Moreover, the overall shape of the CSF changed with lower stimulus luminances.
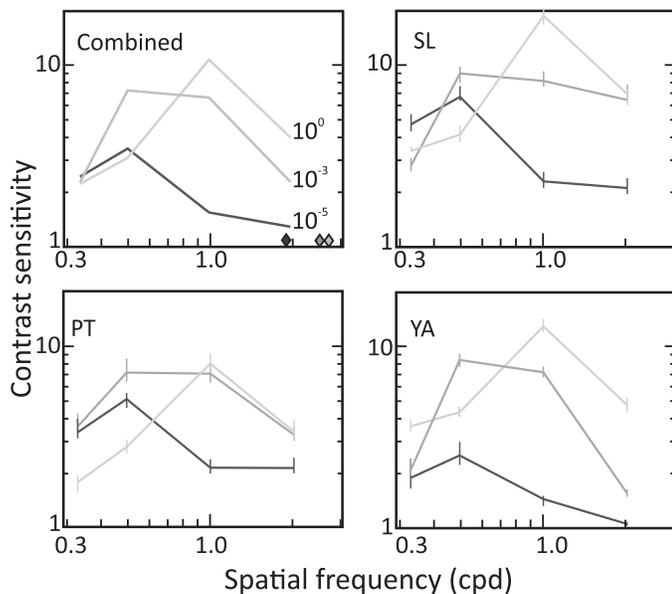
Figure 3. Contrast sensitivity at scotopic (black, 9.32 × 10⁻⁵ cd/m²), mesopic (dark gray, 4.78 × 10⁻³ cd/m²) and photopic (light gray, 3 cd/m²) light levels. Contrast sensitivity is defined as the inverse of the contrast threshold and was plotted as a function of spatial frequency. The top left graph displays the average threshold of three owls. Gray rhombs represent the average grating acuity at the tested light levels. The other graphs show results for each individual owl (SL, PT, and YA) at the three light levels. Error bars are the 95% confidence intervals of these measurements. All functions show an inverted U-shape. With decreasing luminance contrast sensitivity was reduced and the peak sensitivity shifted towards lower spatial frequencies.

Sensitivity to high spatial frequencies decreased when luminance was lowered, but was constant at low spatial frequencies. While this general trend was evident in each owl, there were differences between individuals. Owl SL was always more sensitive than the others, but differences decreased with luminance. SL's maximum contrast sensitivity decreased from photopic to scotopic light levels by a factor of 2.79, PT's by only 1.57, and YA's by 5.15. By comparison, at the tested luminance levels the average grating acuity threshold did decrease only by a factor of 1.45 (photopic: 2.9 cpd, mesopic: 2.6, scotopic 2.0).

Discussion

In a set of behavioral experiments using gratings as stimuli, we determined the visual acuity and contrast sensitivity of three barn owls under photopic to fully scotopic stimulus luminance levels. Given this small set size of tested individuals, care has to be taken not to over assess individual results. Although significant, differences we observed between our individuals are commonly seen in behavioral studies of visual function (Hirsch & Curcio, 1989; Langston, Casagrande, & Fox, 1986; Lind, Sunesson, & Mitkus, 2012; Pasternak & Merigan, 1981).

The owls' average grating acuity threshold decreased only slightly over 5.5 log units from its peak at mesopic light levels to low scotopic conditions. Maximum contrast sensitivity decreased towards scotopic conditions while the U-shaped contrast sensitivity function was shifted leftwards to lower spatial frequencies (Figure 3).

In the following we compare the visual performance of barn owls to other species and discuss their special adaptations for scotopic vision.

Due to their cone dominated foveae, man, eagle (*Aquila audax*), and pigeon (*Columba livia*) surpass barn owls' acuity in bright light by far. However barn owls outperform these species in scotopic conditions (Figure 4; Shlaer, 1937; Pirenne & Denton, 1952; Reymond, 1987; Hodos, Leibowitz, & Bonbright, 1976; Hodos & Leibowitz, 1977). This is also true for the nocturnal great horned owl (*Bubo virginianus*), which has a higher maximal acuity (6 vs. 3.2 cpd), but lower scotopic acuity than barn owls (Fite, 1973). The luminance–acuity curve of barn owls is almost parallel
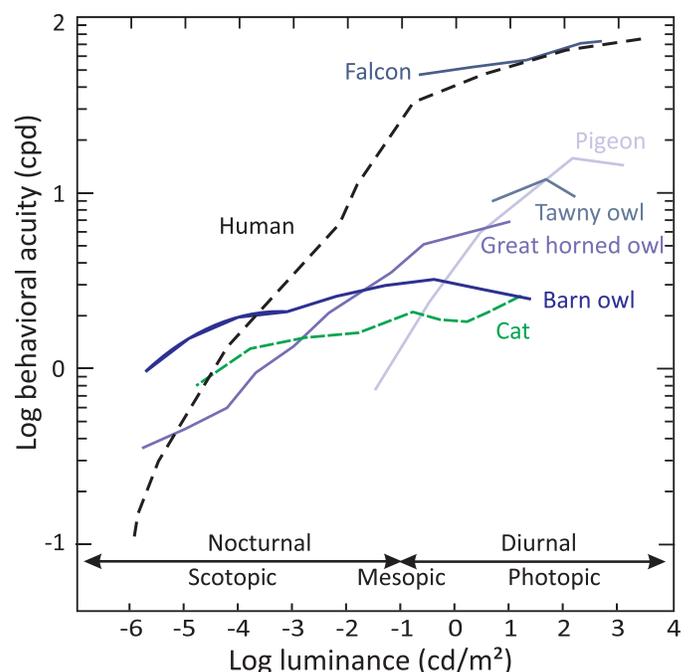

Figure 4. Visual resolution as a function of luminance in several species. Behavioral data for grating acuity are plotted as a function of stimulus luminance on logarithmic axes. Data for other species are taken from: falcon (Reymond, 1987), pigeon (combined photopic and scotopic data, Hodos et al., 1976; Hodos & Leibowitz, 1977), tawny owl (Martin & Gordon, 1974), great horned owl (Fite, 1973), cat (Pasternak & Merigan, 1981), and human (Pirenne, Marriott, & O'Doherty, 1957; Shlaer, 1937).

to that of cats (Pasternak & Merigan, 1981). Both species have quite constant visual acuity across the 7 log unit range of light levels used in this study, although barn owls have higher acuity in mesopic and scotopic light levels.

Data on contrast sensitivity shows the same trend when luminance is lowered as is known from species like man (Meeteren, 1972), macaques (*Macaca* sp., Valois & Morgan, 1974), and cats (Pasternak & Merigan, 1981): Peak contrast sensitivity decreases and shifts towards lower spatial frequencies, although the relative decrease is smaller in barn owls than in the other species. While the attenuation of sensitivity at high frequencies can be attributed to a decrease in resolution, contrast sensitivity is preserved at low frequencies in barn owls. This means, that larger objects have approximately the same contrast to owls at all light levels.

Visual information gain greatly decreases at nocturnal light levels (Warrant, 1999). In birds, several adaptations evolved to cope with the greater tentativeness of visual information at nocturnal light levels. As an extreme, the flightless kiwi (*Apteryx* sp.) has ceased to rely on vision in favor of tactile and olfactory orientation (Martin et al., 2007). A more common adaptation is to increase the sensitivity to light. Oilbirds have small eyes with a very low f-number of 1.07 (Martin, Rojas, Ramirez, & McNeil, 2004), thus increasing retinal image brightness and decreasing retinal image size, resulting in a low absolute threshold at the cost of spatial resolution (Warrant, 1999). However, flying birds require a sufficient resolution to resolve their surroundings. One solution would be to use echolocation to support obstacle avoidance inflight like oilbirds do (*Steatornis caripensis*, Konishi & Knudsen, 1979). However, echolocation in birds is uncommon. Most birds, like barn owls, have no auxiliary sensory means to support flying and rely on visual cues only. Therefore their visual system needs to be not only optimized for sensitivity, but also to preserve enough resolving power over the 6.5 million cd/m^2 range they encounter at night (Martin, 1982).

Eyes optimized for high sensitivity as found in oilbirds, rats, or cats usually have low f-numbers and small axial lengths (Hughes, 1979; Martin et al., 2004; Vakkur, 1963). On the other hand, nocturnal owls in general have eyes that are larger than their body weight would suggest (Howland, Merola, & Basarab, 2004). Barn owls have an f-number of 1.13 and an axial length of 17.48 mm. If only the f-number is taken into account as a measure for sensitivity, barn owls are slightly more sensitive to light than other owls like tawny owls (f-number/axial length 1.3/28.5 mm) or great horned owls (1.42/38.72 mm). The approximately twice higher maximal acuity of other owls fits with the finding that larger focal lengths are correlated with higher spatial

acuity. This seems to reverse in scotopic conditions, under which barn owls have higher acuity (Figure 4).

Martin (2009) argues that overlapping frontal eye fields, and thus binocular vision in owls, is only due to selection for large eyes in a small skull, which also houses large ears. However, binocularity seems to be an important feature in barn owls, which is emphasized by the fact that barn owls are the only bird species known to possess hyperacute stereovision (van der Willigen, 2011; van der Willigen, Frost, & Wagner, 1998). It is reasonable that if hyperacute stereovision is possible, barn owls should be able to correlate the visual input between their eyes to reduce noise. We speculate that one function of binocularity in owls is to prevent a drop in acuity and contrast sensitivity at low light levels.

In conclusion, barn owls have low acuity and contrast sensitivity; they perform poorly at photopic light levels compared with other species and owls. On the other hand, in scotopic conditions this is inverted. Most remarkable is owls' nearly constant visual acuity across the nocturnal light levels. Based on ganglion cell counts their visual resolution could be between 7.9 and 8.4 cpd (Wathey & Pettigrew, 1989), and with their high quality optics, barn owls have a clear retinal image. This is not reflected in their maximal behavioral acuity, which is less than half their possible anatomical maximum. Therefore, visual processing in this bird seems not to be optimized for maximal acuity. We speculate that this visual behavior reflects a tradeoff from maximum acuity not only to increase absolute sensitivity, but to achieve a reliable presentation of a scene at scotopic light levels.

Commercial relationships: None
Corresponding author: Julius Orlowski.
Email: julius@bio2.rwth-aachen.de.
Address: Department of Zoology and Animal Physiology, Rheinisch-Westfaelische Technische Hochschule Aachen University, Aachen, Germany.

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