Published in final edited form as:

J Neurophysiol. 2006 February ; 95(2): 783–790. doi:10.1152/jn.00833.2005.

Comparison of Midbrain and Thalamic Space-Specific Neurons in Barn Owls

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Abstract

Spatial receptive fields of neurons in the auditory pathway of the barn owl result from the sensitivity to combinations of interaural time (ITD) and level differences across stimulus frequency. Both the forebrain and tectum of the owl contain such neurons. The neural pathways, which lead to the forebrain and tectal representations of auditory space, separate before the midbrain map of auditory space is synthesized. The first nuclei that belong exclusively to either the forebrain or the tectal pathways are the nucleus ovoidalis (Ov) and the external nucleus of the inferior colliculus (ICx), respectively. Both receive projections from the lateral shell subdivision of the inferior colliculus but are not interconnected. Previous studies indicate that the owl's tectal representation of auditory space is different from those found in the owl's forebrain and the mammalian brain. We addressed the question of whether the computation of spatial cues in both pathways is the same by comparing the ITD tuning of Ov and ICx neurons. Unlike in ICx, the relationship between frequency and ITD tuning had not been studied in single Ov units. In contrast to the conspicuous frequency independent ITD tuning of space-specific neurons of ICx, ITD selectivity varied with frequency in Ov. We also observed that the spatially tuned neurons of Ov respond to lower frequencies and are more broadly tuned to ITD than in ICx. Thus there are differences in the integration of frequency and ITD in the two sound-localization pathways. Thalamic neurons integrate spatial information not only within a broader frequency band but also across ITD channels.

INTRODUCTION

In the owl's brain, the processing stream that computes sound direction leads to the formation of an isomorphic map of auditory space in the external nucleus of the inferior colliculus (ICx) and optic tectum, which is called the "tectal sound localization pathway" (Knudsen 1982; Knudsen and Knudsen 1983; Knudsen and Konishi 1978, 1979; Moiseff and Konishi 1981; Peña and Konishi 2001; Takahashi et al. 1989; Wagner et al. 1987). Conversely, no map of spatial cues has been found in forebrain structures (Cohen and Knudsen 1994, 1995, 1996, 1998, 1999; Cohen et al. 1998; Knudsen et al. 1977; Proctor and Konishi 1997). However, the barn owl's forebrain contains neurons sensitive to sound direction that are tuned to the same spatial cues that create the spatial selectivity in the midbrain.

Lesions in the tectal pathway render owls unable to accurately localize sound in the area of space represented by the damaged regions (Wagner 1993). During inactivation experiments, the probability of performing an accurate orienting behavior toward sounds decreased (Knudsen and Knudsen 1996a; Knudsen et al. 1993). However, the owls regain their normal localizing ability in the course of a few weeks (Knudsen et al. 1993; Wagner 1993). A

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“forebrain sound localization pathway” that extends from the midbrain to the forebrain via the thalamus appears to be also involved in this localizing ability and recovery (Cohen and Knudsen 1994, 1995, 1998; Cohen et al. 1998; Knudsen et al. 1993; Wagner 1993). Consistent with this hypothesis, lesion or inactivation of both pathways permanently impairs the owl’s ability to localize sounds (Knudsen and Knudsen 1996a; Knudsen et al. 1993; Wagner 1993). Thus owls seem to use either tectal or forebrain structures to determine sound direction. The space-specific neurons of the forebrain do not receive projections from the midbrain map (Arthur 2002; Cohen et al. 1998; Knudsen and Knudsen 1983; Proctor and Konishi 1997). However, both the forebrain and midbrain representations of auditory space use information on binaural cues produced by the same lower brain stem areas. These binaural cues are the interaural level difference (ILD) and the interaural time difference (ITD), which are processed in separate brain stem pathways (Fig. 1). For the owl, ILD and ITD encode the vertical and horizontal coordinates of sound direction, respectively (Moiseff 1989).

The ICx and the thalamic nucleus ovoidalis (Ov) are, respectively, the first areas that belong exclusively to the tectal and forebrain sound localization pathways. Whereas ICx generates the auditory spatial tuning that reaches the optic tectum, Ov is the entry site of auditory information to the forebrain. It is not known whether or not the forebrain and tectal pathways derive spatial information using the same methods of computation. Integration across frequency is used to eliminate the ambiguity inherent to the periodic nature of sound. This mechanism has been observed in the owl’s tectal pathway, where frequency convergence across narrowband channels largely tuned to the same ITD creates neurons that have a characteristic delay (CD) (Mazer 1998; Peña and Konishi 2000; Saberi et al. 1999; Takahashi and Konishi 1986; Wagner et al. 1987). However, studies in the mammalian inferior colliculus (McAlpine et al. 1998) do not find frequency-independent ITD tuning and a large proportion of thalamic neurons have characteristic delays that do not correspond with discharge maxima (Stanford 1992). Because the existing experimental evidence suggests that the owl’s midbrain map of auditory space differs from the representations of auditory space in the owl’s forebrain and in mammalian brain areas, we asked whether or not these pathways compute spatial information in the same way. Thus we compared how Ov and ICx neurons integrate ITD responses from different frequency bands in the barn owl.

METHODS

Adult barn owls (*Tyto alba*) of both sexes were anesthetized by intramuscular injections of ketamine hydrochloride (20 mg/kg; Ketaset) and xylazine (4 mg/kg; Anased) and given prophylactic antibiotics (oxytetracycline; 20 mg/kg; Phoenix Pharmaceuticals). Anesthesia was maintained with supplemental injections of ketamine and xylazine during the experiment. A heating pad (k-20-f; American Medical Systems, Cincinnati, OH) was used to maintain the body temperature and the wings were restrained with a soft leather jacket. A stainless-steel plate was placed on the skull using dental acrylic to hold the head in subsequent experiments, and a reference pin was implanted on the midline point of the interaural plane. Recording sessions began a week after this initial surgery. The owl was anesthetized and placed into a custom-built stereotaxic device that held the head such that the ventral surface of the palatine ridge was at 30° from the horizontal plane. We opened a small hole on the skull area overlying either Ov or ICx and cut a slit in the duramater for electrode insertion. At the end of the experiment, we covered the craniotomy with gelfoam and dental cement and closed the skin incision. Owls were returned to their individual cages and monitored for recovery. Depending on the owl’s weight and recovery conditions, experiments were repeated every 7–10 days for a period of several weeks. These procedures comply with guidelines set forth by the National Institutes of Health and Caltech Institute’s Animal Care and Use Committee.

Acoustic stimuli

Custom software was used to generate sound stimuli, data collection and analysis. Acoustic stimuli were delivered by a stereo analog interface (DD1; Tucker Davis Technologies) through a calibrated earphone assembly. Tonal, broadband, and narrowband noise stimuli (50-ms duration, 5-ms linear rise/fall time) were presented once per second. Broadband stimuli had a band-pass of 1–12 kHz. Narrowband signals were 1-kHz bandwidth noise.

Spikes were recorded during a time window set to start 100 ms before the stimulus onset and ending 200 ms after stimulus offset. ITD was varied in steps of 30 μ s, ILD in steps of 5 dB, and frequency in steps of 100 Hz. We averaged the response ≥ 10 randomized repetitions of the same stimulus. The stimulus intensity could be varied independently for each ear using a pair of digitally controlled attenuators (PA4, Tucker Davis Technologies).

All recordings were performed in a double-walled sound-attenuating chamber. Each earphone consisted of a speaker (Knowles 1914) and a microphone (Knowles 1319) encased in a custom-made metal delivery piece (5 mm long and 7 mm diam) that fits the owl's ear canal. The gaps between the earphone assembly and the ear canal were filled with silicone impression material (Gold Velvet II, All American Laboratory). Simultaneous measurement of sound with both the B&K and the Knowles microphones made it possible to translate the voltage output of the Knowles into sound intensity in dB SPL. The Knowles microphones were then used to calibrate the earphone assemblies at the beginning of each experiment. The calibration data contained the amplitudes and phase angles measured in steps of 100 Hz. The computer automatically smoothed irregularities in amplitude and phase of the frequency response of each earphone from 0.5 to 12 kHz.

Data collection

The activity of single neurons in Ov and ICx was recorded extra-cellularly with tungsten electrodes (1M Ω , 0.005-in, A-M Systems). Action potentials were amplified, filtered (Amplifier System, μ A-200, Beckman Electronic Shop), and converted to transistor-transistor logic (TTL) pulses with a spike discriminator (SD1, Tucker Davis Technologies). The data were stored in a computer via a time converter (ET1, Tucker Davis Technologies) and an A/D converter (DD1, Tucker Davis Technologies) with a sampling rate of 48 kHz and 16-bit resolution.

Ov was localized using stereotaxic coordinates and locating its tonotopically organized region (Proctor 1993; Proctor and Konishi 1997). ICx was localized stereotaxically and by its physiological response properties (Knudsen and Konishi 1978; Peña and Konishi 2000, 2001). The electrodes were advanced with a microdrive (Motion Controller, Model PMC 100, Newport) in steps of 100 μ m until the nucleus was reached. The size of the steps was then reduced to 2–4 μ m to search and isolate single units. The neurons were recorded every approximately 100 μ m in the dorsoventral plane.

The number of impulses obtained for specific values of stimulus parameters such as frequency, ITD and ILD constitutes the raw data in this study. The stimulus parameters were randomly varied during the recording of neural responses. For each Ov and ICx neuron we examined the ITD, ILD, and frequency tuning (Fig. 2). We computed: mean firing rate as a function of ITD (ITD curves), varied in 30- μ s steps within a range from –300 to 300 μ s (negative ITDs indicate ipsilateral ear leading); mean firing rate as a function of ILD (ILD curves), varied in steps of 5 dB in a range from –30 to 30 dB (negative ILDs mean left ear louder); and mean firing rate as a function of the stimulus frequency changed in steps of 100 Hz at a constant sound intensity of 40 dB SPL (iso-intensity frequency tuning curve).

Data analysis

We first determined that a neuron was “sensitive” to ITD or ILD by visual inspection of the tuning curves obtained with broadband noise stimulation. The ITD tuning was later confirmed by the statistics used in fitting the ITD curves obtained with tonal stimulation. The “best ITD” and “best ILD” elicited the maximum response in the ITD and ILD curves, respectively. In the case of ITD curves with multiple peaks of similar amplitude, we used the peak closest to 0 μ s. We used the best ITD to collect the ILD curves and the best ILD to collect the ITD curves. These ITD and ILD values were then used to obtain the neuron’s frequency tuning curve. An Ov neuron was classified as broadly tuned to frequency when it responded to a frequency band equal to or larger than the median half-height width of the iso-intensity frequency tuning curves in the ICx neurons sample (1.4 kHz). In all neurons that were initially considered tuned to ITD and broadly tuned to frequency, we examined the ITD sensitivity across frequency. We performed the same analysis on space-specific neurons of ICx to compare results obtained under identical experimental conditions.

The tuning to ITD in periodic signals (tones) can be expressed in terms of phase differences between the sound arriving to the left and right ears. The interaural phase difference that elicits the maximum mean response will be called the mean interaural phase (MIP) (Goldberg and Brown 1969). ITD curves for tones in Ov and ICx do not show the clear sinusoidal shape of lower brain stem neurons that allows MIP computation by fitting the data to cosine functions (Peña et al. 1996; Viete et al. 1997). Instead, we obtained MIP by folding the ITD curves into a single period of the stimulating frequency, converting ITD to interaural phase difference (IPD), and fitting the data to a Gaussian function using the least-square method. The center of the Gaussian fit was used as MIP. We used visual inspection of each fit and the χ^2 statistical test, based on the residuals between the data and the model, and the degrees of freedom of the fitting equation, to evaluate the goodness of each fit. Only the cells whose fits passed the χ^2 test ($P < 0.05$) were used for further analysis. We then performed a linear regression of the MIP versus stimulating-frequency and quantified the difference between the data and the regression line by computing the mean of the squared differences between each point and the regression line. We carried out the same analysis for Ov and ICx neurons.

We studied the ITD tuning across frequency by examining the relationship between MIP and stimulus frequency. We used the residuals between the data and the regression line to quantify the linearity of this relationship. For linear relationships, this is also the most precise method to determine the characteristic delay (CD) of the neurons (Rose et al. 1966; Yin and Kuwada 1983). Neurons that have a CD respond to a value of ITD with the same relative firing rate at all stimulus frequencies. In such cells, plotting the MIP against the stimulating frequency yields a line whose slope is the CD.

The width of the main peaks of the ITD curves for broadband noise and tones were measured at 50% of the distance between the minimum and maximum response level (“half-height width”). The same criteria were used to measure the frequency-tuning width in iso-intensity frequency tuning curves.

Histology

The recording sites were marked in the last experiment by iontophoretic injection of tracers [fluorescein (FDA) and tetramethylrhodamine (RDA) conjugated dextran amines] and electrolytic lesions in the previously recorded regions of Ov and ICx (Fig. 2, A and B). Four to 6 days after tracer injection, the owls were overdosed with sodium pentobarbital (Nembutal, Abbot Laboratories) and perfused with saline followed by 2% paraformaldehyde (Fisher Scientific). Brains were blocked in the plane of the electrode penetration, removed from the skull and placed in 30% sucrose until they sank. They were then cut in 60- μ m sections and

mounted on slides to verify the location of the recording site. The electrode locations of previous experiments were extrapolated using records of the stereotaxic coordinates of each recording site.

RESULTS

Single-unit extracellular recordings of Ov and ICx neurons were collected from eight anesthetized adult barn owls. We included in this sample 325 Ov neurons that were tuned to ITD and 52 ICx neurons. Given the abundance of studies that have previously described the response of ICx neurons (Knudsen and Konishi 1978, 1979; Knudsen and Knudsen 1983; Knudsen et al. 1977; Mazer 1998; Peña and Konishi 2000, 2001, 2002; Takahashi et al. 1989), we considered our sample representative of ICx responses to the stimuli used in our study. Two hundred and sixteen Ov neurons were sensitive to both ITD and ILD (Fig. 2, *C*, *D*, *F*, and *G*). As in the previous study of Ov neurons (Proctor and Konishi 1997), we found no clear topographic organization such as clusters or groups of neurons tuned to similar ITD. Instead the responses varied widely over sequentially recorded neurons along the same electrode track.

Frequency tuning

We obtained iso-intensity frequency tuning curves in Ov (Fig. 2, *E* and *H*) and ICx neurons (Fig. 2*K*). The best frequencies, frequencies that elicited the maximum response of the neuron, in Ov neurons varied from 0.7 to 7.1 kHz (median = 4.3 kHz). Their frequency tuning width varied from 0.2 to 7.8 kHz (median = 1.7 kHz). The best frequencies of ICx neurons varied from 2.0 to 6.2 kHz (median = 5.2 kHz), and their frequency tuning width varied from 0.4 to 3.4 kHz (median = 1.4 kHz). There was no significant difference in the frequency tuning width in both nuclei (*t*-test, $P = 0.31$). The comparison of best frequencies showed a distribution with significantly lower mean in Ov neurons than in ICx (*t*-test, $P < 0.00001$; Fig. 3).

We used the median frequency tuning width of the ICx neurons sample (1.4 kHz) to divide the population of Ov neurons into two groups: we considered broadly tuned those Ov neurons that responded to a frequency band equal or larger than this value, and narrowly tuned otherwise.

ITD sensitivity

In Ov, ITD curves measured with broadband noise varied from having multiple undistinguishable maxima (phase ambiguous) to a distinctly larger response to a unique ITD (Fig. 2, *C* and *F*). These results are consistent with previous work (Proctor 1993). Of the 325 Ov neurons included in this study, 42.2% ($n = 137$) presented a phase ambiguous ITD tuning curve, while the rest responded maximally to a single ITD. All ICx neurons recorded ($n = 52$; Fig. 2*I*) showed a main peak at a single ITD.

We compared the half-height width of the main peak in ITD tuning curves obtained for broadband noise signals and tones in Ov and ICx (see METHODS). Only broadly frequency-tuned Ov neurons were used to measure the ITD tuning width in broadband noise. The mean half-height width of the ITD curves was $175.6 \pm 125.7 \mu\text{s}$ (median = 136 μs , $n = 148$) in Ov. The same measurement in ICx neurons, with similar frequency response bands, yielded significantly smaller values (mean half-height width = $77.1 \pm 27.3 \mu\text{s}$; median = 69 μs ; $n = 52$; *t*-test, $P < 0.0001$; Fig. 4*A*).

We also measured the width of the ITD curves generated in response to tones. The data obtained from Ov neurons showed that the width of the ITD peaks decreased in a nonlinear manner when the stimulating frequency increased. The same analysis showed that the widths tended to be less dependent on frequency in ICx neurons (Fig. 4*B*). To quantify this difference within

the same frequency range, we computed the linear regression of each sample removing all Ov curves with stimulating frequency smaller than the lowest frequency to which ICx neurons responded (3.2 kHz). Although the linear fit did not account for all the variance in the Ov sample, there was a highly significant correlation between width and stimulating frequency in Ov ($r = 0.5662$, $P < 0.0001$) but not in ICx.

ITD tuning across frequency

We compared the relationship between MIP (see METHODS) and the stimulating frequency in Ov and ICx. We used cells having frequency tuning curves wider than 2 kHz to select for neurons with broader tuning than the coincidence detector neurons of the nucleus laminaris (Peña et al. 2001). This ensured that frequency convergence had taken place along the processing stream leading to each of these neurons. If this relationship is linear, there is a frequency-independent ITD that elicits the same relative response in the neurons. This frequency-independent ITD is called the “characteristic delay” of the neurons (CD) (Rose et al. 1966; Yin and Kuwada 1983). A lack of linear relationship between phase and frequency indicates that the tuning to ITD varies with frequency and that the neurons have no CD.

We computed the linear regression of the MIP versus frequency plots in 61 Ov neurons and 37 space-specific neurons of ICx (Fig. 5). These neurons met the following selection criteria: the frequency tuning curves of Ov neurons had a half-height width of ≥ 2 kHz, four or more stimulating frequencies had been tested for each neuron, and the fit of all the ITD curves passed the χ^2 test. Whereas ICx neurons showed the conspicuous frequency-independent tuning to ITD observed in previous studies (Takahashi and Konishi 1986), Ov neurons did not. We quantified the deviation from linearity of the relationship between MIP and the stimulating frequency by computing the mean squared difference between the data points and the regression line (see METHODS). The mean squared difference in Ov (0.0022 ± 0.0049) was significantly larger than in ICx (0.00065 ± 0.00051 , $P < 0.029$, t -test) indicating that MIP values across frequency are more aligned in the latter. To rely on periodic ITD curves for the measurement of MIP, we used tonal stimulation. However, narrowband stimulation, which is a better representation of a natural sound, yielded similar results (Fig. 6).

A noticeable characteristic observed while examining the response properties of Ov and ICx neurons is the difference in the frequency range to which neurons respond (Fig. 3). Whereas Ov neurons that respond to low frequencies were a common finding, this and other studies (Peña and Konishi 2000; Takahashi and Konishi 1986) have rarely found ICx neurons that responded to frequencies < 3.5 kHz. We then removed from the Ov sample those frequencies that were below this value and tested if the differences in the tuning to ITD across frequencies between Ov and ICx persisted. We found that the mean squared residual in each nucleus (Ov: 0.0018 ± 0.0057 , $n = 42$; ICx: 0.00065 ± 0.00051 , $n = 37$) was no longer significantly different, indicating that the low frequencies make a major contribution to the departure from linearity.

DISCUSSION

We have studied how the owl's thalamic neurons tuned to auditory spatial cues integrate ITD responses across frequency and compared this information with measurements made on midbrain space-specific neurons. We found that the auditory system does not repeat the same process in the two pathways. Whereas the midbrain neurons show frequency convergence along the same ITD channel, thalamic integration occurs not only across frequency but also across ITD.

The width of the main peaks in the ITD curves for broadband stimuli in Ov is significantly broader than in ICx neurons. Because we used broadband signals delivered dichotically, without compensating for the individual neuron's pattern of ITD tuning across frequencies, it

remains to be tested if these neurons are more broadly tuned in natural conditions such as in free-field experiments. However, the weaker dependence of the width of the ITD peaks on the stimulating frequency in ICx than in Ov is consistent with nonlinear processes occurring in ICx, which sharpen the tuning to ITD (Fujita and Konishi 1991).

The neurons of the owl's ICx perform across-frequency integration to extract the frequency independent ITD from its phase equivalents, i.e.; they resolve phase ambiguity (Mazer 1998; Peña and Konishi 2000; Takahashi and Konishi 1986). This computation is necessary for the head-turn-orienting behavior toward a sound source in a unique and unequivocal direction (Saber et al. 1999). However, experimental evidence suggests that owls can use the forebrain representation to perform the same behavioral task (Knudsen and Knudsen 1996a; Knudsen et al. 1993; Wagner 1993). Because some Ov neurons tend to integrate high frequencies along a constant ITD, this information is presumably available to the forebrain as well. This is consistent with multiunit studies in the forebrain that show frequency independent tuning to ITD in the high-frequency range (Miller and Knudsen 2003).

Given that low frequencies contribute significantly to the ITD tuning across frequency in Ov neurons, the difference between the midbrain and forebrain processing of auditory space may rest in the use of different frequency bands to extract information related to sound direction. Recent studies in mammals do not find frequency independent ITD tuning, i.e., a characteristic delay, in the low-frequency range. These results have been explained by a convergence from more than one binaural coincidence detector line (McAlpine et al. 1998). Other studies in mammals determined that a great proportion of thalamic neurons had characteristic delays at neither the peak nor the trough of the ITD curve (Stanford et al. 1992), which is also consistent with convergence across ITD channels. On the other hand, the high-frequency neurons of the tectal pathway of barn owls show characteristic delays (Takahashi and Konishi 1986) despite the ability to adjust the ITD tuning in a frequency-specific manner (Gold and Knudsen 2000). Thus the owl's brain may be using ITD information differently at high and low frequencies. Because the barn owl can perform ITD detection in both high and low frequencies, it constitutes a good model to evaluate unifying hypotheses on sound localization of birds and mammals (Harper and McAlpine 2004).

A question of biological importance is what information the spatially tuned areas of the midbrain and the forebrain encode that requires two distinct types of representation. The clustered arrangement of space-specific neurons described in some forebrain areas of the owl (Cohen and Knudsen 1994, 1995, 1998; Knudsen et al. 1977) indicates that the continuous representation of spatial cues observed in the midbrain and brain stem (Carr and Konishi 1990; Knudsen 1982; Knudsen and Konishi 1978; Manley et al. 1988; Mogdans and Knudsen 1993, 1994; Olsen et al. 1989; Sullivan and Konishi 1986; Wagner et al. 1987) no longer applies in forebrain structures. Although the possibility of curved or distorted maps in Ov cannot be ruled out without combining the recording of the neurons with stimulation in the free field, our results are consistent with the absence of a topographic representation of space. Because the spatial dimensions of neural representations impose limitations on coding dimensions, an isomorphic two-dimensional map may no longer be possible if information other than the one in consideration is being represented or if the computation has changed. Presumably, the forebrain supports diverse and complex functions involving auditory spatial information. For example, it has been shown that the inactivation of the owl's auditory arcopallium interrupts memory-guided orienting responses (Knudsen and Knudsen 1996b), and that the forebrain is involved in the identification and discrimination of complex auditory stimuli in mammals (Diamond and Neff 1957; Diamond et al. 1962; Geissler and Ehret 2004; Heffner and Heffner 1984; Petersen et al. 1988; Poremba et al. 2004; Zatorre et al. 1992). Thus a different organization may be required to combine the representation of auditory space with other parameters of the sound. However, if the forebrain expands the number of variables used to

compute auditory space itself in addition to frequency-independent coordinates of ITD and ILD, a departure from a continuous representation may also become necessary. The frequency-dependent tuning to ITD of Ov neurons described here is consistent with this viewpoint.

ACKNOWLEDGMENTS

We thank M. Konishi for guidance and comments, T. Takahashi, S. Shanbhag, and B. Christianson for reviewing final versions of this manuscript, and G. Akutagawa for helping with the histology.

GRANTS

This work was supported by grants from the National Institutes of Health.

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FIG. 1.

Sound localization pathways in the barn owl. Time (ITD) and intensity (ILD) information are processed in 2 parallel pathways that originate in a bifurcation of the auditory nerve (nVIII) and converge in the inferior colliculus (IC). The IC projects to the forebrain (□) and tectal (■) sound localization pathways. NM, cochlear nucleus magnocellularis; NA, cochlear nucleus angularis; NL, nucleus laminaris; LLDp, nucleus of the lateral lemniscus pars posterior; ICx, external nucleus of the inferior colliculus; OT, optic tectum; Ov, nucleus ovoidalis; AAr, auditory arcopallium.

FIG. 2.

Response properties in Ov and ICx. We located the position of the recording electrodes by the injection of fluorescent tracers. Four different recording sites (seen as white spots) are shown in a photograph of Ov (A) and one recording site in ICx (B). For each neuron we collected ITD-tuning curves (C, F, and I), ILD-tuning curves (D, G, and J) and iso-intensity frequency tuning curves (E, H, and K). *Left and middle*: curves of Ov neurons shown here correspond to units recorded in the site indicated by * and +, respectively. *Right*: ICx neuron was recorded in the location marked by tracer injection in B. Error bars represent SE. Scale bar = 1 mm.

FIG. 3. Distribution of best frequencies (BF) in Ov and ICx. A substantial proportion of Ov neurons (■) responded to low frequencies. No BFs <3 kHz were found in ICx (□).

FIG. 4.

ITD tuning width in Ov and ICx. *A*: half-width of the main peak of ITD curves collected using broadband noise in Ov (■) and ICx (□). The widths were larger in Ov than in ICx. *B*: width of ITD curve peaks obtained with tones as a function of stimulating frequency (Stim. Freq.). In ICx, widths do not change with frequency (see text). - - - and —, the exponential regression for Ov and ICx data, respectively.

FIG. 5. ITD tuning across frequency in ICx and Ov. Overlaid ITD curves for tones of different frequencies (*left*) and plots of mean interaural phase (MIP) as a function of stimulating frequency (*right*), which show a more linear relationship in ICx than in Ov. Each row corresponds to a different unit.

FIG. 6.

ITD curves for tonal and narrow band stimulation in Ov. Examples of ITD curves obtained with tones (*left*) and narrowband stimuli (*right*). We obtained similar results with both types of acoustic signals. Each row corresponds to a different neuron. The stimulating frequencies (in kHz) are indicated above each plot.