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Space and Frequency Are Represented Separately in Auditory Midbrain of the Owl

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SUMMARY AND CONCLUSIONS

1. The influence of sound location and sound frequency on the responses of single units in the midbrain auditory area (MLD) of the owl (*Tyto alba*) were studied using a movable sound source under free-field conditions. With this technique, two functionally distinct regions in MLD have been identified: a tonotopic region and a space-mapped region.

2. MLD units were classified according to their receptive-field properties: *1*) limited-field units responded only to sound from a small, discrete area of space; *2*) complex-field units exhibited two to four different excitatory areas separated by areas of reduced response or inhibition; *3*) space-preferring units responded best to a certain area of space, but their fields expanded considerably with increasing sound intensities; *4*) Space-independent units responded similarly to a sound stimulus regardless of its location in space.

3. Limited-field units were located exclusively along the lateral and anterior borders of MLD. These units were tuned to sound frequencies at the high end of the owl's audible range (5–8.7 kHz). They usually responded only at the onset of a tonal stimulus; but most importantly, the units were systematically arranged in this region according to the azimuths and elevations of their receptive fields, thus creating a physiological map of auditory space. Because of this latter, dominant aspect of its functional organization, this region is named the space-mapped region of MLD.

4. The receptive fields of units in the larger, medial portion of MLD were of the space-independent, space-preferring, or complex-field types. These units tended to respond in a sustained fashion to tone and noise bursts, and these units were arranged in a strict frequency-dependent order. Based on this last property, this region is named the tonotopic region of MLD.

5. Because of the salient differences in the response properties of their constituent units, it is argued that the space-mapped region and the tonotopic region are involved in different aspects of sound analysis.

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INTRODUCTION

The identification of a sound and the localization of its source in space are two primary functions performed by the auditory system, each of which depends on different aspects of the auditory stimulus. Sound identification requires frequency discriminations and the recognition of "meaningful" frequency complexes, whereas sound localization relies on disparities in the time, intensity, and phase of the sound as it arrives at the two ears. Since the neuronal integration required to carry out each of these functions is necessarily different, it would not be surprising to find frequency and spatial analyses of sound taking place in separate auditory processing areas. Evidence that this may be the case comes from numerous neurophysiological studies of unit properties at brain stem, midbrain, and forebrain levels, where units selective either for the spectral content (14, 16, 19, 20, 22, 23) or for the interaural parameters (for a complete review refer to Erulkar, ref 5) of sound stimuli have been described.

Recently (9), direct evidence of spatial analysis of sound stimuli by the auditory system was found in the owl's MLD (mesencephalicus lateralis dorsalis), the avian midbrain auditory nucleus homologous to the mammalian inferior colliculus (7). By delivering sound stimuli with a movable speaker under free-field conditions, we found units that responded only when sound originated from a limited area of space. Furthermore, these units were systematically arranged within a discrete region of MLD according to the area of space to which they each responded, so that they formed a physiological map of auditory space. Consequently, this region will be called the space-mapped region of MLD. Units in the larger, remaining portion of MLD have not been previously studied with respect to their responses to sounds in real space.

In this paper the space-related response properties of units in both regions of the owl's MLD are described in detail. Characteristic frequencies (CF, the frequency to which a unit is most sensitive) and discharge characteristics of the units are also reported. Based on salient differences in the response properties of their constituent units, the two MLD regions, the space-mapped region and the tonotopic region, are hypothesized to be involved in distinct aspects of sound analysis: one being concerned with "where was it?" and the other with "what was it?"

METHODS

Sound Chamber

The experiments were conducted in a 5 x 3 x 3 m anechoic chamber made by the Industrial Acoustics Co. The cutoff frequency of the chamber was rated at 300 Hz; our own calibration showed that sound attenuation at different points along the length of the chamber followed the inverse-square law for frequencies down to at least 500 Hz, indicating the absence of standing waves due to echoes.

Inside the chamber was a semicircular track, 2 cm wide and 200 cm in diameter, on which was mounted a 5-cm speaker (Fig. 1). The track

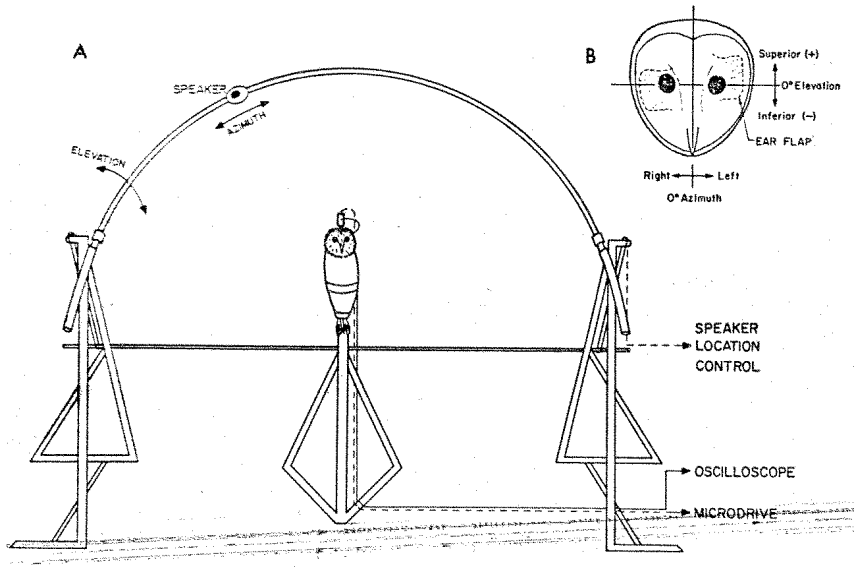

FIG. 1. Experimental apparatus and divisions of auditory space with respect to the owl's head. *A*: an owl is depicted in testing position at the center of the speaker-carriage system, which is located inside the anechoic chamber. The speaker location control, oscilloscope, and hydraulic microdrive are located outside the chamber. *B*: auditory space was divided with reference to the owl's median and visual planes. Speaker locations across the median plane from the side recorded were measured in contralateral degrees (x°c), on the same side were ipsilateral degrees (x°i). Above the visual plane were positive degrees ($+y$°), below were negative degrees ($-y$°).

pivoted around a horizontal axis to provide changes in speaker elevation; the speaker itself moved along the track to provide changes in speaker azimuth. Speaker elevation and azimuth were controlled independently by stepping motors located outside the anechoic chamber. Thus the speaker could be positioned under remote control anywhere on a sphere of radius 1 m, except for a 20° sector blocked by a supporting post for the owl.

Preparation

Five barn owls (*Tyto alba*) were used in these experiments. Four owls were fitted with cylindrical stainless steel "wells" inserted through their skulls so that they could be recorded from repeatedly. The wells were placed at the posterior margin of the visual Wulst, directly dorsal to MLD on one side. Electrode penetrations made through the wells traversed the telencephalon and diencephalon before entering MLD. In the final experiment on each owl, the MLD on the side opposite the well was mapped (described later). This experiment required visualization of the dorsal surface of the optic tectum by removing a posterior section of skull and suctioning the underlying portion of neostriatum. The fifth owl was used exclusively for mapping studies, both sides of its brain being prepared in the above manner.

Anesthesia was induced with an intramuscular injection of ketamine hydrochloride (4 mg/kg), and was maintained at a light level with repeated injections as necessary. The owl was restrained with a soft leather jacket which was fastened to a post in the center of the speaker sphere (Fig. 1). The owl's head was bolted to a specially designed head holder that permitted accurate adjustment of the owl's head position while avoiding distortion of the sound field. The owl was positioned within the sphere so that its visual and median planes corresponded to 0° elevation and 0° azimuth of the speaker. Positioning was accomplished ophthalmoscopically by exploiting retinal landmarks that bear specific relationships to the owl's visual and median planes (10).

MLD units were recorded extracellularly using glass-insulated tungsten electrodes. Electrode trajectory was measured with a protractor assembly with the lower edges of the upper mandible serving as the reference plane (this plane will be defined as the horizontal plane, in accordance with Karten and Hodos (8)). Electrodes were advanced into the brain by means of a hydraulic microdrive, the controls of which were located outside the anechoic chamber. Spike activity was amplified with a Grass P15 preamplifier and was monitored visually and acoustically outside the chamber (Fig. 1). Spike data were processed on-line in the form of peristimulus time (PST) histograms generated by Ortec time histogram and memory-control modules.

Stimulation

Sound stimuli included tone bursts, noise bursts, and clicks. Sine waves were generated by a Wavetek model 111 function generator. Electrical noise, supplied by a Grason-Stadler noise generator, was variably band filtered using a B & K Instruments graphic spectrum equalizer. Sine wave and noise bursts were shaped with a Grason-Stadler electronic switch. The bursts were 100 ms in duration with 2.5-ms rise and decay times, and were repeated every 1–1.25 s. Pulses 7.5 ms in width from a Grason-Stadler timer were used to produce clicks. For control of sound intensity, the stimulus signal was passed through a decade attenuator before being amplified and sent to the track-mounted speaker in the anechoic chamber.

The sound stimuli were calibrated with a General Radio type 1900 wave analyzer in conjunction with a 2.5-cm Bruel and Kjaer condenser microphone placed where the owl would be located. The frequency response of the 5-cm speaker was flat over 3.5–10 kHz. Variations in sound intensity as a function of speaker location were ±2 dB, except in a small area directly beneath the owl.

The acoustic shadow cast by the owl's head and body in this free-sound field was determined by measuring sound level in the ear canal and auditory nerve responses, as a function of speaker location (Fig. 2). Measurements were made at 10° intervals in azimuth and elevation to sound frequencies of 3, 6, and 8 kHz. Ear canal measurements were made with a Knowles model BT-1759 subminiature transducer placed in each ear approximately 0.5 cm inside the ear canal opening, with the transducer diaphragm facing outward. The oscillator signal from the General Radio wave analyzer was fed through an amplifier to the movable speaker; the output of each intraaural transducer was fed to the tracking filter and amplitude detector in the analyzer. The sound pressure level required to give a standard voltage output from the intraaural transducer was measured as a function of speaker location (Fig. 2, top). Auditory nerve responses (N_1) were measured with electrodes implanted near the round windows of each ear. In this case, the sound level that evoked a half-maximal response was plotted as a function of speaker location (Fig. 2, bottom). Our measurements of ear directionality confirm those of Payne (17): the owl's ears are most sensitive to sounds in the frontal area, with the right ear's

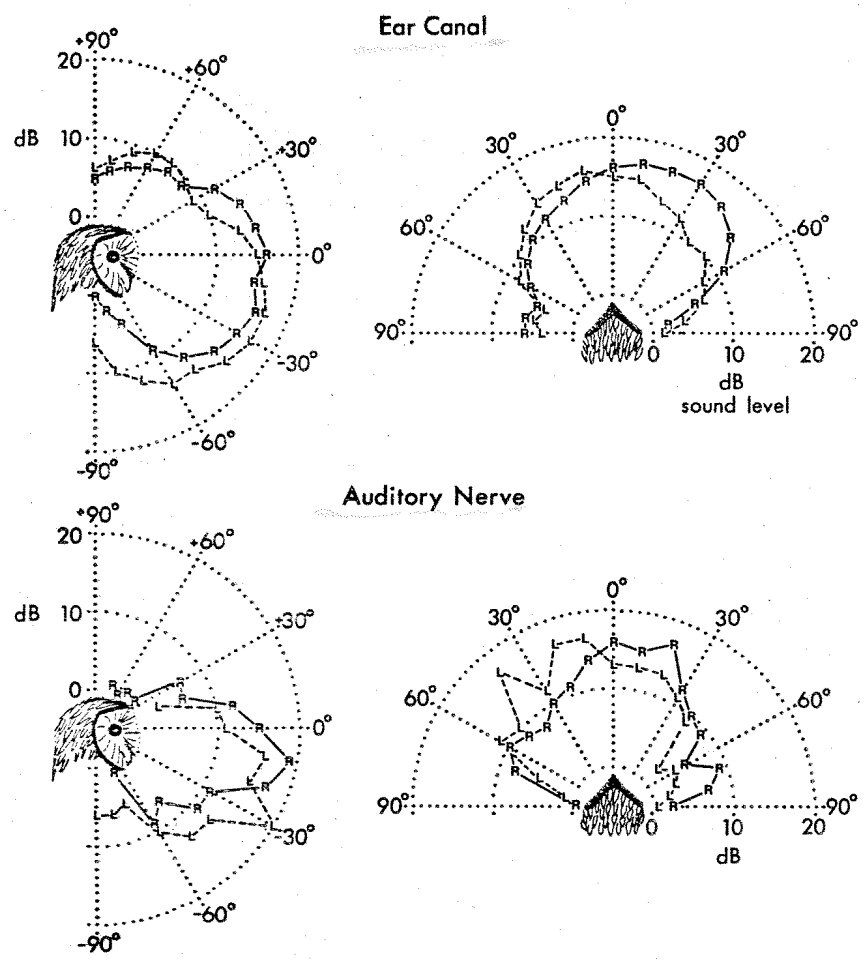

FIG. 2. Sound level and auditory nerve response as a function of sound source location for a 6-kHz tone. Above: the sound level necessary to give standard outputs from microphones placed inside the left (L) and right (R) ear canals, is plotted as a function of speaker location in the median (left) and visual (right) planes. Below: sound level required to give a half-maximal evoked response (N_1) from the left (L) and right (R) auditory nerves is plotted as a function of speaker location in the median (left) and visual (right) planes.

sensitivity being greatest to the right and 10–15° above that of the left ear for frequencies greater than 3 kHz.

Units were tested for sensitivity to visual stimuli by sweeping bars and spots of light across a tangent screen which was temporarily placed 57 cm in front of the owl. The screen was removed during acoustic stimulation.

Electrode track reconstruction and mapping experiments

Recording sites were determined from electrolytic lesions that were placed at critical locations. On the side of the brain that was penetrated in several experiments, lesions were made only during the last experiment before mapping the op-

posite side. These lesions were placed to demarcate the region of brain sampled in the previous experiments.

Acute mapping experiments involved a systematic survey of unit types throughout MLD. Electrode penetrations were made in a grid pattern with the electrode oriented at a constant angle of 45° to the horizontal plane and parallel to the sagittal plane. The sites of the first and last auditory units sampled in each penetration were marked with lesions.

At the conclusion of each mapping experiment the bird was deeply anesthetized with sodium pentobarbital and perfused through the heart with 0.9% NaCl, followed by 10% formal-saline. Frozen sections were cut at a thickness of 30 μm in either the transverse, sagittal, or horizontal plane, and were stained with cresyl violet. Electrode tracks were identified by the relative positions of the lesions in the grid pattern. On an enlarged photograph of the appropriate section, the locations of units along each track were reconstructed from their depths with respect to the top and bottom lesions, as measured by the hydraulic microdrive.

RESULTS

Definition

The term "receptive field" will refer to that area of space within which a sound stimulus can influence the firing rate of an auditory unit.

Plotting auditory receptive fields

The receptive fields of MLD units were determined in the following manner. After a single unit was isolated, the speaker was moved to a location where the unit responded strongly to the search stimulus (usually wide-band noise bursts). With the speaker at this location, the unit's threshold to noise bursts was measured. The intensity of the noise bursts was increased to 10 dB above threshold and the speaker was moved systematically in azimuth and elevation to locations where the unit failed to respond. The coordinates of these locations defined the borders of the unit's receptive field. The intensity of the test stimulus was then increased to 30 dB above threshold and the width ot the unit's receptive field was remeasured (in many cases the entire field was replotted).

On occasion, the unit's receptive field was remapped in the above manner using the other two sound stimuli: clicks and tone bursts at the unit's characteristic frequency (CF, the frequency to which a unit is most sensitive).

Classes of auditory receptive fields

Four classes of MLD units were distinguished based on salient differences in the properties of their receptive fields: *1*) limited-field units, *2*) complex-field units, *3*) space-preferring units, and *4*) space-independent units (Fig. 3). Limited-field units responded only when an appropriate sound originated from within a single, well-defined area in space, the borders of which were little affected by changes in the intensity of the sound stimulus. Complex-field units exhibited two to four strongly excitatory areas separated by areas wherein sounds either inhibited or had a reduced excitatory effect on the unit's activity. Space-preferring units responded best to sounds from a particular area of space, but the borders of their receptive fields were indistinct and they expanded considerably with increasing sound intensities. Space-independent units responded similarly to a sound stimulus regardless of its location in space.

The distributions of these unit classes within MLD were clumped to some extent: limited-field units were confined to the lateral and anterior margins of MLD; the other three classes were located in the remaining major portion of the nucleus. This segregation of unit classes into two distinct regions in MLD can be best appreciated in concert with certain other striking differences in the functional properties of these units. Therefore, details about the various receptive-field classes are reserved for the succeeding sections in which the response characteristics of the units in these two regions are discussed separately.

Space-mapped region of MLD

Forming a strip along the lateral and anterior borders of MLD was a region that contained limited-field units. These units were tuned to sound frequencies at the high end of the owl's audible range and usually responded only at the onset of a tonal stimulus. Most importantly, the units were systematically arranged in this region according to the azimuths and elevations of their receptive fields, and thus created a physiological map of auditory space (9).

Based on this last aspect of its functional organization, this region will be termed the space-mapped region of MLD.

Auditory receptive fields in space-mapped region

The receptive fields of 92 units from the space-mapped region were plotted. The receptive-field borders of these units were demarcated by a cessation of unit responsiveness that was sufficiently abrupt to allow fields to be reproducibly mapped to an accuracy of ±1°. Most (93%) of these fields consisted of an ellipsoidal area of space (Fig. 4) that was vertically oriented or tilted slightly to the owl's right, by up to 10°. In rare cases (7%), a unit's field was in the shape of a ring that encircled the owl, being limited in azimuth while unrestricted in elevation. Receptive-field sizes ranged from 7 to 39° in azimuth (average, 25°), and from 23° to "unrestricted" in elevation (average, excluding six units with ring-shaped fields, 75°).

Units with similar auditory receptive fields were also recorded in the deep layers of the tectum. However, the tectal units were strongly influenced by visual stimuli as well. The units in the space-mapped region showed little or no response to visual stimuli.

Whether its field was ellipsoidal or ring shaped, each limited-field unit responded most vigorously when the sound stimulus was positioned within a specific small area inside its receptive field, called the unit's best area (Fig. 4). As the speaker was moved away from the best area, response reliability declined markedly. A unit's best area could be readily determined by simply monitoring spike activity as a test stimulus was moved through its receptive field. However, when a precise measure of the best area was required, PST histograms were collected at regular intervals across the unit's field; the speaker positions at which the unit first gave a submaximal response defined the boundaries of its best area. By this criterion, best areas ranged in size from 2.5 to 10° in azimuth and from 5 to 45° in elevation.

An impressive feature of unit responses in the space-mapped region was that neighboring units had similar best areas. As described in a previous paper (9), the centers of these best areas were systematically arrayed within the space-mapped region (Fig. 5). The extent of space covered by best-area centers was from +20 to −90° represented dorsoventrally, and from 60 contralateral (60°c) to 15° ipsilateral (15°i) represented posterolaterally to anteromedially. Elevations between −10 and −60° and azimuths between 0 and 20°c were represented in a disproportionately large volume of tissue.

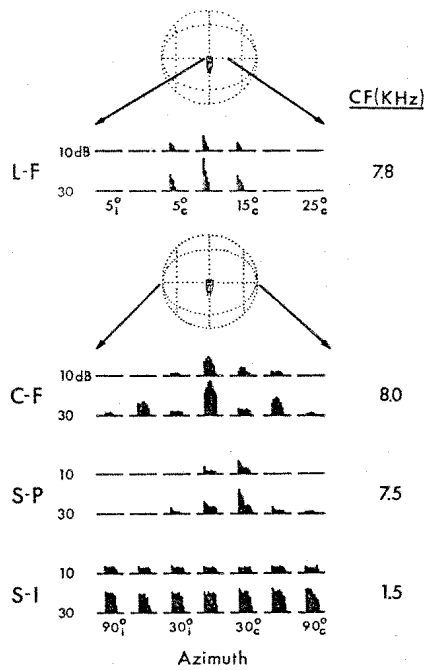

FIG. 3. Responses of four units representing the four classes of auditory receptive fields found in MLD. The top unit was a limited-field unit (L-F) recorded in the space-mapped region. The complex-field (C-F), space-preferring (S-P), and space-independent (S-I) units were recorded from the tonotopic region. PST histograms depict responses of each of the four units to a broad-band noise stimulus delivered at 10 dB (upper row) and 30 dB (lower row) above threshold across their receptive fields. Notice dissimilarities among responses of the L-F, C-F, and S-P units despite their similar characteristic frequencies (on the right). The speaker location during the accumulation of each histogram is indicated at the bottom of the histogram column. Each histogram represents a 200-ms sample of 16 repetitions of a 100-ms noise burst. The dotted globes (above and middle) depict the speaker sphere and indicate the azimuthal range encompassed by histograms.

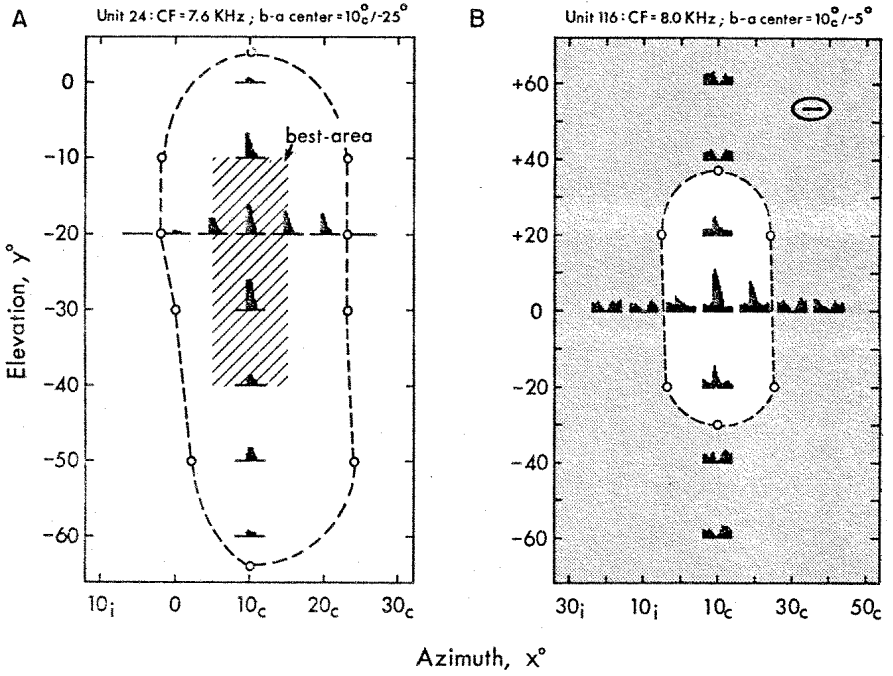

FIG. 4. Receptive-field plots from two limited-field units demonstrating a best area (left) and an inhibitory surround (right). Dashed lines mark the receptive-field boundaries as projected from actual measurement sites (open circles). Fields were plotted and histograms were generated using wide-band noise bursts at 10 dB above threshold. The position of each histogram corresponds to the location of the speaker during the accumulation of that histogram. On the left, a unit's best area is designated by diagonal lines. On the right, a unit's inhibitory surround is stippled. Units were recorded from the MLD on the right side.

Completely surrounding the excitatory areas of four limited-field units was found an inhibitory area, wherein sound stimuli actively suppressed spike activity (Fig. 4). These inhibitory surrounds, which extended as far as 50° beyond the excitatory receptive-field borders, were made evident by the relatively high rate of spontaneous discharge among these units. Since the rest of the units in the space-mapped region exhibited little spontaneous activity (<1 per second), the existence of inhibitory surrounds could not be routinely ascertained. Nevertheless, it is our impression that this is a common property of limited-field units and one worthy of further investigation.

Sound intensity had remarkably little effect on the receptive-field sizes of most limited-field units (Figs. 3, 6). When receptive fields plotted at 30 dB above threshold were compared with those plotted at 10 dB above threshold for 63 units, 43% changed by ±2° or less in azimuth and 22% changed by ±5° or less in elevation. Of those fields that changed substantially in size, 63% expanded in azimuth by 3–11°, and 37% contracted in azimuth by 3–18°. Thus, in the azimuthal dimensional, the receptive fields of limited-field units changed in size by no more than −0.9°/dB to +0.5°/dB, with nearly half of them changing by only ±0.1°/dB or less.

Sound intensity exerted a greater effect on the vertical dimensions of most receptive fields. Although many of the receptive fields changed little in this dimension also (10% decreased 6–18°, 22% remained within ±5°, and 13% increased by 6–40°), 55% expanded dramatically at 30 dB above threshold and approached the form of ring-shaped fields. A property of these receptive fields that emerged

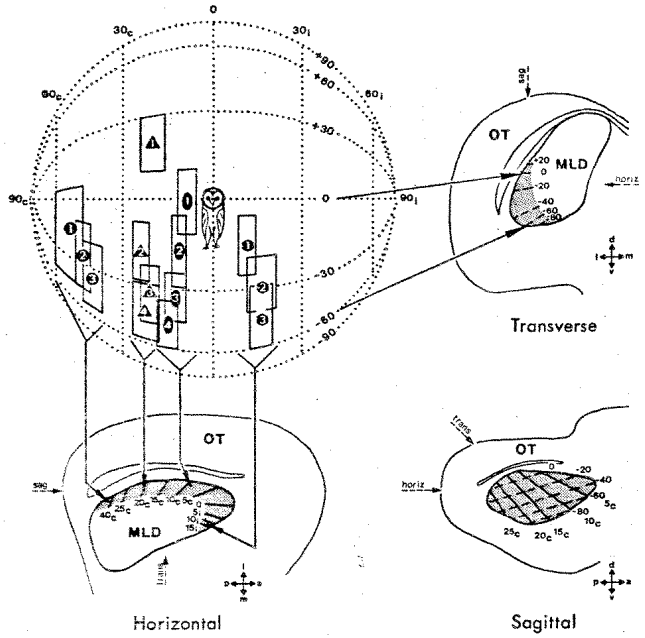

FIG. 5. Representation of auditory space in the midbrain nucleus (MLD), as defined by centers of unit best areas. In the upper left, coordinates of auditory space are depicted as a dotted globe surrounding the owl. Projected onto the globe are the best areas (solid-lined rectangles) of 14 units that were recorded in four separate penetrations. The large numbers backed by similar symbols represent units from the same penetration; the numbers themselves signify the order in which the units were encountered, and are placed at the centers of their best areas. Penetrations were made with the electrode oriented parallel to the transverse plane at positions indicated in the horizontal section by the solid arrows. Below and to the right of the globe are illustrated three histological sections through MLD in the horizontal, transverse, and sagittal planes. The stippled portion of MLD corresponds to the space-mapped region; the remaining portion is the tonotopic region. Isoazimuth contours, based on best-area centers, are shown as solid lines in the horizontal and sagittal sections; isoelevation contours are represented by dashed lines in the transverse and sagittal sections. On each section, dashed arrows indicate planes of the other two sections. Solid, crossed arrows to the lower right of each section define the orientation of the section: a, anterior; d, dorsal; l, lateral; m, medial; p, posterior; v, ventral. The optic tectum (OT) is labeled on each section. (From Knudsen and Konishi (9).)

at high intensities of stimulation was that they contained two strong-response areas, one in front of the owl (its best area) and another behind the owl (secondary area), but both at the same azimuth (Fig. 6). The difference in a unit's threshold to a sound located in its best area, as opposed to one located in its secondary area, was 10 to >40 dB. Spatially separating these two relatively low-threshold areas were zones above and beneath the owl in which a sound could elicit only a weak response, even at high intensities.

Units in the space-mapped region usually responded with low thresholds to all three mapping stimuli (noise, tones, and clicks), and the locations of their best areas were independent of the stimulus that was employed. However, the boundaries of many receptive fields did depend to varying extents on the type of stimulus used (Fig. 6). The receptive-field borders of 20 units were replotted using noise, clicks, and tones at characteristic frequency (CF-tone), each at 10 and 20 dB above threshold for that sound. Thirty-five percent of the receptive fields were independent of the type of sound stimulus used; they remained constant to within ±5°. The rest of the receptive fields changed in size to one or all of the mapping stimuli. Again, it was the vertical dimension of the receptive

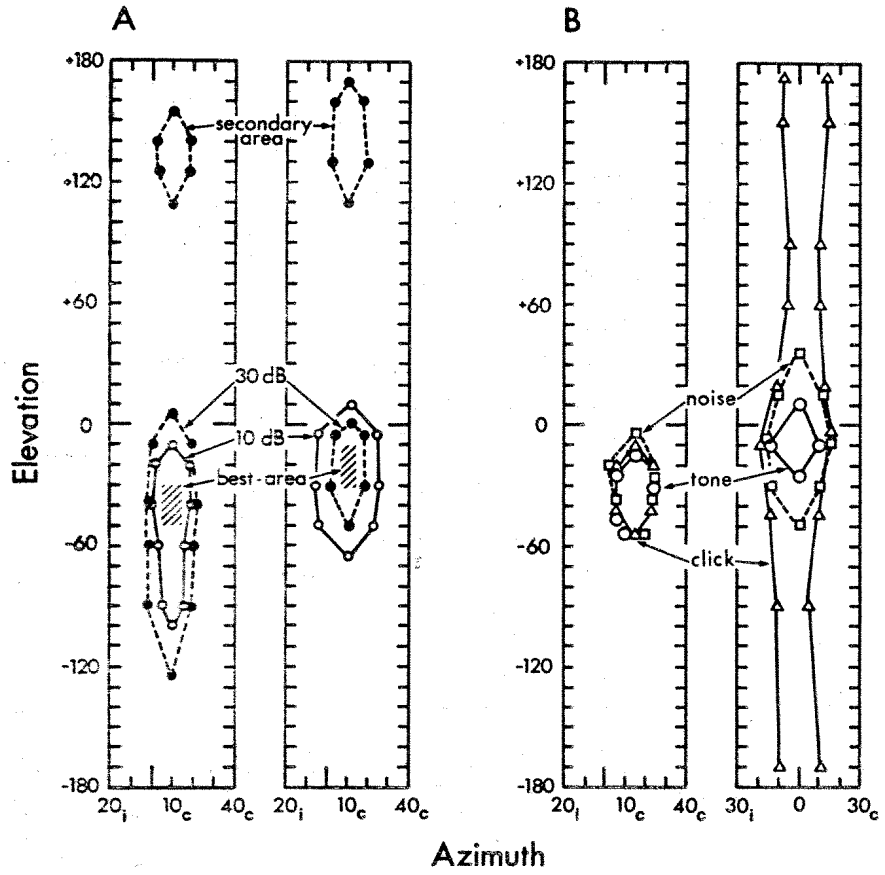

FIG. 6. Effect of sound intensity and sound type on the receptive-field plots of limited-field units. *A*: receptive fields of two units plotted with wide-band noise bursts at 10 dB (open circles) and 30 dB (closed circles) above threshold. The field of the unit on the left expands, and the one on the right contracts at the higher sound intensity. Both units exhibited secondary areas behind the owl's head to 30-dB noise bursts. *B*: receptive fields of two units plotted with noise bursts, CF-tone bursts, and clicks, each presented at 30 dB above threshold. The unit on the left is typical of limited-field units. The unit on the right represents the most extreme case of receptive-field variation due to sound type.

fields that was the most profoundly influenced by changing the nature of the mapping stimulus. The magnitude of the variation in receptive-field sizes was from 5 to 20° in azimuth, and from 10 to >100° in elevation. The large variations (>100°) in the vertical dimension (four units), were due in each case to the unit's having restricted fields to noise and CF-tone bursts, while responding to clicks at virtually any elevation (Fig. 6). A consistent finding throughout these experiments was that whenever a unit's field size varied with the nature of the sound stimulus, the receptive field plotted with CF-tone bursts was the unit's smallest field.

Frequency representation in space-mapped region

The characteristic frequencies of units in the space-mapped region were determined by acoustically monitoring spike activity as the owl's audible frequency range

(0.1–10 kHz) was swept. Stimulus frequency was read from a Hewlett-Packard electronic counter. The range of CFs represented in the space-mapped region was limited to 5–8.7 kHz, with 85% (77 of 92) of the CFs between 6 and 8 kHz. Although there was a tendency for units with lower CFs to be located dorsally and those with higher CFs to be located ventrally within this region, the tendency was by no means strict (Figs. 7, 8): in some penetrations the CF order was reversed (high to low), in others it was erratic.

Unit discharge characteristics in space-mapped region

Unit responses to tone and noise bursts were evaluated as either on or sustained for 67 units in the space-mapped region (Table 1). Each of these stimuli was delivered at 20 dB above threshold in the unit's best area, and the response of the unit was determined from a stimulus-locked display of the unit's activity. On-responses predominated among these units: 90% exhibited on-responses to tone bursts, 54% to noise bursts. The only response combination not observed was a sustained response to tone together with an on-response to noise.

Tonotopic region of MLD

Two hundred thirteen units were recorded from the medial portion of MLD. The receptive fields of these units fell into the space-independent, space-preferring, or complex-field classes. These units tended to respond in a sustained fashion to tone and noise bursts, and they were arranged in a conspicuous frequency-dependent order within this region. Because of the latter aspect of its functional organization, this region will be termed the tonotopic region of MLD.

Frequency representation in tonotopic region

Units in the tonotopic region were arranged strictly according to their CFs (Figs. 7, 8). Low frequencies were represented dorsomedially and high frequencies, ventrally, with isofrequency laminae oriented approximately in the horizontal plane. The lowest CF measured was only 0.7 kHz, due to the low frequency limitations of the speaker (owls can hear down to 0.1 kHz (12)). The highest CF encountered was 9.5 kHz, which is near the upper end of the owl's audible range.

With the electrode oriented in the transverse plane and parallel to the sagittal plane, unit CFs increased as a continuous and linear function of electrode depth (Fig. 8), except for an occasional aberrant CF recorded at the bottom of some tracks, possibly from incoming lemniscal fibers. This linear depth-CF relationship does not necessarily signify a disproportionate representation of high frequencies in the owl, compared to the logarithmic depth-CF relationships found in other animals (1, 2, 4, 6, 15, 18), since relative tilts of the isofrequency laminae within the tonotopic region could cause the same result, and our data were inadequate to confidently reconstruct the three-dimensional contours of the laminae. Of importance, however, was that in each of 15 penetrations through widely separate portions of the tonotopic region, the progression of CFs with unit depth was unerringly systematic.

At the boundary between the tonotopic and space-mapped regions, this relationship was interrupted (Fig. 8). In four penetrations that traversed the boundary, the interruption appeared not as a major jump in CFs, but as a stabilization of subsequent CFs at a frequency between 6 and 8 kHz, or as a limited fluctuation of CFs within this range.

Auditory receptive fields in tonotopic region

Auditory receptive fields in the tonotopic region were in the space-independent, space-preferring, and complex-field classes (Figs. 3, 7). There was no simple relationship between the CF of a unit and its receptive-field properties, except that space-independent units were all tuned to frequencies of less than 3 kHz (although not all low-frequency units were space independent). In sharp contrast to units in the space-mapped region, units in the tonotopic region with comparably high CFs (5–9 kHz) were in the space-preferring or complex-field classes (Figs. 3, 7). Space-preferring and complex-field units were recorded throughout the tonotopic region, and were often grouped by receptive-field class. However, no system to the groupings was discernible.

The receptive fields of space-preferring units ranged in size from 30 to 210° in azi-

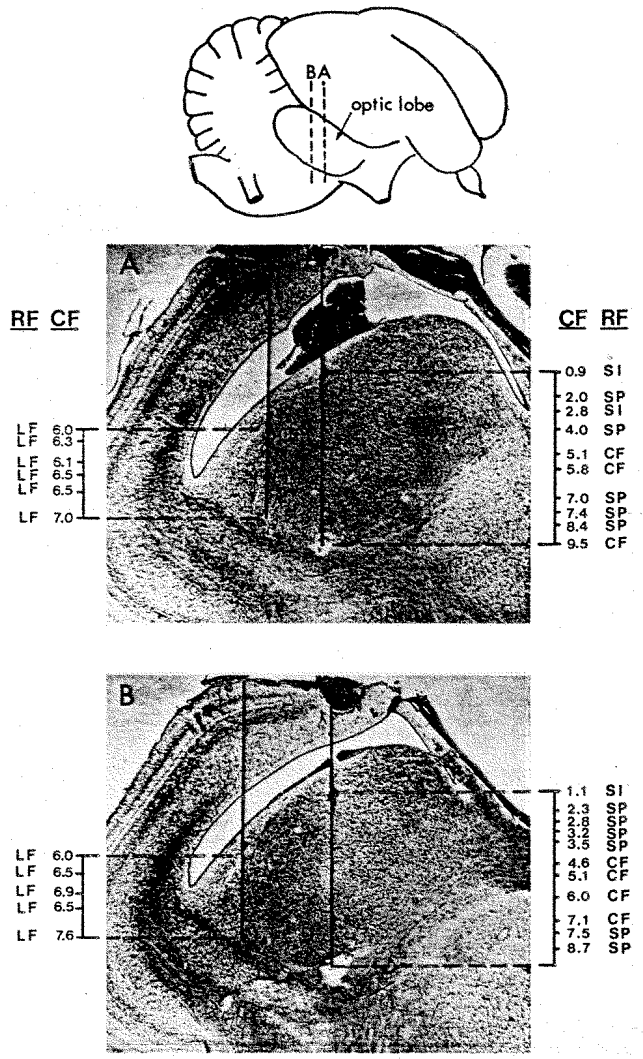

FIG. 7. Characteristic frequencies and receptive-field characteristics of sequentially recorded single units in the space-mapped and tonotopic regions of MLD. Four electrode tracks (solid lines on the photomicrographs) are reconstructed on transverse Nissl sections. Tracks on the left traversed the space-mapped region; tracks on the right traversed the tonotopic region. Numbers to the left and right of each photomicrograph indicate characteristic frequencies in kilohertz. The corresponding letters designate the classification of the unit's receptive field: LF, limited field; CF, complex field; SP, space preferring; SI, space independent. The histological sections were taken at levels indicated by the dashed lines in the illustration of the owl's brain (above). The overlying optic ventricle and optic tectum can be seen in each photomicrograph.

muth, and from 70° to unrestricted in elevation. Their preferred areas were restricted and were predominantly located between 50° contralateral (50°c) and 10° ipsilateral (10°i) in azimuth, and between +10 and −80° in elevation. Thus, the receptive fields of these

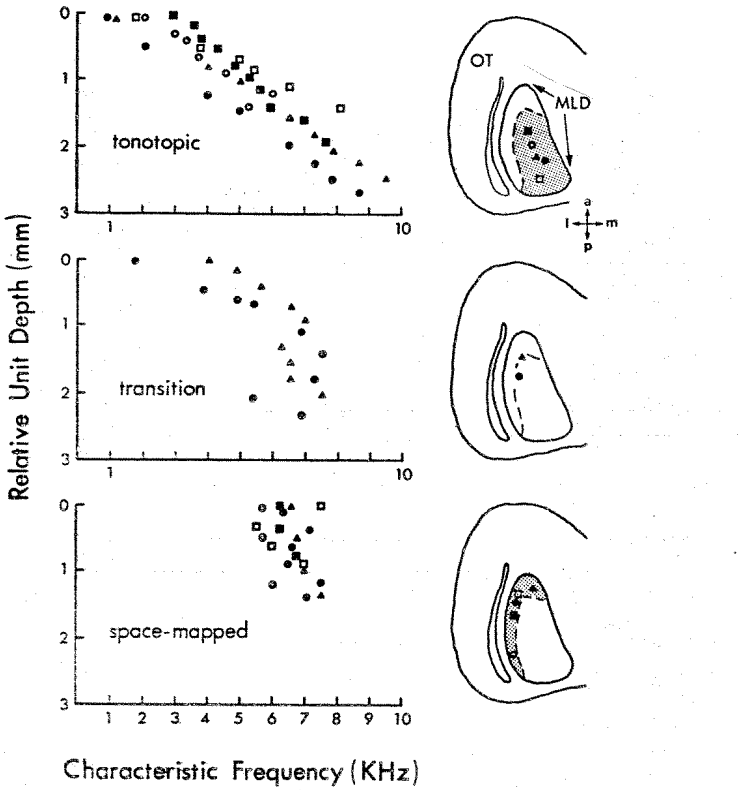

FIG. 8. Characteristic frequencies plotted as a function of relative unit depth for penetrations in the tonotopic region (top), the transitional region (middle), and the space-mapped region (bottom) of MLD. Unit depths were measured with respect to the first MLD unit encountered in each penetration. Each symbol signifies units from a single penetration, the approximate location of which is indicated on the right in a diagram of a horizontal section through the optic lobe. The orientation of the horizontal section is indicated by the crossed arrows: a, anterior; p, posterior; l, lateral, m, medial. The plane of the horizontal section is at 45° to the transverse plane shown in Fig. 6. OT, optic tectum.

units demonstrated a biased representation of the contralateral and inferior areas of auditory space. However, sound intensity had a dramatic effect on their receptive-field sizes, a 20-dB increase causing an azimuthal expansion of 30° to >100° (Fig. 3). In fact, many space-preferring units could be driven from anywhere around the owl, given a sufficiently intense sound.

Complex-field units responded with strong excitation to sounds in several separate areas of space which, taken together, usually spanned the owl's entire frontal area (Fig. 3). At low sound intensities (up to 10 dB above

TABLE 1. *Discharge characteristics of units in tonotopic and space-mapped regions to tone and noise bursts*

Discharge Characteristics		Space-Mapped Region, % (n = 67)	Tonotopic Region, % (n = 129)
Tone	Noise		
On	On	54	22
On	Sustained	36	3
Sustained	On	0	0
Sustained	Sustained	10	57
Selective for tone or noise		0	18

threshold) these units frequently behaved like space-preferring units, their receptive fields expanding rapidly with increasing sound intensity. However, further increases in sound intensity resulted in the appearance of one to three new excitatory areas with intervening inhibitory or poor-response areas (Fig. 3). A change in the type of mapping stimulus used could also alter the number or distribution of these excitatory areas.

Unit discharge characteristics in tonotopic region

The responses of 129 units in the tonotopic region were categorized as on or sustained to tone and noise bursts (Table 1). Unlike the units in the space-mapped region, the majority of these units responded with a sustained discharge to tone and noise stimuli. Also, in the tonotopic region, 18% of the recorded units were unresponsive either to a tone or to a noise stimulus, whereas units in the space-mapped region demonstrated no such selectivity.

DISCUSSION

Functionally distinct regions of MLD

The spatial segregation of complex sound into its basic frequency components, as initially performed by the cochlear partition, is precisely repeated at every subsequent auditory nucleus, up to and including the primary telencephalic projection area, in the form of tonotopic organization. While the ubiquity of tonotopy is well recognized, its functional significance is not. Certainly the mere presence of a frequency-dependent organization, as found in the tonotopic region of MLD, does not signify that frequency analysis is being performed. It does, however, demonstrate that in this region frequency-specific information is at least being preserved, information that is likely to provide the basis for frequency discriminations and ultimately for sound identification at some level (1).

A fundamental question concerning functional organization in the auditory system is whether any other parameter(s) of sound stimuli are represented within the framework of tonotopic organization. Sound location has often been considered to be a likely candidate parameter (6, 15). However, in the owl's MLD this does not seem to be the case. The receptive fields of units in the tonotopic region are highly complex and/or are labile to changes in sound intensity or type. These response properties are not easily compatible with the proposition that this region even encodes auditory space in a meaningful manner, much less that space is systematically arrayed within its isofrequency laminae. Thus, while sound location can be eliminated as a candidate parameter to vary in an orderly fashion in the tonotopic region of the owl's MLD, the sound parameters that are so represented remain to be discovered.

Functional specialization in the space-mapped region of MLD is more definite. Units in the space-mapped region respond well to a wide variety of sounds, but only when the source is located within their receptive fields. The intensity of the sound has little effect on these receptive fields. Most importantly, the units in the space-mapped region are organized according to the locations of their receptive fields so that they create a physiological map of auditory space. These obviously space-dependent functional properties are not a refinement or rerepresentation of the pattern of stimulation arriving at the sensory epithelium, as is true of neural maps of other modalities, but are probably derived from precise comparisons of binaural inputs. Because these unit properties must have been specifically generated by neural integration, it seems probable that the space-mapped region is intimately involved in the analysis of spatial aspects of an auditory signal.

Neurons which are "tuned" to specific values of interaural differences in intensity or time have been reported by many authors. As Starr (21) pointed out, these values are much too large to account for the observed accuracy of sound localization in behavioral tests. For this reason Starr thought it unlikely that auditory space is encoded in terms of single-unit receptive fields and neural maps, as is the case in the visual and somatosensory systems. However, the properties of limited-field units described above would seem to satisfy the conditions for analysis of auditory space at the single-unit level.

Although the evidence is strong that the tonotopic and space-mapped regions of MLD are functionally distinct, there is no evidence

as to whether these regions are arranged in parallel, each receiving already functionally differentiated inputs, or whether they are arranged in series with the space-mapped region receiving selected inputs from the tonotopic region. The substrate for a previous functional segregation of auditory activity might be found in the division of auditory nerve inputs to innervate two discrete second-order nuclei: nucleus angularis and nucleus magnocellularis (considered to be homologous to the mammalian dorsal and ventral cochlear nuclei (3)). In pigeons (13), nucleus angularis projects to the caudal portion of the contralateral MLD, whereas nucleus magnocellularis projects bilaterally to nucleus laminaris, which in turn projects to the anterior portions of MLD. Thus, there is evidence of parallel auditory pathways already at the brain-stem level. However, the limited nature of this evidence and the fact that it was gathered from a phylogenetically distant species that is not specialized for sound localization prevent a rigorous examination of their possible relationships to the functional regions defined here in the owl's MLD.

Behavioral predictions from unit properties in space-mapped region

Assuming that the space-mapped region of MLD plays a key role in sound localization, the properties and limitations exhibited by the units in this region should be manifest in behavioral localization tasks. For example, the finding that the range of unit CFs in the space-mapped region is limited to 5–8.7 kHz suggests that sound frequencies much above or below this range should not contribute to the owl's ability to localize sound. Behavioral experiments confirm this prediction (11, 12): owls located 5- to 9-kHz pure-tone targets far better than they located 3- or 10-kHz targets. Furthermore, "noises containing frequencies between 5.5 and 9.5 kHz were more accurately located than those involving other frequency ranges."

Behavioral predictions that have not yet been tested are the following. *1*) The secondary response areas of limited-field units, which appear behind the owl's head at sufficiently high sound intensities, suggest that under similar conditions the owl will make occasional, front-back errors. *2*) Because of the disproportionately heavy receptive-field representation of the frontal 40° in azimuth and −10 to −60° in elevation demonstrated by the auditory map (Fig. 5), the owl should locate sounds that originate inside this frontal area far more accurately than it does sounds that originate from more peripheral points. *3*) Since the map of auditory space in MLD must assign predetermined spatial coordinates to each binaural input, the owl should be able to perform accurate localization of even a single, short sound. This prediction contradicts Payne's (17) theory of sound localization, in which the owl localizes a sound by turning its head until the intensity of all frequencies is maximized in both ears, which automatically aligns the head with the source. Payne's theory predicts that the owl requires either a repeated or a long-duration sound for accurate localization. The systematic representation of auditory space by limited-field units in MLD indicates that neither condition should be necessary.

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