The role of spectral cues in sound localization by the barn owl

Thesis by

S.E. Roian Egnor

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I have not felt to warble and trill, however sweetly,
I have felt to soar in freedom and in the fullness of power,
joy, volition.

Walt Whitman

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The one constant in my time at Caltech has been the incredibly wonderful people in my life. Members of the Konishi lab, past and present, have taught, cajoled, supported, teased, and generally molded me into a reasonably competent scientist. Of particular note are: Ben Arthur, whose friendship, humor, and help have been wonderful; and Kourosh Saberi, who withstood interminable questioning with grace and who has never failed to encourage me. I also want to thank Ben, Jamie Mazer and Chris Malek, whose computer programs I used for data collection; Gene Akutagawa for sharing his mastery of histology; and Jose-Luis Pena, the Pena Foundation, and Svenja Viete, who made the lab a civilized place. I am indebted to Mark Konishi for subtlety, clarity, kindness and wisdom; I learned an extraordinary amount in his laboratory.

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Finally, I would like to thank my partner, Anthony Leonardo, for infinite support and patience, and for making me happy.

Abstract:

The barn owl (*Tyto alba*) is a nocturnal predator with excellent spatial hearing. Evolutionary pressure on the auditory system of the barn owl has produced numerous adaptations for processing spatial information; my dissertation addresses two new aspects of sound localization in this auditory specialist.

I. Barn owls have been shown to use interaural time differences (ITDs) and interaural intensity differences (IIDs) to localize the sources of sounds. Such binaural difference cues are also used by a variety of mammals, including humans. Mammals also exploit a monaural sound localization cue. When sound arrives at the eardrum it has been filtered by the external ear in a location- and frequency-dependent manner; this spectral cue underlies our ability to localize in the vertical plane. Recent measurements in barn owls have shown that spectral features similar to those thought to encode vertical position in humans also exist in barn owls. I show that radical variations in the monaural spectra which do not produce concomitant changes in the binaural difference spectrum have no effect on barn owl sound localization behavior. In contrast to humans, barn owls do make some use of the frequency-specific IID information in the binaural difference spectrum.

II. In order to use a binaural difference cue, the sound from a source that enters the left ear must be compared with sound from the same source that enters the right ear. This results in the perception of a single auditory image; this process is known as binaural fusion. One feature of sound which is important to fusion is the degree to which the sounds arriving at the two ears are correlated. The ability of both barn owls and humans to localize based on ITD is eliminated if binaural correlation is reduced to zero. However, I show that barn owls can extract the IID of a binaurally uncorrelated signal, and use that IID to control an auditory saccade. In addition I show that neurons in the thalamic auditory pathway, in contrast to the more well understood collicular auditory pathway, encode the IID of binaurally uncorrelated sounds.

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Chapter 1

Introduction

The sound from a snapped twig travels through the air at 340 m/s and is heard by a person walking in the woods. The arriving sound produces vibrations in the ear drum, which, transmitted and amplified by the bones of the middle ear, produce vibrations in the fluid-filled organ of hearing, the cochlea. Waves produced in the fluid of the cochlea activate auditory sensory cells called hair cells. Each hair cell responds only to sound in a given frequency range, and varies its response with the amplitude and phase of the incoming sound. The activation of hair cells produces action potentials in the auditory nerve, which make the first synapse in the central nervous system, on cells in the cochlear nucleus. Sound arriving at the ear is therefore broken down into its component frequencies, and information about sound intensity and phase is encoded in the action potentials in the auditory nerve. From this incoming information a person can perceive the direction and distance to the snapped twig, its identity (thickness, approximate load required to break it), and formulate a response: a small twig requiring a light body to snap located far ahead may induce a slow head turn, whereas a large twig requiring a very heavy body to snap located immediately behind may produce a vertical leap of several feet and a hasty and undignified retreat. This thesis is concerned with the auditory cues and neural circuits involved in determining the location of sound sources.

A brief review of sound localization cues:

There are two broad classes of cues for sound localization--those that depend on a comparison of the sounds arriving at the two ears (binaural cues) and those that require an analysis of the arriving sound across frequency (spectral cues).

Binaural sound localization cues:

In humans, there are two types of binaural cues: interaural time differences (ITDs) and interaural intensity differences (IIDs). Both IID (Venturi, 1796; Rayleigh, 1877) and ITD (Rayleigh, 1907) encode horizontal sound source position in humans. Interaural time differences arise as a result of differences in path length from a sound source to the right and left ears, whereas interaural intensity differences arise as a result of differential attenuation by the head of the sound arriving at the two ears.

ITD:

Humans can detect ongoing interaural phase differences in the fine structure of long duration sounds (Licklider et al., 1950; Zwislocki & Feldman, 1956), in the envelopes of amplitude and frequency modulated sounds (Henning, 1974; McFadden & Pasanen, 1978), and in the onset times of clicks (Stevens and Newman, 1936). When a sound source is on the right of the midline, the path to the right ear is shorter than the path to the left ear--producing a right-ear-leading ITD. The use of ITD depends on the ability of the auditory system to encode time. In humans ITD encoding is most accurate for frequencies below about 1.3 kHz (Middlebrooks and Green, 1991) and ITD encoding, and thus the ability to localize based on ITD declines sharply at progressively higher frequencies.

IID:

A sound source located to the right of the midline will also be attenuated at the left ear relative to the right ear because of the acoustic shadow produced by the head, producing a right-ear-louder IID. IIDs are small for sounds with wavelengths that are larger than the diameter of the head (the head is not an effective sound barrier) and larger for wavelengths that are smaller than the diameter of the head.

The duplex theory:

ITD is therefore important for determining the horizontal location of low frequency sound, while IID is important for determining the horizontal location of high frequency sound; this arrangement is referred to as the duplex theory. The dip in human horizontal sound localization accuracy at about 1.5-3 kHz (Stevens & Newman, 1936; Sandel et al., 1955) is attributed to these frequencies being at the border between ITD and IID cues: too high for good ITD encoding but too low to produce a significant IID.

Spectral sound localization cues:

Spectral cues arise from the location-dependent filtering of the sound spectrum produced by the head, pinnae, and shoulders. The shape of these head-related transfer functions (HRTFs) varies with the horizontal and vertical position of the sound source. In general HRTFs are used for vertical localization only (Batteau, 1967; reviewed in Middlebrooks and Green, 1991), although people who are monaurally deaf from birth can use HRTFs to localize in both the horizontal and vertical planes (Slattery and Middlebrooks, 1994). Because the spectrum received at the eardrum is a combination of the source spectrum and the transfer function of the ear, the use of spectral cues for sound localization requires some knowledge or assumptions about the source spectrum (Blauert, 1969/1970; reviewed in Middlebrooks and Green, 1991).

Auditory scene analysis:

Localizing a sound source is intimately related to perceiving it as an object. In a normal acoustic environment the time-varying sound pressure waveform that arrives at the ear is composed not only of the superposition of multiple sounds that can overlap in time, frequency, and source location, but also of multiple echoes of each sound. This sound-source separation problem is solved automatically and extremely accurately by the auditory system (with a level of accuracy and speed that is as yet unmatched in engineering). Our perception of the location of an object depends heavily on a comparison of the sounds arriving at the two ears. How is acoustic information about object A that enters the left ear matched with information about object A that enters the right ear? The auditory system seems to have evolved to take advantage of most of the potential cues to "fuse" information from the left and right ears into a single object; this process is called binaural fusion. Common fate (common onset and offset time, common amplitude- and frequency-modulation), harmonic relatedness, common ITD and IID, and binaural correlation all contribute to the percept of a single, compact sound object (Bregman, 1990). Although all of these cues have been shown to contribute to auditory object formation, some cues carry more weight than others. For example, when the ITD information about the number of objects and harmonic relatedness information about the number of objects are opposed artificially (using stimuli presented over headphones), the auditory object perceived is consistent with the information conveyed by harmonic relatedness (Buell and Hafter, 1991).

Auditory processing in the central nervous system:

Information in the auditory nerve:

Movement of a hair cell by a stimulating sound opens a mechanically sensitive ion channel; this direct activation allows signal transduction to be both very sensitive (detection is limited by the thermal motion of the detector [Hudspeth and Gillespie, 1994]) and very fast. The mechanical sensitivity of hair cells is directional and graded: movement of a hair cell in one direction increases transmitter release, movement in the opposite direction reduces transmitter release, and the magnitude of increase or decrease depends on the amplitude of the deflection. As activation of hair cells tends to be sinusoidal, this produces sinusoidal transmitter release and thus rhythmic action potentials in the auditory nerve. For low frequencies of sound these action potentials occur at the same phase of the stimulating sound and are said to be "phase-locked." As stimulus intensity (deflection amplitude) increases, the number of action potentials produced increases. Hair cells are sensitive to sound of a restricted range of frequencies. Thus action potentials in the auditory nerve encode the frequency, intensity, and phase of the stimulating sound.

Calculation of ITD:

Most models of binaural hearing include some type of cross-correlation to extract ITD information and a physiologically plausible structure capable of doing so was proposed by Jeffress (1948; Figure 1). The Jeffress model consists of delay lines from the left and right ear, and a mechanism that detects coincident input from the left and right delay lines. In the model, the interaural time delay created by different sound pathlengths outside the head is offset by a neural time delay inside the head; as action

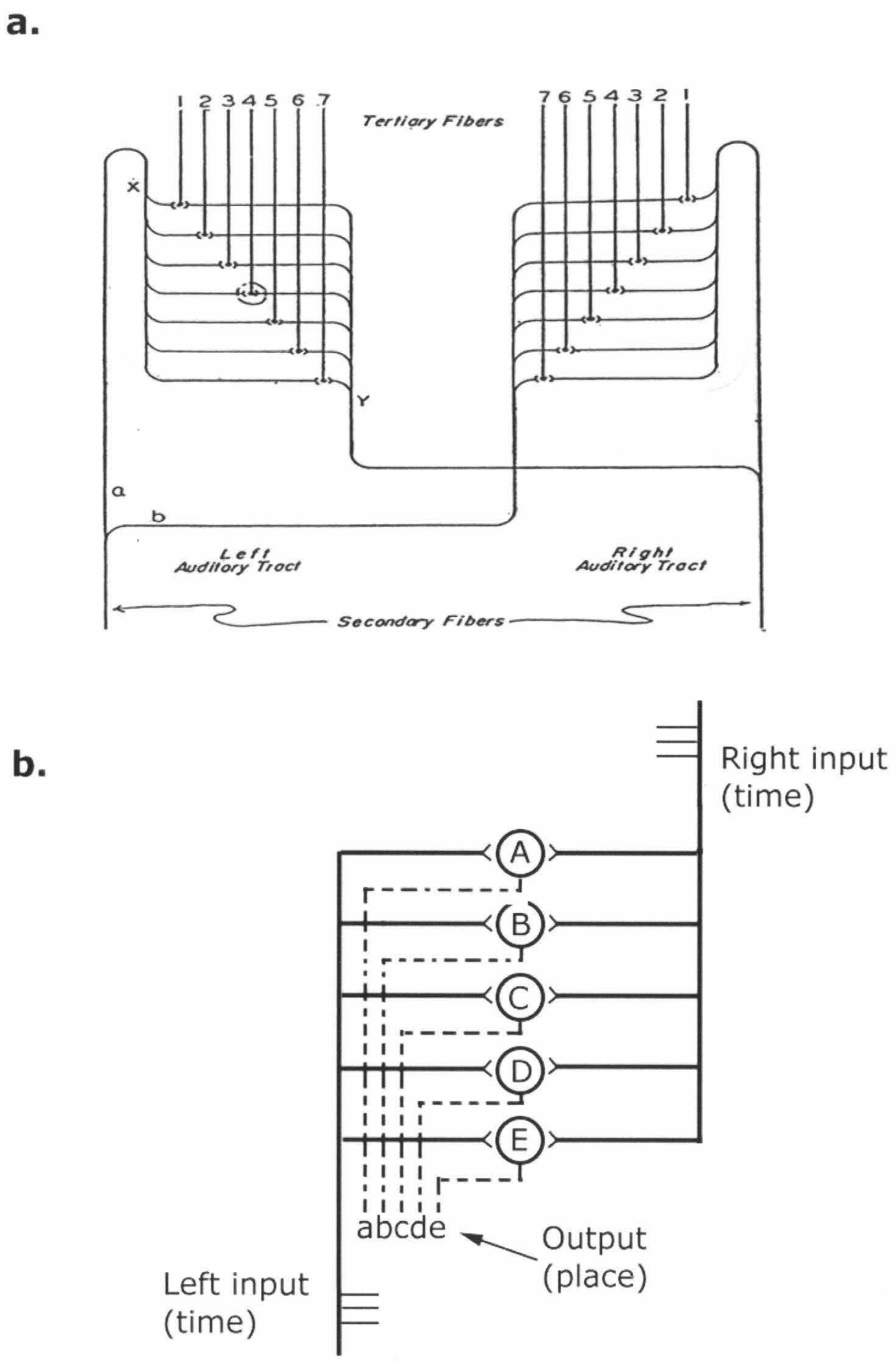


Fig. 1. A place code model of ITD measurement. a) the original model as envisioned by Jeffress in 1948 (while visiting professor of psychobiology at Caltech). b) A modern version of the model, after Konishi et al., 1988.

potentials travel through the circuit, the location of coincidence changes depending on the ITD of the sound. Physiology consistent with such a structure was shown in the dog medial superior olive (MSO; Goldberg and Brown, 1969), a potential anatomical substrate was demonstrated in the chick nucleus laminaris (NL) (Young and Rubel, 1986), and both physiology and anatomy were shown in the barn owl NL (Carr and Konishi, 1988). Because the extraction of ITD depends on phase-locked action potentials, what is encoded is in fact interaural phase difference (IPD), rather than ITD. The response rate of a neuron tuned to IPD as a function of ITD is periodic, i.e., sounds with different ITDs will activate the neuron (Figure 2). This situation is referred to as phase ambiguity. If the sound wavelength is long relative to the diameter of the head (as is the case with humans) this poses no difficulty for localization, as ITDs that would activate a neuron selective for a particular IPD cannot occur.

Maps of auditory space:

Unlike the maps of the retina, the cochlea, or the body surface, a map of auditory space is not a simple projection from a sensory epithelium, but a structure that is generated (Konishi, 1986). The ability of a neuron to respond to a particular location in space is the consequence of many

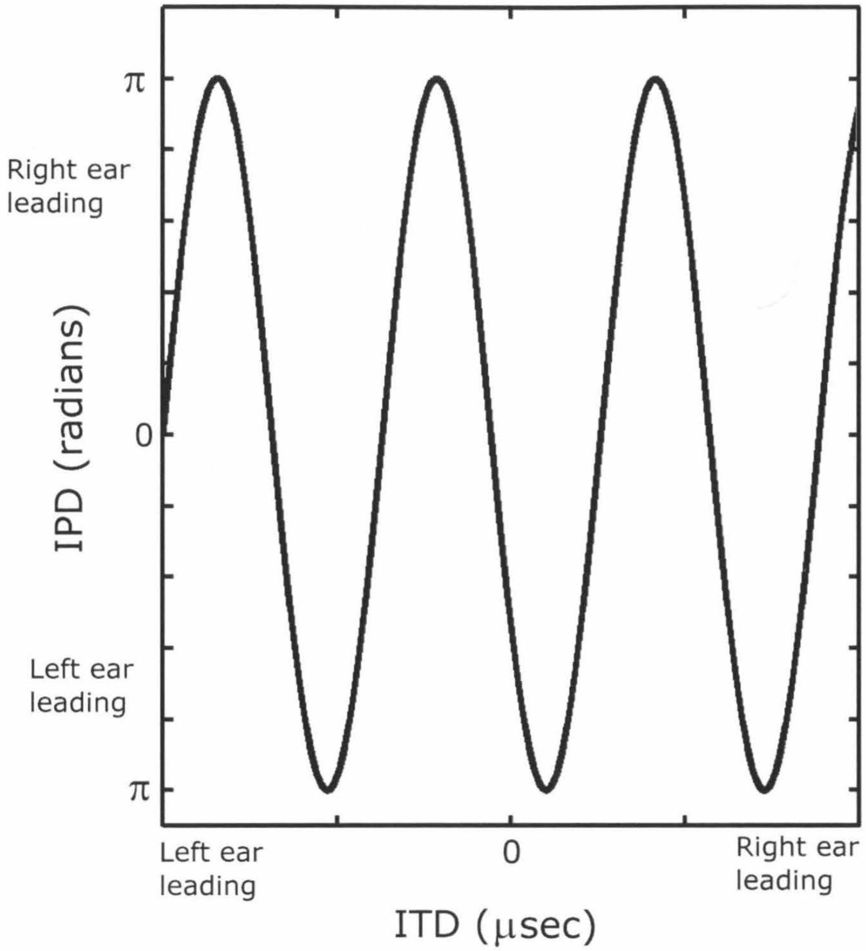


Fig. 2. The response of a neuron to interaural phase difference (IPD) is periodic as a function of interural time difference (ITD).

levels of processing. Neurons sensitive to sound coming from a specific location in space do not necessarily have to be arranged in a map, for example space-specific neurons in Field L of the barn owl are organized according to frequency (Knudsen et al., 1977). Maps of auditory space have been demonstrated in the midbrains of many animals (barn owl: Knudsen and Konishi, 1978; guinea pig: Palmer and King, 1982; cat: Middlebrooks and Knudsen, 1984; bat: Wong, 1984; ferret: King and Hutchings, 1987).

The barn owl -- a sound localization specialist:

The barn owl is a medium sized owl (about 40 cm) and has the widest geographical distribution of any land bird. Like most owls it is a nocturnal predator. The characteristic heart-shaped face of the barn owl is one of many evolutionary adaptations that give the barn owl its excellent spatial hearing (Payne and Drury, 1958; Payne, 1971; Konishi, 1973). This facial disk is a row of densely packed (hexagonally-closest) highly specialized feathers, that surround the ear canal opening. Feathers in the facial ruff (analogous to the pinnae) have extremely thick, flattened shafts (rachises). The feathers that cover the face are auricular feathers, which, as the name implies, are usually only found in the ear. Auricular feathers are nearly acoustically transparent. The facial ruff has been shown to amplify incoming sound by about 15 dB dB, depending on frequency (Coles and Guppy, 1988; Keller et al., 1998). This amplification drops the barn owl's auditory threshold to between -10 and -20 dB SPL, i.e., barn owls are able to detect sounds that are 3-10 times quieter than sound at human threshold (Konishi, 1973; Dyson et al., 1998).

Several species of owls have asymmetrical ears, and ear asymmetry appears to have arisen independently at least 5 times (Norberg, 1977; Pycraft, 1898). In barn owls the asymmetry is in the feathers of the facial ruff, in the vertical location of the ear canal openings, and in the vertical location of the preaural flaps. Pumphrey (1948) and Southern (1955) suggested that such an asymmetry might confer a sound localization advantage in hunting. The asymmetry in the barn owl's facial ruff is such that sound from sources above the horizon are louder in the right ear and sounds from sources below the horizon are louder in the left ear. This means that IID varies with the vertical position of a sound source rather than with the horizontal, as it does in symmetrically eared animals (Payne, 1971). The slope of the iso-IID contours varies as a function of frequency, becoming more horizontal at higher frequencies.

Early experiments (Knudsen and Konishi, 1979) showed that the barn owl, unlike humans, is able to use ITD information up to 8 kHz. Because of the small size of the owl's head (4 cm) and hearing range (0.5-12 kHz), barn owls should experience phase ambiguity over most of their hearing range. When the ability of barn owls to localize pure tones was tested, it was found that they did, in fact, occasionally respond to multiple locations for a single speaker position; however this never occurred in response to broadband sound. Further investigation showed that while NL neurons do exhibit phase ambiguity over the normal range of ITDs experienced by the owl (~200 microseconds leading in either ear, see Figure 3, a), neurons in the auditory space, map do not (Figure 3, b). The elimination of phase ambiguity, which is essential for the production of neurons with azimuthal space-specificity, relies on a convergence of IPD information across frequency. There are several time encoding specializations that support the measurement of high-frequency ITDs. Barn owl auditory nerve fibers have significant phase locking up to about 9 kHz (Sullivan and Konishi, 1984; Koppl, 1997), the terminals (endbulbs of Held) of auditory nerve fibers onto neurons in the cochlear nucleus magnocellularis (NM) are specialized to maintain phase information (Carr

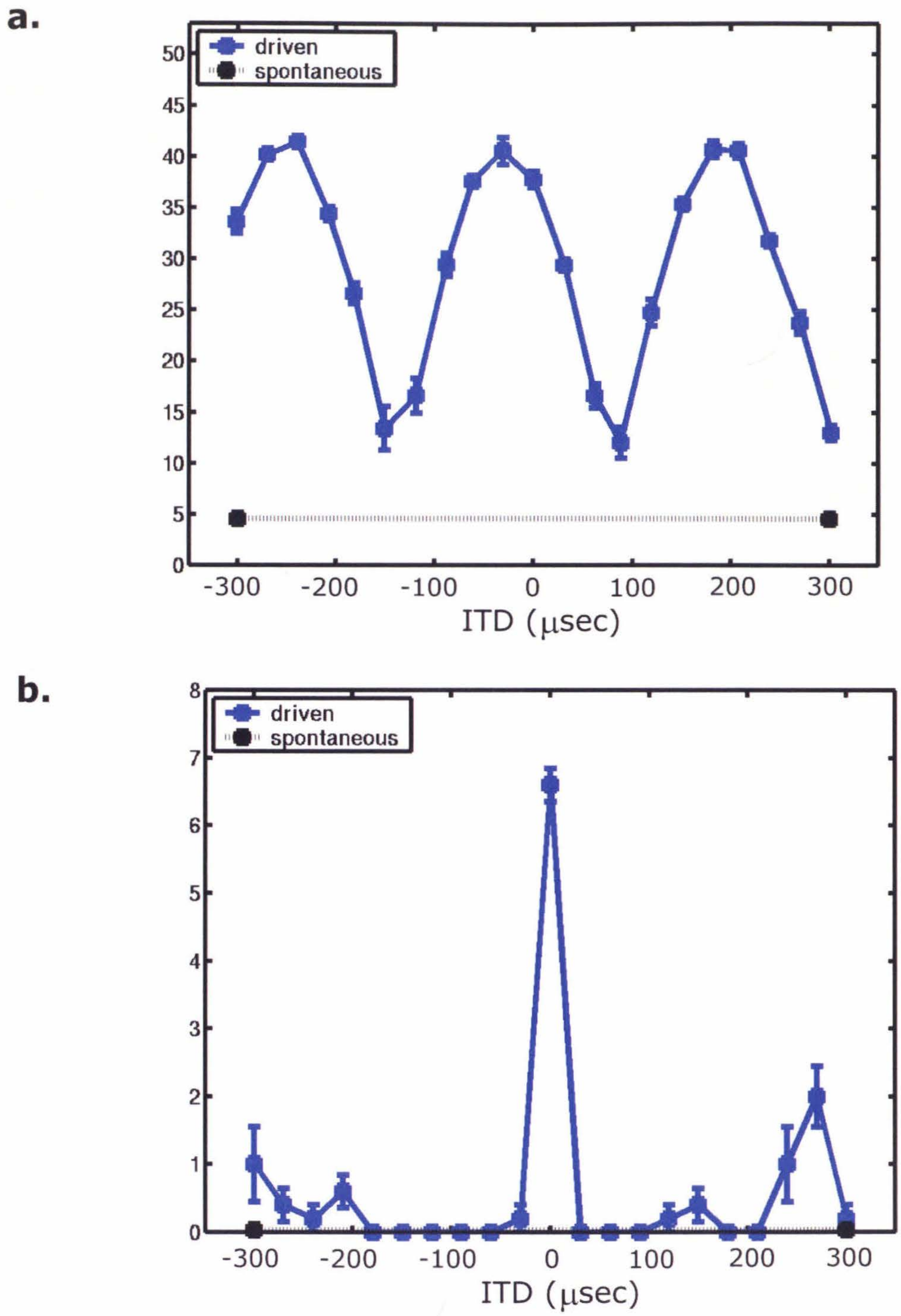


Fig. 3 Response of neurons at different levels of the auditory pathway to variations in interaural time difference (ITD).
a) Neurons in nucleus laminaris (NL) are phase-ambiguous.
b) Neurons in external nucleus of the inferior colliculus (ICx) are space-specific. (Data courtesy of Dr. Jose-Luis Pena).

and Boudreau, 1991), and the projection from NM to nucleus laminaris (NL) is also specialized to maintain phase information: inter-node-of-Ranvier distances on NM axons are unusually short and have unusually low variance (Carr and Konishi, 1990).

Responses to novel sound-localization stimuli in the barn owl:

Although there have been many suggestions based on the acoustics of the barn owl's external ears that spectral cues may be used for localization, and although several electrophysiological and developmental studies show some frequency dependence on sound localization (Knudsen et al., 1991, Gold and Knudsen, 1999), there has been no direct test of the ability of barn owls to use spectral cues for sound localization. This thesis presents data from a series of experiments designed to test this basic question. The results of a preliminary experiment on the use of spectral cues (Chapter 2), though ambiguous regarding the existence of such cues, revealed the possibility of a different, previously unknown sound-localization cue. Chapter 3 addresses this new cue explicitly, and chapters 4 and 5 test the effects of this cue on neurons in the auditory pathway known to be involved in sound localization. Chapter 6 takes advantage of a new technique that allowed me to test the existence of spectral cues explicitly and determine whether such cues are monaural or binaural in nature.

Chapter 2

Effect of a monaural plug on sound localization

Many of the experiments that demonstrate the existence of spectral cues have investigated sound localization ability in monaurally deaf subjects (either natural monaural deafness or artificial monaural deafness simulated with an acute monaural plug). When sound is received at only one ear, any correspondence between binaural difference cues (ITD and IID) and the location of the sound source is removed. Any residual accurate localization must therefore rely on monaural, presumably spectral, cues. There is general agreement that spectral cues are the primary cue for vertical sound localization (Batteau, 1968; Bauer and Blackmer, 1965; Oldfield and Parker, 1986; Butler et al, 1990; Hebrank & Wright, 1974; reviewed in Middlebrooks and Green, 1991). In certain circumstances, monaural cues can also be used for horizontal localization: some people who are congenitally monaurally deaf are capable of good localization in both the horizontal and vertical planes (Slattery and Middlebrooks, 1994), some early experiments found good localization in both horizontal and vertical planes (Angell and Fite, 1901; Hocart and McDougall, 1908; Feree and Collins, 1911; Jongkees and van der Veer, 1958; Bauer, et al.

1966; Fisher and Freedman, 1968; Perott and Elfner, 1968; Starch, 1908), and changing the source spectrum can change the perceived horizontal position of the sound source in people with a monaural plug (Butler and Flannery, 1980; Musicant and Butler, 1985; Butler, 1986), suggesting a role for spectral information in horizontal sound source localization.

Although there is considerable debate about the efficacy of acute monaural plug experiments at producing truly monaural stimuli, and about the interpretation of different experiments, it is clear that monaural plugs demonstrate the presence of a sound-localization cue that does not depend on interaural comparisons.

There have been a handful of experiments on the acute effects of monaural plugging in the barn owl. However, these experiments used plugs that attenuated, rather than eliminated, sound transmission to the plugged ear (Knudsen and Konishi, 1979), did not describe the effect of complete monaural plugging in detail (Knudsen et al., 1984), and did not report whether the plugs eliminated sound transmission completely (Knudsen et al., 1984). Studies with humans have suggested that even a small amount of sound leakage through a monaural plug makes the interpretation of any resulting “monaural” sound localization difficult (Wightman and Kistler, 1997). Therefore, the first step to demonstrating the use of spectral cues by the barn owl is to investigate effect of a complete, acute monaural plug on barn owl sound localization.

2.1 Methods:

Training:

Hand-raised owls were trained to sit on a perch in a large anechoic chamber (Industrial Acoustics Company, Inc., 5 m x 3 m x 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. For a schematic of the behavioral setup, see figure 4 (headphones are used in later experiments).

Monitoring head position:

Adult barn owls were fitted with small metal mounting tabs for the head-

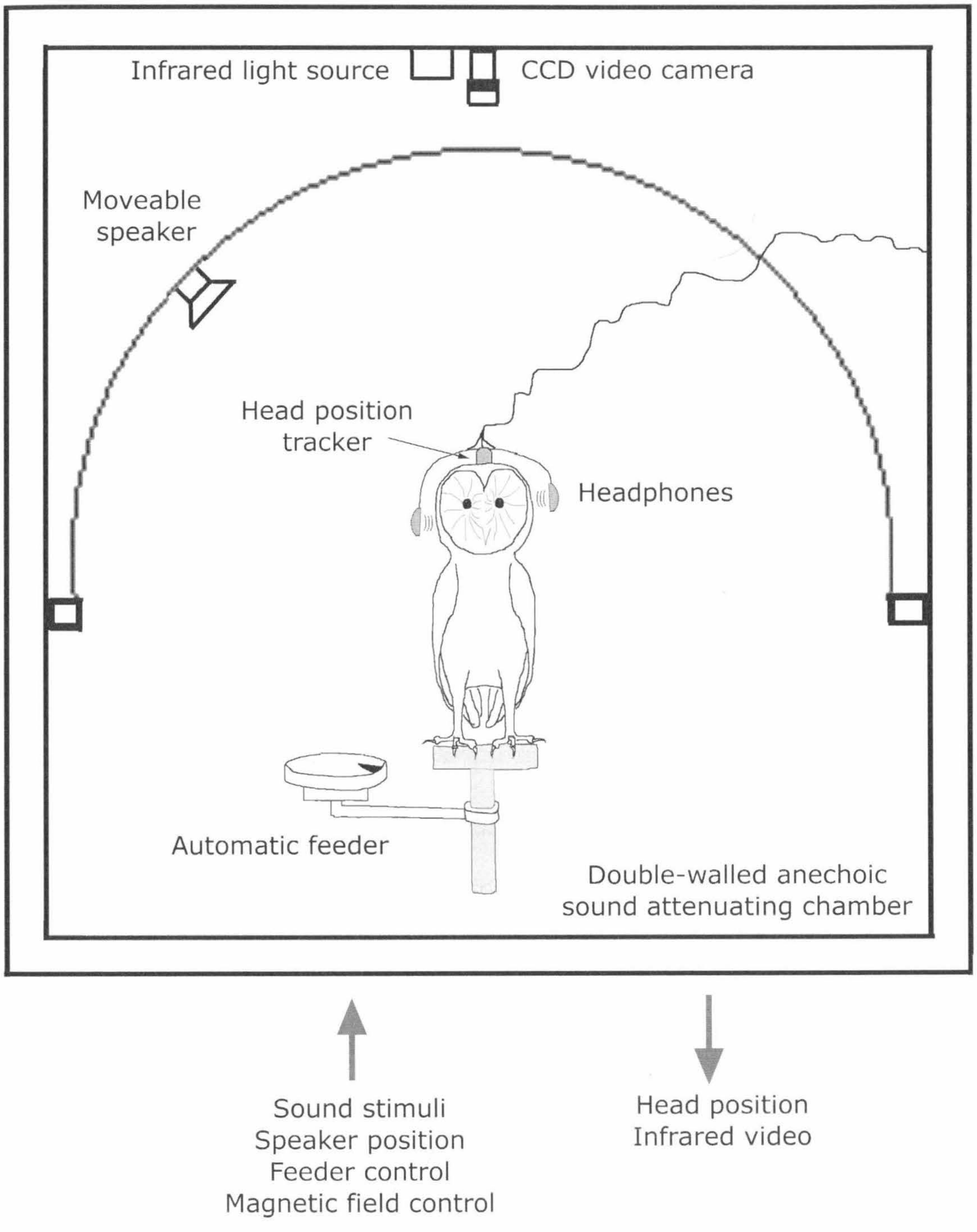


Fig. 4. Schematic of behavioral data collection setup

position tracker using the following procedure: the owl was deeply anesthetized with intramuscular injections of ketamine hydrochloride (20 mg/kg) and diazepam (0.1 mg/kg), the feathers on the top of the head were plucked, the skin was cleaned with an antiseptic solution (chlorhexidine gluconate, .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 75 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 hours before being returned to their home cages.

Before each session the owl was placed on the perch and the head coil was attached to the mounting tab. The head coil consisted of three orthogonally oriented coils of wire, with a diameter of 3 cm. The perch was surrounded by three pairs of magnetic induction coils, one pair operating at 25 kHz with sine phase, one pair at 11 kHz with sine phase, and the third pair operating at 11 and 25 kHz at cosine phase. This "phase coil" setup allowed the head position to be monitored continuously. The voltage induced in the three headcoils at the two frequencies is proportional to the angle of the head within the magnetic field. The use of sine and cosine phase allows the translation of amplitude differences in the induced current (which are hard to measure) into phase differences in the induced current (which are easier to measure). The voltage signals were digitized at 256 Hz by a custom built computer card (B.E.S.) installed in a PC.

Ear plugs:

A 10 cc syringe was filled with newly mixed ear mold compound (Gold Velvet II, All American Mold Laboratories) and the compound was injected, while still soft, deeply into the owls external auditory meatus. A sufficient quantity was injected to completely block the ear canal. Care was taken to leave a large “handle” on the outside so that the plug could be removed. Auditory stimuli were not presented until the plug had hardened. Plugs were removed after each testing session. The attenuation of the plug was measured by using an owl that had been implanted with probe tubes for an experiment by Ben Arthur, another member of the lab. The probe tube ran from the skin behind the ear to approximately 2 mm from the tympanum; there was one probe tube in each ear. Small microphones (Knowles Electronics, ED-1939) were coupled to the probe tubes using short pieces of polyethylene tubing. Pure tones of different frequencies were played from the target speaker and the amplitude of the sound was measured at each frequency in the absence of a plug. A monaural plug was then introduced and allowed to harden and amplitude measurements at the same frequencies were taken. The attenuation of the plug was then calculated as the difference between the unplugged and plugged conditions (Figure 5).

Sound stimuli:

Target sounds consisted of segments of white noise, 50 ms long, bandpassed from 4 kHz to 13 kHz, with 10 ms on and off ramps. The low end of the passband was chosen because plug attenuation was lower for lower frequencies, and because the owl's interaural canal allows sound leakage from the open ear at low frequencies (Moiseff and Konishi, 1981). The high end of the passband is slightly above the high end of the owl's hearing range. Sound intensity was calibrated using a 1" Brüel & Kjær microphone (model 4179) with a sensitivity of 101 mV/Pa positioned where the owl's head would be during testing. Target sounds were played at 10 dB SPL, which insured no leakage through the plug. Testing took place in a large (3 m x 5 m x 5 m) double-walled, sound-attenuating anechoic chamber (Industrial Acoustics Co., Inc).

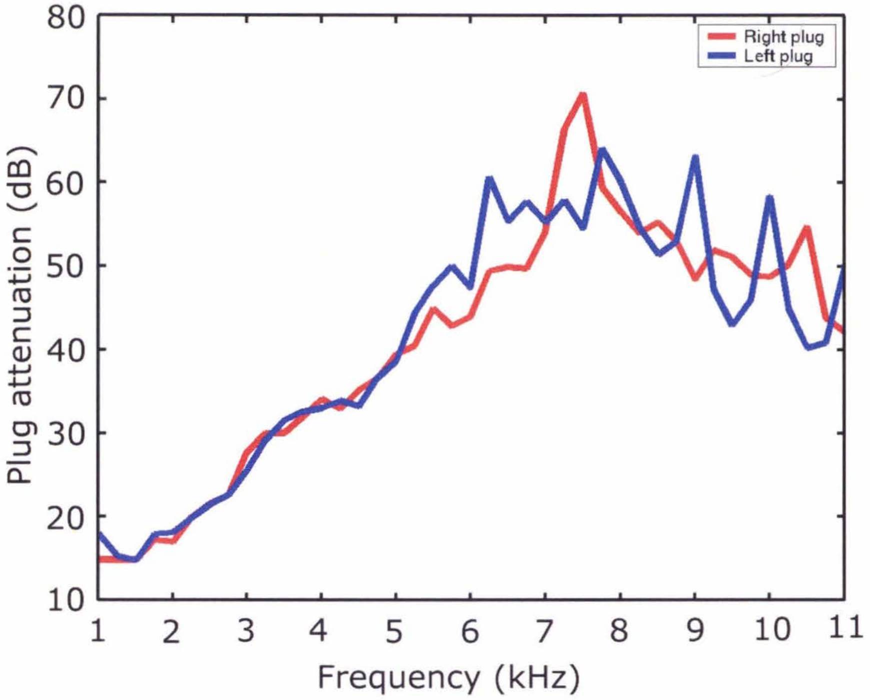


Fig. 5. Ear plug attenuation as a function of frequency

Coordinate system:

Stimulus locations are described in terms of their double-pole coordinates (described in Knudsen et al., 1979), which describes the horizontal and vertical location of the speaker on a sphere whose center is the owl's head. The elevation of the speaker relative to the owl's head is related to the elevation of the hoop by the equation:

$$\textit{elevation} = \arcsin(\cos\alpha \sin\theta)$$

where α is the azimuthal position of the speaker and θ is the elevation of the hoop.

Presentation of stimuli:

Sounds were played over a small (6 cm diameter) speaker mounted on a hoop with a radius of 1 meter. The speaker could be moved horizontally on the hoop and the angle of the hoop could be changed, which allowed stimulus presentation from anywhere from +/- 80 degrees azimuth and +/- 80 degrees elevation.

Experimental Session:

To insure that the owl's head turns were indicative of where the sound was located, each experimental session started with about 10 trials of normal sound localization. If the owl was not performing well during these trials the session was aborted. If the owl's sound localization performance was normal, one ear was plugged, and approximately 20 plugged trials were collected. The side that was plugged was alternated on successive sessions. The owl was rewarded for the first ballistic head movement after zero fixation during the monaural plug phase (regardless of direction). At the end of each session the plug was removed and another 10 trials of normal sound localization were presented.

2.2 Results:

Unplugged condition:

Both owls varied their final head position with the location of the target speaker (fig 6., black symbols). Final head position versus speaker location for both horizontal and vertical planes was well fit by a linear regression for both owls (table 1). The average standard deviation of final head positions was under 2 degrees in the horizontal plane and under 3

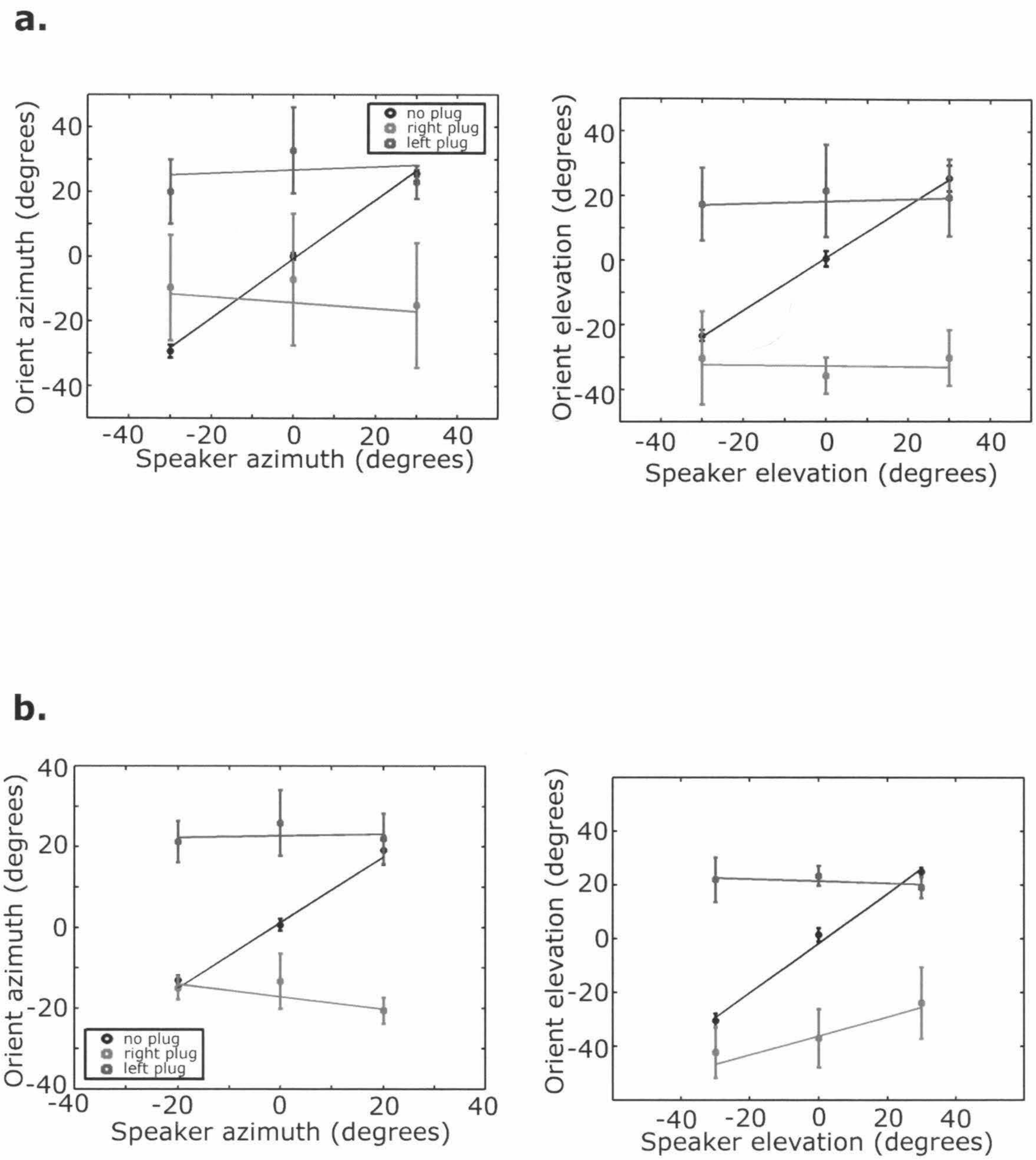


Fig. 6. The effect of monaural plugging on orient accuracy. a) final head position in azimuth and elevation for left plug (●), right plug (●), and unplugged (○) conditions for Io. b) The same data for Callisto.

a.

	Speaker Azimuth versus Orient Azimuth					
	Unplugged		Right Plug		Left Plug	
	slope	r^2	slope	r^2	slope	r^2
Io	0.91	0.99	-0.09	0.01	0.05	0.01
Callisto	0.81	0.94	-0.15	0.04	0.02	0.001

b.

	Speaker Elevation versus Orient Elevation					
	Unplugged		Right Plug		Left Plug	
	slope	r^2	slope	r^2	slope	r^2
Io	0.81	0.98	-0.01	0.001	0.04	.004
Callisto	0.92	0.98	0.35	0.31	-0.04	0.02

Table 1. Effect of monaural plugging on orient accuracy. a) Azimuthal accuracy. b) Elevational accuracy.

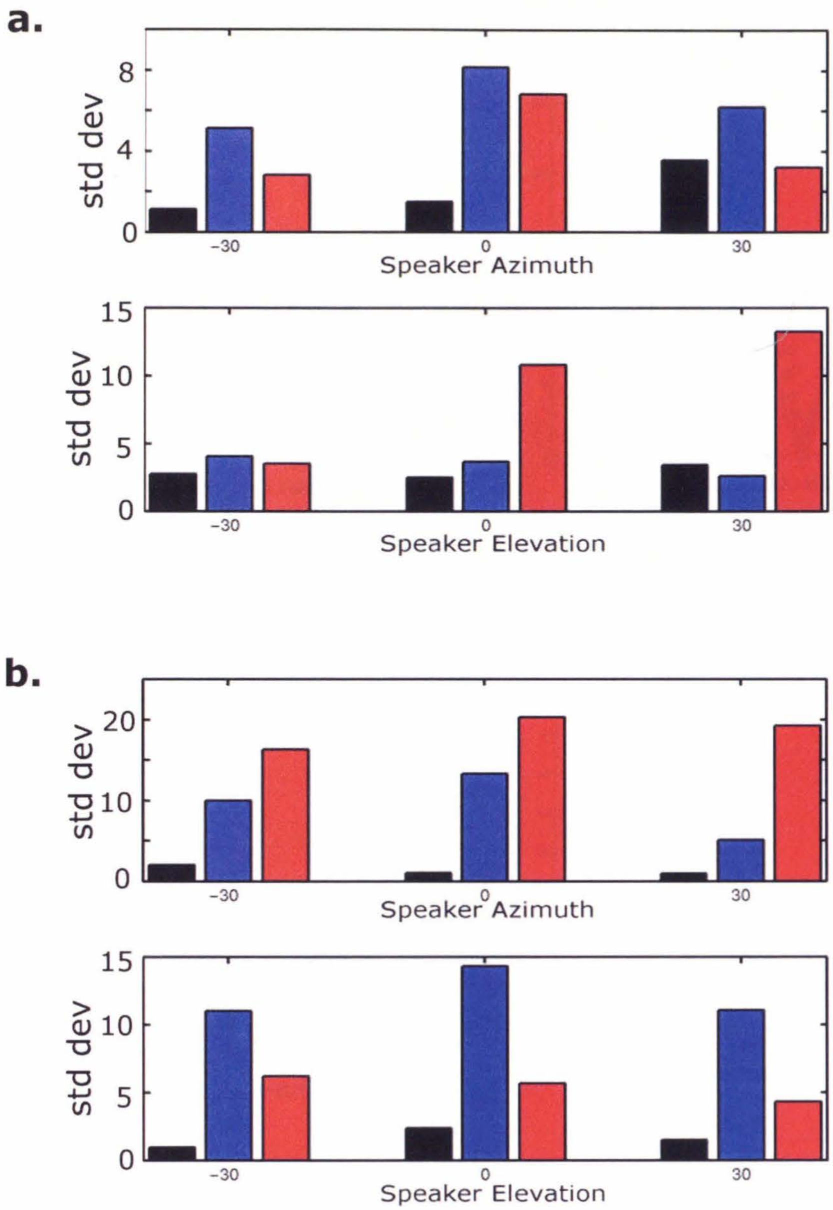
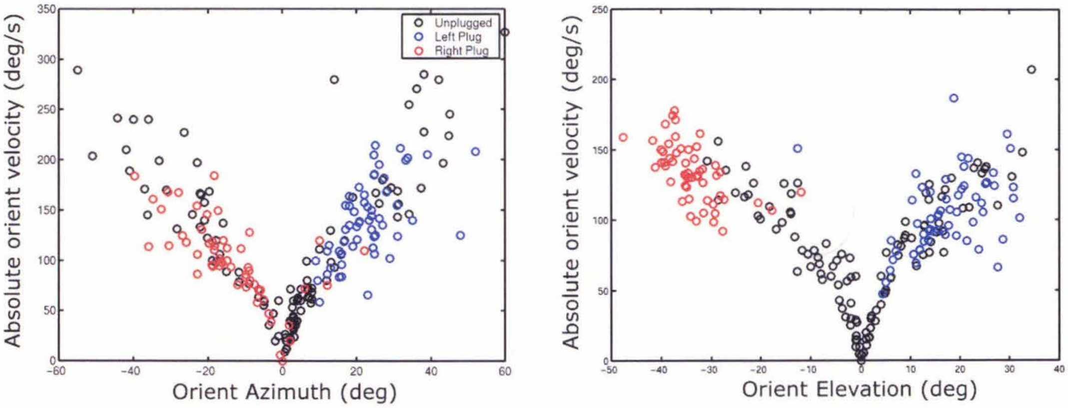


Fig. 7. The effect of monaural plugging on orient precision. a) Data for Callisto. b) Data for Io.

a.



b.

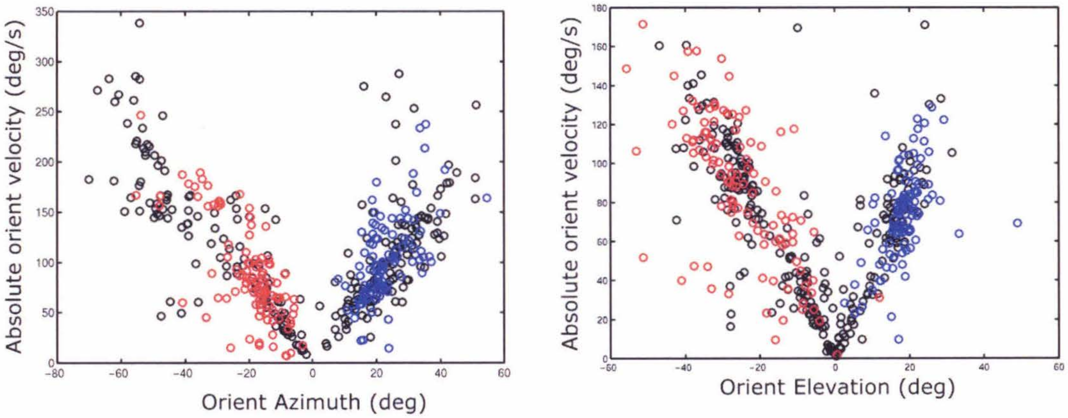


Fig. 8. The effect of monaural plugging on orient velocity.
a) Data for Io. b) Data for Callisto

degrees in the vertical plane for both owls (Figure 7). Orient speed increased as orient magnitude increased (Figure 8, black symbols).

Plugged conditions:

For both right and left monaural plugs neither the azimuth nor the elevation of final head position was positively correlated with the location of the target speaker (fig 2, red and blue symbols). Both owls looked up and to the right for all locations of the target speaker when wearing a left plug, and down and to the left for all locations of the target speaker when wearing a right plug. The goodness of fit of the linear regression was low for both owls and both plug conditions (table 1). Variance of final head position was generally, though not always, larger in plugged versus unplugged orients (Figure 3). Average orient magnitude was approximately the same for all speaker locations. The orient velocities in the plugged condition varied as a function of orient magnitude and were similar to those in the unplugged condition (Figure 4, blue and red symbols).

2.3 Discussion:

Barn owls with a monaural plug show no residual sound localization ability, which suggests that monaural spectral cues are not used. In humans, when spectral cues are removed by filling in the pinnal convolutions of the open ear, sounds from any location in space are perceived as coming from a restricted area on the side of the open ear (Oldfield and Parker, 1986). The sound-orienting response of barn owls wearing monaural plugs is very similar to the response of humans using this restricted cue.

The existence of monaural spectral cue use in barn owls cannot be completely ruled out, however, because of the radical changes in binaural difference cues produced by monaural plugging (Wightman and Kistler, 1997). Monaural plugs do not remove binaural difference cues; rather, they change these cues. The auditory system receives normal excitatory input from the unplugged ear and spontaneous activity from the hair cells in the cochlea of the plugged ear. All sounds will therefore have an open-ear-louder IID and no coherent ITD across frequency. Thus, although monaural plugs remove any correspondence between binaural difference cues and sound source location, allowing any monaurally based sound localization to be observed, they also introduce a mismatch between the monaural and binaural estimates of sound source location. This mismatch may prevent the expression of monaural localization. In humans the effect of this binaural/monaural mismatch can be seen in the bias in horizontal localization seen in many studies of monaural localization: sound sources are perceived as coming from the side of the open ear (Belendiuk and Butler,1975; Butler and Naunton, 1967; Butler and Planert,1976). Vertical localization is relatively unaffected by monaural plugging in humans, probably because there are no binaural difference cues for vertical localization, and thus no mismatch. In the barn owl, however, IID encodes elevation and ITD encodes azimuth, and thus a monaural plug will produce a mismatch between the known binaural cues and the putative monaural cues. In addition, monaural plug experiments suffer from the same technical difficulty: sound may leak through the plug and despite all efforts to the contrary, the stimuli may not be completely monaural.

The response of barn owls fitted with monaural plugs to auditory stimuli was surprising since several lines of evidence suggest that space-specific neurons in the barn owl auditory midbrain are less active, or silenced completely, in the absence of a coherent ITD signal. Knudsen and Konishi (1980) showed that about a third of neurons in the ICx were silenced by a tight monaural plug, even for stimuli that were probably not completely monaural. More recent experiments by Saberi and colleagues (1998) have explicitly addressed the dependence of space-specific neurons on coherent ITD, by using binaurally uncorrelated noise as a stimulus. Two independently generated white noises have, by definition, a correlation of zero. Since ITD is extracted using a cross-correlation-like function, binaurally uncorrelated noise also has no coherent ITD. This stimulus allowed Saberi et al. to investigate the effect of varying levels of binaural correlation on the spike rate and space-specificity of OT neurons. They found that when binaural correlation was reduced to zero, OT neurons did not fire significantly differently than their spontaneous rate. Thus, any auditory orient (accurate or not) by barn owls to monaural stimuli cannot be supported by the tectal pathway.

Chapter 3

Behavioral response to binaurally uncorrelated noise

Most neurophysiologically plausible models of binaural hearing include some type of binaural cross-correlation (e.g. Colburn and Durlach, 1978; Saberi, 1995; Trahiotis and Stern, 1995; Colburn, 1996). Cross-correlation models not only account for ITD extraction from broad-band and tonal signals, but also are able to predict a wide variety of psychoacoustic responses to variations in the binaural correlation of the stimulating sound.

Effect of binaural correlation on cross-correlation functions:

The location in time of the peak of a cross-correlation function 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 (ρ) of one and there is a large peak in the cross-correlation function (fig 9, a). If the signals at the two ears are completely uncorrelated, the sound has a ρ of zero, and there is no peak in the cross-correlation function (fig 9, b). Experiments that vary the binaural correlation of sound stimuli have

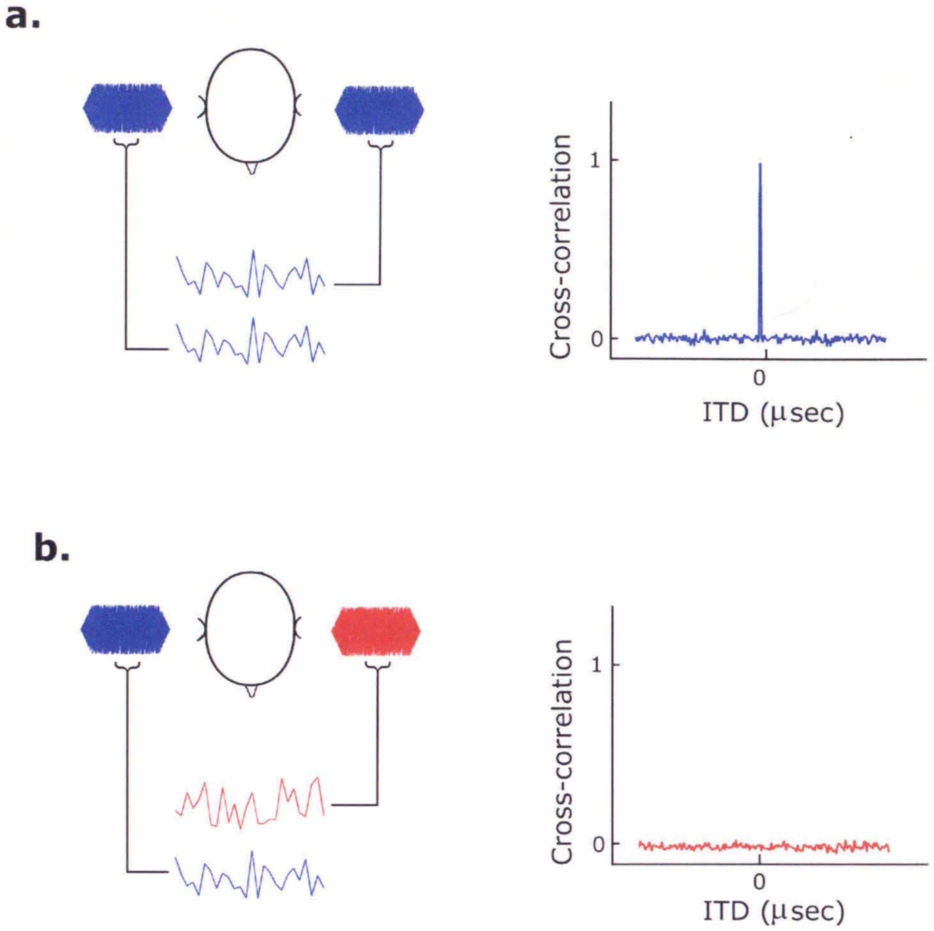


Fig. 9. The effect of binaural correlation on the shape of the cross-correlation function. Binaurally correlated signals (a) have a peak in the cross-correlation function and binaurally uncorrelated signals (b) do not.

shown that binaural correlation is extremely important for binaural fusion (directly, or indirectly via masking or detection) and for sound localization.

Effect of varying binaural correlation on binaural fusion:

A high binaural correlation is essential for binaural fusion in humans. When sounds with a binaural correlation of one are played over headphones, humans perceive a single, compact auditory image, whose location in the mediolateral plane depends on the IID and ITD of the sound (Sayers, 1964; Durlach and Colburn, 1978; Yost, 1981). As binaural correlation drops 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 ρ of 0.4; at lower correlations humans perceive two auditory objects, one at each ear (Blauert and Lindemann,1986; Licklider, 1948) or perceive a very diffuse object that fills the head (Gabriel and Colburn, 1981).

The ability of humans to detect variations in binaural correlation and the sensitivity of binaural unmasking to binaural correlation can both be understood in terms of the effect of binaural correlation on auditory object formation. Just-noticeable differences (jnds) in binaural correlation are small near $\rho=1$ and large near $\rho=0$ (Pollack and Trittipoe, 1959; Gabriel and Colburn, 1981), as would be expected if a high binaural correlation is important for auditory object formation, and thus detection and discrimination. In binaural unmasking, decreasing binaural correlation increases masking threshold (Durlach et al., 1986; Robinson and Jeffress, 1963; Osman, 1971): changing the binaural correlation can be thought of as moving the location of the masker from a position where it doesn't overlap the target (when $\rho=1$ and the masker is near the ear opposite the target) to a position where it does overlap the target (when $\rho=0$ and the decorrelated masker splits into two maskers, one of which overlaps the target).

Effect of varying binaural correlation on sound localization:

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 the case in humans: when subjects were presented noise over headphones and allowed to control the interaural delay, the ability to center the noise dropped to chance when $\rho = 0$ (Jeffress et al., 1962). Recently Saberi and colleagues (1998) have shown this to be the case in barn owls: as in humans, barn owl sound-localization ability based on ITD falls to chance as binaural correlation is reduced to zero.

The failure of binaurally uncorrelated signals to produce a single, binaurally fused image in humans suggests that variations in the IID of these signals could not be used as a cue for sound location. Although similar perceptual data is not available for barn owls, the congruence between human and barn owl horizontal localization ability predicts that barn owls would also be insensitive to variations in the IID of binaurally uncorrelated noise. This prediction is in conflict with the observation that barn owls fitted with monaural plugs continue to orient to auditory stimuli in a manner consistent with an open-ear-louder IID, despite the presumable lack of a coherent ITD. In order to determine whether owls could respond to IID cues in the absence of a coherent ITD, I tested the ability of two barn owls to detect and respond to variations in the IID of binaurally and uncorrelated signals.

3.1 Methods:

Training:

Two adult barn owls, with previous experience in sound-localization experiments, were trained to wear headphones, a head-position monitor, and to localize sounds played over the headphones. Headphones were used because they allow closer control of binaural correlation, and a binaural correlation of zero, in particular, is difficult to achieve in the free field. Owls were rewarded for fast, accurate localization with small pieces of mice presented using an automatic, stepper-motor-controlled feeder (R.E.S., model #1).

Sound stimuli:

Sound stimuli (tones and Gaussian noise, linear ramps) were generated using software libraries written by Dr. Jamie Mazer, and maintained by Ben Arthur and Chris Malek. Mex files, which allowed Matlab to access the libraries, were written by Chris Malek. Drivers for sound-generation hardware were ported by Chris Malek. A software experimental interface, (based in Matlab, 5.3.0, The Mathworks) to play sounds, and record head position and sound data, was written by the experimenter. This program allowed the intensity, bandwidth, ITD, IID, binaural correlation, duration, and rise and fall time of the sound to be controlled from trial to trial. The binaural correlation of the sounds was controlled by either playing the same sound to the right and left ears ($\rho=1$ condition) or by independently generating two noises and playing one to each ear ($\rho=0$ 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 make sure filtering or playing the sound hadn't introduced any binaural correlation. Sounds played with a binaural correlation of zero had no 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:

Input: Sounds were recorded using microphones (Knowles Electronics, ED-1939), analog signals were filtered with an anti-aliasing filter (FT6-2, TDT, frequency cutoff: 24 kHz), sampled at 48077 Hz with a digital to analog converter (AD2, TDT), and read into a PC (200 MHz Pentium, running RedHat Linux 5.2) using a DSP card (AP2, TDT).

Output: 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-1914 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. A small (2 cm diameter) pickup coil was mounted on the head, using the same connector used for monaural plug experiments. The Isotrak II generates three orthogonal alternating magnetic fields, in series, at about 8 kHz, reads the current induced in three orthogonally oriented loops of wire in the pickup coil on the head, and smooths and averages the data over several samples. 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).

3.2 Results:

When sounds with a ρ of one were presented over headphones, the owls varied the elevation of their final head position with IID (fig 10, squares) as expected (Moiseff and Konishi, 1981). When sounds with a ρ of zero were presented, the barn owls continued to localize correctly in the vertical plane (fig 10, circles). Final head positions in the vertical plane for $\rho=0$ stimuli were positively correlated with those for $\rho=1$ stimuli in both owls (owl 1: r=0.98, owl 2: r=0.98). Variance in both the horizontal and vertical component of final head positions increased for binaurally uncorrelated stimuli, but the increase in the horizontal dimension was much larger (Figure 11, a,b). Elevation speed as a function of the elevation

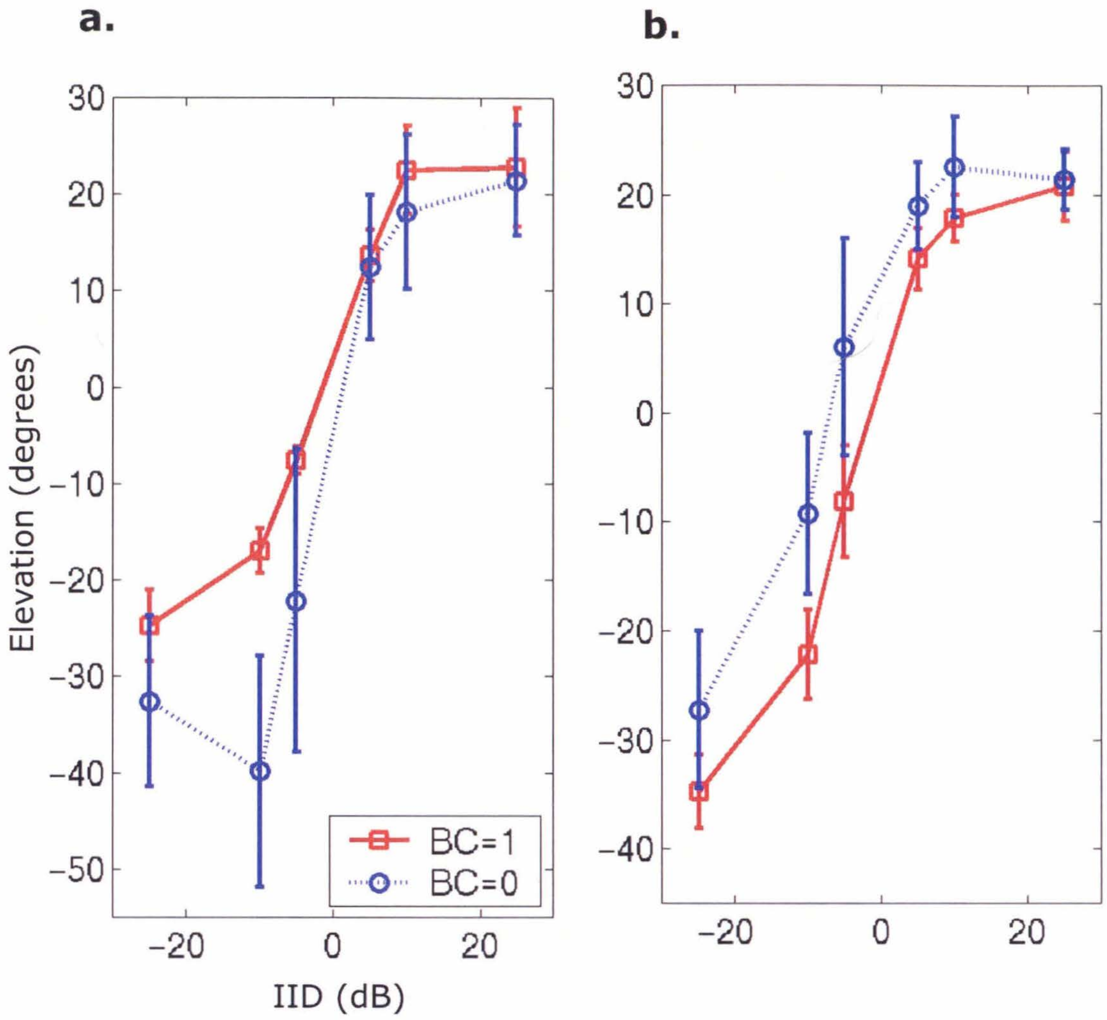


Fig. 10. Vertical localization of binaurally correlated and uncorrelated stimuli. Elevation of final head position varies with IID in both conditions in two owls. a) Data from Io. b) Data from Callisto.

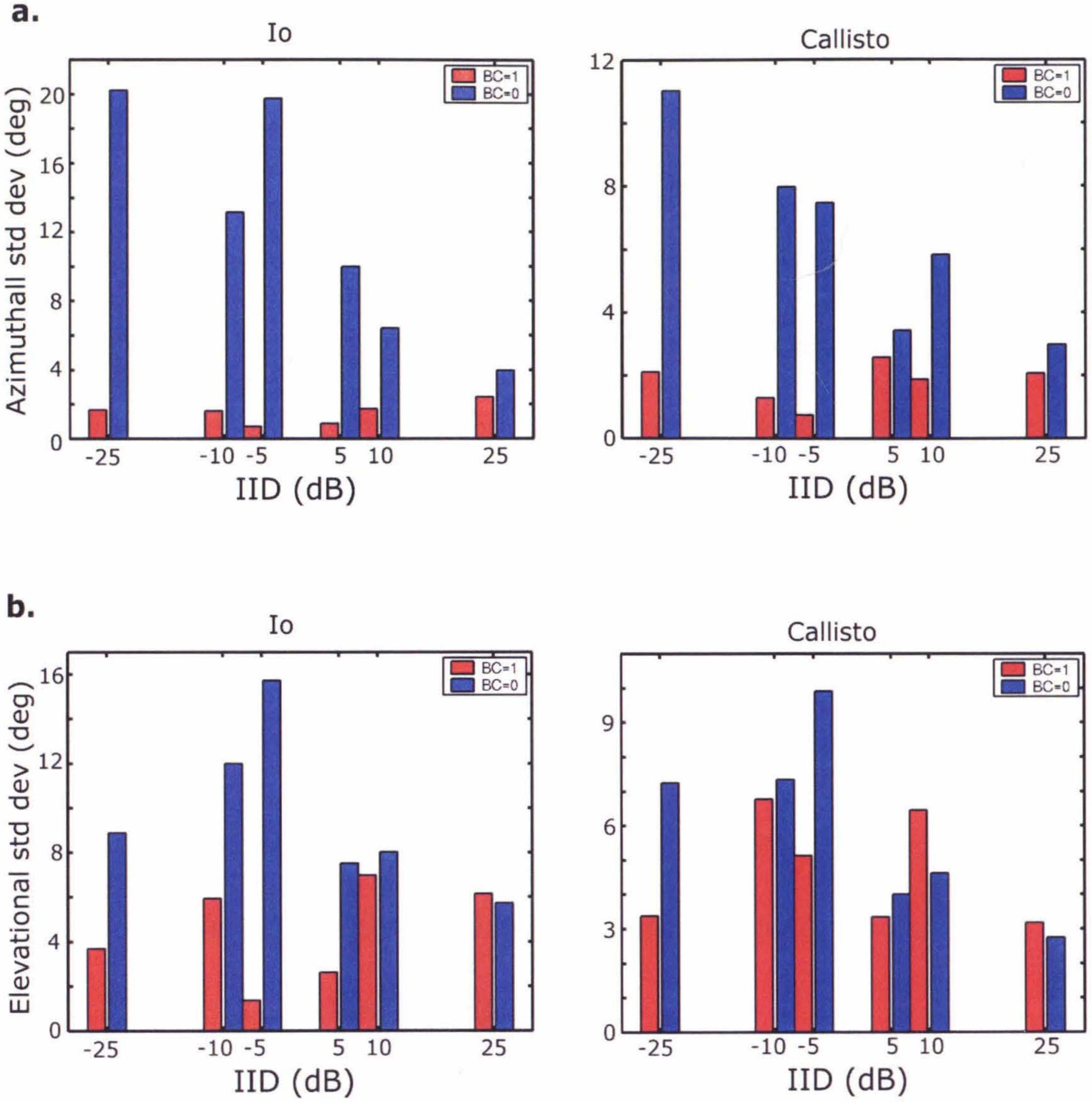


Fig. 11. Effect of binaural correlation on the variance of final head positions as a function of IID. a) Azimuthal standard deviations. b) Elevational standard deviations.

component of head turns for binaurally correlated sounds was similar to that in the free field (Figure 12, red and black symbols) in both owls. For one owl elevation speed as a function of turn angle was also similar in the binaurally uncorrelated condition, but in the other owl, the speed of downward orients was significantly slower in the binaurally uncorrelated condition (Figure 12, blue symbols). Both owls also exhibited an increase in orients in which initial turn direction was reversed mid-orient (double-take orients; Figure 13, a,b).

3.3 Discussion

These experiments demonstrate that barn owls can extract IID from binaurally uncorrelated stimuli and use that information to control the vertical component of sound localization.

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 (Saberi et al., 1998), why does lack of binaural correlation increase elevational variance? There is nothing intrinsic to an IID that depends on binaural correlation. One possible explanation is

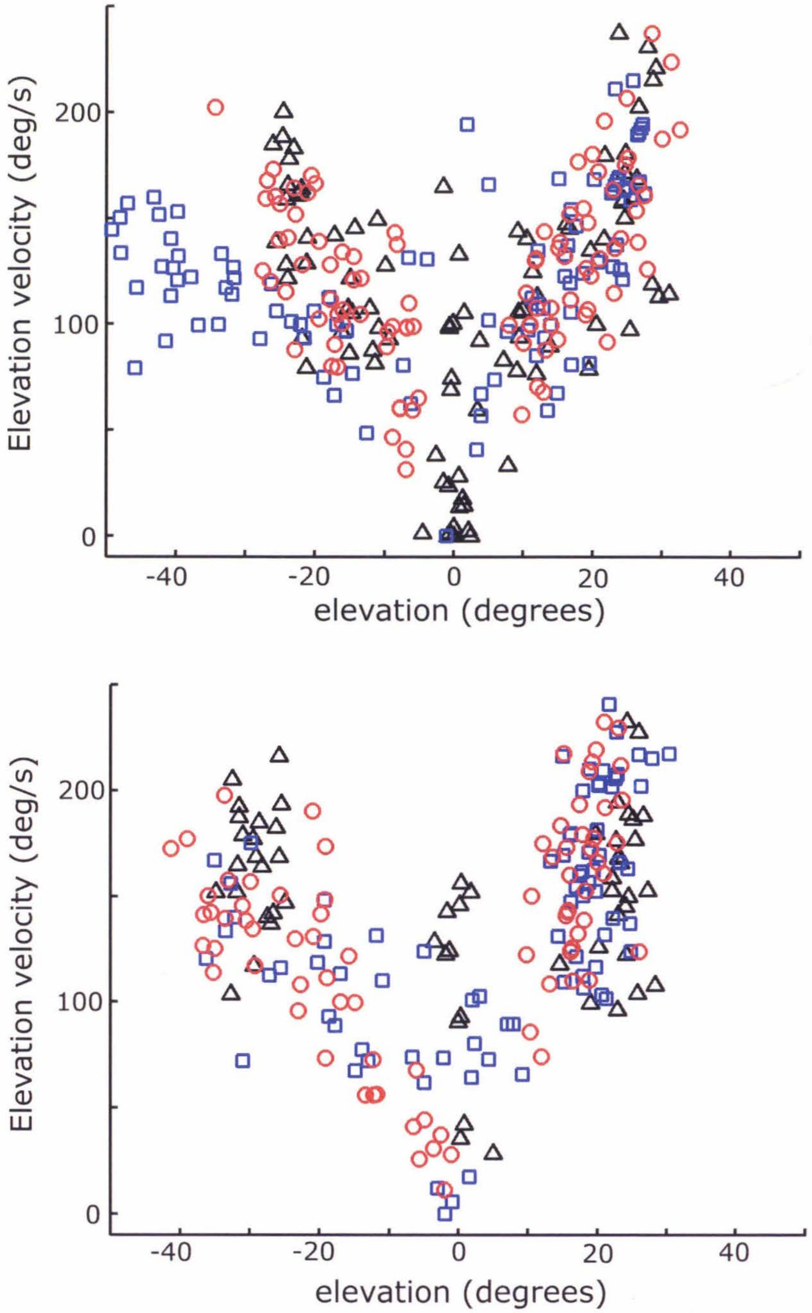


Fig. 12. Elevation speed as a function of the elevation component of head turns for free-field (△), binaurally correlated (○), and binaurally uncorrelated (□) stimuli in two owls. a) Data from Io. b) Data from Callisto.

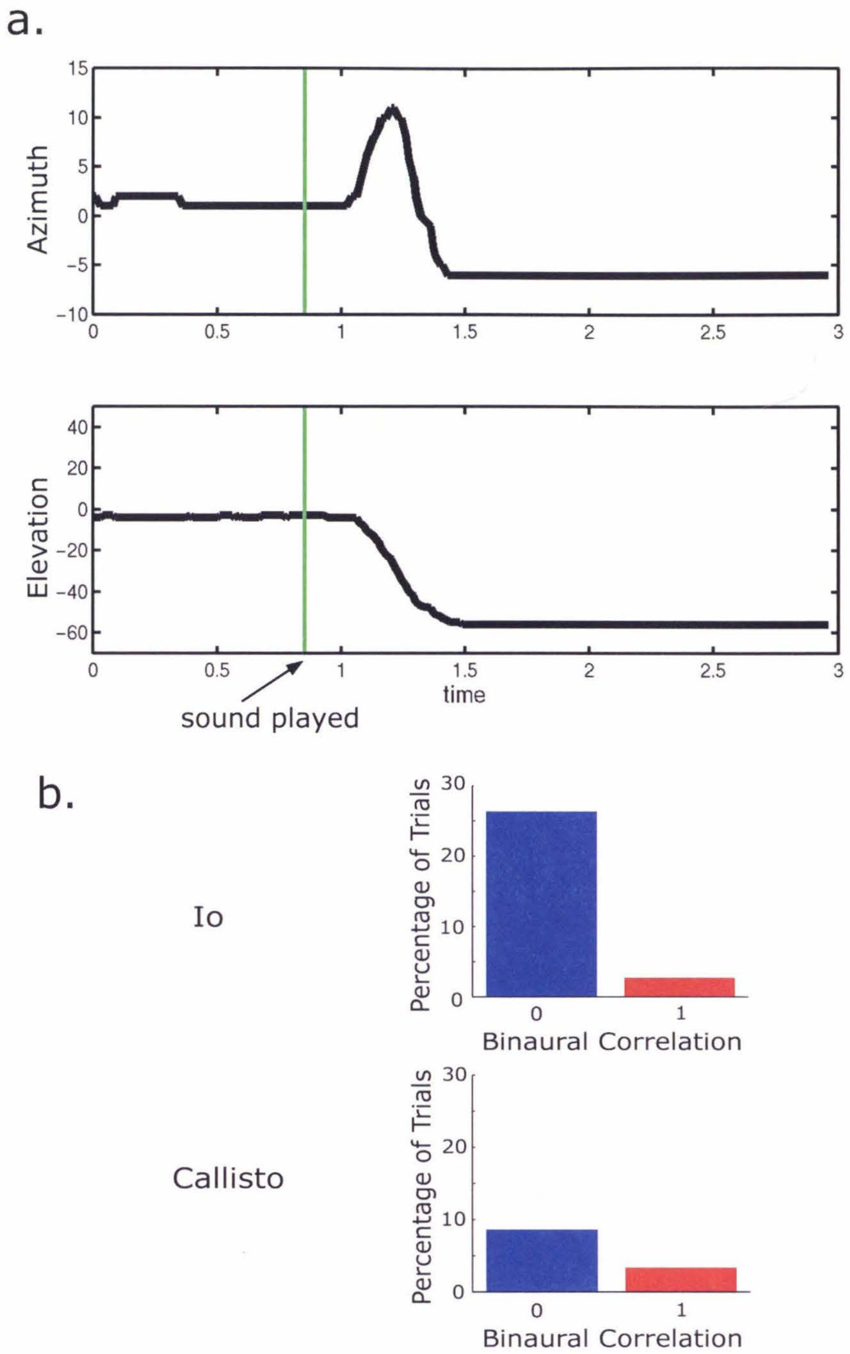


Fig. 13. Binaural decorrelation increases double-take frequency. a) azimuth and elevation component of head turn during a double-take orient. b) Double-take frequency for binaurally correlated and uncorrelated stimuli in two owls.

that, in the absence of a coherent ITD, a particular IID does not correspond to a particular location in space, but to a family of locations, which varies depending on the magnitude of the IID (Moiseff, 1989; 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 effect on the speed of the movements and the increase in double-take frequency suggest that binaurally uncorrelated sounds are perceptually different to barn owls. However, the behavior suggests that although there is no compact auditory image in the horizontal plane, that there is a detectable and localizable image in the vertical plane.

The ability of owls to localize based on the IID of a binaurally uncorrelated signal suggests the existence of IID sensitive neurons in the auditory system which maintain their tuning in the absence of binaural correlation. Experiments on neurons in the auditory space map in the optic tectum (Saberi et al., 1998; Takahashi,Y., personal communication) suggest that these space-specific neurons are obligatory AND gates--that is, that they require information about both the elevation (IID) and azimuth (ITD) of a sound source to fire. Auditory neurons which can direct head movements in the absence of binaural correlation would not be obligatory AND gates, and this suggests that a) there exists another area which can support auditory orients and b) space-specificity in this area is generated differently than it is in the OT.

Chapter 4

Brainstem Response to Variations in Binaural Correlation

IID and ITD are processed by separate and parallel pathways in the barn owl brainstem and midbrain (Takahashi et al., 1984). The barn owl's brainstem nucleus ventralis lemnisci lateralis pars posterior (VLVp) is the first stage in the intensity pathway that contains neurons sensitive to IID. As the name suggests, VLVp is embedded in the lateral lemniscus. VLVp neurons receive excitatory input from the contralateral cochlear nucleus angularis (NA) and inhibitory input from the contralateral VLVp (Takahashi and Konishi, 1988; Takahashi and Keller, 1992). VLVp neurons are excited by sounds that are louder in the contralateral ear and inhibited by sounds that are louder in the ipsilateral ear (fig 14, a; Moiseff and Konishi, 1983). The location of the IID at half-height (cutoff) of the sigmoid varies with depth in the nucleus; neurons with cutoffs nearer the contralateral ear are located more dorsally and neurons with cutoffs nearer the ipsilateral ear are located more ventrally (Manley et al., 1988; Mogdans and Knudsen, 1994). VLVp neurons are narrowly frequency tuned (fig 14, b) and are arranged tonotopically, with low frequencies anterior and high frequencies posterior (Manley et al., 1988).

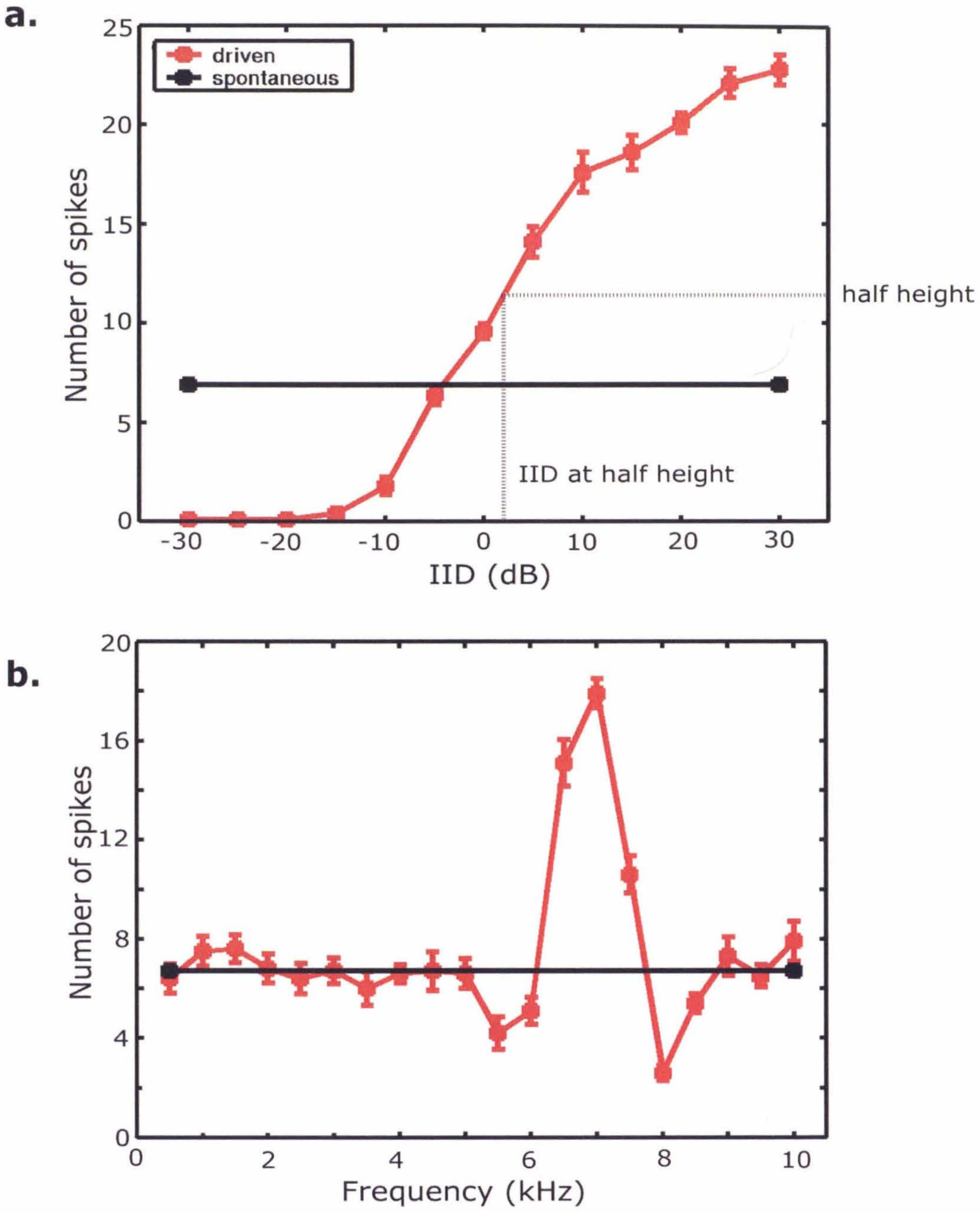


Fig. 14. Response of a VLVp neuron to IID and frequency. a) Spikes as a function of IID. The dotted line indicates the IID at half height. b) Spikes as a function of the frequency of stimulating sound. By convention negative values of IID correspond to sounds louder in the ipsilateral ear and positive values of IID to sounds louder in the contralateral ear.

VLVp neurons are not sensitive to ITD (Moiseff and Konishi, 1983).

Is there an effect of binaural decorrelation on IID encoding?

All of the information that exists about VLVp suggests that IID encoding in VLVp should be completely unaffected by changes in binaural correlation, since there is no known mechanism by which VLVp neurons could acquire interaural phase sensitivity. It has been shown, however, that variation in binaural correlation reduces responses to both IID and ITD in the external nucleus of the inferior colliculus (ICx; Albeck and Konishi, 1995) and eliminates neuronal responses altogether in the OT (Saberi et al., 1998). In addition, although barn owls continue to be able to localize binaurally uncorrelated stimuli in the vertical plane, orients to these stimuli are much more variable than to binaurally correlated stimuli. Is the source of this variability an effect of binaural correlation on initial IID encoding, or does binaural correlation affect elevation in the vertical plane indirectly by creating ambiguity in the location of the sound image in the horizontal plane? In order to see if initial IID encoding is affected by variations in binaural correlation, I recorded extracellularly from VLVp neurons and tested the effect of variations in binaural correlation on their IID sensitivity.

4.1 Methods:

Surgery:

Owls were anesthetized with intramuscular injections of ketamine hydrochloride (20 mg/kg) and diazepam (0.1 mg/kg) 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, .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 (1.5 x 1 x 1 cm) and a small metal zero post were attached to the skull using dental acrylic (Perm Reline & Repair Resin, Hygenic Corp.). 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 stereotactic coordinate system. Once the dental acrylic has hardened, the ear bars and beak plate are removed and the head is fastened to the stereotax using the head plate. A 4 mm by 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 & Upjohn Co.) soaked in .05% chlorhexidine and covered in dental acrylic. The skin was sutured closed and intramuscular buprenorphine hydrochloride (.06 mg/kg) and subcutaneous fluids (5 cc lactated Ringers solution) were administered. The owl was placed in a small, well-heated cage and monitored for 24 hours after surgery before being returned to its home cage.

Sound presentation:

Auditory stimuli were presented and neural data was collected using a data acquisition program (xdphys) originally written by Dr. Jamie Mazer and revised and maintained by Ben Arthur and Chris Malek. Sounds were calibrated by measuring the left and right headphone transfer functions before each experiment, using small microphones in the headphone assembly (Knowles Electronics, ED-1939) and using the inverse of the respective transfer functions to filter all sound played through the headphones. 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) and played through headphones (Knowles Electronics, ED-1914 receiver with a Knowles BF-1743 damped coupling assembly). 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 10x gain current buffer (B.E.S, headstage), filtered from 1 to 10 kHz, and amplified by 100x (B.E.S., μA108). Analog signals were digitized at 48 kHz (Proport, Ariel), read into the computer using a DSP card (S56X, Berkeley Camera Engineering), and thresholded and recorded using xdphys.

Electrophysiology:

Electrodes consisted either of 1.0 mm O.D. glass pipettes, with a capillary fiber, double pulled (puller), with tip widths of 5-10 μm, and filled with 3 M K-Acetate, 3M NaCl, or Wood's metal with 7-10 μm widths plated with gold and platinum. All electrodes had impedances between .2 and

1.8 M Ω at 1 k Hz. Electrodes were moved with a microdrive (B.E.S, μD 100) in steps of 100 μm until VLVp was reached, and in steps of 2-10 μm while isolating. Neurons were characterized based on their tuning to IID, ITD, binaural correlation, average binaural intensity (abi; [intensity of left channel + intensity of right channel)/2]), and frequency or frequency range of stimulating sound. All data were recorded at 20 dB above threshold. The number of trials recorded varied from 5-20. Isolation was based on consistency of action potential shape and an inter-spike interval (ISI) histogram, which showed no ISI smaller than 1 ms. Binaurally correlated and uncorrelated noise IID trials were interleaved. Recordings were made with the owl placed in a small (1 m^3) double-walled sound attenuating chamber (Acoustic Systems).

Statistical tests:

For each neuron, spike number as a function of IID for both binaurally correlated and binaurally uncorrelated stimuli was calculated and then an ANOVA was performed, with IID as the variable factor. Spikes as a function of IID for binaurally correlated noise were plotted versus spikes as a function of IID for binaurally uncorrelated noise for each neuron (Figure 15, a). The response of the neuron to a particular IID for ρ=0 for

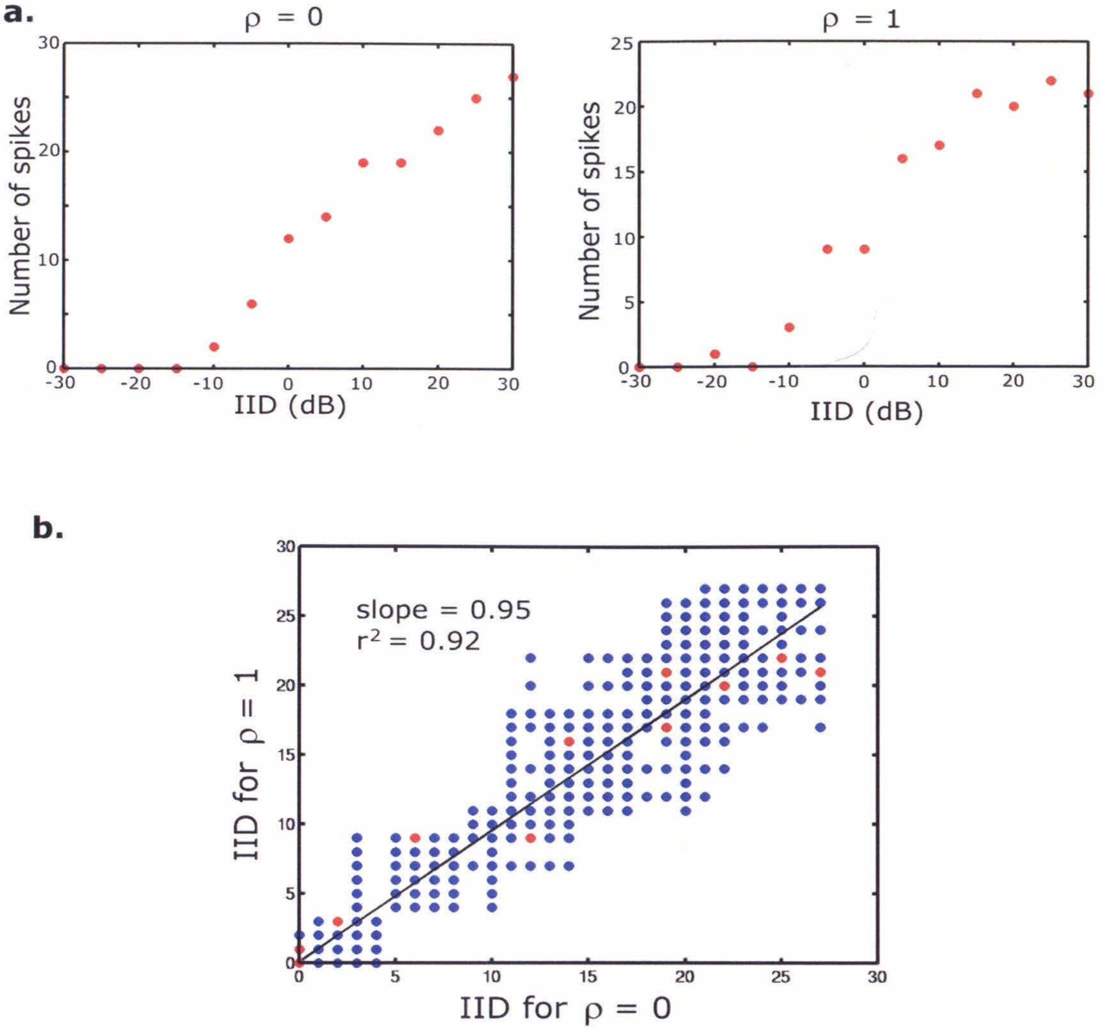


Fig. 15. The effect of varying binaural correlation on IID sensitivity in VLVp. a) Spike rate vs. IID for a single trial for $\rho = 0$ and $\rho = 1$. b) Spike rate for IID for all trials. The trial combination shown in part a) above is shown in red.

a single trial was plotted against the response of the neuron to that same IID for $\rho = 1$ for a single trial. All possible $\rho=1$ trial:$\rho=0$ trial combinations were used, so that the total number of points for a given neuron is: ($\rho=0$ number of trials) times ($\rho=1$ number of trials). Although overlapping points do not show up in the plot (fig 11, b), all points were used in calculating correlation coefficients (r), coefficients of determination (r^2) and slope 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 x -4 A for 10 s), the owls were deeply anesthetized with an overdose of sodium pentobarbital (80 mg/kg) and perfused with 0.9 % warm saline and 4 % paraformaldehyde in .2 M phosphate buffer. The brain was cryoprotected with 30% sucrose and 40 μm sections were cut on a freezing microtome. Sections were mounted on glass slides, cleared, dehydrated, and stained with a Nissl stain (Neutral Red or Cresyl Violet) and coverslipped and recording sites were verified anatomically.

4.2 Results:

I recorded extracellularly from 11 well-isolated VLVp neurons. The best frequencies of the neurons ranged from 3-7.5 kHz (Fig.16, a), and IIDs at half height had values between 0 and 10 dB (Figure 16, b). All VLVp neurons tested maintained their IID sensitivity with binaurally uncorrelated noise ($p < 0.01$). Figure 17, a shows the effect of binaural correlation on the IID tuning of a single neuron. Both neurons are inhibited below the spontaneous rate for left-ear-louder IIDs and excited by right-ear-louder IIDs. IID 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 (Figure 17, b). The plot of $\rho = 1$ versus $\rho = 0$ produces slopes and correlation coefficients that, in general, are very close to one (Table 2, see methods and Figure 11 for details of slope and r^2 calculation). All neurons had values of correlation coefficients for $\rho = 1$ vs $\rho = 0$ which were significantly greater than zero ($p < 0.01$).

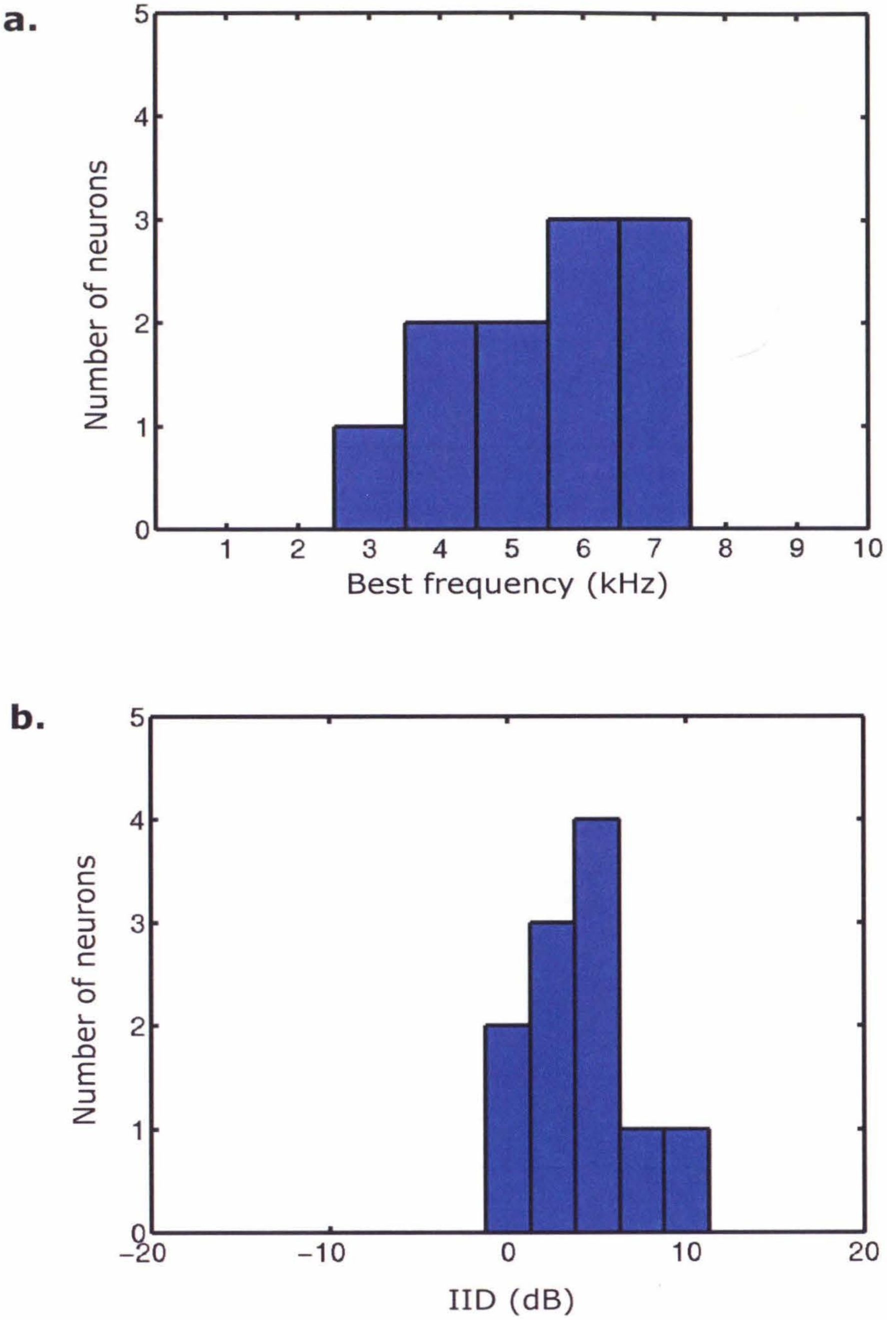


Fig. 16. The distribution of best frequencies and IIDs of neurons recorded in VLVp. a) Distribution of best frequencies. Distribution of IIDs at half height.

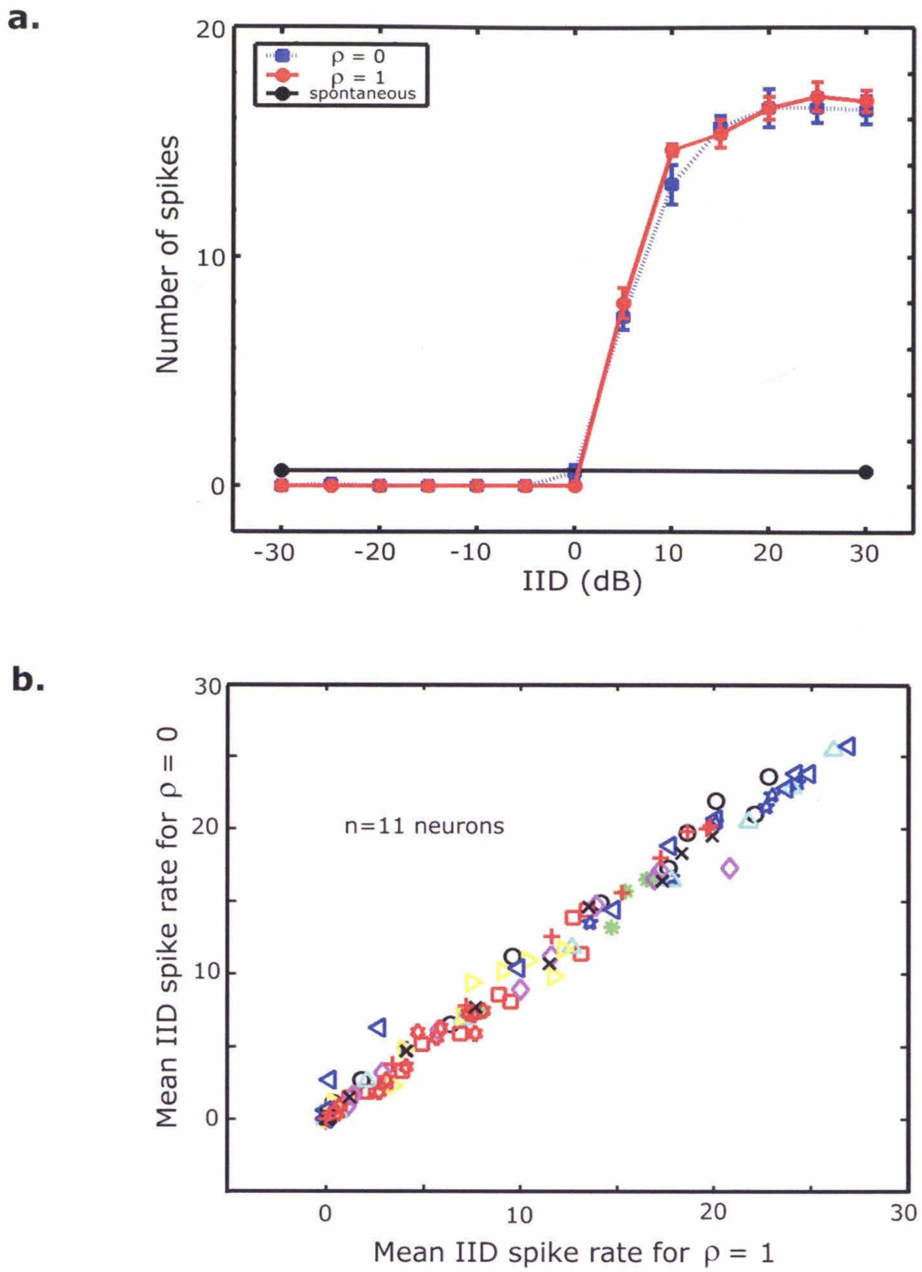


Fig. 17 Effect of varying binaural correlation on IID tuning in VLVp a) IID sensitivity to binaurally correlated (—●—) and binaurally uncorrelated (··■··) noise. Both ρ = 1 and ρ = 0 are inhibited below the spontaneous rate (—●—) for left-ear-louder IIDs and excited by right-ear-louder IIDs. b) Mean spike rate as a function of IID for ρ = 1 plotted vs. mean spike rate for ρ = 0 for 11 VLVp neurons.

	Slope	r^2
	0.95	0.92
	0.86	0.71
	1.02	0.97
	0.99	0.94
	0.96	0.78
	1.03	0.95
	0.82	0.69
	1.02	0.91
	0.99	0.93
	0.96	0.99
	0.75	0.51
Average	0.94	0.85
Std dev	+/- 0.09	+/- 0.15

Table 2. The IID sensitivity of VLVp neurons is similar for binaurally correlated and binaurally uncorrelated noise. Slopes and coefficients of determination (r^2) are shown calculated from spikes as a function of IID for $\rho = 1$ plotted vs. $\rho = 0$ for each neuron.

4.3 Discussion:

The fact that IID encoding in VLVp neurons is unaffected by the degree of binaural correlation was expected, considering that there is no known phase-sensitive input to this nucleus. It is important, however, to demonstrate that the IID of binaurally uncorrelated noise can be encoded, since binaurally uncorrelated stimuli fail to drive neurons in the auditory space map (Saberi et al., 1998), and reduce the output of in lower order ITD sensitive neurons (Albeck and Konishi, 1995). In addition, although initial IID encoding is insensitive to variations in binaural correlation, vertical sound localization ability based on IID is not. Higher auditory areas are getting an IID signal for binaurally uncorrelated noise, which is virtually indistinguishable from that for binaurally correlated noise, but this is not translating into precise vertical localization of binaurally uncorrelated stimuli. The response of VLVp neurons to IID is sigmoidal; further processing of IID in higher auditory areas creates neurons with sensitivity to a restricted range of IIDs (peaked neurons). The mechanism by which peaked IID responses are generated is a subject of debate, but it has been shown to occur in parallel with the reduction in the phase ambiguity of responses to ITD. An increase in the phase sensitivity of a neuron seems likely to also decrease its response to binaurally uncorrelated noise. Since barn owls can localize based on the IID of binaurally uncorrelated signals, there must exist a population of neurons which can both access head movement circuitry and maintain IID tuning for binaurally uncorrelated noise. A potential candidate for such an area is the auditory thalamic nucleus ovoidalis.

Chapter 5

Thalamic response to variations in binaural correlation

Tectal and thalamic auditory pathways:

Early investigations of auditory spatial processing in the barn owl revealed two sites that contained space-specific auditory neurons--the forebrain nucleus Field L (Knudsen et al., 1977) and the midbrain nucleus ICx (Knudsen and Konishi, 1978). More recent experiments have shown that the forebrain pathway can support auditory orients following lesions to the auditory space maps in ICx and OT (Knudsen et al., 1993; Wagner, 1993). Although sound-localization ability is not eliminated, the orients of barn owls with such midbrain lesions to auditory targets in the contralateral hemifield are less precise, and have longer latencies than those of unlesioned owls. Owls with lesions in the auditory thalamus (nucleus ovoidalis, NO), which is the primary input to Field L, are still able to localize contralateral auditory targets, with no consistent loss of precision or increase in latency (Knudsen et al., 1993). Owls with lesions to both NO and OT, however, are unable to localize auditory spatial targets contralateral to the lesions (Knudsen et al., 1993). As there are two independent pathways capable of supporting auditory orienting responses in the barn owl, the failure of neurons in the tectal space map to respond to stimuli (binaurally decorrelated sound) that can support auditory localization behaviorally suggests that the thalamic pathway might be involved.

Anatomy of NO:

NO receives ipsilateral input from ICc (Karten, 1967; Proctor and Konishi, 1997), and from nuclei in the lateral lemniscus (Wild, 1987; Proctor, 1993) and projects ipsilaterally to the forebrain nucleus Field L (Karten, 1968; Bonke et al., 1979; Durand, et al., 1992; Wild et al., 1993; Proctor, 1993; Vates et al., 1996; Cohen et al., 1998).

Physiology of NO:

There have been few studies of the physiological property of NO neurons. A recent study in slice (Strohmann et al., 1994) showed that there are two biophysically distinct types of neuron in NO. Earlier *in vivo* work in zebra finches, starlings, and ring doves showed that NO neurons have variable frequency tuning; they may be narrowly tuned in frequency, broadly tuned, or have multiple peaks in their tuning curves (Biederman-Thorson,1970; Bigalke-Kunz et al., 1987; Diekamp and Margoliash, 1991) and that these neurons are arranged tonotopically (Bigalke-Kunz et al., 1987). This variability in frequency tuning has also been seen in the barn owl, as has the tonotopy; neurons with high best frequencies are located dorsally and neurons with low best frequencies are located ventrally (Proctor, 1993; Proctor and Konishi,1997). In contrast to other lower order nuclei in the barn owl, the representation of frequency in NO does not match the representation of frequency in the cochlea--there is no overrepresentation of frequencies between 5-10 kHz (Proctor; 1993).

Tuning of NO neurons to spatial cues:

The response of NO neurons to binaural sound localization cues has only been studied in the barn owl. All neurons in NO respond to at least one binaural spatial localization cue; most neurons are tuned to both ITD and IID, but a substantial fraction are tuned only to IID (Proctor, 1993). The responses of NO neurons to binaural sound localization cues is complex. Tuning to spatial cues can be thought of as ranging from spatially ambiguous to spatially restricted. A neuron with phase-ambiguous ITD tuning, or sigmoidal IID tuning will respond to auditory targets over a large region of space. A neuron with side-peak suppressed ITD tuning and peaked IID tuning will respond only to auditory targets in its restricted receptive field. In the brainstem and midbrain a neuron is spatially ambiguous for a single binaural cue, partially space-specific for both cues, or completely space-specific for both cues (Mazer, 1998). While these types of tuning occur in NO, they are accompanied by response types that do not occur in the brainstem and midbrain. In NO a neuron can be spatially restricted in IID, but spatially ambiguous in ITD or spatially restricted in IID and not tuned to ITD at all.

If the forebrain pathway supports auditory orients to binaurally uncorrelated stimuli, some neurons in NO must encode the IID of binaurally uncorrelated noise. I therefore recorded from neurons in NO and tested their IID response for binaurally correlated and binaurally uncorrelated noise.

5.1 Methods:

Methods for surgery, presenting stimuli, recording data, and histology are the same as in the previous chapter.

Measuring neuronal response properties:

The approximate IID and ITD of the neuron was calculated by hand and then responses to IID for $\rho = 0$ and $\rho = 1$ (trials interleaved), ITD, and frequency were collected. All responses were collected at between 15 dB and 20 dB above threshold.

Analysis:

Quantifying response to frequency:

The frequency response of NO neurons is heterogenous. Some NO neurons respond to a narrow range of frequencies (Figure 18, a), some neurons to a broad range (Figure 18, b), and some neurons have multiple peaks in their tuning curves (Figure 18, b). The best frequency of a neuron is defined, in this thesis, as the center of mass of the excitatory portion of the frequency tuning curve (Figure 18, a,b). Two different measures of bandwidth were calculated. Bandwidth range is defined as the highest frequency with a response greater than 50% of the maximum rate minus the lowest frequency with a response greater than 50% of the maximum rate. Effective bandwidth is defined as the sum of the frequencies with response greater than 50% of the maximum rate. For a frequency tuning curve with a single peak effective bandwidth and the bandwidth range will be

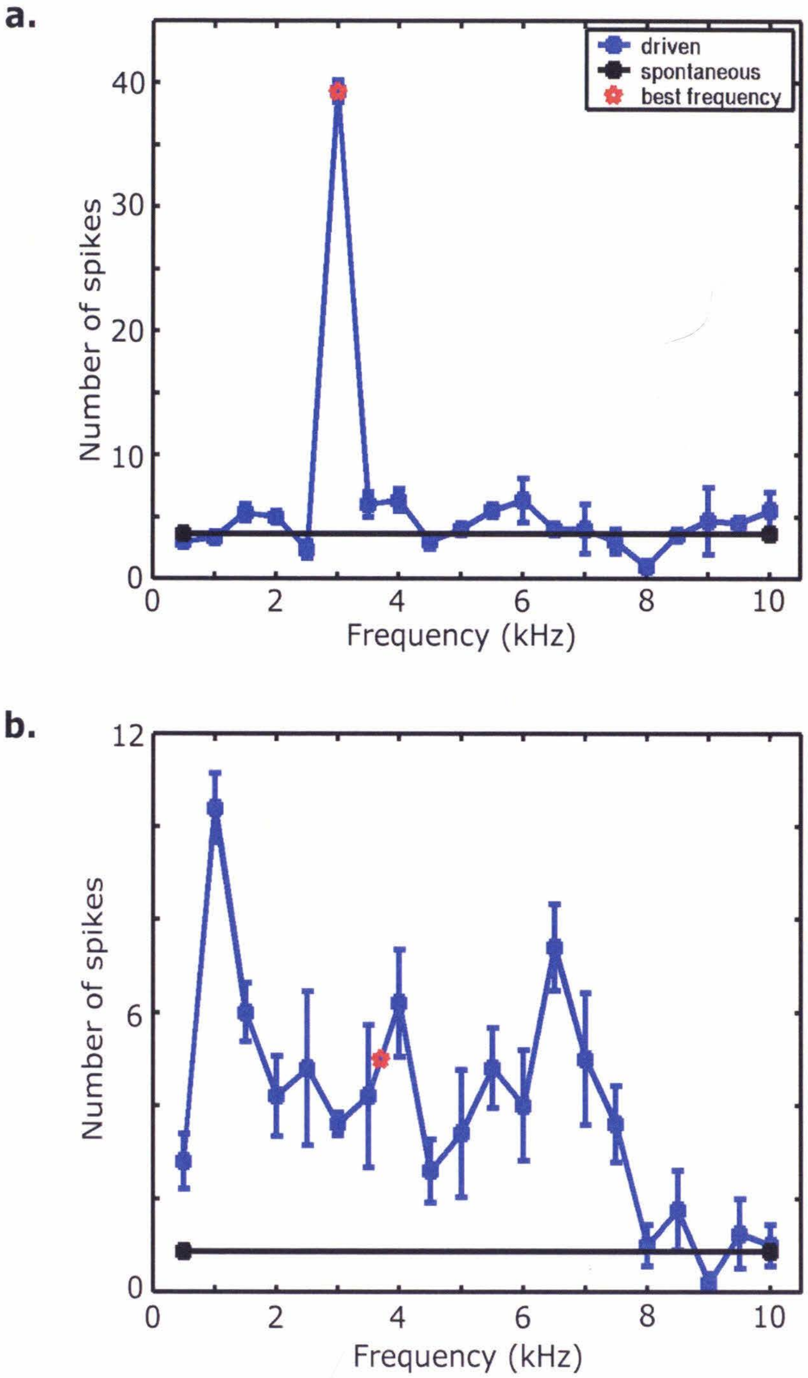


Fig. 18. Characterization of the best frequencies of NO neurons. a) A narrowly tuned neuron. b) A broadly tuned neuron with multiple peaks. Center of mass best frequency is indicated (✱).

the same. For a frequency tuning curve with multiple peaks the effective bandwidth will be smaller than the bandwidth range.

Quantifying response to IID:

An ANOVA was used to test whether a neuron was IID tuned or not. Neurons were classified as either sigmoidal or peaked. Neurons intermediate between sigmoidal and peaked were classified as sigmoidal if the response at the shoulder was less than 50% of the maximum response and as peaked if the response at the shoulder was more than 50% of the maximum response. IID responses were also characterized by the IID to which the neuron responded maximally (best IID, Figure 19, a,b,c).

Quantifying response to ITD:

An ANOVA was used to test whether a neuron was ITD tuned or not. Two different measures of ITD were used. For neurons with a defined main peak (MP) and side peaks, an index of side peak suppression (SPS) was calculated (see Figure 20, a). For all neurons an index of ITD modulation (IM) was calculated (see Figure 20, b).

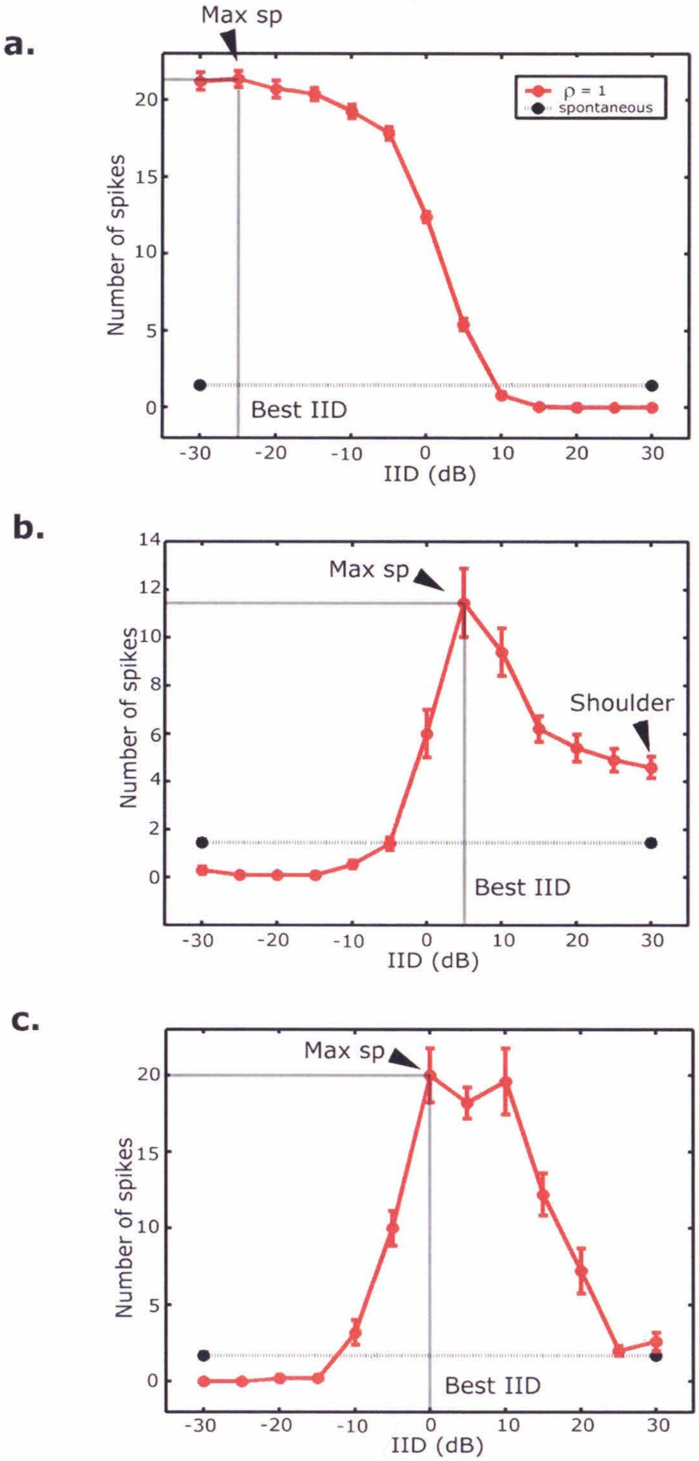
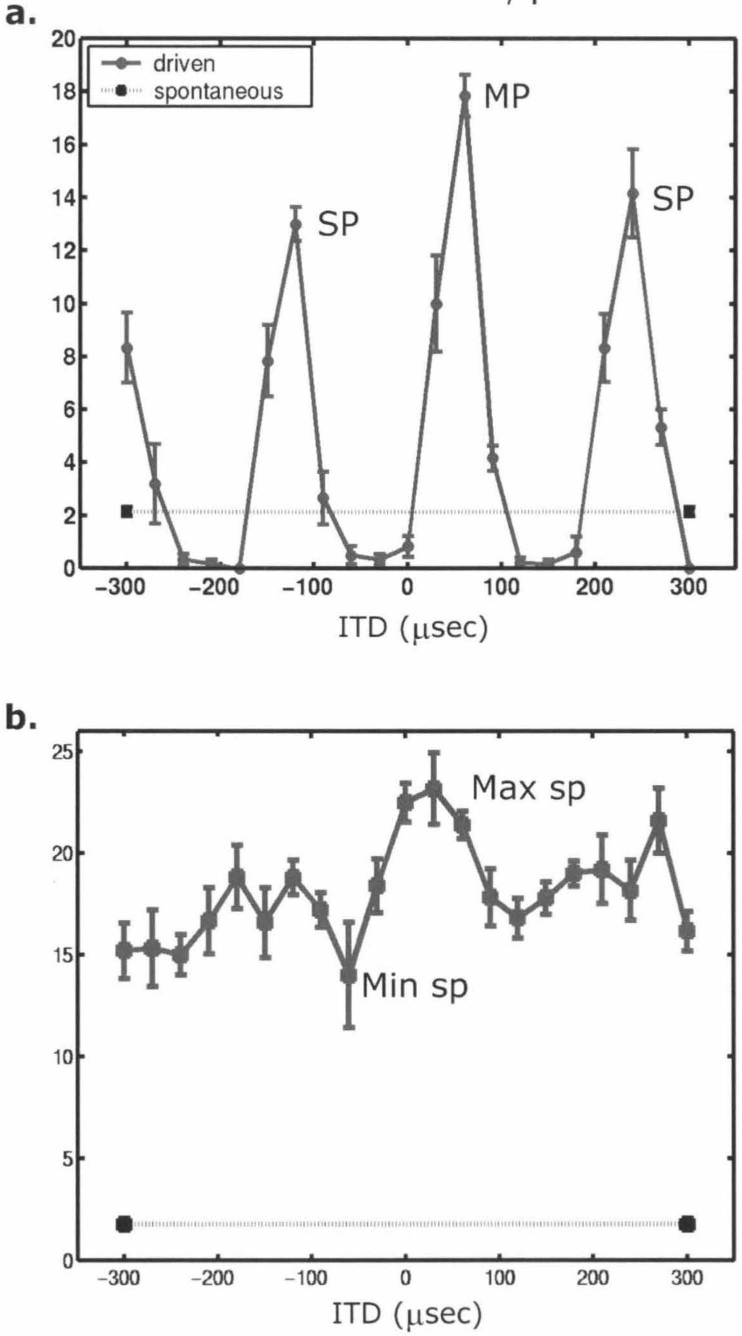


Fig. 19. Characterization of IID responses in NO neurons. a) A neuron with sigmoidal IID tuning. b) A shoulder neuron with peaked IID tuning. c) A neuron with peaked IID tuning. Best IID is indicated for each neuron.



$$\mathrm{SPS} = \frac{(\mathrm{MP}-\mathrm{SP})}{\mathrm{MP}}$$

$$\mathrm{IM} = \frac{(\mathrm{Max\ sp} - \mathrm{Min\ sp})}{\mathrm{Max\ sp}}$$

Fig. 20. Characterization of ITD tuning in NO neurons. a) The ITD response of a neuron with a clear main peak (MP) and side peaks (SP). A side-peak suppression index (SPS) can be calculated for neurons of this type. b) The ITD response of a neuron without a clear MP or SP, with maximum spike number (Max sp) and minimum spike number (Min sp) indicated. An ITD modulation index (IM) can be calculated for all neuronal types.

5.2 Results:

Types of neuronal response in NO:

I recorded extracellularly from 35 well-isolated NO neurons. The best frequencies of the neurons ranged from 1 to 8.9 kHz, with an average of 4.9 kHz (Figure 21). The minimum bandwidth range was 0.5 kHz and the maximum was 8 kHz, with a mean of 2.3 kHz (Figure 22, a). The minimum effective bandwidth was 0.5 kHz and the maximum was 5.0 kHz, with a mean of 1.8 kHz (Figure 22, b). 22 of 35 neurons recorded from were sensitive to ITD (ANOVA, $p< 0.01$). Of those 22, 13 had identifiable side peaks. All SPS values were below 0.4 (Figure 23, a). The average ITD modulation index for all neurons was 0.7 (Figure 23, b). All of the neurons recorded from were sensitive to IID (ANOVA, $p<0.01$). There were approximately the same number of neurons with peaked and sigmoidal IID tuning curves (Figure 24, a), and one neuron had a shape that could not be classified. The average best IID of the neurons recorded from was 3.7 dB (Figure 24, b).

Effect of variations in binaural correlation on IID tuning:

Nine of 35 neurons showed no change in response between $\rho=0$ and $\rho=1$

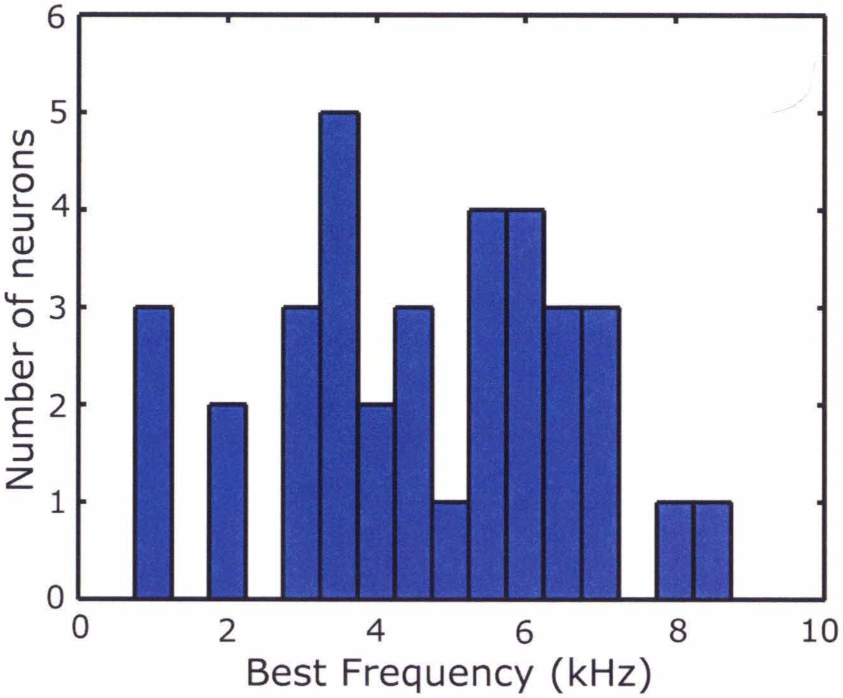


Fig. 21. Distribution of best frequencies of NO neurons

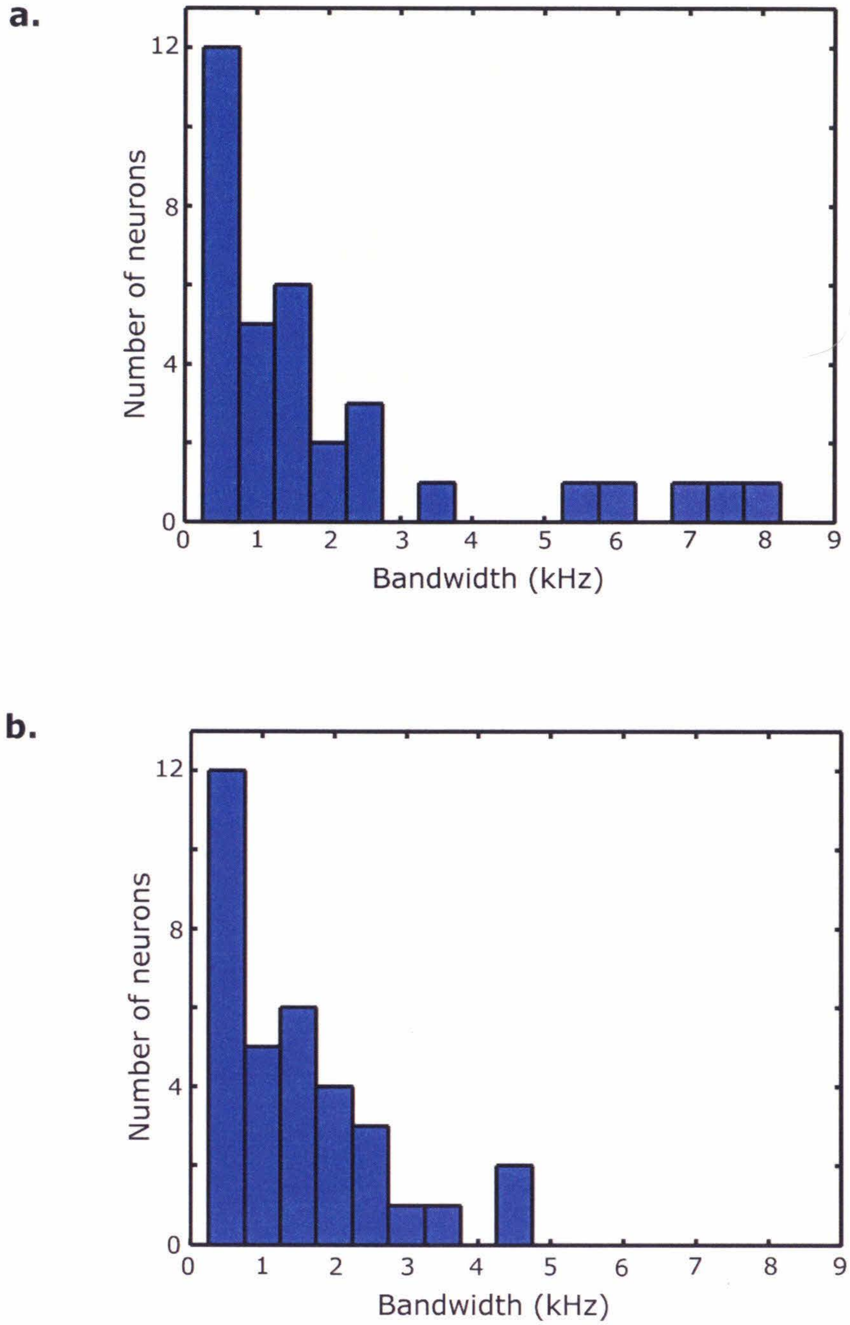


Fig. 22. Distribution of the bandwidth of neurons recorded in NO. a) Distribution of bandwidth ranges. b) Distribution of effective bandwidths.

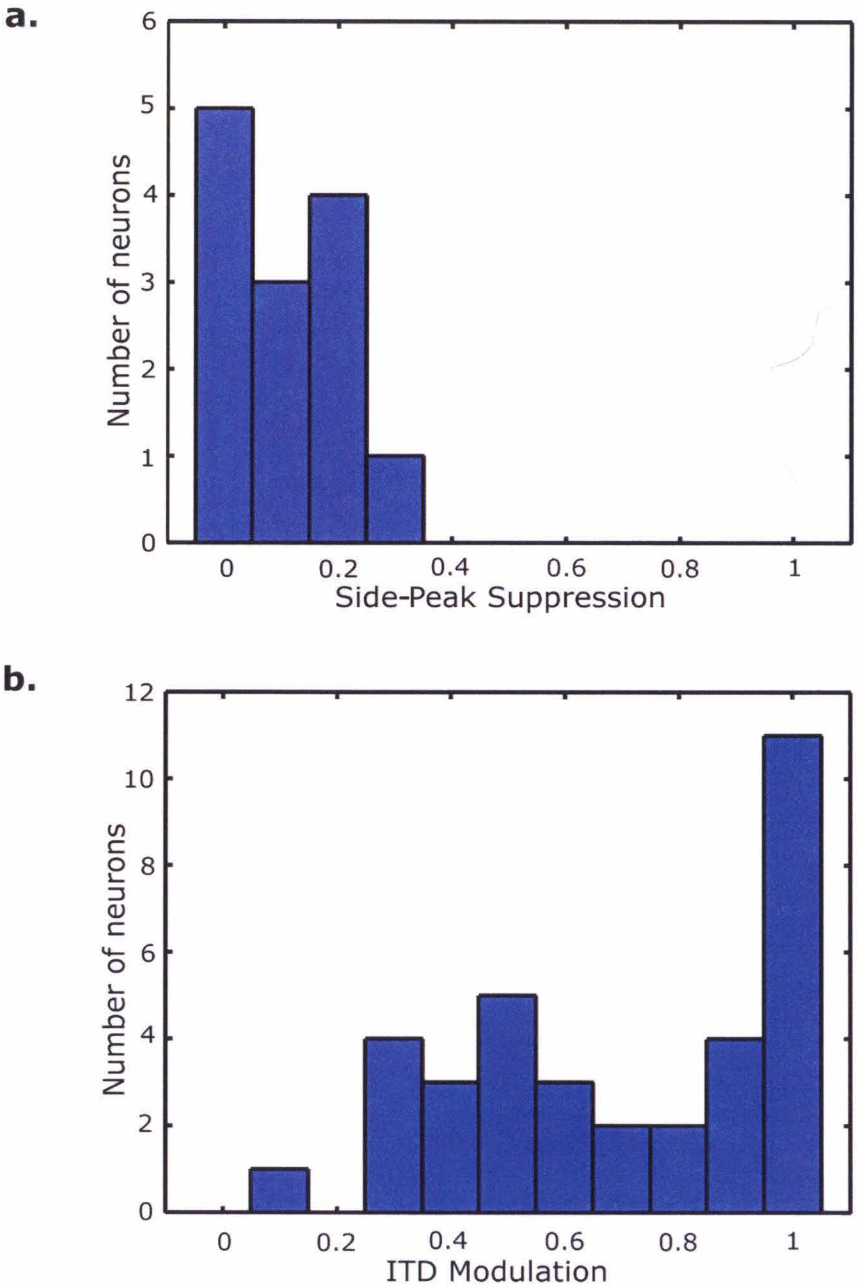


Fig. 23. ITD response of NO neurons. a) Distribution of side-peak suppression (SPS). b) Distribution of ITD modulation (IM).

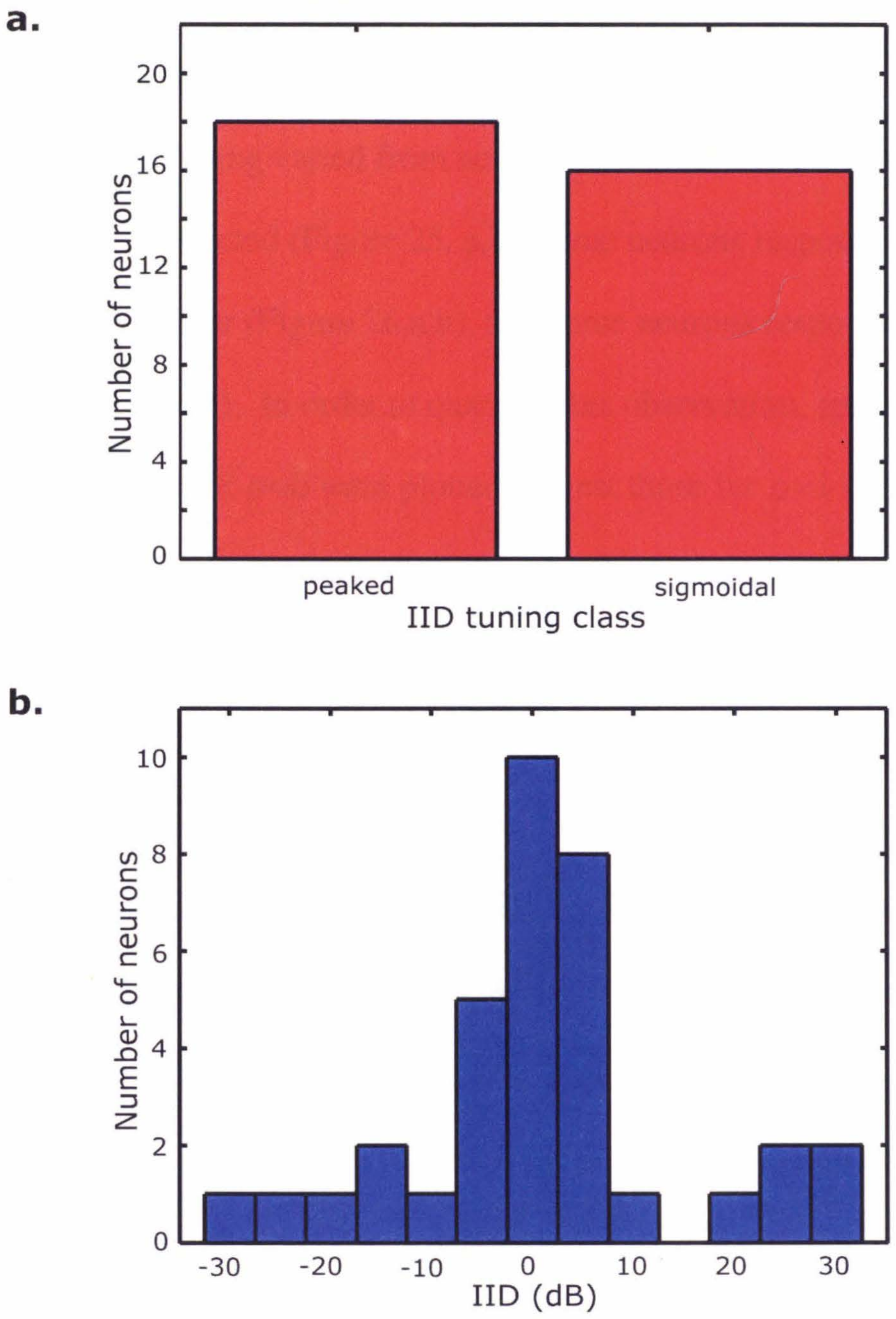


Fig. 24. IID responses in NO. a) Distribution of peaked and sigmoidally IID tuned neurons. b) Distribution of best IIDs.

(ANOVA, $p<0.01$). All neurons recorded from responded to some degree to binaurally uncorrelated noise. The effect of changing binaural correlation on IID tuning varied from neuron to neuron: some neurons were relatively unaffected (Figure 25, a,b), some neurons responded less but in a similar manner (Figure 26,a,b), and some neurons responded quite differently (fig 27, a,b). In order to quantify this observation, spike rates as a function of IID for $\rho=0$ were plotted against those for $\rho=1$ (Figure 28), and regression lines and slopes calculated for each neuron (Table 3). Unlike the responses of VLVp neurons, the response of many NO neurons was not well fit by a line (Table 3, col 1). For those neurons that were well fit by a line, y-intercepts tended to be greater than zero (Figure 29, a) and slopes tended to be positive (Figure 29, b). Regardless of r^2 value, the points in Figure 24 tended to lie above the line $y=x$, i.e., in general neurons tended to fire less for $\rho=0$ than for $\rho=1$. Because the binaural correlation sensitivity of many of the neurons was not well described by fitting a regression line to $\rho=0$ vs. $\rho=1$, an index of sensitivity to binaural correlation (BCS) was calculated. BCS is defined as the ratio of maximum spike rate in the $\rho=0$ condition to the maximum spike rate in the $\rho=1$ condition. Neurons that responded similarly to $\rho=0$ and $\rho=1$ have BCS values near one, neurons that respond more for rho=0 have

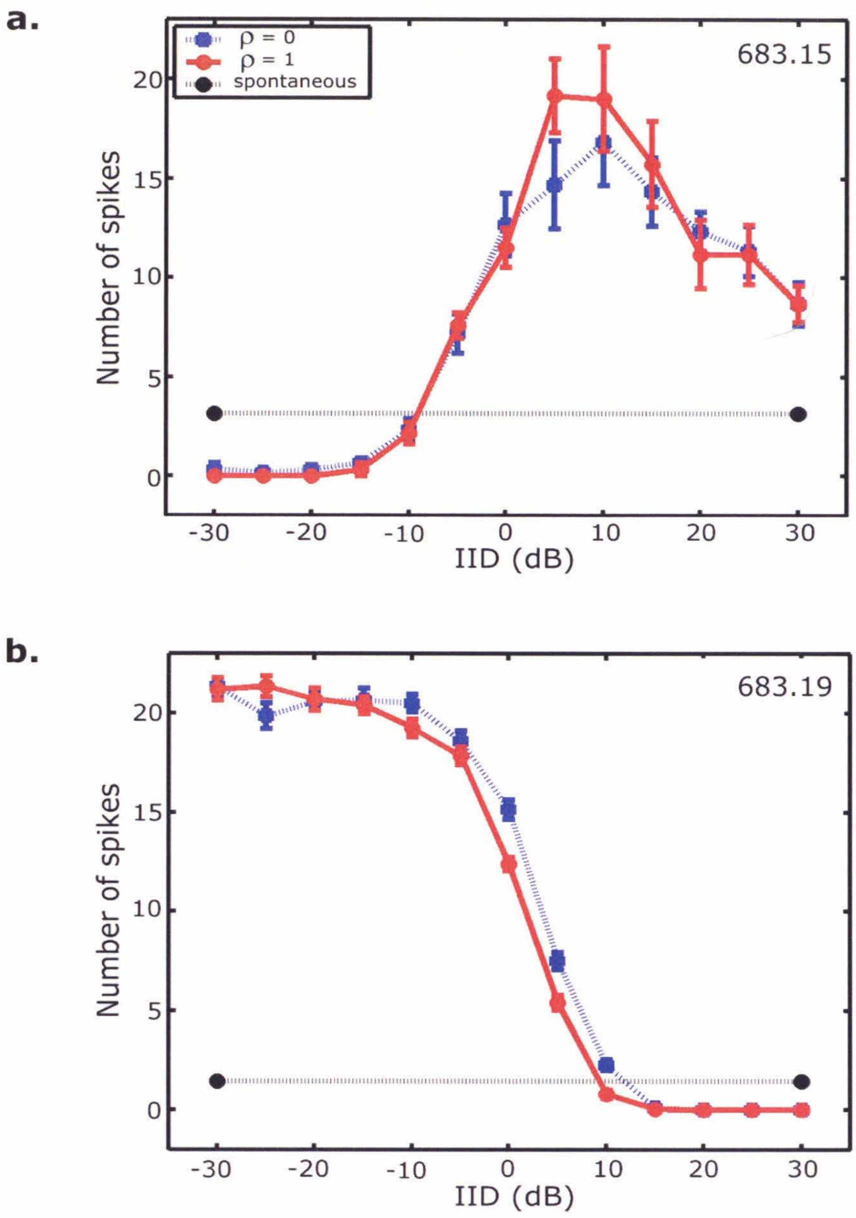


Fig. 25. Neurons with similar IID respnses to binaurally correlated (●) and binaurally uncorrelated (■) noise. a) a neuron with a shoulder IID response. b) A neuron with a sigmoidal IID response.

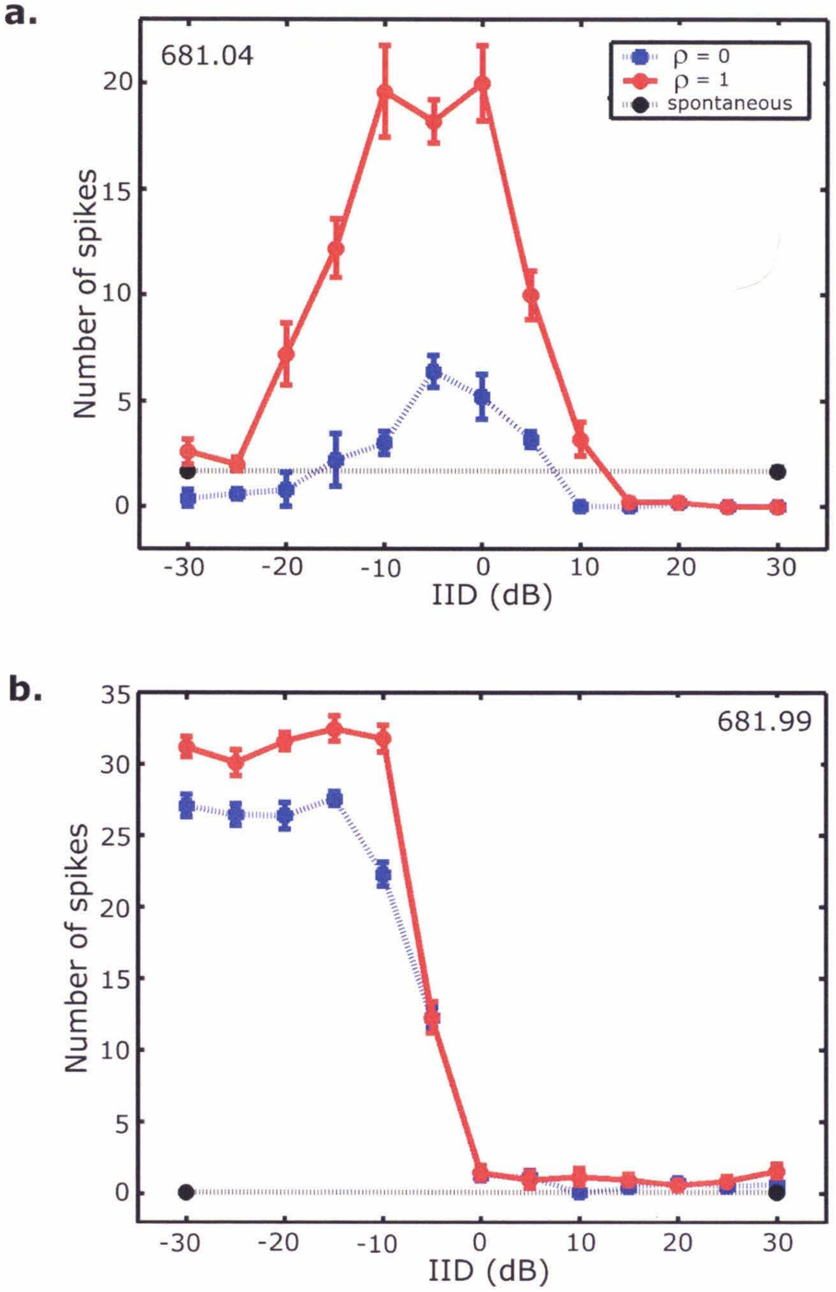


Fig. 26. Neurons whose responses to binaurally correlated (●) and binaurally uncorrelated (●) noise are scaled versions of each other. a) A neuron with a peaked IID response. b) A neuron with a sigmoidal IID response.

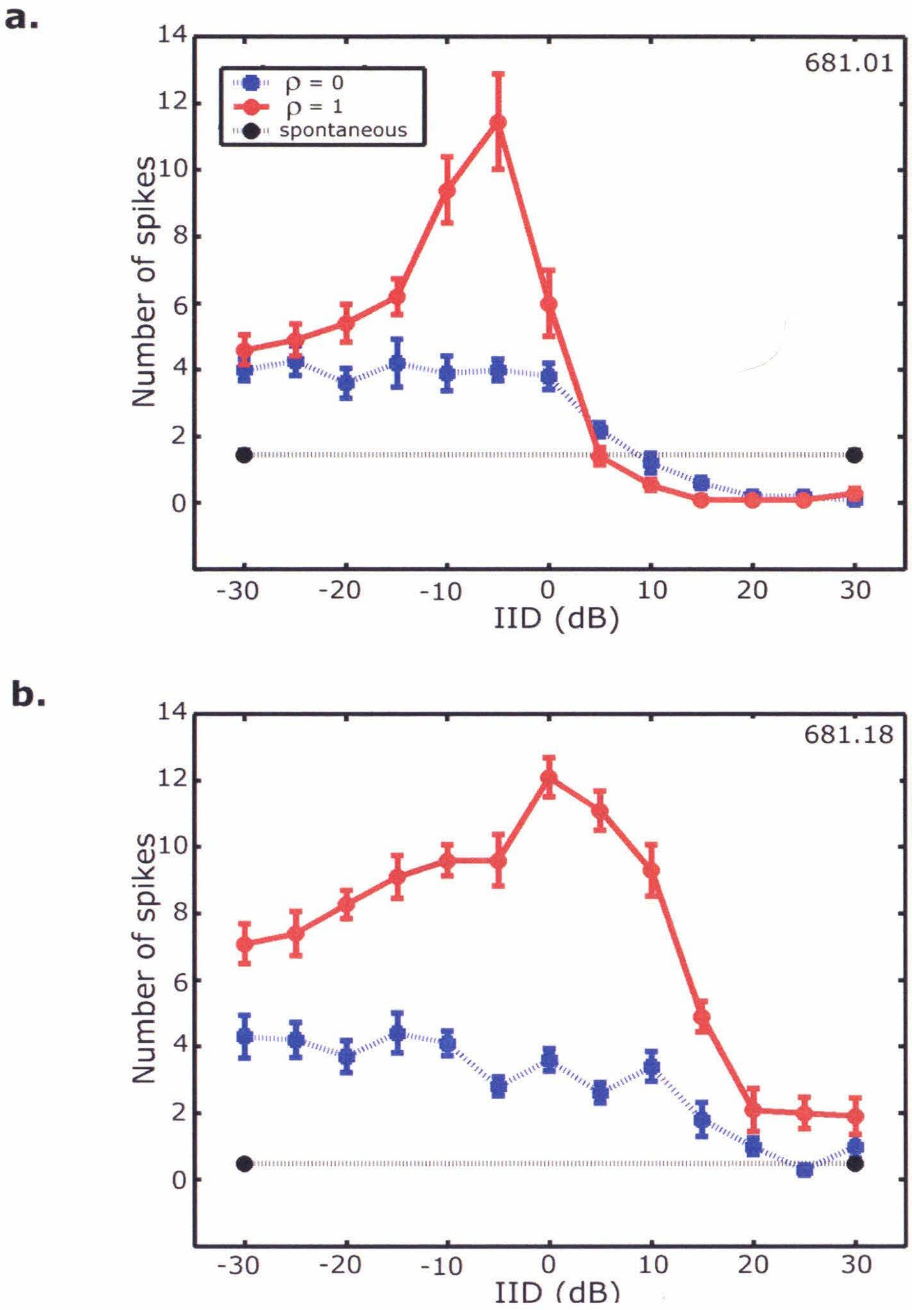


Fig. 27. Neurons with different IID response types for binaurally correlated (●) and binaurally uncorrelated (■) noise. a) A neuron with a should IID response for binaurally correlated noise and a sigmoidal response for binaurally uncorrelated noise. b) A different neuron with the same response types as in part a.

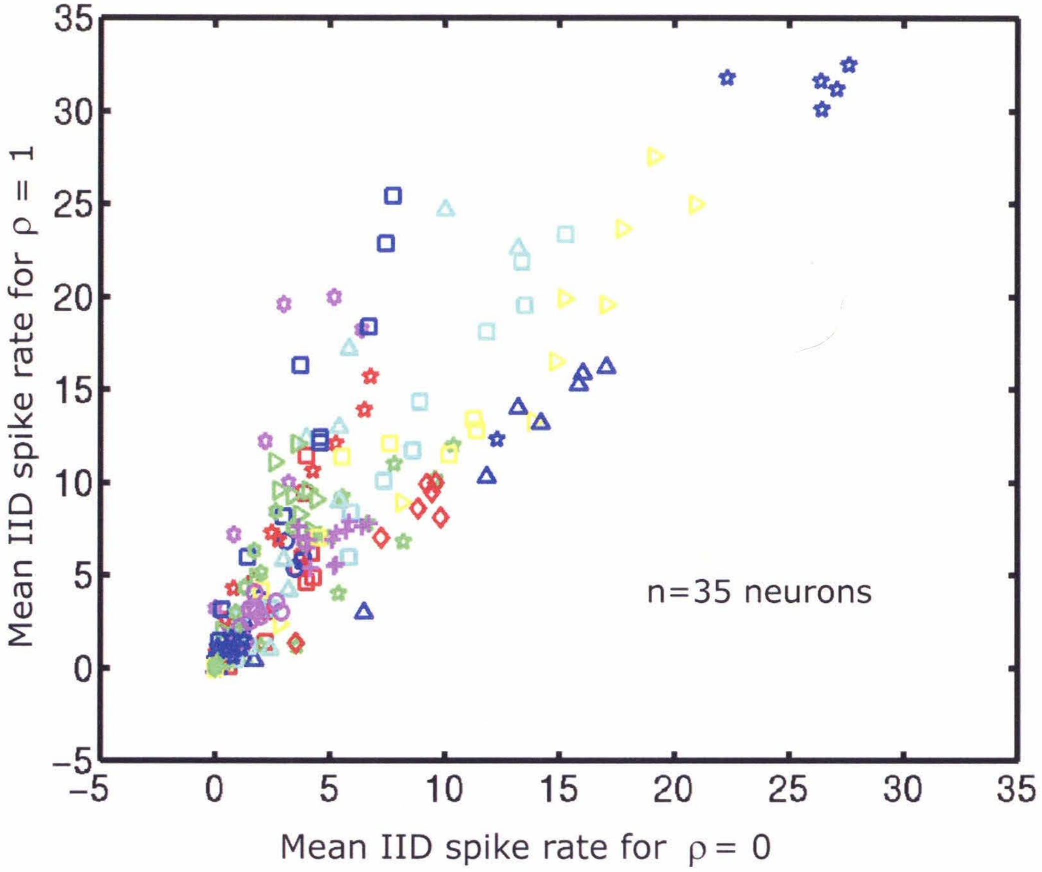


Fig. 28. The effect of binaural correlation on IID tuning in NO.

Table 3. Binaural correlation has a variable effect on the IID sensitivity of NO neurons. Slopes and coefficients of determination(r^2) are shown calculated from spikes as a function of IID for $\rho = 1$ plotted vs. $\rho = 0$ for each neuron.

	r^2	Slope
	0.37	0.53
	0.59	1.01
	0.23	0.40
	0.62	0.82
	0.40	1.30
	0.33	0.94
	0.44	0.85
	0.60	2.50
	0.71	1.80
	0.82	1.15
	0.74	1.77
	0.83	0.89
	0.28	1.08
	0.46	1.77
	0.77	0.89
	0.90	1.50
	0.63	1.02
	0.43	1.38
	0.04	0.26
	0.00	-0.01
	0.96	1.17
	0.68	0.94
	0.73	0.96
	0.95	0.99
	0.65	1.70
	0.48	0.79
	0.34	0.48
	0.12	0.43
	0.44	0.61
	0.53	1.12
	0.15	0.93
	0.01	0.14
	0.25	0.60
	0.55	0.83
	0.19	0.38
Average	0.49	0.97
Std dev	+/- 0.27	+/- 0.53

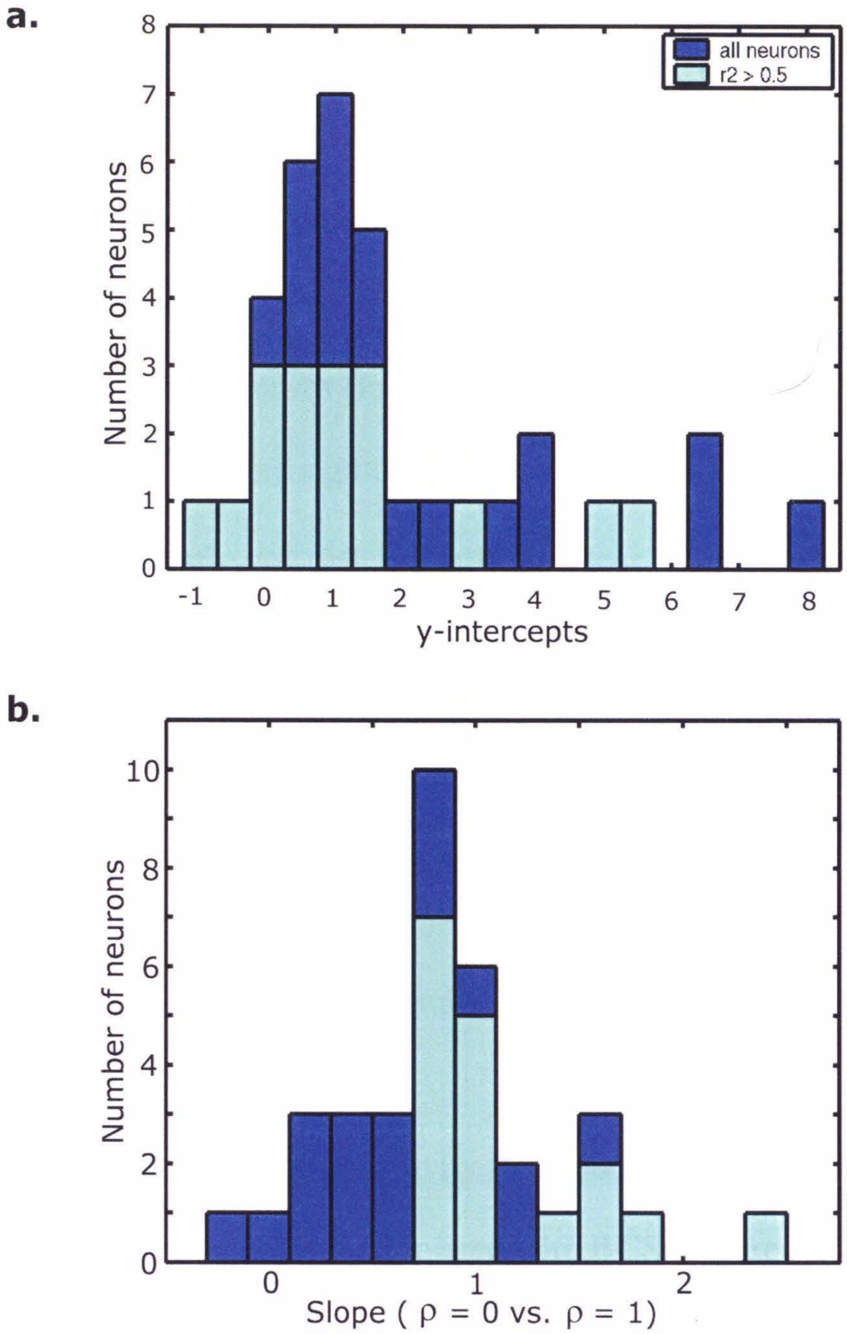


Fig. 29. NO neurons vary in the similarity of responses to $\rho = 0$ and $\rho = 1$. a) The distribution of y-intercepts for regression lines calculated from $\rho = 0$ vs. $\rho = 1$. b) The distribution of slopes for $\rho = 0$ vs. $\rho = 1$. Dark blue bars plot all data, light blue bars plot data with r^2 values greater than 0.5.

BCS values greater than one and neurons that responded more for $\rho=1$ have BCS values near zero. The distribution of BCS values for the NO neurons recorded from is shown in figure 30. Changing binaural correlation also changed the relative number of neurons that had peaked vs. sigmoidal tuning curves (Figure 31, a). Four neurons that were peaked for $\rho= 1$ became sigmoidal for $\rho=0$. In addition, the two different IID classes were affected differentially by a loss of binaural correlation (Figure 31, b); neurons that had peaked IID tuning curves for $\rho =1$ had lower BCS values, on average, than neurons that had sigmoidal IID tuning curves for $\rho =1$. The average BCS value for neurons that had peaked IID tuning curves for $\rho=1$ was 0.66, whereas the average BCS value for neurons that had sigmoidal IID tuning curves was 0.85.

<u>Effect of response type on sensitivity to binaural correlation</u>:

ITD modulation is inversely correlated with BCS (Figure 32, a); neurons with larger ITD modulation tend to have smaller BCS values, while neurons with smaller ITD modulation tend to have larger BCS values. The effect of bandwidth on sensitivity to binaural correlation can be seen in Figure 32, b. For neurons with narrow bandwidths (between 0 and 3 kHz) bandwidth was not a good predictor of BCS. Neurons with

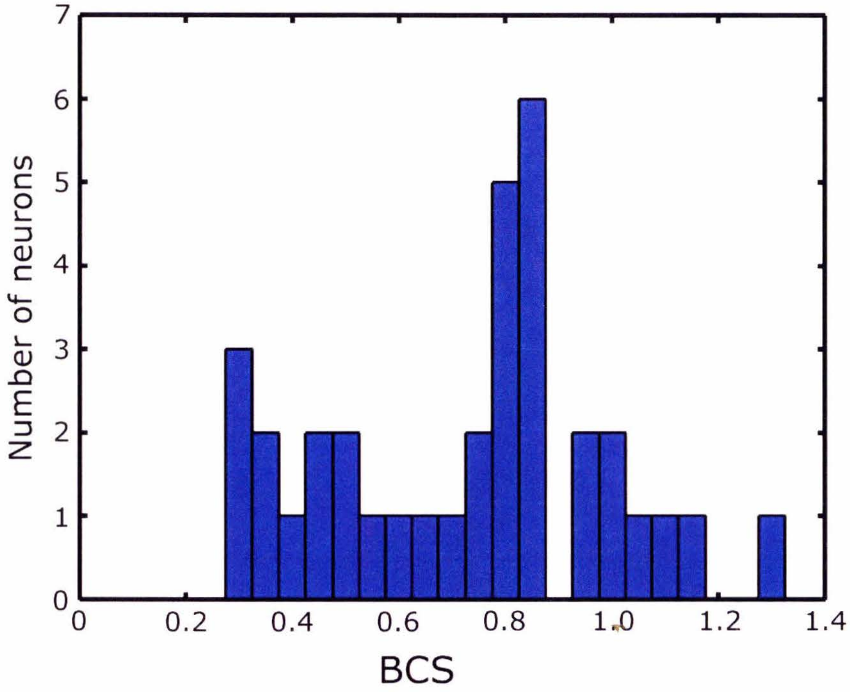


Fig. 30. Variation in sensitivity to binaural correlation in NO neurons. The distribution ofthe binaural correlation sensitivity index (BCS; ratio of maximum spikes for $\rho = 0$ to maximum spikes for $\rho = 1$).

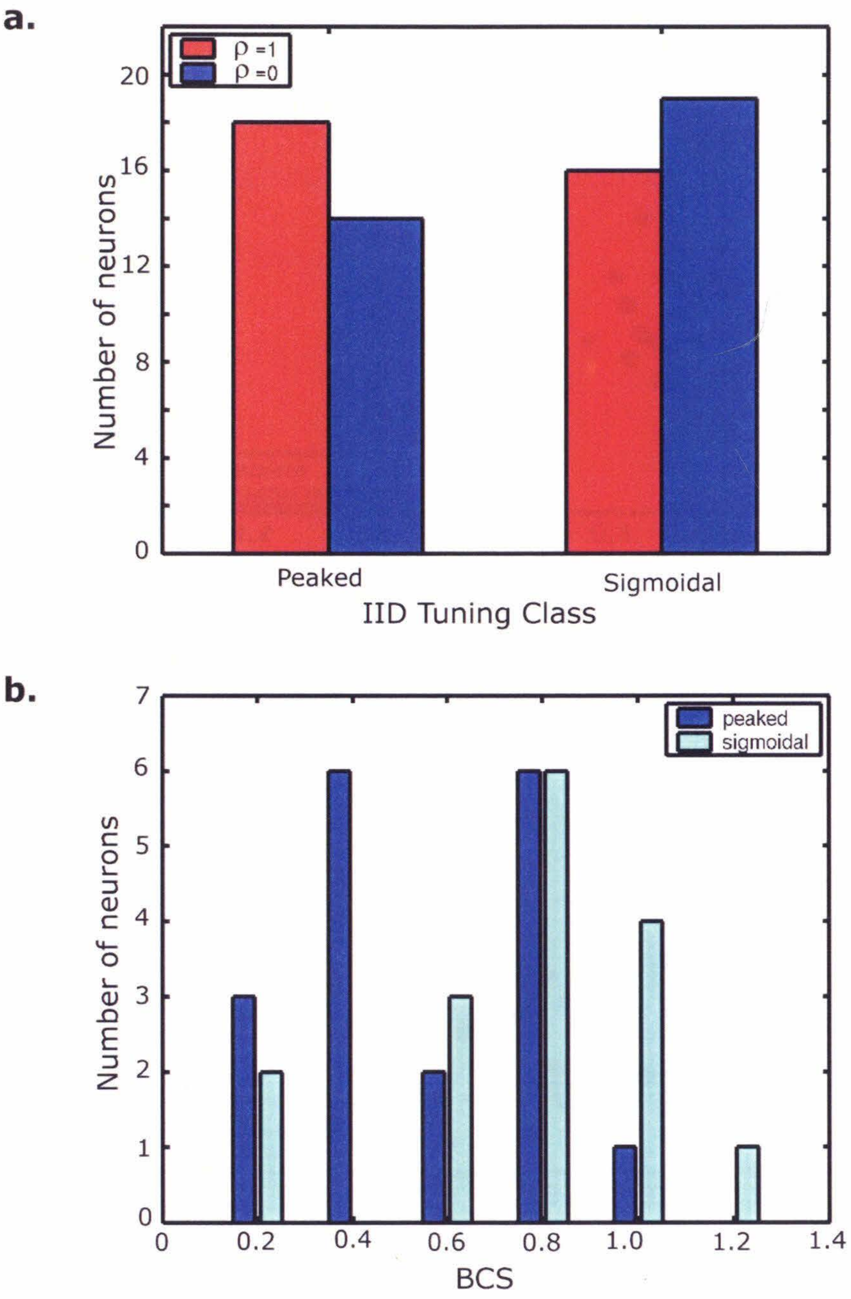
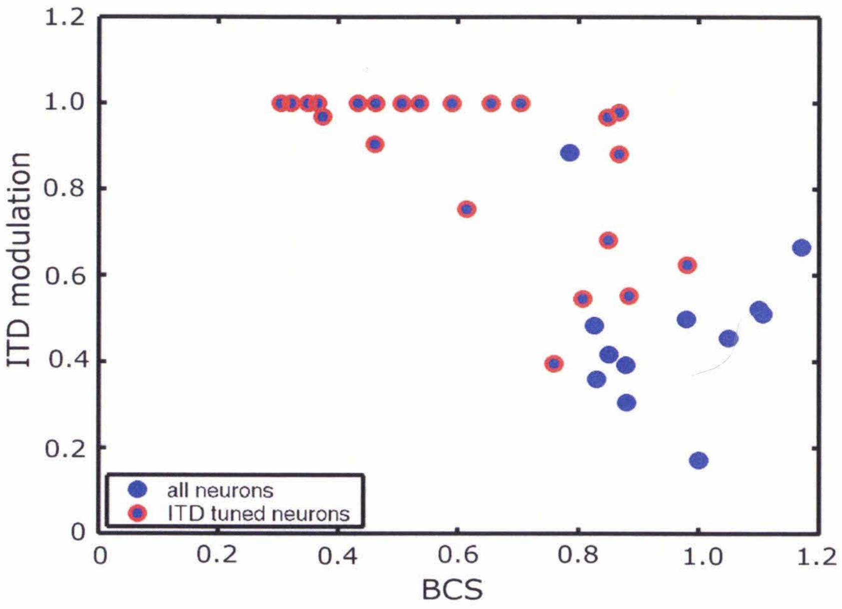


Fig. 31. Effect of binaural correlation on IID tuning
a) Number of neurons with peaked and sigmoidal tuning curves as a function of binaural correlation. b) Binaural correlation sensitivity (BCS) for neurons with peaked and sigmoidal IID tuning.

a.



b.

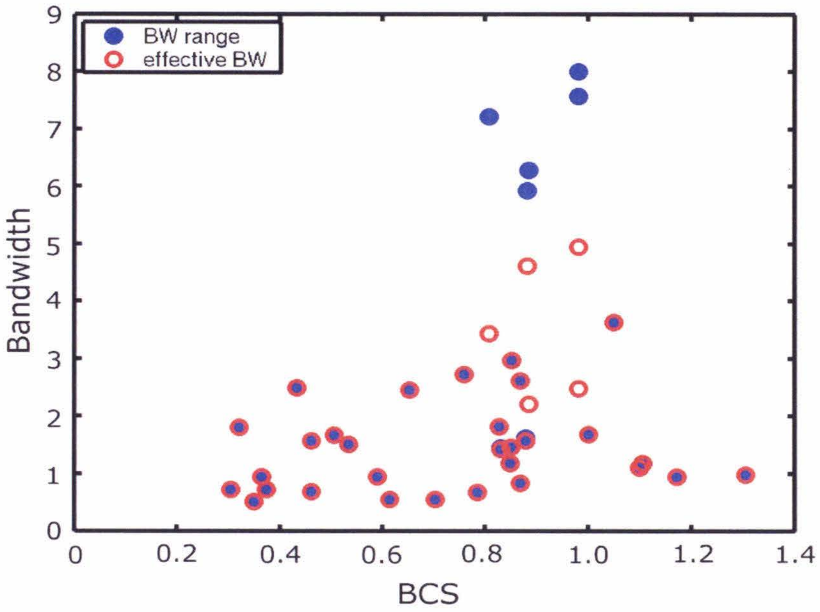


Fig. 32. Effect of binaural correlation on response properties of NO neurons. a) ITD modulation as a function of binaural correlation sensitivity (BCS). b) Bandwidth as a function of BCS.

large bandwidth ranges, however, tended to have BCS values near 1. In addition, Figure 28, b shows that these neurons have multiple peaks in their frequency tuning curves, since their effective bandwidths and bandwidth ranges are different.

5.3 Discussion:

The major result of this study is that a subset of NO neurons have spatially restricted IID responses for binaurally uncorrelated noise. This means that information about the elevation of a binaurally uncorrelated stimulus exists at the level of NO. These neurons are capable of supporting the accurate vertical sound localization behavior seen for binaurally uncorrelated noise. Unlike the optic tectum, all neurons in NO responded at least somewhat to binaurally uncorrelated noise, and many neurons were relatively unaffected by it. In addition, although there was a slight correlation between ITD modulation and degree of sensitivity to binaural correlation, many neurons with strong ITD tuning were also strongly responsive to binaurally uncorrelated noise. In fact, even for neurons with complete ITD modulation, the reduction in spike rate for $\rho=0$ stimuli never dropped below 70% of $\rho=1$, the average reduction in spike rate was closer to 50%, and one completely ITD modulated neuron had a drop in spike rate of only 30%. The general result that ITD tuned neurons continue to respond to $\rho=0$ stimuli shows that either NO neurons get excitatory drive from both IID and ITD channels, and that IID activation is enough to drive the cells in the absence of input from the ITD channel, or that $\rho=0$ stimuli activate NO neurons to some degree. This latter is more likely for neurons with phase-ambiguous ITD tuning, because such tuning implies a narrow frequency bandwidth, and sounds that are binaurally uncorrelated become progressively more correlated as they are filtered by narrower and narrow bandpass filters. The fact that the neuronal bandwidth is wide does not necessarily imply that the bandwidth of the ITD input is also wide. Proctor (1993) presents several neurons with broad frequency tuning but phase-ambiguous ITD response, and notes that one of those neurons was only ITD tuned for a narrow bandwidth.

For neurons for which a plot of $\rho=0$ vs. $\rho=1$ was well fit by a regression line, the increase in slopes above 1 indicate a decrease in tuning-curve steepness for binaurally uncorrelated stimuli, and the positive y-intercepts indicate a change in the breadth of the IID tuning curve (which would be expected with a vertical shift down in the curve). That many of the neurons were not fit by a line is not surprising: several of the neurons had different tuning-curve shapes for binaurally correlated and binaurally uncorrelated stimuli, which would not produce a line, and several neurons had IID tuning curves that were the same shape but shifted horizontally relative to each other, which would also not produce a line.

It will be interesting to discover whether accurate vertical localization to binaurally uncorrelated stimuli is dependent on those NO neurons that are only tuned to IID, and that show the least decrement in spike rate for binaurally uncorrelated noise, or on those NO neurons that are also tuned to ITD. If this later group is responsible, do they become more side-peak suppressed? No one knows how side-peak suppressed you need to be to be spatially specific, in fact there is some indication that the increase in neuronal space-specificity between ICx and OT may be a simple threshold.

Although this study demonstrates that information about the IID of a binaurally uncorrelated noise exists in NO, it is important to remember that NO is not the only avenue for auditory information to enter the forebrain. There are also projections from the intermediate nucleus of the lateral lemniscus to nucleus basalis (NB) (Arends and Zeigler, 1986; Delius, et al., 1979), an auditory nucleus in the forebrain. Neurons in NB in the barn owl may be tuned to binaural spatial cues (Wild, J.M. and Carr, C.E. personal communication).

Chapter 6

Sound localization with head-related transfer functions

General attributes of spectral cues:

By the time a sound from a distant source hits your ear drum it has already been heavily filtered. Sound is reflected and absorbed, attenuated and amplified by interactions with our torso, shoulders, head, ear canals, and especially by our pinnae. Early experiments that either occluded the convolutions of the pinna (Gardner and Gardner, 1973; Oldfield and Parker, 1984) or bypassed the pinna by inserting tubes into the ear canals (Jongkees and Groen, 1946; Fisher and Freedman, 1968) demonstrated the importance of these pinnal cues for localization in the vertical plane. In all animals in which this filtering has been studied, it has been found to be direction and frequency-dependent (starling: Klump and Larsen, 1992; pigeon: Lewald, 1990; bat: Fuzessery, 1996; cat: Musicant et al., 1990; ferret: Carlile, 1990; guinea pig: Sinyor and Laszlo, 1973; human: Wiener and Ross, 1946; mouse: Chen et al., 1995; wallaby: Coles and Guppy). Although experimenters have been measuring these head-related transfer functions (HRTFs) for over fifty years (Wiener and Ross, 1946; Butler and Belendiuk, 1977; Plenge, 1974; Shaw, 1974; Mehrgardt and Meller, 1977; Wightman and Kistler, 1989a,b), there is still considerable debate about what features of the HRTF encode sound-source location. Both peaks (e.g., Middlebrooks; 1992) and notches (Bloom, P.J., 1977; Hebrank and Wright, 1974; Watkins, 1978; Rice et al., 1992) have been suggested as important for vertical sound localization. Whatever features are responsible, they may not need be as spectrally sharp as previously believed--a recent experiment (Kulkarni and Colburn, 1998) has shown that HRTFs can be smoothed considerably before a difference between the smoothed HRTFs and an actual free-field sound source can be detected.

Plasticity of spectral cues:

Spectral cues also seem to be distinct from ITD and IID in that they remain plastic well into adulthood. In a beautiful experiment, Hofman et al. (1998) created artificial pinnae that altered their own natural HRTFs; immediately after being fitted with the artificial pinnae, their vertical localization ability disappeared. However, after several weeks of constant experience with the new pinna, vertical localization ability gradually returned. Intriguingly, when the pinnae were removed, vertical localization ability remained good, showing that the acquisition of new pinnal cues did not overwrite the subjects' original pinnal cues.

Effect of pinnal cues in development:

Monaural spectral cues are sufficient to produce a map of auditory space in the superior colliculus (mammalian analog of the OT), which is aligned with the visual map of space (King, Hutchings and Moore, 1987; King, Moore, and Hutchings, 1993), although only for near-threshold sound. When the pinnae are removed bilaterally in young ferrets, however, a map of auditory space fails to develop, showing that the spectral cues provided by the pinnae are necessary, as well as sufficient to instruct the developing auditory space map (King and Carlile, 1989; Schnupp et al, 1998). A less invasive method of changing spectral cues was used by Gold and Knudsen (1999; 2000). They investigated the effect of a monaural ear-plug with defined frequency-specific delay and attenuation on the development of space-specific responses in the auditory space map in the OT. Small frequency-dependent shifts relative to control animals were seen in the pure tone IID tuning, and in the location of pure tone receptive fields. The shifts seen were adaptive, in the sense that they were in the correct direction to offset the filtering effect of the earplug, but they were of a much smaller magnitude than expected. In addition, the general topography of the auditory space map was preserved in owls raised wearing such a device. This observation is consistent with the unmasking of frequency-specific binaural sound localization cues in blind-reared owls (Knudsen et al., 1991).

Spectral cues in barn owls:

Many other experiments have demonstrated the frequency-specific directional sensitivity of the barn owl external ear (Payne, 1971; Coles and Guppy, 1988; Moiseff, 1989; Olsen et al., 1989; Brainard et al., 1992). In the owl, the HRTFs depend on the feathers of the facial ruff, the preaural flaps (analogous to the tragus in humans), and the ear canal. Recently Keller and colleagues (1998) have recorded high quality HRTFs from a large number of positions in 12 owls. These data have shown, in agreement with early observations by Payne (1971), that there are sharp notches in the monaural spectrum. The authors also note that these notches are especially common in the lower hemifield and seem to vary from owl to owl. Both Knudsen et al., 1991, and Keller et al., 1998, found that binaural difference spectra were very similar between owls. All experiments that have demonstrated a dependence of auditory localization on spectral information in the barn owl have been electrophysiological and have focused on frequency-dependent shifts in ITD and IID, particularly IID.

Are spectral cues monaural or binaural?

Although demonstration of spectral cues has often relied on monaural stimulation (see Chapter 2), there is some question as to whether spectral cues are monaural or binaural in character. It is well known that although vertical localization is relatively unimpaired in monaural conditions, localization accuracy increases if both ears are used (see, for example, Butler et al., 1990). The monaural hypothesis states that two independent estimates of sound-source elevation are generated based on the monaural cues, and the increased accuracy in vertical localization in the binaural condition is due to averaging the two independent estimates. The binaural hypothesis suggests that in addition to monaural spectral estimates of sound-source elevation, a comparison of the two monaural spectra is used to provide additional information about sound-source elevation, and it is this binaural cue that is responsible for the increased accuracy in binaural vertical localization (Searle et al., 1975). One attractive feature of using a comparison of the spectra at the two ears (the binaural difference spectrum) is that use of a difference renders one immune to variations in the source spectrum. Unfortunately for this elegant hypothesis, not only is there no unambiguous experimental evidence in humans of the existence of such a cue, the sensitivity of vertical localization to changes in sound source spectrum argues against it. In addition, a recent experiment by Hartmann and Wittenberg (1996) has demonstrated that presenting human listeners with an accurate binaural difference spectrum, but unnatural monaural spectra, is insufficient for normal sound-location perception.

Although there is no strong evidence for the use of the binaural difference spectrum in humans, it has long been hypothesized to be important for barn owls (Payne, 1971; Knudsen and Konishi, 1978). This study takes advantage of the newly available high quality HRTFs to directly test whether barn owls use monaural and/or binaural spectral cues. In order to accomplish this, two different types of stimuli were generated: inverted-reversed HRTFs and flat-average HRTFs.

Inverted-reversed HRTFs:

One of the major difficulties with disambiguating monaural from binaural cues is that changing the monaural spectra usually changes the binaural spectra, and vice-versa. However, when the left and right HRTFs for a particular sound-source location (Figure 30, a, +30 ° elevation, 0 ° azimuth) are inverted, the inverted left spectrum played in the right ear and the

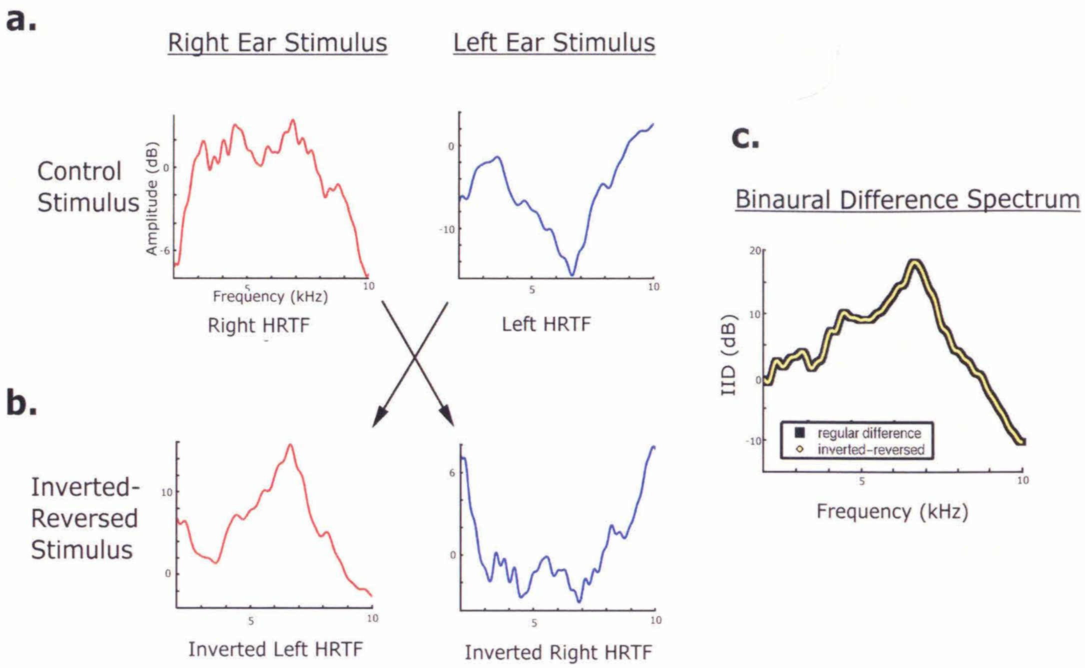


Fig. 33. Generation of inverted-reversed stimuli for comparison with regular difference spectra. a) Regular left and right HRTFs. b) In the inverted-reversed condition the left and right HRTFs are inverted and played through opposite ears. c) Regular and inverted-reversed difference spectra.

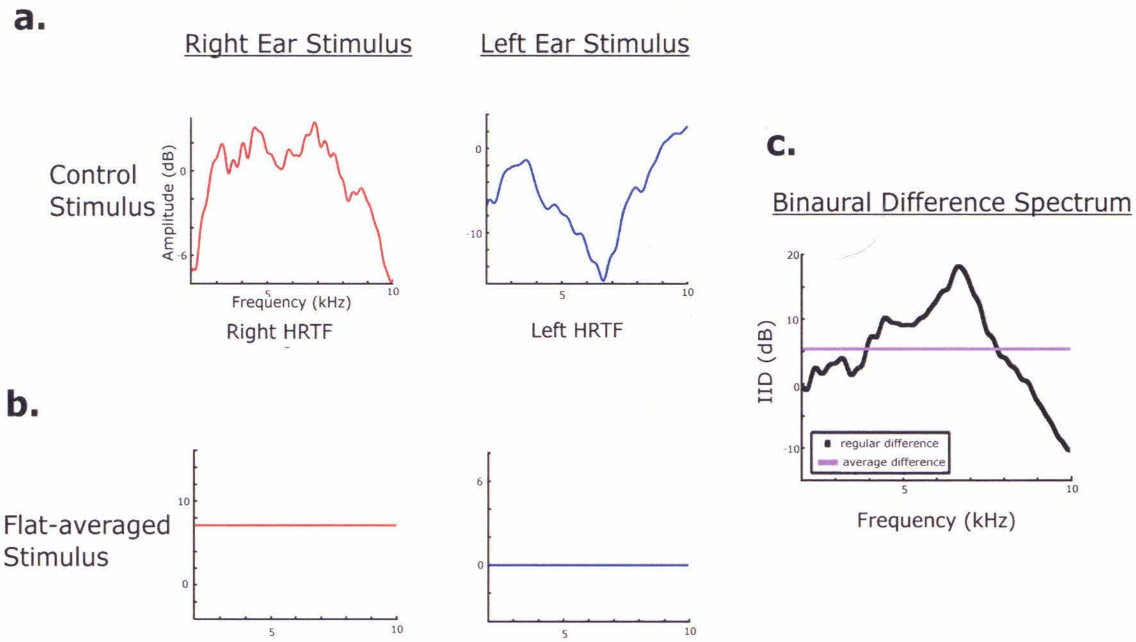


Fig. 34. Generation of flat-average stimuli for comparison with regular difference spectra. a) Regular left and right HRTFs. b) Flat left and right transfer functions calculated such that the average IID matched the average IID of the regular difference spectrum for a particular location. c) Regular and flat-average difference spectra.

inverted right spectrum played in the left ear (Figure 33, b), the resulting difference spectrum is the same as the uninverted, unreversed difference spectrum (Figure 33, c). This produces a stimulus condition in which monaural cues alone can be assessed.

Flat-average HRTFs:

There is also a confound in testing the effect of spectral cues, in that the known binaural difference cues (average ITD and average IID) are also affected by changes in the monaural and binaural spectrum. In order to control for effects of average IID and average ITD, a flat-average difference spectrum was calculated for each tested elevation (Figure 30, c). The average IID and average ITD were calculated for a particular difference spectrum and then flat transfer functions for the left and the right ears were generated, which would produce the average IID and ITD. This changes the binaural and monaural spectra without changing average IID and ITD, and allows the existence and character of putative binaural spectral cues to be tested.

In addition, although electrophysiological recordings from neurons in the barn owl inferior colliculus have shown that neural responses to free-field stimuli are very similar to neural responses to stimuli filtered with the HRTFs presented over headphones (Keller et al., 1998), these HRTFs have not been tested behaviorally. Part of the aim of this study was to demonstrate whether or not the HRTFs could support normal sound localization to virtual targets.

6.1 Methods:

Training:

Two owls with previous experience in sound localization were used for these experiments. General behavioral methods were the same as described in detail in the methods section of Chapter 3.

Presentation of normal HRTFs:

The HRTFs of two owls (#880 and #884) sampled at 685 sound-source locations in frontal space were generously donated by Kip Keller and Terry Takahashi. HRTFs were presented headphones. Care was taken to reproduce the spectral features of the HRTFs. The measured transfer functions of the left and right headphones were multiplied by the inverse left and right HRTFs for each location tested (-30, -15, 0, +15, and +30 degrees of elevation, and 0 degrees of azimuth) to create five headphone calibration files. The inverse of these combined transfer functions were used to filter stimuli played from the headphones. HRTFs are described using the same double-polar coordinate system described in Chapter 2 (Knudsen, 1982).

HRTF coordinate system:

The correspondance between the virtual locations measured and the perceived direction of the sound source when the HRTFs are played back will depend on the exact position of the owl's head when the HRTFs were measured; that is, the HRTFs were measured on a particular coordinate system, and how well this matches the actual perceptual coordinate system of the barn owl depends on how well the defined HRTF zero matches the perceptual zero of the owl (in both azimuth and elevation). Keller et al. (1998) defined zero as the position of the owls head when "the inner flat of the beak pointed downwards at 45 degrees resulting in a natural looking head posture." I suspect that this position is tilted slightly downward, at least from the head positions of the two owls in this study, as responses to HRTFs in both owls tended to be higher by about 5 degrees than the stated virtual elevation.

Experimental session:

Because the transfer function of the headphone and ear canal are sensitive to small changes in the position of the headphone assembly in the ear canal, extra care was taken to ensure that the headphones were positioned correctly before testing. For each session sounds filtered by regular HRTFs and either inverted-reversed or flat-averaged HRTFs were presented interleaved and in random order (without replacement).

6.2 Results:

Virtual stimuli:

Both owls varied the elevation of their orients with virtual elevation (Figure 35, a,b, red symbols). A comparison of HRTF mediated orients and free-field orients revealed that final head positions for virtual elevations were in general higher than those to the corresponding real-world source elevation (Figure 35 a,b, black symbols). Regression lines were fit to both HRTF and free-field data and the resulting slopes were not significantly different in either owl (t-test; $p < 0.01$).

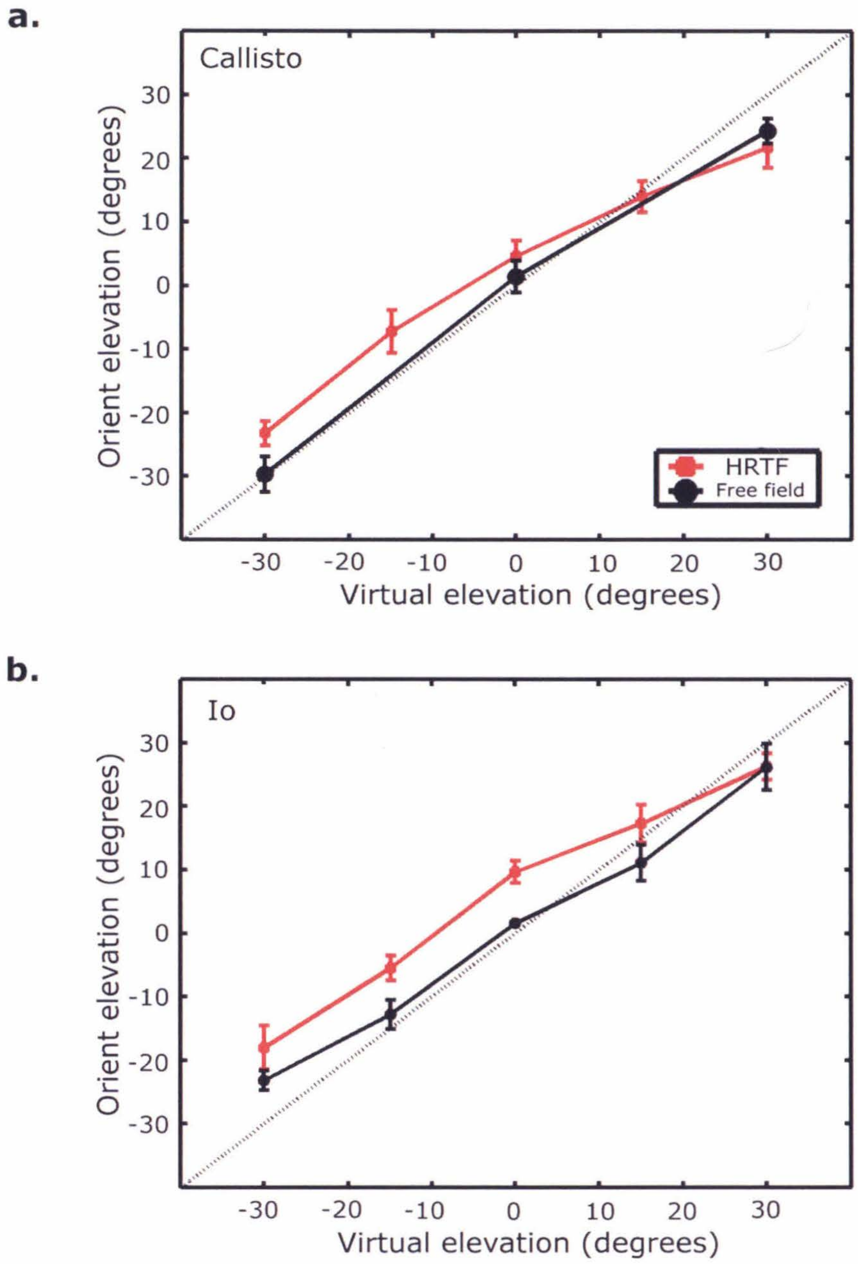


Fig. 35. Vertical localization to free field (●) and virtual (🟥) stimuli in two owls. a) Data from Callisto. b) Data from Io.

Disrupted monaural spectral cues:

Both owls continued to vary the elevation of their orients with virtual elevation, even when the left and right HRTFs were inverted and presented to opposite ears (inverted-reversed condition; Figure 36, a,b, blue symbols). There was no difference between responding to normal HRTFs (Figure 36, a,b, red symbols) and to inverted-reversed HRTFs in either owl (ANOVA, $p < 0.01$).

Disrupted monaural and binaural spectral cues:

When both monaural and binaural spectral cues were disrupted (flat-average condition), vertical localization was affected in both owls (Figure 37, a,b, blue symbols). This difference was statistically significant in one owl (Io; ANOVA, $p<0.01$), and not in the other (Callisto; ANOVA, $p=.13$).

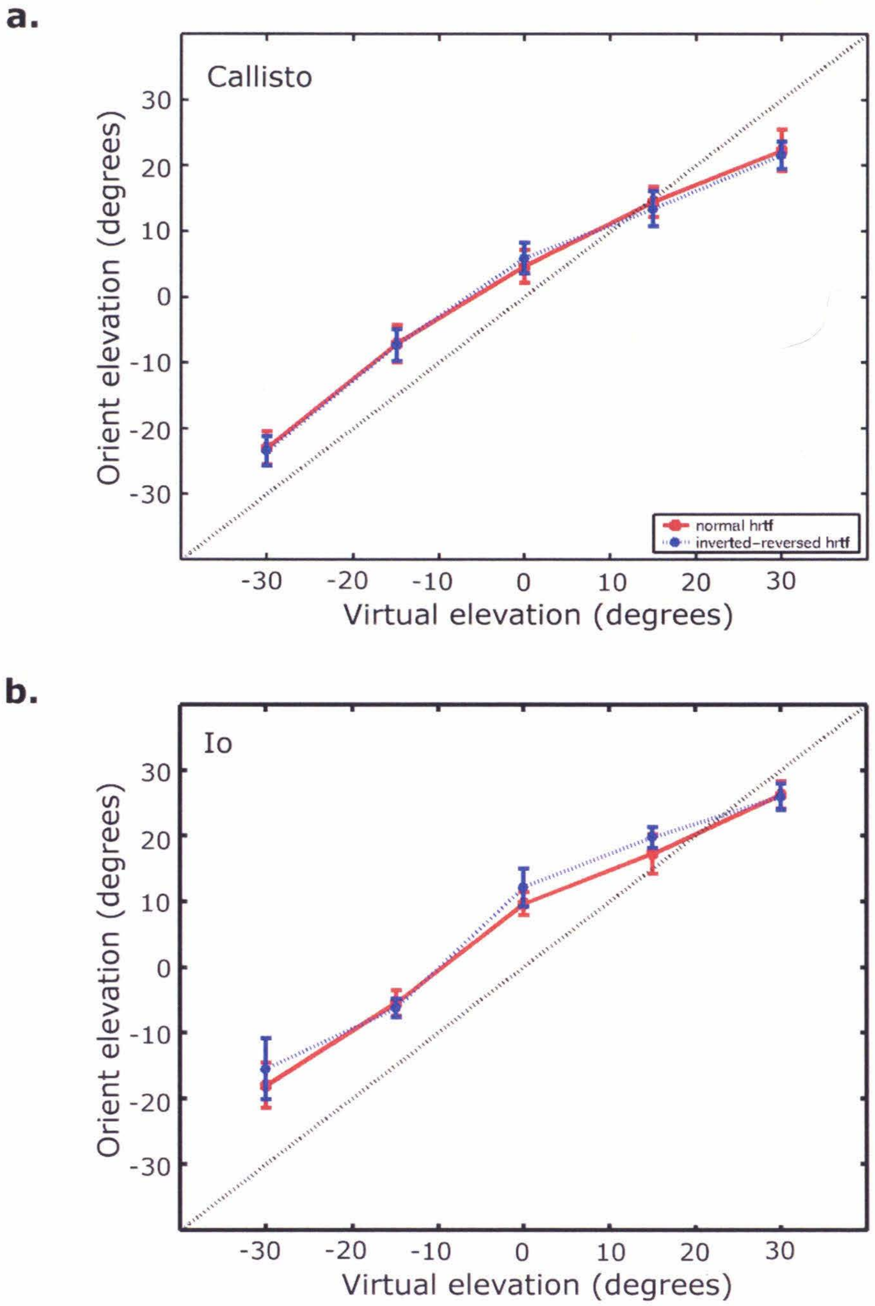


Fig. 36. The effect of inverted-reversed and regular HRTFs on vertical localization. a) Data from Callisto. b) Data from Io.

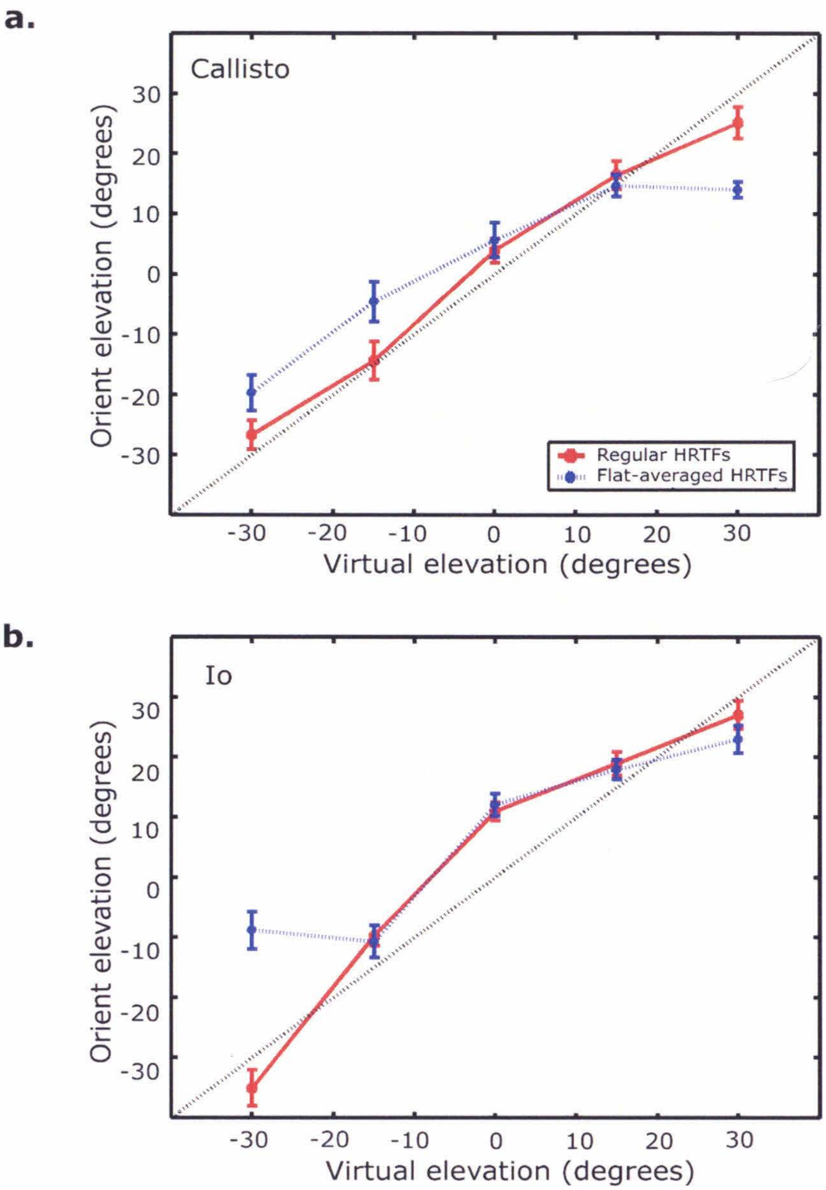


Fig. 37. Vertical localization to regular HRTFs (●) and flat-average HRTFs (●).

6.3 Discussion:

There was good agreement between sound localization to free-field and virtual stimuli; this is the first time that barn owl HRTFs have been tested behaviorally.

The vertical offset between free-field and virtual stimuli is probably the result of differences between the experimenter defined acoustic zero for the HRTF recordings and perceptual zero.

Monaural spectral cues:

The results of the inverted-reversed experiment demonstrate that barn owls are completely insensitive to changes in monaural spectra that do not produce concomitant changes in the binaural difference spectrum. This is in sharp contrast to human auditory spatial perception, which is severely disrupted if monaural cues are impaired, even if the binaural difference spectrum is maintained (Hartmann and Wittenberg, 1996).

Binaural spectral cues:

The results of the flat-average experiment demonstrates that binaural spectral differences do play a role in barn owl sound localization, but that this role is minor in comparison to average IID and ITD.

Accuracy of reproduction of HRTF fine structure:

Although neurons in the inferior colliculus respond as well to other owls HRTFs as to their own (Keller et al., 1998), it is possible that there are some individual-specific features of the HRTFs that are missing, which would have improved sound localization. Localization is already so good that it might not be possible to detect any improvement if such features do exist, however. Another caveat is that the HRTFs used in this study were measured on anesthetized owls. The entire facial ruff, and probably the preaural flap, are movable, and so features important for sound localization that are present when the owl is awake may be missing. It would be interesting to compare the HRTFs of an awake owl with those recorded while the same owl was anesthetized.

Why no monaural spectral cues?

Although barn owls possess the physical substrate for spectral localization, in the form of sharp and directionally-selective notches in the monaural spectrum, they do not appear to take advantage of it. Perhaps once ear asymmetry developed, and IID allowed accurate vertical localization, there was no pressure to develop monaural spectral cues, especially since these cues are less robust to noise than binaural difference cues. It's certainly true that humans do not use spectral cues for horizontal localization in general, although we can in some cases: in congenital monaural deafness (Slattery and Middlebrooks, 1994) or restricted cue conditions (Belendiuk and Butler, 1975). The fact that barn owls do seem slightly sensitive to the binaural difference spectrum is a basic consequence of the acoustic properties of the facial ruff: neurons that have IID tuning that is flat across frequency will be less space-specific than neurons that are tuned to the particular frequency-specific IID contour of a particular spatial location. What is surprising is what a small effect on sound localization a radical change in the binaural difference spectrum produces. Are barn owls really so insensitive to the binaural difference spectrum? Perhaps final head position is too coarse a measure to detect perceptual differences that exist. Barn owls are capable of making very fine discriminations in the spectrum of broadband noise (Konishi and Kenuk, 1975), so it seems likely that they are able to detect the difference between the regular HRTF and flat-average conditions.

Chapter 7

Conclusions

Barn owls do not use monaural spectral cues to localize sound:

Despite the existence of spectral features which could potentially support accurate sound localization, barn owls do not appear to use monaural pinnal cues. As a nocturnal predator specialized for audition, barn owls are under evolutionary pressure to localize sound accurately; it seems odd that cues that exist are not exploited. If barn owls have lost the ability to use spectral cues over time, this would suggest that such cues did not confer the advantage they appear to. Perhaps the development of ear asymmetry and the consequent availability of IID cues for the vertical plane rendered monaural cues obsolete. Alternatively, it is possible that no barn owl predecessor used spectral cues, and that the development of asymmetrical ears removed the pressure to find another method of localizing in the vertical plane. Neurons in the ICx of closely related symmetrically-eared owls have auditory receptive fields that are not restricted in the vertical plane and that do not respond to frequencies above 5.5 kHz (Volman and Konishi, 1990). The lack of vertical specificity in these neurons and the low frequency cutoff are both consistent with a lack of spectral cues (Heffner and Heffner, 1995). The pressure to use IID for vertical localization appears to have been quite intense, as ear asymmetry is believed to have arisen at least five times in different owl species (Norberg, 1977). That ear asymmetry developed, perhaps as opposed to the use of monaural spectral cues, may stem from the fact that binaural difference cues are more robust to noise, and, unlike monaural spectral cues, are not sensitive to variations in the source spectrum.

Barn owl sound localization is sensitive to the binaural difference spectrum:

Changes in the binaural difference spectrum do change barn owl sound localization, independent of average IID and ITD, although these changes are relatively small. The effect of such a manipulation on sound localization may be more pronounced for more peripheral targets than were tested in this study. Despite the computational attractiveness of the binaural difference spectrum as a cue for sound localization, this is the first unequivocal demonstration of its importance for sound localization in any species.

Barn owls can orient to sounds that lack a coherent ITD

Barn owls are able to extract the IID of a binaurally uncorrelated stimulus, and use the IID to localize in the vertical plane. This ability is in contrast to the effect of binaural decorrelation on horizontal sound localization (Saberi 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. Although both humans and barn owls depend on ITD and IID for sound localization, the loss of coherent ITD affects the two species differently.

Auditory thalamic neurons encode the IID of binaurally uncorrelated sounds:

The fact that barn owls can localize the vertical component of binaurally uncorrelated stimuli implies the presence in the auditory system of neurons that encode the IID of binaurally uncorrelated stimuli. Previous experiments had already shown that the more well understood collicular pathway could not support this behavior (Saberi et al., 1998). Recordings from VLVp neurons show that the initial IID encoding of binaurally uncorrelated sounds is indistinguishable from that of binaurally correlated sound. Recording from neurons in NO show that neurons maintain IID tuning for binaurally uncorrelated noise. Information about the elevation of a binaurally uncorrelated stimulus is therefore 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 IID 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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