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Vernier acuity in barn owls

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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.

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 (Seymoure & 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 illusionary 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

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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/m^2). 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/m^2 peak luminance, 0.43 cd/m^2 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).

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

(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 ($p \leqslant 0.05$) 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.