REVIEW

From optics to attention: visual perception in barn owls

Wolf M. Harmening · Hermann Wagner

Abstract Barn owls are nocturnal predators which have evolved specific sensory and morphological adaptations to a life in dim light. Here, some of the most fundamental properties of spatial vision in barn owls are reviewed. The eye with its tubular shape is rigidly integrated in the skull so that eye movements are very much restricted. The eyes are oriented frontally, allowing for a large binocular overlap. Accommodation, but not pupil dilation, is coupled between the two eyes. The retina is rod dominated and lacks a visible fovea. Retinal ganglion cells form a marked region of highest density that extends to a horizontally oriented visual streak. Behavioural visual acuity and contrast sensitivity are poor, although the optical quality of the ocular media is excellent. A low *f*-number allows high image quality at low light levels. Vernier acuity was found to be a hyperacute percept. Owls have global stereopsis with hyperacute stereo acuity thresholds. Neurons of the visual Wulst are sensitive to binocular disparities. Orientation based saliency was demonstrated in a visual-search experiment, and higher cognitive abilities were shown when the owl's were able to use illusory contours for object discrimination.

Keywords Stereopsis · Hyperacuity · Gaze control · Grating acuity · Contrast sensitivity

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Introduction

Evolution has shaped sensory systems to the ecological needs of an animal, and comparative physiology is the discipline to investigate the resulting specializations. The studies of evolutionary specialists have played a pivotal role in the understanding of neuroethology, both at the behavioral and neural level (Siemers and Schnitzler 2004; Jones and Holderied 2007; Kawasaki 2009; Borst et al. 2010). Moreover, neuroethologically well characterized systems often serve as role models for biomimetic applications, such as photomechanical sensors based on the IR receptors of pyrophilous beetles, insect brain based control architectures, an analogue parallel vision system inspired by the visual system of the house fly, or snake-inspired robot designs (Bleckmann et al. 2004; Wessnitzer and Webb 2006; Davis et al. 2008; Hopkins et al. 2009).

The barn owl is a specialist for hunting. It can bring prey every 10 min to the nesting box to feed its hungry babies. Observations at the institute's breeding stock in Aachen showed that the clutch may have up to seven babies, each of which needs five mice per day during the phase of rapid growth. Thus, a barn owl may need to catch up to 35 mice a night, equalling 6 h of hunting without intermission if it succeeds every 10 min. The hunting area has a size of several square kilometres. The owl has to leave the nesting box, forage, attack, catch a prey and return to the nest. The tight temporal sequence necessitates that the birds do not make many failures during hunting.

The barn owls' exquisite hunting system requires many adaptations, and indeed such adaptations have been described. Most conspicuous is the facial ruff, consisting of auricular and reflector feathers (Koch and Wagner 2002; von Campenhausen and Wagner 2006) that reflects the specializations of this animal for the processing of sounds

Fig. 1 A photograph of the barn owl's head. The conspicuous feather-ruff is comprised of specialized feathers that filter and direct sounds to their ears, which are hidden at the ruff's edges, and placed asymmetrically above the eye-level. The forward orientation of both eyes engages barn owls in three-dimensional vision

(Fig. 1). Indeed, the barn owl is well known for its exquisite sound-localization capabilities (Payne 1971; Konishi 2006; Takahashi 2010) and low hearing threshold (Konishi 1973; Wagner 1993; Dyson et al. 1998). In order to hear faint sounds, the owl should not make much noise during flight, and therefore, feather and wing structures show adaptations for silent flight (Bachmann et al. 2007; Bachmann and Wagner 2011). Almost equally conspicuous as the ruff are the frontally oriented eyes, indicating also a specialization of the visual system. These visual specializations will be reviewed in the following in some detail. For brevity, we omit the literature on audio-visual neural plasticity, because this has been reviewed elsewhere (Knudsen 2002).

The eye

Morphology

With only a few exceptions, birds are highly visual animals. The avian eye globe, in relation to the size of the skull, is generally large, advantageous to allow a larger image to be projected onto the retina, and thus to potentially contribute to visual acuity (Güntürkün 2000). The eyes of barn owls, with an axial length of about 17.5 mm, are large (Schaeffel and Wagner 1996), almost twice as long as allometry based on body weight would suggest (Howland et al. 2004). The overall shape of the barn owl eye is tubular (Fig. 2a), with a concave elongated intermediate segment, forming a tube before joining the posterior segment at a sharp angle (King and McLelland 1984;

Kern 1991). This special eye design is believed to improve visual acuity at low light levels due to the larger retinal image with a constrained focal length (Martin 1982). The ratio between focal length and maximal entrance pupil diameter, the f-number, is 1.3 in barn owls (Schaeffel and Wagner 1996). A low f-number ultimately results in a bright retinal image, a feat generally considered to reflect an adaptation to a nocturnal lifestyle (Warrant 1999).

As a result of the large size of the globe and its fit within the orbit, any torsional movement of the globe is strongly limited, although all six extra-ocular eye muscles are present (Williams 1994). Eye movements in the barn owl were reported to be limited to about 2° (Steinbach and Money 1973; Dulac and Knudsen 1990). The functional significance of these small movements is yet unclear. For example, whether or not the owls can perform vergence eye movements poses interesting implications for their binocular vision (see "Stereovision"). However, due to a long and flexible neck, barn owls can turn their head quickly up to 270°. This high flexibility is thought to compensate for the limitations set by their eyes' immobility (Knudsen and Konishi 1979; Knudsen and Knudsen 1985; Dulac and Knudsen 1990; Masino and Knudsen 1993). Contrasting typical eye movements, their head rotations are not pure rotations, but are always accompanied by a translatory component, probably due to structural and biomechanical constraints (Ohayon et al. 2006).

Optical quality

The optical quality of the eye was assessed by measuring the ocular wavefront aberrations with state-of-the-art aberrometry (Harmening et al. 2007b). Wavefront aberrations are a product of the spatial irregularities of curvature of the refractive surfaces, in particular those of the cornea and the crystalline lens (Liang and Williams 1997). Because the ocular aberrations can affect retinal-image quality to large degrees, their impact takes a central position in the complex process of visual perception (Westheimer 2009). Measured under natural viewing conditions in eight eyes of four barn owls, the total RMS wavefront error was between 0.06 and 0.15 μm (mean: 0.10 μm) for a 6 mm pupil and with cancelled defocus (Harmening et al. 2007b). Astigmatism was low in all eyes, ranging from 0.014 and 0.065 D (mean: 0.03 D), being about 3–10 times lower than in emmetropic human eyes (McKendrick and Brennan 1996). These results together with the earlier observation that adult barn owl eyes are generally emmetropic (Schaeffel and Wagner 1996) suggest that image quality in barn owl eye is excellent. In fact, the higher-order aberrations reported for the barn owl are lower than those reported in the eyes of other animals (Thibos et al. 2002; Ramamirtham et al. 2003, 2006; de la Cera et al. 2006).

Fig. 2 Anatomy of the owl's eye and retina. **a** A frozen section of the barn owl's eye, showing its tubular shape and the large crystalline lens. *Numbers* represent distance measures along the *horizontal line* in millimetres (modified after Schaeffel and Wagner 1996). **b** Flat mount retina with iso-density contour lines of retinal ganglion cell counts, given in thousands per square millimetre. The black vertical structure is the protrusion of the pecten (modified after Wathey and Pettigrew 1989). **c** Retinal cross section at foveal region, marked with *asterisk*. Note that most of the owl's retina is comprised of rods (modified after Oehme 1961). **d** Sketch of optical and visual axes superimposed on a photograph of the barn owl's skull and scleral ossicles. The optical axes diverge by about 62°, while the visual axes are almost parallel. *Arrows mark* area of highest ganglion cell density derived from **b**
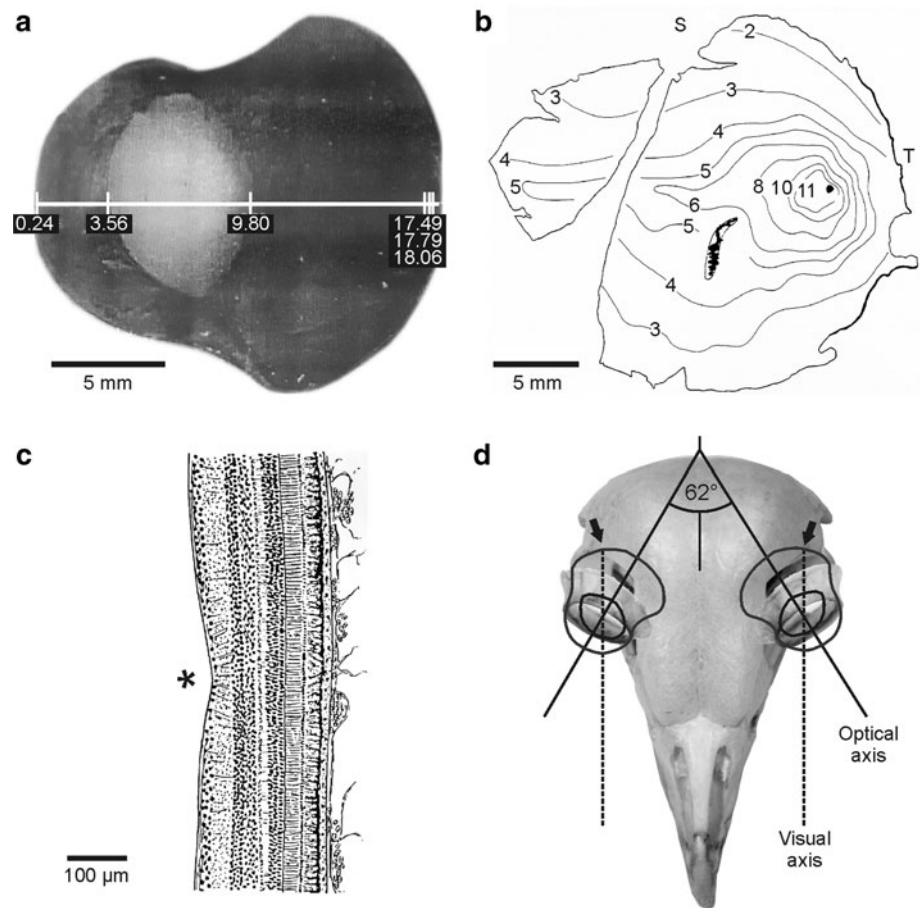
The higher-order aberrations of human eyes are on average about three times higher than those of the barn owl (He et al. 2000). The relative and absolute magnitude of aberrations of the owl eye compare well to those found in the cat eye, when measured at the same pupil size with similar techniques (Huxlin et al. 2004).

Accommodation

As outlined above, barn owls have the typical lens-eye found in all vertebrates, with a transparent, avascular crystalline lens that, together with the cornea, serves to refract incoming light, and to focus it on the retina to create a sharp image. In order to keep the retinal image focused at different viewing distances, the refractive power of the lens and also the cornea can change, a process called accommodation. In contrast to mammals, the avian lens has an annular pad around its central core, which might serve as a hydrostatic mechanism for transmitting pressure from the ciliary muscle to the central core to facilitate accommodation (Evans and Martin 1993; Samuelson 1991). Compared to other owls, the accommodative range in barn owls is large, amounting to about 6–12 D (Murphy and Howland 1983; Schaeffel and Wagner 1992). Barn owls have been shown to use

accommodation as a distance cue for short distances (Wagner and Schaeffel 1991). They are not able to accommodate independently in both eyes and thus have coupled accommodation, which might indicate that binocular vision is of elevated importance for these animals (see also "Stereovision"). On the other hand, pupillary responses to light are independent in the two eyes (Schaeffel and Wagner 1992).

Retina

The retina of birds is comprised of the typical cell-layers found in other vertebrates. However, there are differences regarding vascularization, morphology, and areas of higher visual acuity. First, the vascularization of the retina of birds is reduced, and it receives nourishment by the pecten oculi. The pecten extends from the optic nerve into the vitreous chamber (Fig. 2b), and by saccadic oscillations of the pecten during eye and head movements nourishment is performed via diffusion through the vitreous body (Pettigrew et al. 1990). The pecten also provides an oxygen gradient to the retina, subserves acid-base balance, and maintains a constant intraocular temperature (Jones et al. 2007). Second, the bird retinae contain, as in humans, cones and rods. While the retinae of diurnal birds are

dominated by a special double-cone cell type (Meyer 1977), nocturnal owls like the barn owl have rod-dominated retinae, with a mean rod:cone ratio in the barn owl of about 30:3 (Oehme 1961). Third, many birds have specialized regions within the retina capable of producing visual acuity greater than outside those regions (termed visual streak or area centralis), achieved by a larger density of photoreceptors and ganglion cells. In primates and some birds, these areas display a typical physical depression, named fovea. Most raptorial birds are bifoveate, having a fovea located in the temporal retina in addition to the more common centrally located fovea (Jones et al. 2007). Owls have only temporal foveae, and, uniquely to them, those foveae contain primarily rods (Fite 1973; Fite and Rosenfield-Wessels 1975). In the barn owl retina, only a scarcely distinct temporal fovea is present (Fig. 2c). The position of the barn owl fovea coincides with a retinal area of elevated ganglion cell density (Fig. 2b), and determines the visual axes of both eyes to be almost parallel (Fig. 2d). In addition, a visual streak with higher ganglion cell density, proceeding from the temporal area centralis to nasal regions could be identified (Wathey and Pettigrew 1989).

Spatial vision

Absolute sensitivity

Absolute visual sensitivity refers to the smallest amount of light that just elicits visual perception, and serves as a good indicator for the kind of lifestyle a visual system is exposed to. Dice (1945) was the first to study absolute sensitivity thresholds in barn owls. He determined the weakest illumination in which the birds were able to find dead mice in laboratory conditions. He found that barn owls were able to see and to approach dead prey directly from a distance of 2 m or more under an illumination calculated to be as low as 7×10^{-8} lux. In a more recent psychophysical study, using sinusoidal gratings as stimuli, visual resolution under dark adaptation was measured (Orlowski 2009). In these experiments, barn owls had to discriminate vertical and horizontal oriented gratings at different display luminances, ranging from photopic to full scotopic light levels (23 cd/m^2 to 2×10^{-7} cd/m^2). The grating acuity threshold was determined for all conditions. The decrease in acuity at low luminances was remarkably small in comparison to the great horned owl (Fite 1973) or the cat (Pasternak and Merigan 1981). Over a span of nearly 5.5 log units (mesopic to low scotopic conditions) barn owls retain approximately a quarter of their maximal visual acuity, a paramount performance that might be facilitated by the excellent optics of the owls' eye which raise the modulation transfer across the whole spatial frequency

spectrum (Harmening et al. 2007b). The absolute visual sensitivity threshold was estimated from video footage recorded during trials with the lowest display luminances (Orlowski 2009). Although the owls' discrimination performance failed under those conditions, a clear change of behavior could be observed with the onset of each trial. Absolute sensitivity was estimated to be 6.4×10^{-7} cd/m^2. The barn owl's absolute sensitivity threshold is outperformed by the cat (1.6×10^{-7} cd/m^2, Gunter 1951). It is about equal within a half log unit to other nocturnal animals, for instance the tawny owl (2.8×10^{-7} cd/m^2, Martin 1977) or the rat (7.9×10^{-7} cd/m^2, Naarendorp et al. 2001), and even to humans (7.6×10^{-7} cd/m^2, Pirenne et al. 1957). It may be interesting to note that the differences in sensitivity values do not strictly adhere to the corresponding minimal f-numbers of the species' eyes (cat: 0.92, owl: 1.3, rat: 0.83, human: 2.13, Martin 1982), possibly because sensitivity is limited by neural signal-to-noise ratios, rather than purely optically.

Contrast sensitivity

One key feature that makes objects visually distinguishable is the amount of light that is reflected relative to the background or relative to other objects. This relative luminance difference is referred to as luminance-contrast, or simply contrast. The so-called spatial contrast sensitivity function (CSF) relates the ability of an observer to visually detect spatial gratings of different spatial frequencies to the amount of contrast present in the grating. The behaviorally measured CSF incorporates visual functions of both physical (i.e. the visual transfer function of the eye) and, to a greater extent, physiological nature (i.e. visual processing in the nervous system). The CSF may, therefore, be regarded as one of the fundamental functional descriptions of a visual system. In virtually all animals that have been tested so far, the CSF renders a band-limited inverted U-shaped function, with a typical high- and low-frequency attenuation (Uhlrich et al. 1981). The high frequency roll-off in humans is regarded as a combined consequence of physical constraints leading to optical degradation (such as the diffraction limit and ocular aberrations), and receptor cell spacing on retina level (Campbell 1965; Cornsweet 1970). The low frequency attenuation can be explained solely by neural factors, such as extent of lateral inhibition (Cornsweet 1970), antagonistic surround mechanisms (Westheimer 1972), or relative insensitivity of low spatial frequency channels (Graham 1972).

For the barn owl, the CSF was determined both in a series of behavioral experiments (Harmening et al. 2009), and with the pattern electro-retinogram (Ghim and Hodos 2006). Considering the different methodology and luminance conditions, the results of both studies were found to
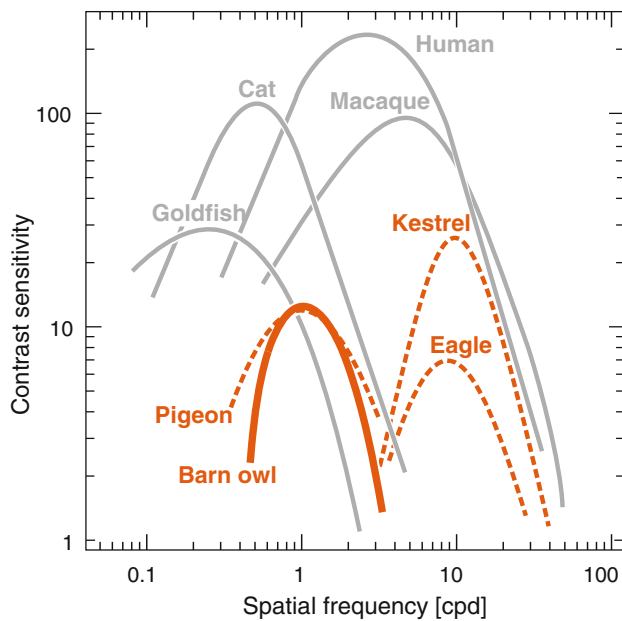
Fig. 3 Contrast sensitivity functions across species. Bird's maximum contrast sensitivity is comparably low, and bandwidth is generally narrow (modified after Harmening et al. 2009)

be in reasonable agreement. The CSF of the barn owl renders the typical band-limited, inverted U-shaped function, with a low maximum sensitivity below 20 at a spatial frequency of about 1 cycle per degree (cpd, Fig. 3). 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 et al. 1997). While low contrast sensitivity and narrow bandwidth is common among all birds, the location of the CSF on the spatial-frequency axis differs among species (Fig. 3). This is easily explained by the individual maximum acuity of a species. While the eagle and kestrel, both equipped with high resolution capabilities (70–140 cpd), have CSFs with maximum sensitivity at a spatial frequency of around 10 cpd (Hirsch 1982; Reymond and Wolfe 1981), the pigeon's and barn owl's maximum sensitivities are shifted towards lower spatial frequencies (Hodos et al. 2002; Harmening et al. 2009). Consistently, these two species exhibit visual acuities that are essentially lower than those of the two raptorial species (pigeon: 6–12 cpd, barn owl: 4–8 cpd, see also following section).

Visual acuity and vernier acuity

The term visual acuity refers to the ability of an observer to resolve fine spatial details in a visual scene. It is often measured as grating acuity, i.e. the smallest distance between single elements of a periodical pattern that is just

resolved, and is then reported as cycle per degree (cpd) at threshold. In an anatomical study, retinal ganglion cell density was used as the basis for a theoretical grating-acuity estimation in barn owls. Maximum ganglion cell density was 11,000–12,500/mm^2 at the area centralis. By application of the Shannon sampling theorem and an assumptive retinal magnification factor of 0.15 mm/deg, grating acuity was calculated to be 7.9–8.4 cpd (Wathey and Pettigrew 1989). While the geometry of barn owl eyes and thus retinal magnification is known (Schaeffel and Wagner 1996), it remains unclear how many of the ganglion cells in area centralis are involved in spatial acuity tasks. Considering the topography of ganglion cell density in the retina of barn owls, displaying a horizontal streak of lower cell density (5,000–8,000/mm^2), behavioral acuity values lower than the theorized 8 cpd become reasonable. With the pattern electro-retinogram visual acuity was estimated from the CSF high frequency cut-off and yielded 6.9 cpd (Ghim and Hodos 2006). In a behavioral study, visual acuity was both estimated from the CSF (3.8 cpd), and measured directly with adaptive psychophysical techniques (2.6–4.0 cpd) (Harmening et al. 2009).

Among other raptors and birds, these results put barn owls at the very low end of the acuity spectrum. For a comparison with other bird species, refer to Fig. 4 (compiled from Table 2 in Harmening et al. 2009). Human thresholds in visual acuity tasks are usually in the range of 30–60 cpd (Campbell 1965). This finding is, as in the barn owl, in good agreement with the retina's sampling capacities (Curcio et al. 1990; Merigan and Katz 1990). On the other hand, pure optical considerations do not explain the barn owl's poor resolution performance (Harmening et al. 2007b). This constitutes a marked optics-acuity disagreement, similar as has been described in a wavefront study of cat eyes (Huxlin et al. 2004). In contrast, it is known 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 1965; Reymond 1985). It was suggested 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 (Harmening et al. 2009; Huxlin et al. 2004).

When discriminative performance was tested with vernier stimuli, i.e. a pair of vertical bars that are relatively offset horizontally, the barn owls' thresholds were as low as 0.58 min of arc of visual angle (arcmin, Harmening et al. 2007a). The mean binocular bar threshold was 2.51 arcmin. Thresholds with single bars were generally
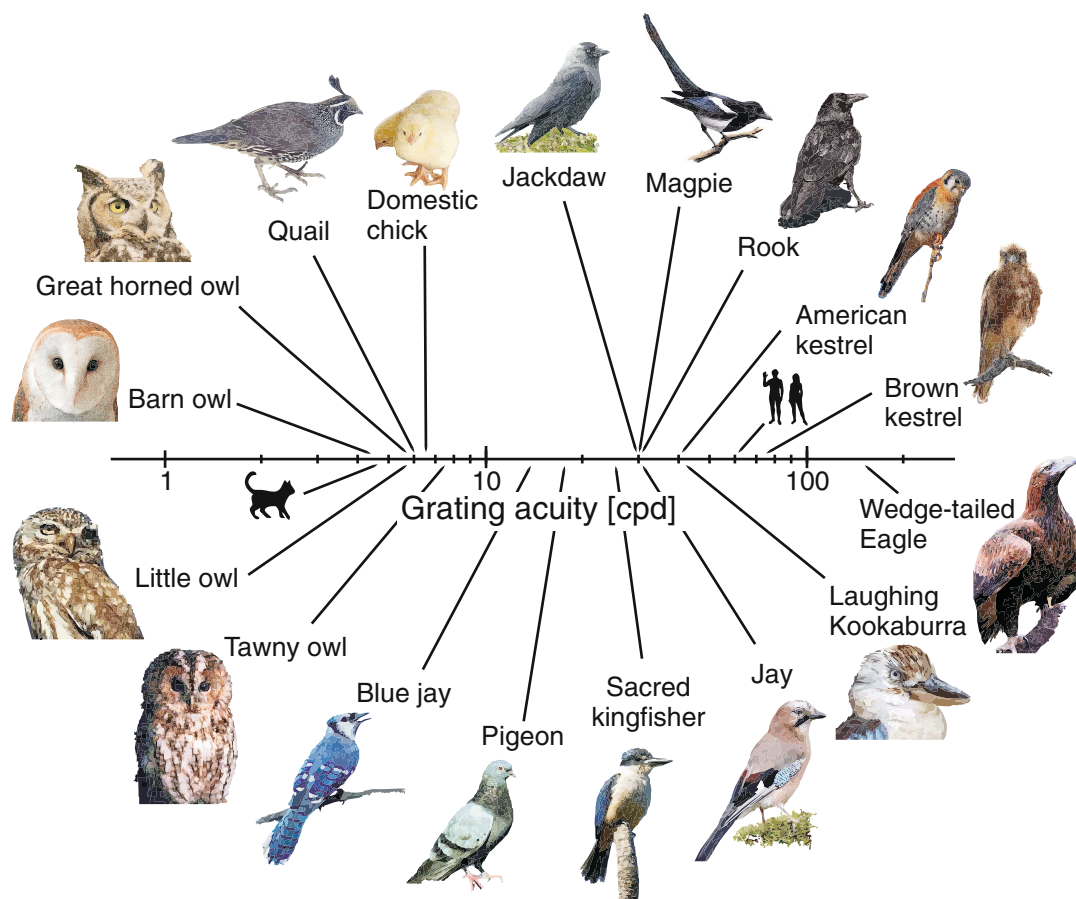
Fig. 4 Grating acuity across bird species. Nocturnal species, as the barn owl, are at the lower end of the acuity spectrum. This is contrasted by the high visual resolution of diurnal raptors. Herbivore and insectivore species populate the medium domain of the spectrum. Typical values for humans and cats are shown for comparison. Where possible, the highest behaviourally measured acuity values are shown (compiled from data of Table 2 in Harmening et al. 2009)

lower than those obtained with a repetitive pattern of identical bars (=grating). Monocular thresholds, obtained in one bird only, were higher than binocular thresholds. With a behavioural grating acuity of 4 cpd in this bird (equalling $30/4 = 7.5$ arcmin between the grating elements), these findings strongly suggest that vernier acuity is a hyperacute phenomenon in barn owls (Harmening et al. 2007a, 2009). The mean hyperacuity factor, i.e. grating acuity divided by vernier acuity, was about 3 in the barn owl. This is comparable to findings with untrained human subjects (McKee and Westheimer 1978) and in cats (Belleville and Wilkinson 1986).

Stereovision

Stereopsis

Probably the most interesting feature of the visual system of owls is the frontal orientation of their eyes. Being confronted with the owl's face, one gets the impression as if their eyes look straight ahead (Fig. 1). However, the optical axes diverge by approximately 62°. The geometrical setup of the eyes in the owl skull can be reviewed in Fig. 2d. In another nocturnal owl, the tawny owl (*Strix aluco*), the optical axes diverge to a similar degree, and it was shown that both monocular fields of view overlap to form an unusual large binocular field of view of around 50° (Martin 1984). Essentially, objects that reside within the binocular field can be viewed with both eyes at the same time, a prerequisite for stereopsis.

Stereopsis is a capability of animals with frontally oriented eyes, including humans, and it relies, to the largest extent, on the neural comparison of the images falling on the retinae in both eyes (for a review see Howard and Rogers 1999). Since the eyes are located at slightly different horizontal positions within the head, corresponding image locations on the right retina are slightly shifted relative to the left retina, predominantly in the horizontal direction. These local differences are called binocular disparities and their magnitude is a function of viewing distance, vergence angle, and relative distance between the

objects in the binocular field of view. Our brain and the brains of animals can make use of disparities to construct a three-dimensional percept from the two-dimensional retinal images.

To investigate whether barn owls experience depth from disparities, van der Willigen et al. (1998, 2011) tested owls psychophysically with a display of random-dot stereograms. In such displays, each eye is presented a stimulus that contains randomly distributed dots. The stimuli for the two eyes are identical, except for a central region in which the dots are relatively shifted between the right and left eyes' view. This shift generates retinal disparities and, in humans, the percept of relative depth of the central region against the background (Julesz 1971). In a figure-ground discrimination tasks, barn owls were able to discriminate the central region when it was defined by binocular disparities alone (van der Willigen et al. 1998). Furthermore, the owls were able to discriminate relative depth as a perceptual category when the central region was defined by negative or positive disparities, respectively (perceived as object vs. hole configuration in humans). The owls could immediately transfer this discrimination to novel stimuli where the equivalent categories were available only through differences in motion information produced by head movements (observer-produced motion parallax) (van der Willigen et al. 2003). Motion-parallax discrimination did occur also under monocular viewing conditions and reliable performance depended heavily on the amplitude of side-to-side head movements. The best measured stereo acuity was 2 arcmin in the barn owl. Following the observations on visual resolution discussed earlier ("Visual acuity and vernier acuity"), this value is about three times better than the sampling capacities of the owl's eye. Thus, just as in humans, depth perception based on horizontal disparities is hyperacute in the barn owl (van der Willigen et al. 1998, 2002).

By employing corrugated random-dot stereograms as stimuli, the spatial disparity-contrast sensitivity function (DSF) was measured in the barn owl (van der Willigen et al. 2010) (Fig. 5). In principle, the DSF is the stereo analogue of the CSF (Tyler 1974). Together, the DSF and CSF portray a visual system's ability to detect spatial modulation as specified by changes in binocular disparity and luminance, respectively. The DSF has the form of an inverted-U envelope, or band-pass characteristic. To be more precise, the DSF provides a disparity-based transfer characteristic at threshold, showing a distinct peak and decreasing sensitivity on either side of this peak (i.e. a high and low frequency fall-off in sensitivity, respectively) (Bradshaw and Rogers 1999). A striking relationship between the owl and human ability to detect shape-from-stereo was observed. In particular, the shift in absolute position between the human and owl DSF closely
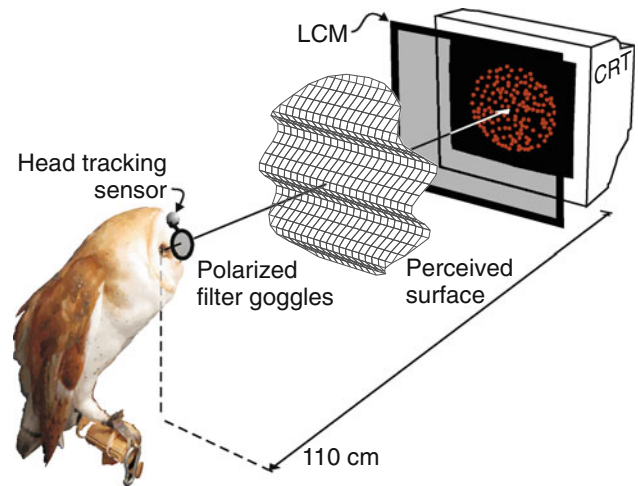

Fig. 5 Example for binocular viewing conditions during stereo experiments. A liquid crystal modulator (*LCM*) grants successive viewing of alternating random dot stereo pairs, shown on the stimulus display (*CRT*). When viewed through polarized filter goggles, relative depth is perceived. In this example, a stimulus that elicits the percept of a corrugation in-depth was used to study the disparity sensitivity function in barn owls (modified after van der Willigen et al. 2010)

corresponded to the shift in absolute position between their respective CSFs. DSF peak sensitivity was shifted towards lower spatial frequencies by a factor of 10 compared to CSF peak sensitivity. Maximum stereoscopic sensitivity is reduced by the same amount relative to the reduction of maximum contrast sensitivity compared with human values. It was argued that these quantitative consistencies might turn the CSF into a valid predictor for the limits of stereovision in species with similar stereoscopical capabilities (van der Willigen et al. 2010).

Neural substrate

In mammals, binocular neurons are first found in the primary visual cortex (V1) (Hubel and Wiesel 1962). Many of these neurons are sensitive to disparity with an increased complexity of coding in complex cells compared to simple cells (Anzai et al. 1999a, b). Therefore, it was logical to look for disparity sensitivity in the avian homologue structure, the visual Wulst. Although the projection of the retina in the barn owl is exclusively contralateral, the Wulst receives binocular information via a thalamo-telencephalic commissure (Karten et al. 1973). Indeed, already an early study demonstrated many similarities in neuronal characteristics between Wulst neurons and V1 neurons, including disparity sensitivity (Pettigrew and Konishi 1976). This was later confirmed in search for the underlying mechanisms (Wagner and Frost 1993; Nieder and Wagner 2000). These studies revealed a representation of stereovision in the barn owl's brain that may be described by algorithms analogous to those that are used to quantify the neural

Fig. 6 Disparity tuning of visual forebrain neurons. Responses of two neurons are shown. For each neuron, tuning curves to correlated-RDS (*solid circles*, **a**, **c**) and anticorrelated-RDS (*open circles*, **b**, **d**) are shown. Gabor functions (*solid lines*) were fitted simultaneously to both tuning curves of each cell. *Error bars* are standard error of the mean. Neuron #1 showed a pronounced inverted tuning curve to a-RDS, whereas Neuron #2 responded only weakly to disparity in contrast-inverted images. Neurons like #2 showed a longer response latency and where thus regarded to represent higher processing stages. Its response explains why no depth is perceived in a-RDS (modified after Nieder and Wagner 2001)
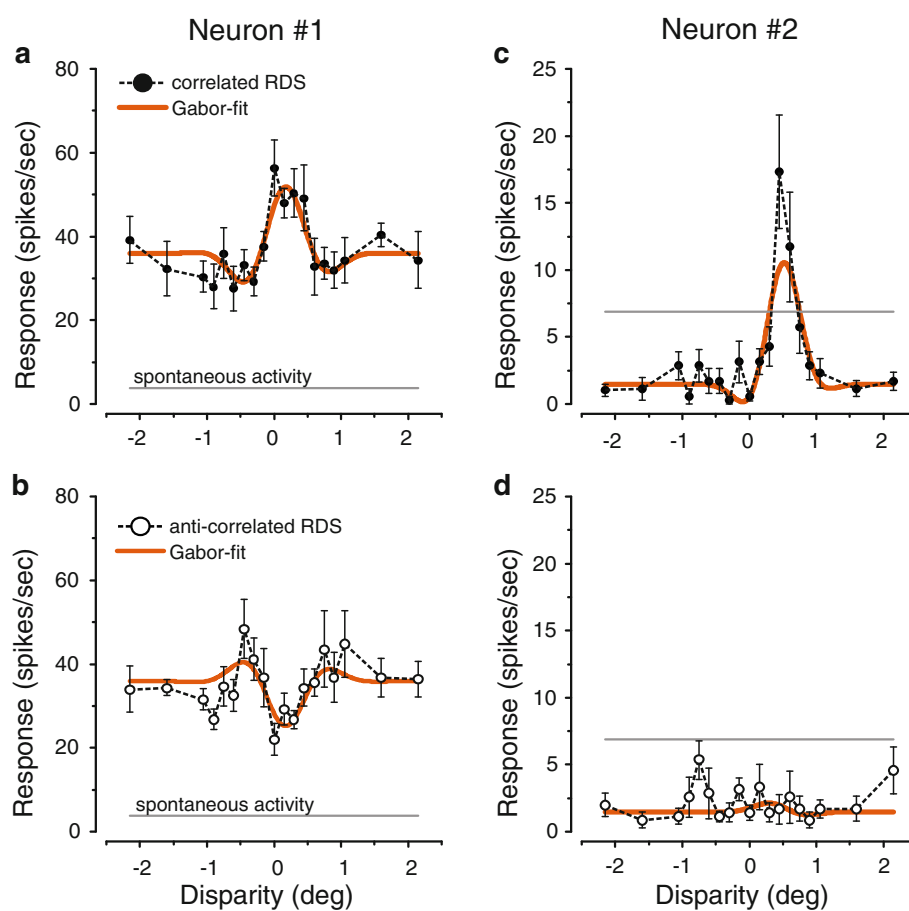
representation of interaural time difference (Wagner and Frost 1993; Wagner 2004), if one takes into account that the stereo problem requires a spatial disparity, while the sound-localization algorithm builds on a temporal disparity. The responses of the neurons in early visual areas are not sufficient to account for the phenomenon of stereopsis. Because of their restricted receptive fields and input-filter characteristics, the neurons respond to disparity in false-matched images. They also exhibit multiple response peaks in their disparity-tuning profiles. Nieder and Wagner (2001) observed a hierarchy of processing in the visual Wulst as demonstrated by increasing response complexities and latencies. In the hierarchically highest neurons, false binocular matches were discarded, and the activity of neurons in the primate inferior temporal cortex correlated directly with conscious depth perception (Fig. 6).

Active vision

Head movements

Barn owls exhibit a rich repertoire of head movements before taking off for prey capture (Ohayon et al. 2006),

which was hypothesized to reflect the barn owl's capacity to efficiently follow a moving prey by vision and audition (Fux and Eilam 2009). These movements occur mainly at light levels that allow for the visual detection of prey. To investigate these movements and their functional relevance, the pre-attack behavior of barn owls was video-taped. Off-line image analysis enabled reconstruction of all six degrees of freedom of head movements. Three categories of head movements were observed: fixations, head translations and head rotations. The observed rotations contained a translational component. Head rotations did not follow Listing's law, but could be well described by a second order surface, which indicated that they are in close agreement with Donder's law. Head translations did not contain any significant rotational components. Translations were further segmented into straight-line and curved paths. Translations along an axis perpendicular to the line of sight were similar to peering movements observed in other animals. It was suggested that these basic motion elements (fixations, head rotations, translations along a straight line, and translation along a curved trajectory) might be combined to form longer and more complex behavior. During preying of live, moving voles barn owls orient their heads towards a prospective clash point and then return to the

target itself, a pattern that fits an interception rather than tracking mode of following a moving target (Fux and Eilam 2009). The typical large horizontal movements (peering) may mainly underlie estimation of distance during prey capture (van der Willigen et al. 2002).

Illusory contours

Robust form perception and its underlying neuronal mechanisms require a generalized representation of object boundaries independent of how they are determined. One of the most striking visual abilities concerning form perception is the reconstruction of contours that are not present in the retinal image. Nieder and Wagner (1999) showed that barn owls are able to perceive subjective contours defined by grating gaps and phase-shifted abutting gratings (Fig. 7). Moreover, single-unit recordings from the visual forebrain of awake, behaving birds revealed a high proportion of neurons that signaled these types of subjective contours independent of local stimulus attributes. These data suggest that the visual Wulst plays an important role in contour-based form perception and exhibits a functional complexity reminiscent to mammalian extrastriate cortical areas (Nieder 2002).

Attention mechanisms

In a number of physiological studies, the barn owl has proved suitable to serve as a model system to research the neural machinery underlying attention and gaze control. In particular, the avian homologue to the superior colliculus in mammals, the optic tectum, has been demonstrated to be involved in orienting gaze toward salient stimuli by containing a multi-modal saliency map (Wagner 1993; Mysore et al. 2010). Neuron responses of the optic tectum show a high integration of visual and auditory sensory inputs (Reches and Gutfreund 2008), which poses interesting questions of how competing stimuli across modalities may drive the animal's behavior during target selection. Neurons of a cholinergic midbrain nucleus that interconnects with the optic tectum were shown to respond to a wide range of auditory and visual features, and to encode the relative strength of stimuli across the entirety of space, while not being tuned to particular values of those features (Asadollahi et al. 2010). Switch-like neural mechanisms have been proposed to constitute a winner-take-all target selection for gaze and attention across modalities (Mysore et al. 2011). A higher-level processing stage was found in the forebrain of the owl that benefited from the integration of auditory and visual information during a novelty detection task (Reches et al. 2010).

In a behavioral approach, visual attention properties of freely behaving barn owls were investigated with the
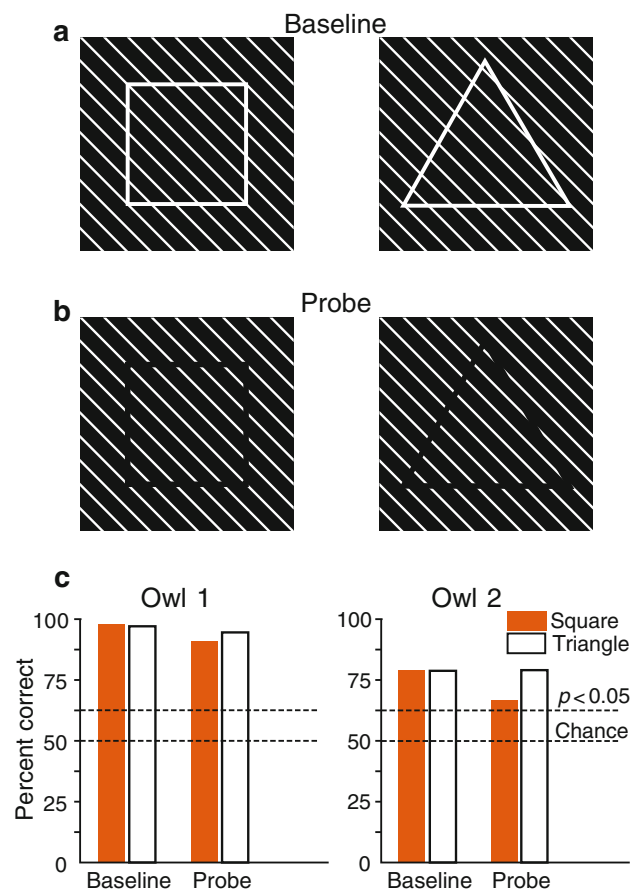

Fig. 7 Barn owls perceive illusory contours. Stimuli used in behavioural tests (**a**, **b**) and corresponding psychophysical performance of two owls (**c**). Two owls were trained to discriminate the stimuli shown in **a**. In transfer tests, geometric objects were defined by subjective contours (**b**). The bar graphs in **c** display the performance of two owls for the baseline stimuli ($n = 730$, *left pair*) and the subjective-contour figures ($n = 80$, *right pair*). Chance level (50%) and the confidence interval above chance ($P < 0.05$, binomial test, two-tailed, $n = 80$) are displayed. Both owls significantly transferred contrast-border figures to subjective-contour probes (modified after Nieder and Wagner 1999)

OwlCam (Ohayon et al. 2008; Harmening et al. 2011), a head-mounted, lightweight micro camera combined with a video broadcasting board, cast into a customized frame of dental cement. Due to its small and rigid physical properties, it can be worn by small animals (e.g. rats, mice, birds) to achieve a genuine, first-person view along the animal's line of sight. Due to the immobility of the eyes of barn owls (see "Morphology"), the view of a properly aligned Owl-Cam is registered along the owls' line of sight at all times.

During an active search task, owls repeatedly and consistently directed their gaze in a way that brings objects of interest to a specific retinal location (retinal fixation area). Using a projective model that captures the geometry between the eye and the camera, the image fixation area was recovered. Recording in various types of environments

(aviary, office, outdoors) revealed significant statistical differences of low level image properties at the image fixation area compared to values extracted at random image patches. These differences are in agreement with results obtained in primates in similar studies (Parkhurst and Niebur 2003). To investigate the role of saliency and its contribution to drawing the owl's attention, a popular bottom-up computational model was used (Itti and Koch 2001). Saliency values at the image fixation area were typically greater than at random patches, yet were only 20% out of the maximal saliency value, suggesting a top-down modulation of gaze control.

Overt attention mechanisms, and in particular, the barn owl's susceptibility to orientation based saliency was studied in a free-viewing experiment (Harmening et al. 2011). Here, barn owls were confronted with visual scenes that contained one differently oriented target among similarly oriented distracters. Although no particular task was given, the owls looked significantly longer, more often, and earlier at the target. This behavior resembles visual search strategies that were thus far shown in primates only. It was concluded that orientation saliency has computational optimality in a wide variety of ecological contexts and therefore that it constitutes a universal building block for efficient visual information processing in general.

Conclusion

With the above descriptions, we have a good account of the basic properties of the eye and of the barn owl's visual capacities. What is least known is whether barn owls have color vision. Martin (1974) trained tawny owls to discriminate blue and green or red and green lights. He concluded that while this species does possess color vision, the wavelength was not of great importance in controlling color-vision guided behavior. Other nocturnal species indeed have color vision (Roth and Kelber 2004). An indirect hint to color vision in barn owls comes from the successful use of anaglyphic displays in stereo-discrimination experiments, where the single dots were defined by hue but not luminance differences (van der Willigen 2011). In addition, it would be interesting to find out more about the function of the barn owls' conspicuous head movements and their specific contribution to depth vision (van der Willigen et al. 2002; Fux and Eilam 2009).

The adaptations in barn owl vision we have described in this review may all be seen in the context of the lifestyle of this animal as a predator that mainly hunts under crepuscular conditions. This would favor high absolute sensitivity at the cost of spatial acuity. As a hunter, one would also expect good depth vision, and this is what the barn owl's stereo system provides. Moreover, not only do these birds have stereopsis, the stereo system is also adapted to function reasonably well under mesopic light conditions. The findings on visual search fit well into this line of arguments. As a predator living under high selective pressure as indicated above, the barn owl should make use of every possible cue available in order to find its prey. The observation of pop-out in these animals supports this notion. We expect many more such adaptations on the cognitive level such as visual and auditory object recognition and segregation, and, therefore, see it as a challenge for the future to investigate and understand more about the cognitive abilities of this species and how they relate to its lifestyle.

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