

Vernier acuity in barn owls

Wolf M. Harmening*, Katrin Göbbels, Hermann Wagner

Department of Zoology and Animal Physiology, RWTH Aachen University, Kopernikusstrasse 16, 52056 Aachen, Germany

Received 23 September 2006; received in revised form 10 January 2007

Abstract

Vernier acuity thresholds were obtained psychophysically in three adult barn owls with vertical bars and sinusoidal gratings. A minimal displacement threshold of 0.58 arcmin was observed with the bar stimulus under binocular viewing conditions. The mean binocular bar threshold was 2.51 arcmin. Bar thresholds were lower than grating thresholds. Monocular thresholds, obtained in one bird only, were typically higher than binocular thresholds. With grating acuity being about 3.75 arcmin in this species, we conclude that the findings reported here indicate that vernier acuity is hyperacute in the barn owl. The data presented here are the first demonstration of vernier acuity thresholds in birds.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Vernier acuity; Hyperacuity; Binocular summation; Crowding; Animal behaviour; Barn owl

1. Introduction

The ability of humans to detect tiny spatial offsets in paired lines, dots, or objects is known as vernier acuity. Psychophysical measures of vernier thresholds yield values down to 1–5 s of arc (Levi & Klein, 1982; Sullivan, Oatley, & Sutherland, 1972; Westheimer & McKee, 1977). Compared to thresholds derived from tasks that are physically limited by foveal cone spacing, such as two-point or grating acuity, vernier acuity thresholds are about 6- to 30-fold lower (Curcio, Sloan, Kalina, & Hendrickson, 1990; Edelman & Weiss, 1995; McKee, 1991). Thus, humans can determine the relative positional difference of spatially non-aligned features with a precision that corresponds to only a fraction of the eye's resolving power. This makes vernier acuity a 'hyperacuity' phenomenon (Westheimer, 1975). So far vernier thresholds have been obtained with humans (Wülfing, 1892), monkeys (Kiorpes, Kiper, & Movshon, 1993), cats (Murphy & Mitchell, 1991) and rats (Seymour & Juraska, 1997), but not in birds.

The barn owl is a highly specialized nocturnal predator with exceptional preying skills. In particular, barn owls are renowned for their superior sound-localization capabilities (Wagner, Brill, Kempter, & Carr, 2005). However, also the visual system in this bird shows anatomical, functional and physiological specializations. The barn owl has frontally oriented eyes with high-quality optics (Schaeffel & Wagner, 1996) that create an unusual large binocular field of view compared to other birds (Martin, 1984). The barn owl has coupled accommodation in both eyes (Schaeffel & Wagner, 1992), and an enlarged visual Wulst with a high degree of binocular interaction and selectivity for binocular disparity (Nieder & Wagner, 2000; Wagner & Frost, 1993; Pettigrew, 1979). It has been shown that owls possess stereopsis and use disparity as a depth cue with hyperacute precision (van der Willigen, Frost, & Wagner, 1998, 2002). Furthermore, barn owls are also able to perceive illusory contours (Nieder & Wagner, 1999). Spatial visual acuity (i.e. minimum separable) in barn owl has been indirectly reported as an anatomical measure of ganglion cell density (Wathey & Pettigrew, 1989) and electrophysically in a Pattern Electro Retino Gram (PERG) study (Ghim & Hodos, 2006). These studies found a theoretical grating acuity of 8.4 and 6.9 cyc/deg, respectively. The question asked here

* Corresponding author. Fax: +49 241 8022133.

E-mail address: wolf@bio2.rwth-aachen.de (W.M. Harmening).

is whether the barn owl displays hyperacuity in a vernier task. This was tested behaviourally with two kinds of stimuli under binocular and monocular viewing conditions.

2. Materials and methods

2.1. Subjects

Experimental animals were three male adult barn owls (*Tyto alba pratincola*, Subjects SL, OL, PT) taken from the institute's breeding stock. Earlier during life a small aluminium stick was fixed to the owls' skull with dental cement under anaesthesia (for details see Nieder & Wagner, 1999). This stick was used to fix a custom made spectacle frame to the owls' head with which one eye could be occluded. Training and experiments took place on 6 days per week. Owls were given food (chick meat) only in the experimental booth via a food dispenser or as a reward directly after the experiment inside the lab. When no experiment took place owls were fed in their aviary. Care and treatment of the owls were in accordance with the guidelines for animal experimentation as approved by the Regierungspräsidium Köln, Germany, and complied to the "NIH Guide for the care and use of laboratory animals".

2.2. Experimental setup and general procedure

The birds were trained extensively with the largest vernier shift which was used in the experiments until they reached significant performance, i.e. 68% correct in the discrimination task. After this training phase, the experimental phase started. All experiments were performed inside a sound-attenuated and darkened booth. Birds were sitting on a perch 85 cm in front of a 17" TFT panel (ran at its native resolution: 1280 × 1024 pixels). Whenever the owl oriented its gaze toward the screen, a trial was initiated and a fixation target was shown in the centre of the screen. The fixation target consisted of a small flashing diamond-shaped bright surface (30 arcmin in square, 2 Hz, 180 cd/m²). After a variable time delay (2–5 s), the fixation target disappeared and the vernier stimulus appeared. The birds had to peck one of two response bars, corresponding to a left or right vernier shift in the stimulus. The response bars were symmetrically placed to the left and right of a remotely operated food dispenser that delivered, only on correct responses, small pieces of chick meat. False responses were neither rewarded nor punished. The time course was self-paced to allow owls an accurate examination of the stimulus. A trial was interrupted whenever the birds made large head movements and stopped fixation of the screen. Head movements and fixation were controlled by observing the gaze and eyes under infrared illumination on a TV monitor. Behavioural performance was controlled and monitored by custom-written software (ANSI-C application using the OpenGL Utility Kit/GLUT) running on a Silicon Graphics workstation that also delivered the visual stimuli.

2.3. Visual stimuli and data acquisition

Two different vernier stimuli were used in the experiments. The first stimulus ('grating') was a vertical sine wave grating presented on dark background (180 cd/m² peak luminance, 0.43 cd/m² minimum luminance, 7 deg in square). Michelson contrast was calculated from the measured values to be 0.995. Spatial frequency was constant and set to a non-critical large value (0.6 cyc/deg). The vernier shift was introduced as a horizontal phase shift of the lower part of the grating relative to its upper part. The second stimulus ('bar') can be regarded as a cut-out of one cycle from the grating stimulus (compare inset in Fig. 3. Note that, for illustrative purposes the stimuli here are drawn as square wave gratings). Grating or bar stimuli and monocular or binocular viewing conditions were applied in a random order.

A typical experiment consisted of about 120 trials of stimulus presentation and owl responses. Since we presented either left or right vernier shifts, owls could response left or right exclusively (2-AFC). Two staircases were recorded in parallel in a randomly interleaved manner. On every

correct response the vernier shift in the stimulus decreased by one step, false responses lead to a shift increment (1-up 1-down). The initial value was set to a 20 pixel vernier shift. Following steps were 17, 14, 12, 10, 9, 8, 7, 6, 5, 4, 3, 2, 1, 0.75, 0.5, 0.25 pixel. At the 0.85 m viewing distance one pixel equalled 1.0526 min of arc. In order to present sub-pixel shifts we used anti-aliasing procedures which come along as built-in functions with the OpenGL Utility Kit.

At least eight reversal points in each staircase pair were taken to calculate the arithmetic mean for each left and right track. After statistical check for equality, reversal points for both tracks were pooled and the threshold was expressed as their overall mean. Thus, single threshold values presented here are the mean values of at least 16 reversal points. In order to present a precise estimation of true absolute thresholds we omitted all staircases from the estimation which were biased according to two bias criteria. First we calculated the binomial distribution for every case and rejected all results in which owls answered significantly unbalanced (1).

$$P(k) = \binom{n}{k} p^k (1-p)^{n-k} \leq 0.05 \quad (1)$$

(With $P(k)$: probability for k left responses, k : number of left responses, p : probability for left stimulus, n : trials). Second we did a statistical comparison between thresholds for left and right stimulus configuration after averaging reversal points. If differences were significant ($p \leq 0.05$) according to the Mann-Whitney U -test we rejected the staircase.

3. Results

3.1. Staircase procedure and response bias

Due to our criteria to account for bias, we first categorized our results into valid, invalid and unusable cases. Out of a total of 98 staircases we used 44 staircases for threshold estimation (valid case, Fig. 1). We defined a valid case as a staircase in which the reversal points for left and right tracks converged to values that were statistically equal (U -test, $p < 0.05$). The other 54 staircases were excluded from the estimation due to a statistical difference for left and right threshold values (27 invalid, compare Fig. 2a) and unbalanced responding (27 unusable, compare Fig. 2b). In total, we could record 10 valid staircases for subject SL, 22 for subject PT, and 12 for subject OL. Due to a strong response bias in subject OL and SL under monocular conditions (i.e. wearing the spectacle frame and occluding one eye), all but one monocular thresholds were obtained in subject PT. The number of trials needed to reach the first reversal point below threshold value in each staircase was counted. On average owl PT needed 58.9 trials to reach threshold level, owl OL needed 60.7 trials, and owl SL needed 45.8 trials, which is significantly earlier than the two others (U -test, $p < 0.01$). No significant difference between conditions in single subjects was observed. Table 1 gives a detailed view on numbers of valid, invalid and unusable staircases for each subject, stimulus configuration and viewing condition. This table demonstrates that all three owls were reliable in binocular tests, with the least number of unusable cases occurring for binocular bar stimuli. Monocular tests were impossible in owl SL and resulted in many unusable cases in owl OL.

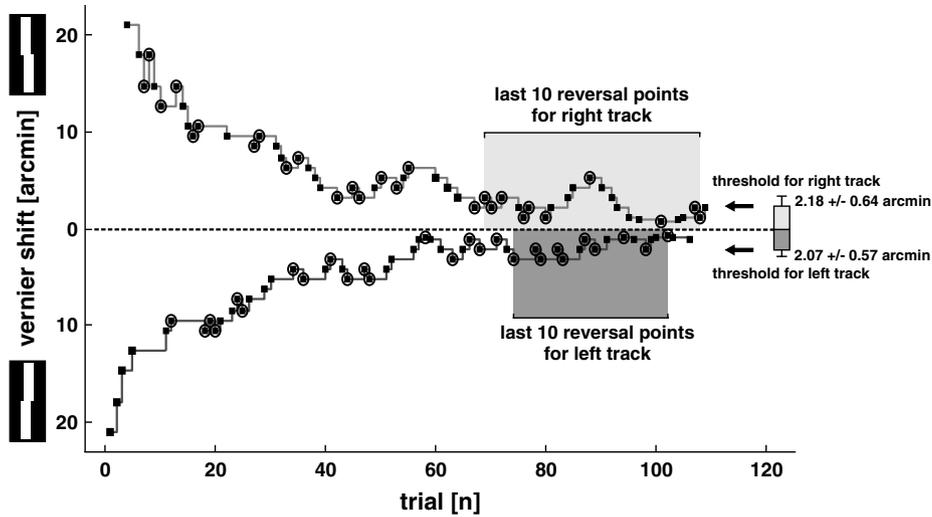


Fig. 1. Staircase procedure. Exemplary result for subject PT under binocular viewing conditions with bar stimulus. Two randomly interleaved staircases were presented at the same time. Ordinate values indicate trial number, abscissa indicates vernier shift in minutes of arc for right and left shifts, respectively. Squares are trials, circles mark reversal points in the staircase. For illustrative purposes trials are connected by a grey line. In this case, the last 10 reversal points were averaged for threshold estimation. Dotted line corresponds to zero shift. Black arrows together with bar plot mark calculated thresholds for left and right track. Error bars are standard deviations.

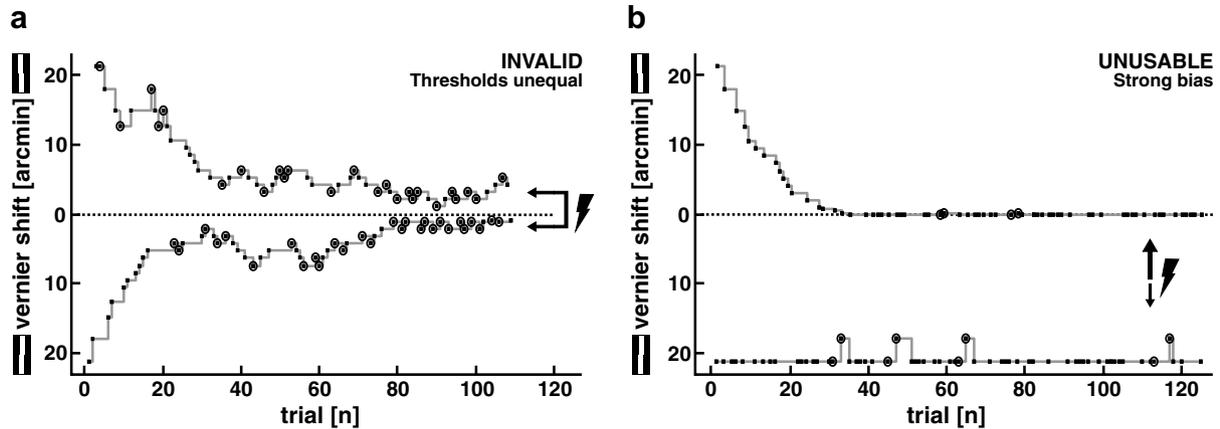


Fig. 2. Biased response behaviour. (a) Exemplary staircase result of owl PT under monocular viewing conditions with the bar stimulus. After averaging the last 10 reversal points, thresholds for left and right track are unequal according to the *U*-test. (b) Exemplary result of a strong bias in subject OL (monocular, grating), preferring RIGHT over LEFT responses, regardless of the presented stimulus. OL pushed in almost 80% of the cases the right response key. These staircase curves were excluded from the threshold estimation. See Section 2.3 part for further explanation of exclusion criteria.

Table 1
Staircase experiments for all owl subjects and all conditions

Owl subject	Number of thresholds		
	SL	PT	OL
Bar binocular	8 (4/4/—)	6 (4/2/—)	7 (6/1/—)
Grating binocular	15 (6/4/5)	9 (4/5/—)	13 (5/4/4)
Bar monocular	—(—/—/—)	12 (7/4/1)	9 (—/1/8)
Grating monocular	—(—/—/—)	9 (7/2/—)	10 (1/—/9)
Total	23 (10/8/5)	36 (22/13/1)	39 (12/6/21)

Bold numbers are total number of experiments for each condition. Numbers in brackets are valid/invalid/unusable cases.

3.2. Vernier thresholds

We could estimate vernier thresholds for all animals and conditions. However, monocular thresholds were mainly based on data from one animal. The thresholds differed from animal to animal, and they differed in the four test conditions. Owl SL had significantly lower minimal and mean thresholds, compared to the other owls (*U*-test, $p < 0.05$). Owl OL had the highest thresholds, except for minimal binocular grating threshold. The lowest absolute threshold value ($0.58 \text{ arcmin} \pm 0.23 \text{ SD}$) was found in sub-

ject SL under binocular viewing conditions with the bar stimulus. The highest threshold (7.07 ± 1.27 arcmin) was derived from measures with subject OL under binocular viewing conditions with the grating stimulus. Except for owl OL, minimal and mean thresholds for the bar stimulus measured under binocular viewing conditions yielded lowest values across all animals (see Table 2). Highest thresholds were found for the bar stimulus under monocular viewing conditions in owl OL. Except for owl OL, all thresholds measured with the bar stimulus yielded lower minimal and mean thresholds than those measured with the grating stimulus. Threshold scatter between animals differed. While subjects SL and PT had a mean standard deviation of about 0.6 arcmin across all thresholds, subject OL's standard deviation was about 3-fold higher (mean SD: 1.70 arcmin, compare Fig. 3).

3.3. Bar versus grating stimuli

Results from all subjects were used to compare the influence of stimulus configuration on performance. A total of $n = 21$ thresholds were derived with the bar stimulus under test and $n = 23$ with the grating stimulus (both binocular and monocular). In two out of three subjects (PT and SL) a significant difference between the two stimulus configurations was observed (see Fig. 4). In subject PT mean threshold for bar stimulus was 2.46 arcmin ($SEM = 0.26$) while grating thresholds averaged to 3.47 arcmin ($SEM = 0.25$). *U*-test was significant ($p < 0.025$). Even more significant was the difference found in owl SL ($p < 0.01$). Here, mean bar threshold was 1.21 arcmin ($SEM = 0.24$) and grating threshold was 2.77 arcmin ($SEM = 0.36$). Thresholds for bar and grating stimuli in subject OL were on average almost identical (3.98 arcmin for bar and 3.67 arcmin for grating). Thresholds of owl OL were the highest in an absolute sense and showed the highest standard deviations ($SD_{Bar} = 1.47$ arcmin, $SD_{Grating} = 1.94$ arcmin) as well.

3.4. Monocular versus binocular viewing conditions

For this comparison data from subject PT were used. In total $n = 8$ staircases were recorded under binocular conditions and $n = 14$ under monocular conditions (both with bar and grating stimuli). We recorded monocular thresholds with right ($n = 7$) and left eye ($n = 7$) occluded, respec-

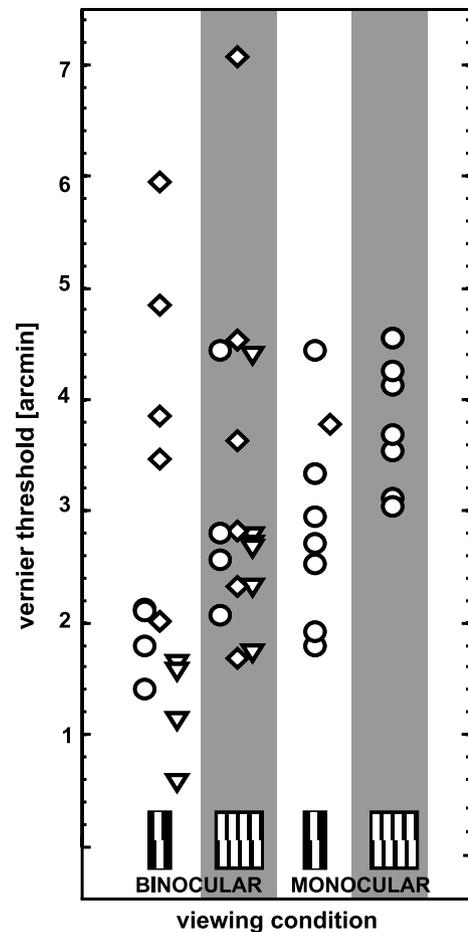


Fig. 3. Summary of threshold values for all subjects and conditions. Marker differences indicate the three owl subjects (circle: PT, diamond: OL, triangle: SL). Insets at the bottom show stimulus configuration (grating versus bar). Thresholds for subject OL show the largest scatter. The lowest thresholds are clearly lower than the anatomical resolution.

tively. Thresholds for the two eyes were not significantly different (*U*-test, $p > 0.2$). Therefore, the data were pooled. The arithmetic mean of binocular bar measurements yielded 1.86 arcmin ($SEM = 0.09$), while monocular bar thresholds averaged to 2.81 arcmin ($SEM = 0.18$). The 1.86 arcmin were used as a normalization factor, and, thus, monocular thresholds were about 1.5 times higher than the binocular thresholds (Fig. 5). The *U*-test did reveal a significant difference between the two conditions ($p < 0.001$). The arithmetic mean of binocular grating measurements yielded 2.97 arcmin ($SEM = 0.17$), while monocular grating thresholds averaged to 3.76 arcmin ($SEM = 0.07$). Normalization demonstrated that monocular thresholds were about 1.3 times higher than the binocular thresholds. Again, the *U*-test showed a significant difference ($p < 0.005$).

4. Discussion

By using the simple one-up one-down staircase method, we demonstrated that barn owls can discriminate vernier

Table 2
Minimal and mean vernier thresholds for all subjects and conditions

Owl subject	Vernier thresholds (arcmin)					
	SL		PT		OL	
	Min	Mean	Min	Mean	Min	Mean
Bar binocular	0.58	1.21	1.41	1.86	2.02	4.02
Grating binocular	1.73	2.77	2.08	2.97	1.69	3.67
Bar monocular	—	—	1.80	2.81	3.78	3.78
Grating monocular	—	—	3.04	3.75	—	—

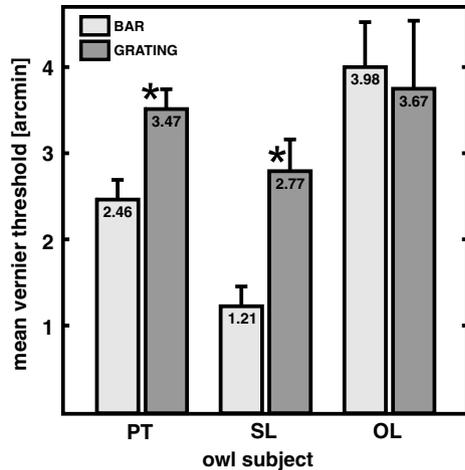


Fig. 4. Comparing the effect of stimulus configuration in subjects. According to the *U*-test, grating vernier acuity yielded significant higher thresholds than bar vernier acuity in subjects PT ($n = 22$, $p < 0.025$) and SL ($n = 11$, $p < 0.01$). For subject OL no differences were found. Note that subject OL not only had the highest mean thresholds for both stimulus configurations, but also highest standard deviations. Numbers are arithmetical means of thresholds, error bars are standard error of means (*SEM*), and asterisks denote significantly different means.

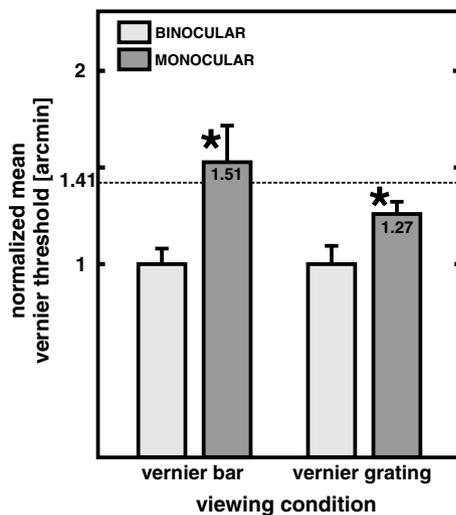


Fig. 5. Comparing monocular and binocular viewing conditions in owl PT. Bar heights are the mean threshold for each condition. Threshold values were normalized to the mean binocular thresholds for each bar and grating stimulus. A normalized threshold of 1 indicates no disadvantage compared to the binocular condition. Thus, a normalized threshold of 1.5 indicates that monocular thresholds were on average 1.5 times worse than binocular thresholds. Asterisks denote that the differences measured either with bar and grating stimulus were significant (*U*-test, $p < 0.005$). The dotted line represents a $\sqrt{2}$ degrading factor. Error bars are *SEM*.

offsets in computer generated visual stimuli. It is discussed whether this finding is evidence that in this bird, as in the human visual system, vernier acuity is a hyperacuity phenomenon. Furthermore, our results showed that discrimination performance in the vernier task is affected by two conditions, i.e. binocular versus monocular viewing conditions and bar versus grating stimulus configuration.

4.1. Method

Reproducibility of threshold values indicates that the staircase method is a feasible tool for testing barn owls on difficult visual tasks. Earlier attempts were conducted using the method of constant stimuli and calculating the complete psychometrical function. Since data points in such functions consisted of records made on several days, this method suffered from reproducibility (compare De Weerd, Vandebussche, & Orban, 1990). On the other hand, staircase experiments yielded valid results in about 45% of the cases.

4.2. Is vernier acuity a hyperacuity phenomenon in the barn owl?

The data presented here are the first behavioural report of vernier acuity thresholds in an avian visual system. We showed that barn owls can discriminate tiny spatial offsets in vertical bars and gratings. In order to benchmark this finding our thresholds needed to be compared with conventional spatial visual acuity thresholds. Spatial visual acuity, i.e. two-point acuity or grating acuity, has been determined in the barn owl only indirectly in an anatomical study (Wathey & Pettigrew, 1989) and by PERG (Ghim & Hodos, 2006). The results estimate spatial visual acuity to be 8.4 and 6.8 cyc/deg, respectively. In our results lowest values for vernier acuity were on the order of 0.6 arcmin. In our stimulus situation, using bars as a stimulus, an argument put forward by Harris and Fahle (1995) might hold, and, thus, the measured values have to be doubled to obtain the true vernier thresholds. Thus, we arrive at 1.2 arcmin. If half of a cycle in a grating is regarded as the separable visual entity, 1.2 arcmin equals 25 cyc/deg. This is a 3-fold better threshold value than the grating acuities reported (Wathey & Pettigrew, 1989; Ghim & Hodos, 2006). $7/44 = 16\%$ of the threshold values were in the hyperacute range, even after the above mentioned correction. This was observed in each of the three animals. Therefore, we conclude that barn owls can determine the relative positional difference of spatially non-aligned features with a precision that corresponds to only a fraction of their eye's resolving power. Following terminology in human visual research, vernier acuity is a hyperacuity phenomenon in barn owls.

4.3. Influence of stimulus configuration and viewing conditions

In two out of three animals bar thresholds were significantly lower than thresholds measured with the grating stimulus. The reason why this effect was not observed in the third owl is unclear. Earlier studies of human vernier acuity reported that a competing stimulus placed adjacent to a vernier offset results in a reduction of vernier thresholds (Westheimer & Hauske, 1975). In the context of vernier acuity this effect may be produced by either lines that

flank a single line vernier stimulus, or by increasing the number of periods of a vernier-grating stimulus (Barrett, Whitaker, & Bradley, 1999; Levi, Klein, & Aitsebaomo, 1985), a situation comparable to our grating stimulus. This interference of spatially adjacent stimuli in the human visual system is often referred to as crowding, or masking effect (Pelli, Palomares, & Majaj, 2004). Its presence in the barn owl visual system could indicate that common mechanisms may underlie vernier acuity in these two species.

Furthermore, the results presented here showed that binocular vernier acuity outperformed monocular vernier acuity by some 30–50%, depending on the stimulus configuration (grating versus bar). An improvement in performance by $\sqrt{2}$ (41%) would indicate that binocular summation plays a role, which is due to the doubling of receptors (i.e. eyes) solving the task (Campbell & Green, 1965). Earlier studies with human subjects reported that vernier discrimination is better with two eyes than with one, showing summation ratios around 40–60% (Banton & Levi, 1991; Frisen & Lindblom, 1988; Lindblom & Westheimer, 1989). This binocular advantage is similar to that found for contrast-detection thresholds in humans, and the amount of summation is dependent on the stimulus contrast. Therefore, a direct comparison of the here found summation ratios and the human summation ratios will be accomplished satisfyingly only if data of the contrast sensitivity function in the barn owl are available.

Our finding that vernier thresholds are hyperacute in the barn owl together with the presence of a crowding/masking effect and binocular summation lead to the speculation that the neural mechanisms underlying vernier acuity share common features in man and bird.

5. Conclusions

The current data show that barn owls can discriminate vernier stimuli below 1 arcmin displacement angle. Based on grating acuity estimation our findings indicate that vernier acuity is a hyperacute percept in this species. The lowest threshold (0.58 arcmin) is 3-fold lower (better) than the assumed grating acuity. Statistical analysis of different viewing conditions indicates that binocular viewing outperforms monocular viewing by some 30–50%. Thus binocular summation seems to play a role in vernier discrimination by owls. Performance is similarly affected as in humans by the choice of stimulus configuration. Bar stimuli yielded lower values than grating stimuli, an effect referred to as crowding in human subjects.

References

Banton, T., & Levi, D. M. (1991). Binocular summation in vernier acuity. *Journal of the Optical Society of America A*, 8, 673–680.

Barrett, B. T., Whitaker, D., & Bradley, A. (1999). Vernier acuity with compound gratings: the whole is equal to the better of its parts. *Vision Research*, 39, 3681–3691.

Campbell, F. W., & Green, D. G. (1965). Monocular versus binocular visual acuity. *Nature*, 208, 191–192.

Curcio, C. A., Sloan, K. R., Kalina, R. E., & Hendrickson, A. E. (1990). Human photoreceptor topography. *Journal of Comparative Neurology*, 292, 497–523.

De Weerd, P., Vandenbussche, E., & Orban, G. A. (1990). Staircase procedure and constant stimuli method in cat psychophysics. *Behavioural Brain Research*, 40, 201–214.

Edelman, S., & Weiss, Y. (1995). Vision, hyperacuity. In M. Arbib (Ed.), *The handbook of brain theory and neural networks* (pp. 1009–1012). Cambridge, MA: MIT Press.

Frisen, L., & Lindblom, B. (1988). Binocular summation in humans: evidence for a hierarchical model. *The Journal of Physiology*, 402, 773–782.

Ghim, M. M., & Hodos, W. (2006). Spatial sensitivity of birds. *Journal of Comparative Physiology A*, 192, 523–534.

Harris, J. P., & Fahle, M. (1995). The detection and discrimination of spatial offsets. *Vision Research*, 35, 51–58.

Kiorpes, L., Kiper, D. C., & Movshon, J. A. (1993). Contrast sensitivity and vernier acuity in amblyopic monkeys. *Vision Research*, 33, 2301–2311.

Levi, D. M., & Klein, S. (1982). Differences in vernier discrimination for grating between strabismic and anisometropic amblyopes. *Investigative Ophthalmology & Visual Science*, 23, 398–407.

Levi, D. M., Klein, S. A., & Aitsebaomo, A. P. (1985). Vernier acuity, crowding and cortical magnification. *Vision Research*, 25, 963–977.

Lindblom, B., & Westheimer, G. (1989). Binocular summation of hyperacuity tasks. *Journal of the Optical Society of America A*, 6, 585–589.

Martin, G. R. (1984). The visual fields of the tawny owl, *Strix aluco* L. *Vision Research*, 24, 1739–1751.

McKee, S. P. (1991). The physical constraints on visual hyperacuity. In J. Cronly-Dillon (Ed.), *Vision and visual dysfunction* (Vol. 5, pp. 221–233). London: Macmillan Press.

Murphy, K. M., & Mitchell, D. E. (1991). Vernier acuity of normal and visually deprived cats. *Vision Research*, 31, 253–266.

Nieder, A., & Wagner, H. (1999). Perception and neuronal coding of subjective contours in the owl. *Nature Neuroscience*, 2, 660–663.

Nieder, A., & Wagner, H. (2000). Horizontal-disparity tuning of neurons in the visual forebrain of the behaving barn owl. *Journal of Neurophysiology*, 83, 2967–2979.

Pelli, D. G., Palomares, M., & Majaj, N. J. (2004). Crowding is unlike ordinary masking: distinguishing feature integration from detection. *Journal of Vision*, 4, 1136–1169.

Pettigrew, J. D. (1979). Binocular visual processing in the owl's telencephalon. In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 204, 435–454.

Schaeffel, F., & Wagner, H. (1992). Barn owls have symmetrical accommodation in both eyes, but independent pupillary responses to light. *Vision Research*, 32(6), 1149–1155.

Schaeffel, F., & Wagner, H. (1996). Emmetropization and optical development of the eye of the barn owl (*Tyto alba*). *Journal of Comparative Physiology A*, 178, 491–498.

Seymour, P., & Juraska, J. M. (1997). Vernier and grating acuity in adult hooded rats: the influence of sex. *Behavioural Neuroscience*, 111, 792–800.

Sullivan, G. D., Oatley, K., & Sutherland, N. S. (1972). Vernier acuity as affected by target length and separation. *Perception & Psychophysics*, 12, 438–444.

van der Willigen, R. F., Frost, B. J., & Wagner, H. (1998). Stereoscopic depth perception in the owl. *Neuroreport*, 9, 1233–1237.

van der Willigen, R. F., Frost, B. J., & Wagner, H. (2002). Depth generalization from stereo to motion parallax in the owl. *Journal of Comparative Physiology A*, 187, 997–1007.

Wagner, H., Brill, S., Kempter, R., & Carr, C. E. (2005). Microsecond precision of phase delay in the auditory system of the barn owl. *Journal of Neurophysiology*, 94, 1655–1658.

- Wagner, H., & Frost, B. (1993). Disparity-sensitive cells in the owl have a characteristic disparity. *Nature*, *364*, 796–798.
- Wathey, J. C., & Pettigrew, J. D. (1989). Quantitative analysis of the retinal ganglion cell layer and optic nerve of the barn owl *Tyto alba*. *Brain, Behavior and Evolution*, *33*, 279–292.
- Westheimer, G. (1975). Visual acuity and hyperacuity. *Investigative Ophthalmology & Visual Science*, *14*, 570–572.
- Westheimer, G., & Hauske, G. (1975). Temporal and spatial interference with vernier acuity. *Vision Research*, *15*, 1137–1141.
- Westheimer, G., & McKee, S. P. (1977). Spatial configuration for visual hyperacuity. *Vision Research*, *17*, 941–947.
- Wülfing, E. A. (1892). Über den kleinsten Gesichtswinkel. *Zeitschrift für Biologie*, *29*, 199–202.