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## Effects of binaural decorrelation on neural and behavioral processing of interaural level differences in the barn owl (*Tyto alba*)

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**Abstract** The effect of binaural decorrelation on the processing of interaural level difference cues in the barn owl (*Tyto alba*) was examined behaviorally and electrophysiologically. The electrophysiology experiment measured the effect of variations in binaural correlation on the first stage of interaural level difference encoding in the central nervous system. The responses of single neurons in the posterior part of the ventral nucleus of the lateral lemniscus were recorded to stimulation with binaurally correlated and binaurally uncorrelated noise. No significant differences in interaural level difference sensitivity were found between conditions. Neurons in the posterior part of the ventral nucleus of the lateral lemniscus encode the interaural level difference of binaurally correlated and binaurally uncorrelated noise with equal accuracy and precision. This nucleus therefore supplies higher auditory centers with an undegraded interaural level difference signal for sound stimuli that lack a coherent interaural time difference. The behavioral experiment measured auditory saccades in response to interaural level differences presented in binaurally correlated and binaurally uncorrelated noise. The precision and accuracy of sound localization based on interaural level difference was reduced but not eliminated for binaurally uncorrelated signals. The observation that barn owls continue to vary auditory saccades with the interaural level difference of binaurally uncorrelated stimuli suggests that neurons that drive head saccades can be activated by incomplete auditory spatial information.

**Keywords** Sound localization · Auditory · ITD · Cross-correlation · Binaural fusion

**Abbreviations** *BC* binaural correlation · *ICc* central nucleus of the inferior colliculus · *ICx* external nucleus of the inferior colliculus · *ILD* interaural level difference · *ITD* interaural time difference · *OT* optic tectum · *VLVp* ventral nucleus of the lateral lemniscus, posterior part

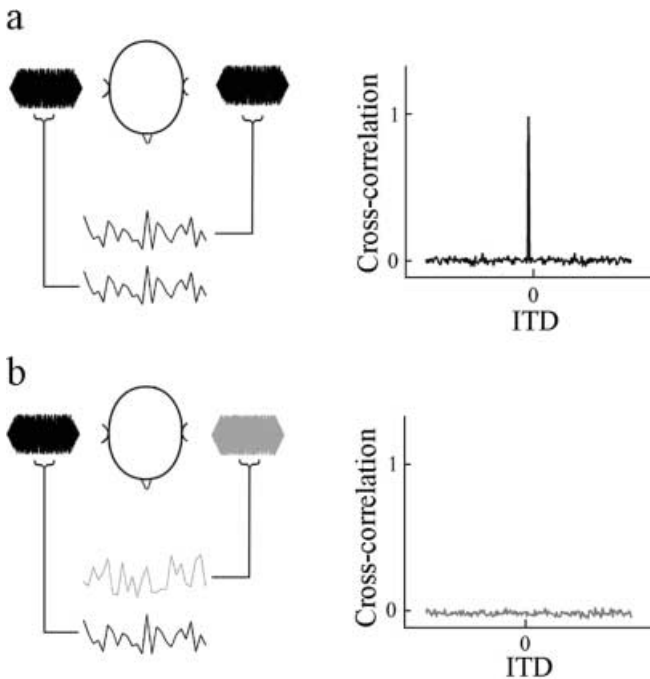
### Introduction

Humans (and many other symmetrically eared animals) use two binaural cues for horizontal sound source position: interaural time differences (ITDs; Rayleigh 1907) and interaural level differences (ILDs; Venturi 1796; Rayleigh 1877). ITDs arise as a result of differences in path length from a sound source to the right and left ears, whereas ILDs arise as a result of differential attenuation by the head, of the sound arriving at the two ears.

Most neurophysiologically plausible models of binaural hearing include some type of binaural cross-correlation for the extraction of ITD (e.g., Colburn and Durlach 1978; Saberi 1995; Trahiotis and Stern 1995; Colburn 1996). The location in time of the peak of a cross-correlation function of the signals arriving at the two ears depends on the ITD, and the height of the peak depends on the degree of correlation between the two input signals. When the signals at the two ears are identical, the sound has a binaural correlation (BC) of one and there is a large peak in the cross-correlation function (Fig. 1a).

A strong prediction of a cross-correlation model of sound localization is that reducing or eliminating binaural correlation should reduce or eliminate localization based on ITD. This is because when the signals at the two ears are completely uncorrelated (BC=0), there is no peak in the cross-correlation function (Fig. 1b). This has been shown to be the case in humans: when subjects are presented noise over headphones and allowed to control the interaural delay, the ability to center the noise drops to chance for BC=0 stimuli

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**Fig. 1a, b** Schematic of the effect of binaural correlation on the cross-correlation function. Binaurally correlated signals (a) have a peak in the cross-correlation whose location in time is determined by the interaural time difference (ITD), while binaurally uncorrelated signals (b) have no peak in the cross-correlation function

(Jeffress et al. 1962). Recently Saberi et al. (1998) have shown that the barn owl, a nocturnal predator with excellent spatial hearing, also depends on binaural correlation for ITD extraction. As in humans, barn owl sound-localization ability based on ITD falls to chance as binaural correlation is reduced to zero.

Although sound localization based on ITD is eliminated by binaural decorrelation, the effect of this manipulation on ILD-based sound localization has never been tested. In the barn owl the first stage of ILD processing is the posterior part of the ventral nucleus of the lateral lemniscus (VLVp). VLVp neurons receive excitatory input from the contralateral cochlear nucleus angularis and inhibitory input from the contralateral VLVp. VLVp neurons are therefore excited by sounds that are louder in the contralateral ear and inhibited by sounds that are louder in the ipsilateral ear (Moiseff and Konishi 1983). VLVp neurons have no ITD sensitivity (Moiseff and Konishi 1983). This lack of ITD sensitivity predicts that binaural decorrelation would not interfere with ILD encoding. However, two other observations suggest that binaural decorrelation would interfere with ILD-based sound localization. In humans, interfering with binaural correlation also interferes with binaural fusion (auditory image formation). When sounds with a BC of one are played over headphones, humans perceive a single, compact, auditory image whose location in the mediolateral plane depends on the ILD and ITD of the sound (Sayers 1964; Durlach and Colburn 1978; Yost 1981). As binaural correlation is reduced from one

towards zero, which can happen naturally in a very reverberant or noisy environment, humans perceive an expansion of the auditory object to a maximum at around a BC of 0.4. At lower correlations humans perceive two auditory objects, one at each ear (Licklider 1948; Blauert and Lindemann 1986) or perceive a very diffuse object that fills the head (Gabriel and Colburn 1981). In addition, it has been shown that decorrelation reduces neuronal responses in the external nucleus of the inferior colliculus (ICx; Albeck and Konishi 1995) and eliminates them altogether in the optic tectum (OT; Saberi et al. 1998). Cells in the ICx and OT are tuned for both ITD and ILD and are therefore space-specific (Knudsen and Konishi 1978; Knudsen 1982). Neurons in the ICx have recently been shown to perform a multiplication of ILD and ITD inputs (Pena and Konishi 2001). The inability of BC = 0 stimuli to drive neurons in the OT can therefore be understood as the result of a reduction in the ITD input. The failure of binaurally decorrelated sounds to drive OT neurons above the spontaneous rate suggests that these neurons would not remain ILD tuned for such stimuli.

The barn owl is a particularly good species in which to test the sensitivity of ILD detection to the degree of binaural correlation because in this species ITD and ILD are used for different axes in sound localization. While symmetrically eared animals use ITD and ILD for horizontal localization, ILD in the barn owl encodes vertical sound source position. This is because the facial ruff of the barn owl (analog of the pinnae of mammals) is bilaterally asymmetric. As a result of this asymmetry, sound from sources above the horizon are louder in the barn owl's right ear while sounds from sources below the horizon are louder in the left ear. This asymmetry transforms ILD from a cue for the horizontal location of a sound source into a cue for vertical location (Payne 1971). Thus in the barn owl, one has an assay for the detection of ILD which is orthogonal to the detection of ITD – a manipulation that interferes with ITD detection, but spares ILD detection will eliminate horizontal sound localization while sparing vertical sound localization.

The failure of binaurally uncorrelated stimuli to drive OT neurons in barn owls, to elicit behavioral responses to ITD in humans and owls, or to produce a compact auditory image in humans all suggest that variations in the ILD of these stimuli could not be used as a cue for sound location. However, ILD and ITD are processed in two independent parallel pathways in the brainstem (Takahashi et al. 1984) suggesting that at least the early stages of ILD extraction would be insensitive to changes in binaural correlation. The experiments presented here were designed to address (1) whether ILD sensitivity in VLVp neurons is maintained for binaurally uncorrelated signals, and (2) whether barn owls can detect and respond to variations in the ILD of these signals. The results offer insight into the process by which ITD and ILD information are combined to produce an auditory image compact in the horizontal and vertical planes.

## Methods and materials

### Behavioral experiment

#### Training

Two adult, hand-raised owls were trained to sit on a perch in a large anechoic chamber (Industrial Acoustics; 5 m × 3 m × 3 m, low-frequency anechoic cutoff 500 Hz), fixate an LED, and then orient to target sounds played from a moveable speaker positioned anywhere in frontal space. Owls were rewarded for target localization and fixation with small pieces of mouse presented in a remote-controlled feeder located at their feet. Once good localization was achieved, the owls were trained to wear a head-position monitor and headphones. Headphones were used because they allow closer control of binaural correlation, and because a binaural correlation of zero is difficult to achieve in the free field. Owls were rewarded for fast, accurate localization with small pieces of mice presented using a stepper-motor-controlled feeder.

#### Sound stimuli

Sound stimuli (100-ms segments of 4–9 kHz bandpassed Gaussian noise with 10 ms linear ramps at 50 dB SPL) were generated using software libraries. Each trial used a different, independently generated noise. A custom-built software interface, (based on Matlab, 5.3.0, The Mathworks) was used to play sounds, and record head position and sound data. The intensity, ILD, and binaural correlation of the sound were varied from trial to trial. Left-ear-louder ILDs correspond to sounds arriving from below the horizon and are designated as negative, while right-ear-louder ILDs correspond to sounds arriving from below the horizon and are designated as positive. ITD for all stimuli was set to 0. The binaural correlation of the sounds was controlled by either playing the same sound to the right and left ears (BC = 1 condition) or by independently generating two noises and playing one to each ear (BC = 0 condition). The efficacy of binaural decorrelation was tested by recording sound from the headphones in the binaurally uncorrelated condition using probe tube microphones implanted near the tympanic membrane. These sounds were then cross-correlated to ensure filtering or other stages of signal processing prior to stimulus presentation hadn't introduced any binaural correlation. Sounds played with a binaural correlation of zero had no significant peak in a cross-correlation function. The transfer function of the left and right headphone speakers was compensated for by recording the left and right transfer functions using microphones implanted in probe tubes in each ear, and then filtering the sound played through each headphone speaker with the inverse of its respective transfer function.

#### Input-output hardware

Sounds were recorded using Knowles Electronics microphones (ED-1939). Analog signals were filtered with an anti-aliasing filter (FT6-2, TDT, frequency cutoff: 24 kHz) sampled at 48077 Hz with an analog-to-digital converter (AD2, TDT), and read into a PC (200-MHz Pentium, running RedHat Linux 5.2) using a DSP card (AP2, TDT). 16-bit digital signals were converted to analog with a digital-to-analog converter (DA1, TDT). Intensity was controlled with a programmable attenuator (PA4, TDT), and sound was played through headphones (Knowles, ED-receiver with a Knowles BF-1743 damped coupling assembly).

#### Monitoring head position

Head position was monitored using a Polhemus Isotrak II, with a 60 Hz sampling rate. Head-position measurement accuracy was within 1.5° in elevation. A small (2 cm diameter) pickup coil was mounted on the head using a small metal mounting tabs implanted with the following procedure: the owl was deeply anesthetized with

intramuscular injections of ketamine hydrochloride (20 mg kg<sup>-1</sup>) and diazepam (0.1 mg kg<sup>-1</sup>). The feathers on the top of the head were plucked, the skin was cleaned with an antiseptic solution (chlorhexidine gluconate, 0.05%), an incision was made in the skin, the top of the skull was cleaned and a small portion of the top layer of bone removed. A small metal tab was cemented onto the skull and the skin was sutured around its base so that about 7.5 mm of the tab showed above the skin. The owls were allowed to recover in a heated isolation cage and kept under observation for 24 h before being returned to their home cage. Head-position data were read into the PC through the serial port.

#### Experimental session

A small number of free-field stimuli were presented at the beginning of each experimental session. If free-field sound localization was abnormal, no headphone data were taken. If free-field sound localization was normal, the owl was fitted with headphones and binaurally correlated and uncorrelated stimuli were presented in random order (without replacement).

#### Statistical tests

Final head position as a function of ILD for binaurally correlated noise were plotted versus final head position as a function of ILD for binaurally uncorrelated noise for each owl. All possible BC = 1 trial:BC = 0 trial combinations (sorted by ILD) were used, so that the total number of points for each bird is: (BC = 0 number of trials) times (BC = 1 number of trials). All points were used in calculating correlation coefficients (*r*) for each neuron. An *F*-test was used to determine if the correlation coefficients were greater than zero.

### Electrophysiological experiment

#### Surgery

Three adult owls were anesthetized with intramuscular injections of ketamine hydrochloride (20 mg kg<sup>-1</sup>) and diazepam (0.1 mg kg<sup>-1</sup>) and maintained with supplemental doses during each recording session. The owl was fitted with ear bars and a beak plate to stabilize the head during head plate implantation. The owl was restrained with a soft leather jacket and warmed with a heating blanket. The feathers on the top of the head were plucked, the skin cleaned with an antiseptic solution (chlorhexidine gluconate, 0.05%), and an incision was made to expose the top of the skull. The top of the skull was cleaned and then the top layer of skull was removed to expose the trabecular layer. A stainless steel head plate and a small metal zero post were attached to the skull using dental acrylic (Perm Reline and Repair Resin; Hygenic). The head plate allows the head to be held fixed in the same position on successive surgery days, and the metal post marks the zero point of our stereotaxic coordinate system. Once the dental acrylic hardened, the ear bars and beak plate were removed and the head was fastened to the stereotax using the head plate. A 4 mm × 4 mm craniotomy was opened in the skull, a small hole was made in the dura, and electrodes were lowered into the brain. At the end of each recording session the craniotomy was filled with gelatin foam (Gelfoam; Pharmacia and Upjohn) soaked in .05% chlorhexidine and covered in dental acrylic. The skin was sutured closed and intramuscular buprenorphine hydrochloride (0.06 mg kg<sup>-1</sup>) and subcutaneous fluids (5 ml lactated Ringer solution) were administered. The owl was placed in a small, well-heated cage and monitored for 24 h after surgery before being returned to its home cage.

#### Sound presentation

Auditory stimuli were presented and neural data was collected using a custom-written data acquisition program. Sounds were

calibrated by measuring the left and right headphone transfer functions before each experiment with small microphones in the headphone assembly (Knowles Electronics, ED-1939). All sounds were filtered with the inverse of the respective transfer functions and played through the headphones (Knowles Electronics, ED-receiver with a Knowles BF-1743 damped coupling assembly). Auditory stimuli (16 bit) produced by a computer workstation (Sparc/IPX, Sun Microsystems) were converted to analog (Proport, Ariel). The intensity of the left and right channels was controlled with programmable attenuators (PA4, TDT). Sound leakage between the headphones was attenuated by sealing the each headphone into the ear canal with ear-mold compound (Gold Velvet II, All American Mold Laboratories) at the beginning of each experiment.

#### Data collection

Neural signals were passed through a  $10 \times$  gain current buffer (B.E.S, headstage), filtered from 1 kHz to 10 kHz, and amplified by  $100 \times$  (B.E.S., microA108). Analog signals were digitized at 48 kHz (Proport, Ariel), read into the computer using a DSP card (S56X, Berkeley Camera Engineering), thresholded and recorded.

#### Electrophysiology

Electrodes consisted either of 1.0 mm o.d. capillary fiber glass pipettes with tip widths of 5–10  $\mu\text{m}$  filled with 3 mol  $\text{l}^{-1}$  K-Acetate or filled with 3 mol  $\text{l}^{-1}$  NaCl, or 1.0 mm o.d. glass pipettes with tip widths of 5–10  $\mu\text{m}$  filled Wood's metal and plated with gold and platinum. All electrodes had impedances between 0.2 M $\Omega$  and 1.8 M $\Omega$  at 1 kHz. Electrodes were moved with a microdrive (B.E.S., microD 100) in steps of 100  $\mu\text{m}$  until VLVp was reached, and in steps of 2–10  $\mu\text{m}$  while isolating. Neurons were characterized based on their tuning to ILD, ITD, binaural correlation, average binaural intensity, ABI [(intensity of left channel + intensity of right channel)/2], and frequency or frequency range of stimulating sound. Broadband noise (500–12,000 Hz, independently generated for each trial) was used to assess ILD, ITD and level tuning. Tones were to assess frequency tuning. All data were recorded at 20 dB above threshold. The number of trials recorded varied from 5–20. An acceptable isolation was defined as a consistent action potential shape throughout the recording period and an inter-spike interval (ISI) histogram with no ISI smaller than 1 ms. Binaurally correlated and uncorrelated noise ILD trials were interleaved and ILD values randomly presented. Recordings were made with the owl placed in a small (1 m<sup>3</sup>) double-walled sound attenuating chamber (Acoustic Systems).

#### Statistical tests

Spikes as a function of ILD for binaurally correlated noise were plotted versus spikes as a function of ILD for binaurally uncorrelated noise for each neuron. All possible BC=1 trial:BC=0 trial combinations (sorted by ILD) were used, so that the total number of points for a given neuron is: (BC=0 number of trials) times (BC=1 number of trials). All points were used in calculating correlation coefficients ( $r$ ) for each neuron. An  $F$ -test was used to determine if the correlation coefficients were greater than zero.

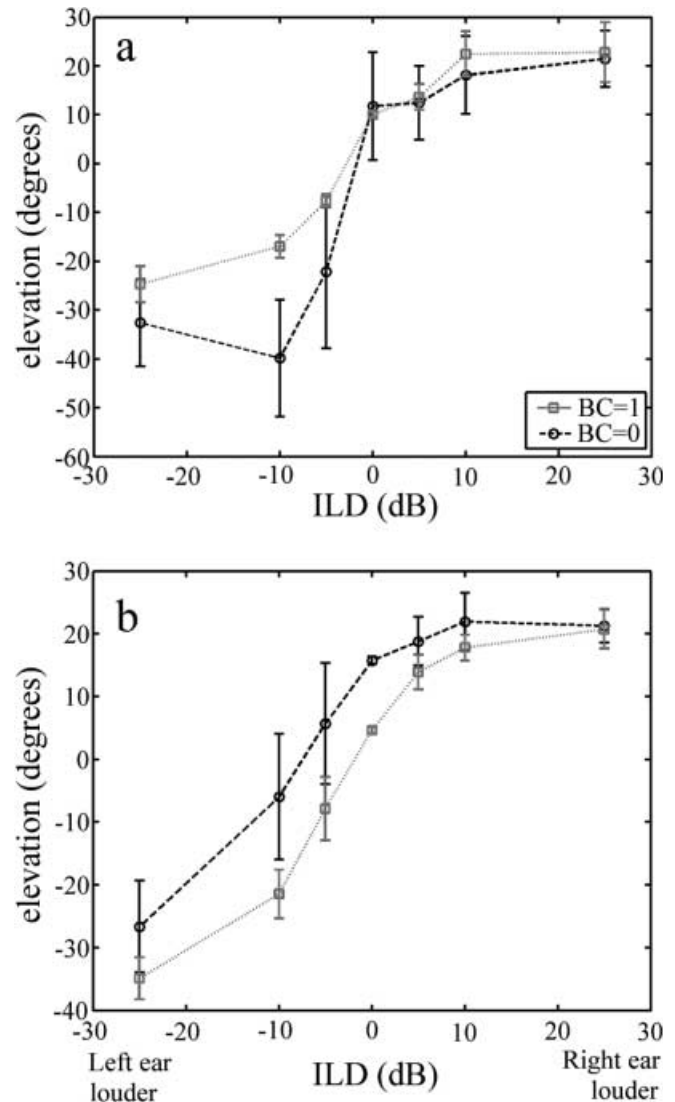
#### Histology

Recording sites were marked with electrolytic lesions ( $2 \times 4 \mu\text{A}$  for 10 s), the owls were deeply anesthetized with an overdose of sodium pentobarbital (80 mg  $\text{kg}^{-1}$ ) and perfused with 0.9% warm saline and 4% paraformaldehyde in 0.2 mol  $\text{l}^{-1}$  phosphate buffer. The brain was cryoprotected with 30% sucrose and 40- $\mu\text{m}$  sections were cut on a freezing microtome. Sections were mounted on glass slides, cleared, dehydrated, stained with a Nissl stain (neutral red or cresyl violet) and coverslipped, and recording sites were verified anatomically.

## Results

### Behavioral response to variations in binaural correlation

When broadband (4–9 kHz) noise with a BC=1 were presented over headphones, both owls varied the elevation of their final head position with ILD (Fig. 2a, b; squares) as has been shown previously (Moiseff 1989a). When the same stimuli with a BC=0 were presented, the barn owls continued to vary the elevation of their final head position with ILD (Fig. 2a, b; circles). Final head positions in the vertical plane for BC=0 stimuli were positively correlated with those for BC=1 stimuli in both owls (owl 1:  $r=0.98$ ,  $F=98.99$ ,  $P \ll 0.001$ ; owl 2:  $r=0.98$ ,  $F=98.99$ ,  $P \ll 0.001$ ). Average elevational standard deviation increased from approximately  $3^\circ$  in both owls

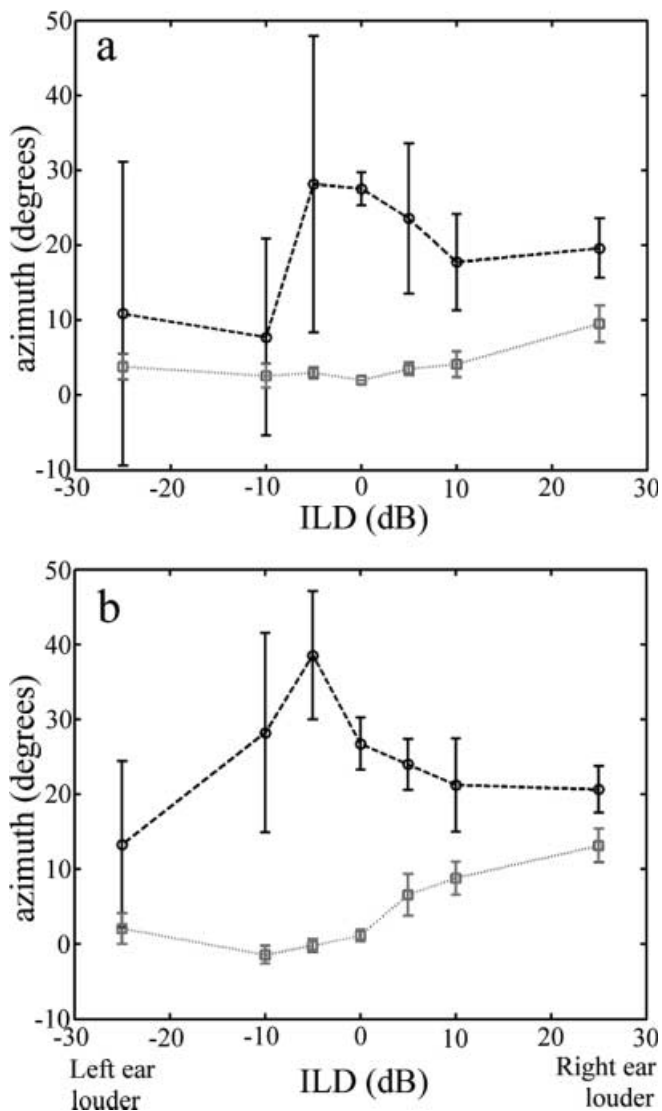


**Fig. 2a, b** Vertical localization of binaurally correlated and binaurally uncorrelated sounds in two owls. Elevation of final head position varies with interaural level difference (ILD) in both conditions in both owl 1 (a) and owl 2 (b)

(owl 1:  $3.5^\circ$ , owl 2:  $3.4^\circ$ ) for  $BC=1$  stimuli to  $9.6^\circ$  in owl 1 and  $6.4^\circ$  in owl 2 for  $BC=0$  stimuli. Final head positions in the horizontal plane for  $BC=0$  stimuli were not correlated with those for  $BC=1$  stimuli in either owl (owl 1:  $r=-0.06$ ,  $F=1.15$ ,  $P>0.25$ ; owl 2:  $r=-0.47$ ,  $F=2.74$ ,  $P>0.1$ ). The azimuth of the final head position of both owls varied slightly as a function of ILD for both  $BC=1$  and  $BC=0$  stimuli (Fig. 3a, b; squares and circles). Average azimuthal standard deviation increased from approximately  $1^\circ$  in both owls (owl 1:  $1.3^\circ$ , owl 2:  $1.7^\circ$ ) for  $BC=1$  to  $10.8^\circ$  in owl 1 and  $7^\circ$  in owl 2.

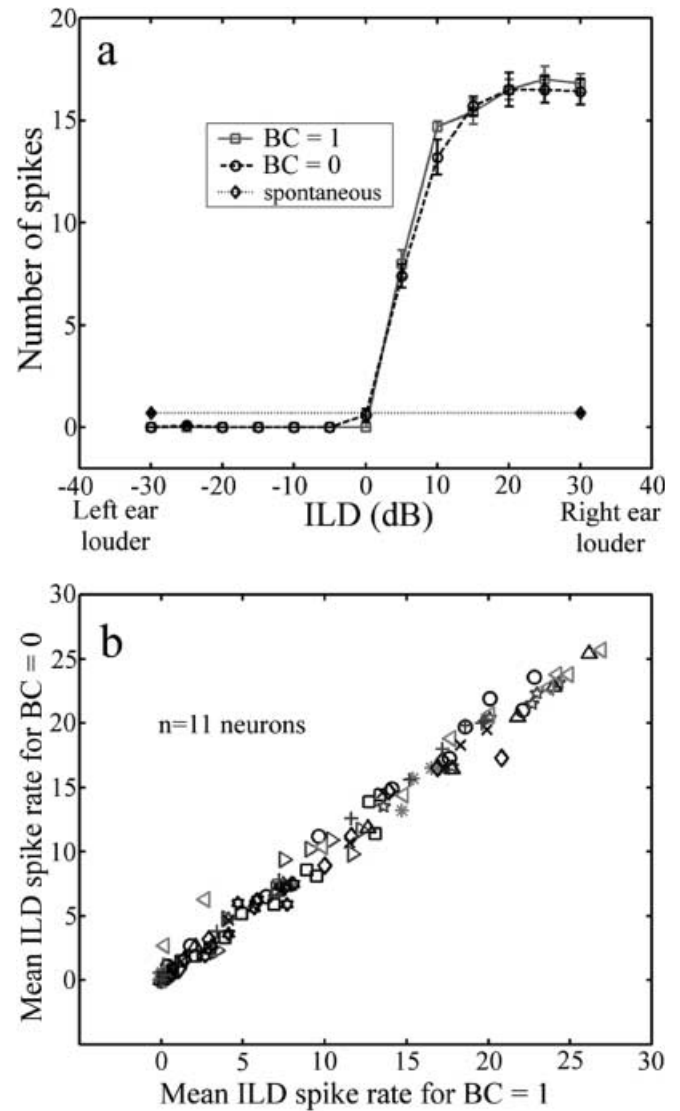
#### Brainstem response to variations in binaural correlation

Extracellular recordings were made from 11 well-isolated VLVp neurons. The best frequencies of the



**Fig. 3a, b** Horizontal localization of binaurally correlated and binaurally uncorrelated sounds in two owls. Azimuth of final head position varies slightly with interaural level difference (ILD) for binaural correlation ( $BC$ ) = 1 in both owl 1 (**a**) and owl 2 (**b**)

neurons ranged from 3 kHz to 7.5 kHz, and ILD tuning curves at half height had values between 0 dB and 10 dB. All neurons maintained their ILD sensitivity with binaurally uncorrelated noise. Figure 4a shows the effect of binaural correlation on the ILD tuning of a single neuron. The neuron is inhibited below the spontaneous rate for left-ear-louder ILDs and excited by right-ear-louder ILDs for both binaurally correlated (squares) and binaurally uncorrelated (circles) stimuli. ILD tuning to binaurally correlated and binaurally uncorrelated noise was very similar in all 11 neurons. This can be most easily seen by looking at the mean neural response to binaurally uncorrelated noise plotted as a function of the mean neural response to binaurally correlated noise



**Fig. 4** The effect of varying binaural correlation on interaural level difference (ILD) tuning in the posterior part of the ventral nucleus of the lateral lemniscus (VLVp). **a** Single neuron ILD sensitivity. This neuron is inhibited below the spontaneous rate (diamonds) for left-ear-louder ILDs and excited by right-ear-louder ILDs for both binaurally correlated and binaurally uncorrelated noise. **b** Mean spike rate as a function of ILD for  $BC=1$  plotted against mean spike rate for  $BC=0$  for 11 VLVp neurons

(Fig. 4b). All neurons had values of correlation coefficients for BC=1 versus BC=0 that were significantly greater than zero (Table 1,  $P < 0.01$  for all neurons).

## Discussion

### Behavioral experiment

These experiments demonstrate that barn owls can extract ILD from binaurally uncorrelated stimuli and use that information to control the vertical component of sound localization. This ability is in contrast to the effect of binaural decorrelation on horizontal sound localization (Sabeti et al. 1998); barn owls are unable to localize binaurally uncorrelated stimuli in the horizontal plane. It is also in contrast to the effect of binaural decorrelation on binaural fusion in humans (Blauert and Lindemann 1986; Licklider 1948; Gabriel and Colburn 1981); binaural fusion is radically reduced or eliminated for binaurally uncorrelated sounds.

In barn owls the slope of iso-ILD contour lines varies as a function of frequency (Moiseff 1989b; Brainard et al. 1992). For low-frequency sound iso-ILD contour lines are nearly vertical in barn owls as they are in humans (Rayleigh 1877). As the frequency of sound is increased, iso-ILD contour lines become progressively more horizontal, allowing ILD to encode elevation. At 4 kHz (the lower end of the frequency range of the stimulus used in the behavioral experiments) iso-ILD contour lines still have a significant azimuthal component. The slight effect of ILD on final azimuthal head position for both BC=1 and BC=0 stimuli is probably the result of this azimuthal dependence.

Although it is expected that lack of binaural correlation should increase azimuthal variance, based on the inability of barn owls to extract ITD from such stimuli (Sabeti et al. 1998), why does lack of binaural correlation increase elevational variance? One possible explanation is that, in the absence of a coherent ITD, a particular ILD does not correspond to a particular

location in space, but to a family of locations, which varies depending on the magnitude of the ILD (Moiseff 1989b; Brainard et al. 1992). Another explanation for the increase in elevational variance might be that the auditory image is broadened and more diffuse in barn owls, as it is in humans. The behavioral results suggest that although there is no compact auditory image in the horizontal plane, there is a detectable and localizable image in the vertical plane.

### Electrophysiology experiment

The ability of owls to localize based on the ILD of a binaurally uncorrelated signal suggests the existence of ILD sensitive neurons in the auditory system that maintain their tuning in the absence of binaural correlation. This hypothesis is borne out by the observation that ILD encoding in VLVp neurons is unaffected by the degree of binaural correlation. The midbrain target of VLVp, the central nucleus of the inferior colliculus (ICc), therefore receives an ILD signal for binaurally uncorrelated noise which is indistinguishable from that for binaurally correlated noise. At the level of the ICc there are two parallel pathways by which auditory spatial information can access head movement circuitry: one collicular pathway through the OT (Knudsen 1982; du Lac and Knudsen 1990) and one thalamic pathway through nucleus ovoidalis (Knudsen et al. 1993). However, experiments on neurons in the OT (Sabeti et al. 1998) have shown that these neurons do not fire in response to binaurally uncorrelated noise. The collicular pathway, therefore, cannot support the observed response to the ILD of binaurally uncorrelated noise. This is mostly likely because space-specific neurons in this pathway are obligatory AND gates for ITD and ILD input (Pena and Konishi 2001). BC=0 stimuli, which contain no coherent ITD, eliminate ITD tuning and would not activate such neurons.

The results of these experiments strongly suggest that information about the elevation of a binaurally uncorrelated stimulus is available to the forebrain circuit that produces head saccades to auditory targets. The fact that a stimulus exists that can be processed by one sound localization pathway and not the other suggests that the generation of space specificity is different in the two pathways. Perhaps there is a simple difference in the convergence of ILD and ITD information, or perhaps the difference reflects a more general ability of the telencephalic auditory pathway to deal with ambiguous or incomplete information.

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**Table 1** Correlation coefficients ( $r$ ) and  $F$  statistics calculated from spikes as a function of interaural level difference (ILD) for binaural correlation (BC)=1 versus BC=0 for 11 well-isolated neurons in the posterior part of the ventral nucleus of the lateral lemniscus (VLVp). All values of  $F$  are statistically significant at  $P < 0.01$

$r$	$F = \frac{1+r}{1-r}$
0.97	65.7
0.85	12.3
0.99	199.0
0.98	99.0
0.93	27.6
0.96	49.0
0.74	6.7
0.98	99.0
0.99	199.0
0.83	10.8
0.95	39.0

programs used in data collection. These experiments comply with the "Principles of animal care", publication No. 86-23, revised 1985 of the National Institutes of Health and also with the current laws of the United States.

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