The Hearing of the Barn Owl

The bird exploits differences between the sound in its left and right ears to find mice in the dark. It can localize sounds more accurately than any other species that has been tested

by Eric I. Knudsen

For the barn owl life depends on hearing. A nocturnal hunter, the bird must be able to find field mice solely by the rustling and squeaking sounds they make as they traverse runways in snow or grass. Like predators that hunt on the ground, the barn owl must be able to locate its prey quickly and precisely in the horizontal plane. Since the bird hunts from the air, it must also be able to determine its angle of elevation above the animal it is hunting. The owl has solved this problem very successfully: it can locate sounds in azimuth (the horizontal dimension) and elevation (the vertical dimension) better than any other animal whose hearing has been tested.

What accounts for this acuity? The answer lies in the owl's ability to utilize subtle differences between the sound in its left ear and that in its right. The ears are generally at slightly different distances from the source of a sound, so that sound waves reach them at slightly different times. The barn owl is particularly sensitive to these minute differences, exploiting them to determine the azimuth of the sound. In addition the sound is perceived as being somewhat louder by the ear that is closer to the source, and this difference offers further clues to horizontal location. For the barn owl the difference in loudness also helps to specify elevation because of an unusual asymmetry in the owl's ears. The right ear and its opening are directed slightly upward; the left ear and its opening are directed downward. For this reason the right ear is more sensitive to sounds from above and the left ear to sounds from below.

The differences in timing and loudness provide enough information for the bird to accurately locate sounds both horizontally and vertically. To be of service to the owl, however, the information must be organized and interpreted. Much of the processing is accomplished in brain centers near the beginning of the auditory pathway. From these centers nerve impulses travel to a network of neurons in the midbrain that are arranged in the form of a map of space. Each neuron in this network is excited only by sounds from one small region of space. From this structure impulses are relayed to the higher brain centers. The selection of sensory cues and their transformation into a map of space is what enables the barn owl to locate its prey in total darkness with deadly accuracy.

The barn owl has a wide range, both as a species and as an individual hunter. Barn owls are found throughout the tropical and temperate areas of the world. Many live close to human settlements, often nesting in barns or in belfries; they also nest in hollow trees and in holes in earth banks or rocks. Like most other owls they remain paired for long periods, sometimes for life, returning to breed in the same place year after year. The birds hunt in open areas, and they cover more ground than any other nocturnal bird. Studies of the bird's pellets (small objects coughed up by the bird that contain the indigestible remnants of prey) have shown that more than 95 percent of its prey are small mammals, mainly field mice; the rest are amphibians and other birds.

The nine species of barn owls are different enough from other owls to form their own family: the Tytonidae. The common barn owl, *Tyto alba,* is the most numerous species. It stands between 12 and 18 inches high and has a white face, a buff-colored back and a buff-on-white breast; its lower parts are mostly white with dark flecks. Each of the bird's middle toes has a small comb with which it dresses its feathers.

The most striking anatomical feature of the barn owl, and the one that plays the most important role in its location of prey, is the face. The skull is relatively narrow and small and the face is large and round, made up primarily of layers of stiff, dense feathers arrayed in tightly packed rows. The feathered structure, called the facial ruff, forms a surface that is a very efficient reflector of high-frequency sounds.

Two troughs run through the ruff from the forehead to the lower jaw, each about two centimeters wide and nine centimeters long. The troughs are similar in shape to the fleshy external pinna of the human ear, and they serve the same purpose: to collect high-frequency sounds from a large volume of space and funnel them into the ear canals. The troughs join below the beak but are separated above it by a thick ridge of feathers. The ear openings themselves are hidden under the preaural flaps: two flaps of skin that project to the side next to the eyes. The entire elaborate facial structure is hidden under a layer of particularly fine feathers that are acoustically transparent. The acoustic properties of the facial ruff are closely associated with the bird's method of locating the source of the sound.

In order to survive the barn owl must be able to locate prey with sound alone. Field mice are difficult to see even in broad daylight because their coloring blends with that of their surroundings; in addition they tend to travel through tunnels in grass or snow. By night, when the mice forage, they are essentially invisible even to the keen eyes of the owl. Hunting from the air makes the task even more difficult, since the owl must determine the angle of elevation above the prey. A determination of azimuth alone would leave an entire line of possi-

STRIKE OF THE BARN OWL in total darkness is shown in this sequence of exposures made in the laboratory with infrared radiation, to which the eyes of the owl are not sensitive. Unlike ground-living predators, the bird must determine its elevation above the prey as well as the direction in the horizontal plane. The owl can locate mice solely by sound. Moreover, just before striking it aligns its talons with the long axis of the mouse's body, as is shown in the final exposure. This action shows that the bird can infer the direction of the prey's motion from sound.

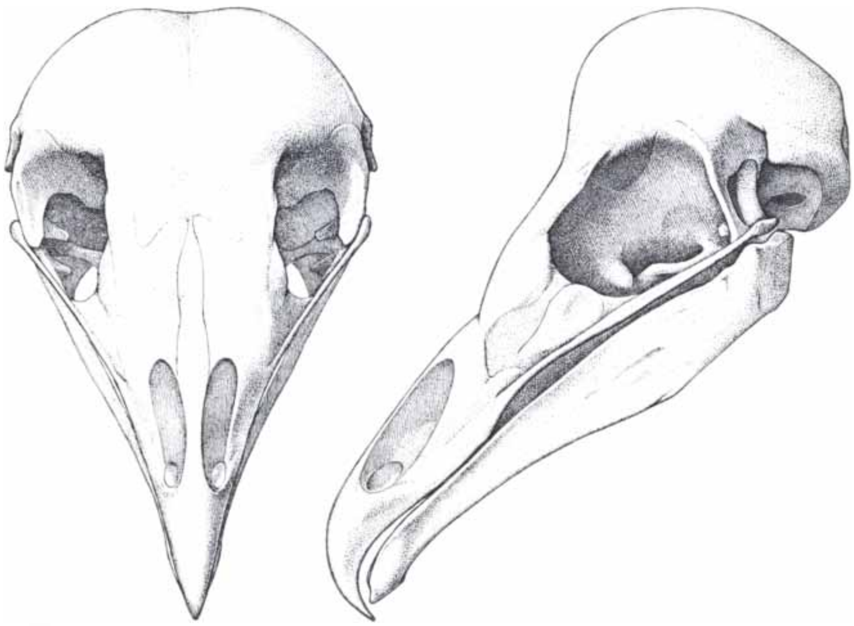
ble target sites along the ground below.

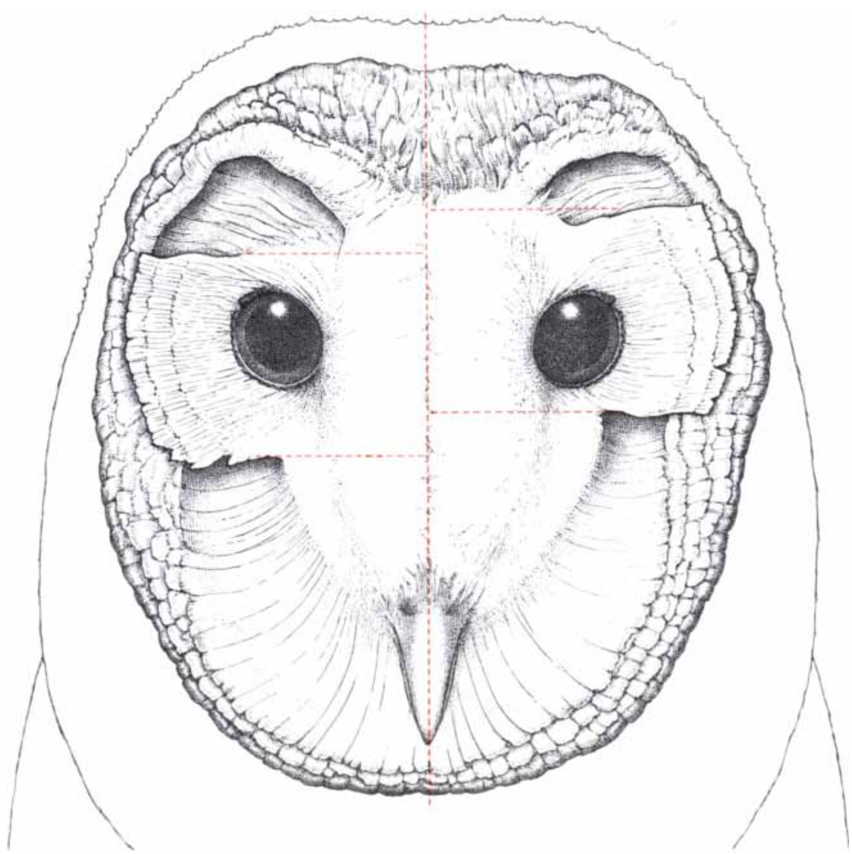
The barn owl locates sounds in two spatial dimensions with great accuracy. Roger S. Payne, and later Masakazu Konishi and I, demonstrated that the bird is capable of locating the source of a sound within a range of one to two degrees in both azimuth and elevation; one degree is about the width of a little finger at arm's length. Surprisingly, until the barn owl was tested, man was the species with the greatest known ability to locate the source of a sound; human beings are about as accurate as the owl in azimuth but are three times worse in elevation. Monkeys and cats, other species with excellent hearing, are about four times worse than owls in locating sounds in the horizontal dimension, the only one in which they have been tested.

The sensitivity of the barn owl's hearing is shown both by its capacity to locate distant sounds and by its ability to orient its talons for the final strike. When the owl swoops down on a mouse, even in a completely dark experimental chamber, it quickly aligns its talons with the body axis of the mouse. It was Payne who first suggested that this behavior is not accidental. When the mouse turns and runs in a different direction, the owl realigns its talons accordingly. This behavior clearly increases the probability of a successful strike; it also implies that the owl not only identifies the location of the sound source with extreme accuracy but also detects subtle changes in the origin of the sound from which it infers the direction of movement of the prey.

Several kinds of experiments have helped to elucidate how the barn owl accomplishes these difficult tasks. Experiments with birds in free flight have measured how accurately the owl flies toward and strikes at an invisible sound source. Head-orientation experiments, where the bird was perched on a testing stand, have helped to measure the precision with which it aligns its head with an incoming sound. Experiments where the brain of an anesthetized owl was probed with a microelectrode while the bird was exposed to various sounds have shown how the sensory information is organized and interpreted by the central nervous system.

Konishi and I have done a series of head-orientation experiments. This experimental system has several advantages over tests conducted with birds in free flight. In free-flight tests flight errors may be confused with sound-location errors. In addition the angle of the sound source in relation to the bird's head at the moment the bird decides to strike cannot be determined. Free-flight trials are also complicated and time-consuming to conduct. In contrast, head-orientation experiments are relatively simple to conduct, and they allow the rela-





FACIAL STRUCTURE of the barn owl is responsible for much of the bird's precision in hearing. The face is formed by rows of tightly packed feathers called the facial ruff extending from the relatively narrow skull. The external ears are troughs formed by the ruff that run down the length of the face to join below the beak. They collect sounds and funnel them into ear-canal openings hidden under the preaural flaps (flaps of skin projecting outward from next to the eyes). The left ear is more sensitive to low-frequency sounds from the left and the right ear is more sensitive to those from the right. At high frequencies, however, the right ear is more sensitive upward, because the preaural flap and opening are lower on the right and the trough is tilted up. The opening and the flap are higher on the left side and the trough is tilted down. The left ear is more sensitive to sounds coming from below. Differences in perceived loudness can therefore yield clues to the elevation of a source of sound as well as to its horizontal direction.

tion between the head and the sound source to be measured.

These experiments take advantage of a natural response of the owl when it is hunting. On hearing a noise the bird turns its head in a rapid flick that brings the source of the sound directly in front of it. This movement brings the sounds into the region where the bird's hearing is keenest. The eyes of the barn owl are immobile, and so the movement also enables the bird to see a target with maximum acuity. Konishi and I monitored this behavior by mounting a lightweight "search" coil on top of the owl's head. Magnetic fields generated by other coils were centered so that when the bird perched normally, the search coil was at the intersection of the horizontal field and the vertical one. The electric current induced in the search coil varied with its orientation to these fields. By evaluating the magnitude of two distinguishable signals one could measure the horizontal and vertical components of the orientation of the owl's head.

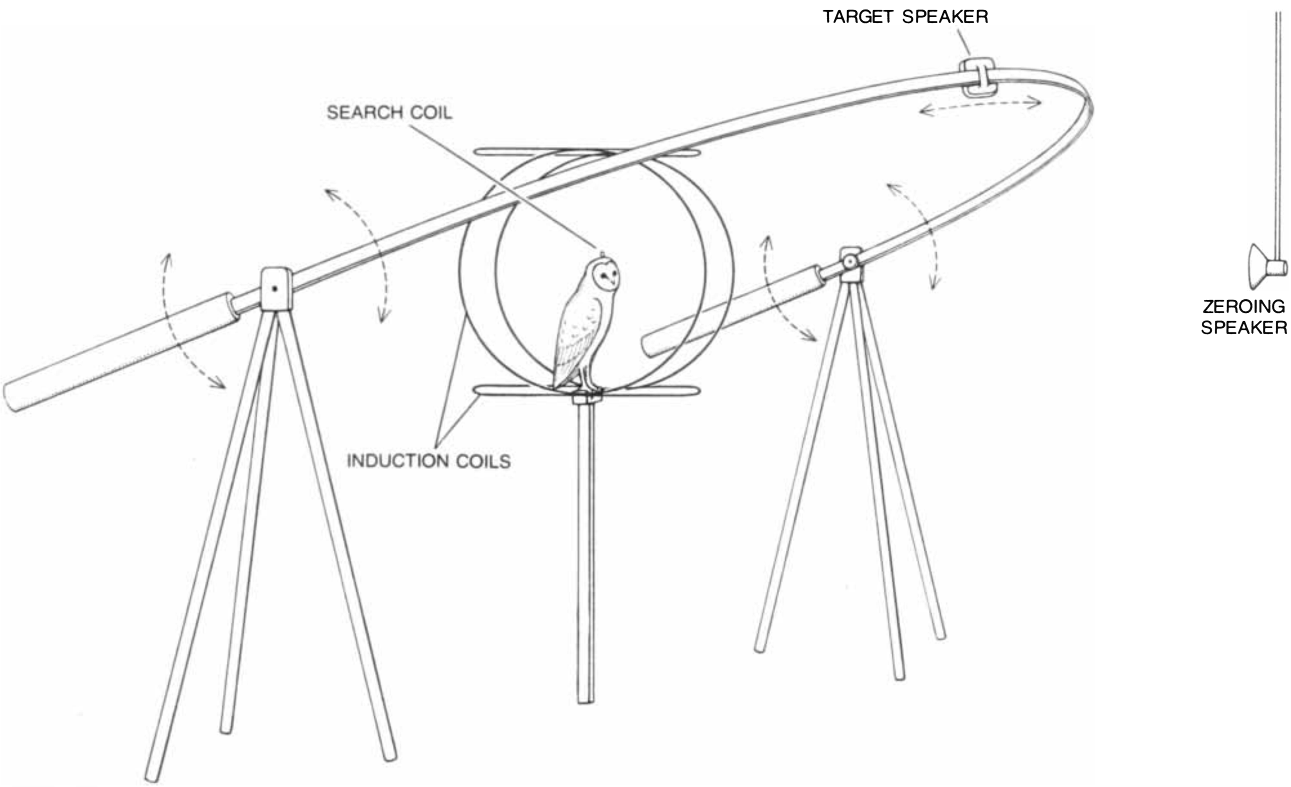
The tests were done in a totally dark chamber lined with materials that eliminate echoes. Sounds were generated by a stationary speaker (the "zeroing" speaker) and a movable speaker (the "target" speaker). The owl first turned to face a sound from the zeroing speaker, placed in front of its perch; a sound delivered by the target speaker then caused the bird to turn its head in the characteristic flicking movement. A computer controlled the location of the target speaker and recorded its location and the alignment of the owl's head.

The head-orientation trials have yielded much information about how the owl determines the origin of a sound. One of the important features of the process is that it can achieve maximum accuracy even with sounds that end before the head movement begins. This indicates that the owl's auditory system determines the azimuth and elevation of a sound without head movement and then utilizes the information to direct the head-orientation response. The head-movement tests also show that the owl's accuracy deteriorates with increases in the angle between the source of the sound and the orientation of the bird's head.

Our experiments and those of others have shown that the barn owl's ability to locate the origin of a sound is dependent on the presence of high frequencies in the sound. Although the owl's hearing is sensitive to a broad range of frequencies, from 100 hertz (cycles per second) to 12,000 hertz, it can locate accurately only sounds with frequencies between 3,000 and 9,000 hertz. In addition experiments in which one of the bird's ears is plugged show that both ears are necessary for the accurate locating of targets. If one ear is plugged, the owl makes large errors in the direction of that ear.

With these characteristics in mind we proceeded to investigate the exact information the barn owl selects from natural sounds. To locate the source of a sound the owl must determine the direction of propagation of the sound waves based on information from detectors at two points, namely its ears. The most useful spatial information is gained by comparing information from these two sources, since the differences between them depend not on the absolute sound level but only on the orientation of the ears in the sound field.

One valuable cue of this kind is the difference in the time of arrival of the sound in the two ears. When the sound comes directly from the side, the difference is at its maximum; when the sound is directly in front of the bird, there is no difference in the arrival time at the two ears. Between these limits the time difference varies with the angle of the



HEAD-ORIENTATION TESTS measured the accuracy of the owl's hearing. These experiments take advantage of a natural response made by the hunting owl: on hearing a noise the bird turns its head to face the source of sound. In the experimental situation the bird remained perched on a stand. A "search" coil mounted on its head was placed at the intersection of horizontal and vertical magnetic fields induced by stationary coils. Any head movement caused a measurable change in the current in the search coil. The owl's attention was first directed to a sound coming from a fixed "zeroing" speaker. A sound from a movable "target" speaker then caused the bird to turn its head in a rapid movement. A computer controlled the location of the target speaker and recorded movements of the bird's head. It was thereby possible to measure the accuracy with which the owl responded to sounds coming from various positions in space.

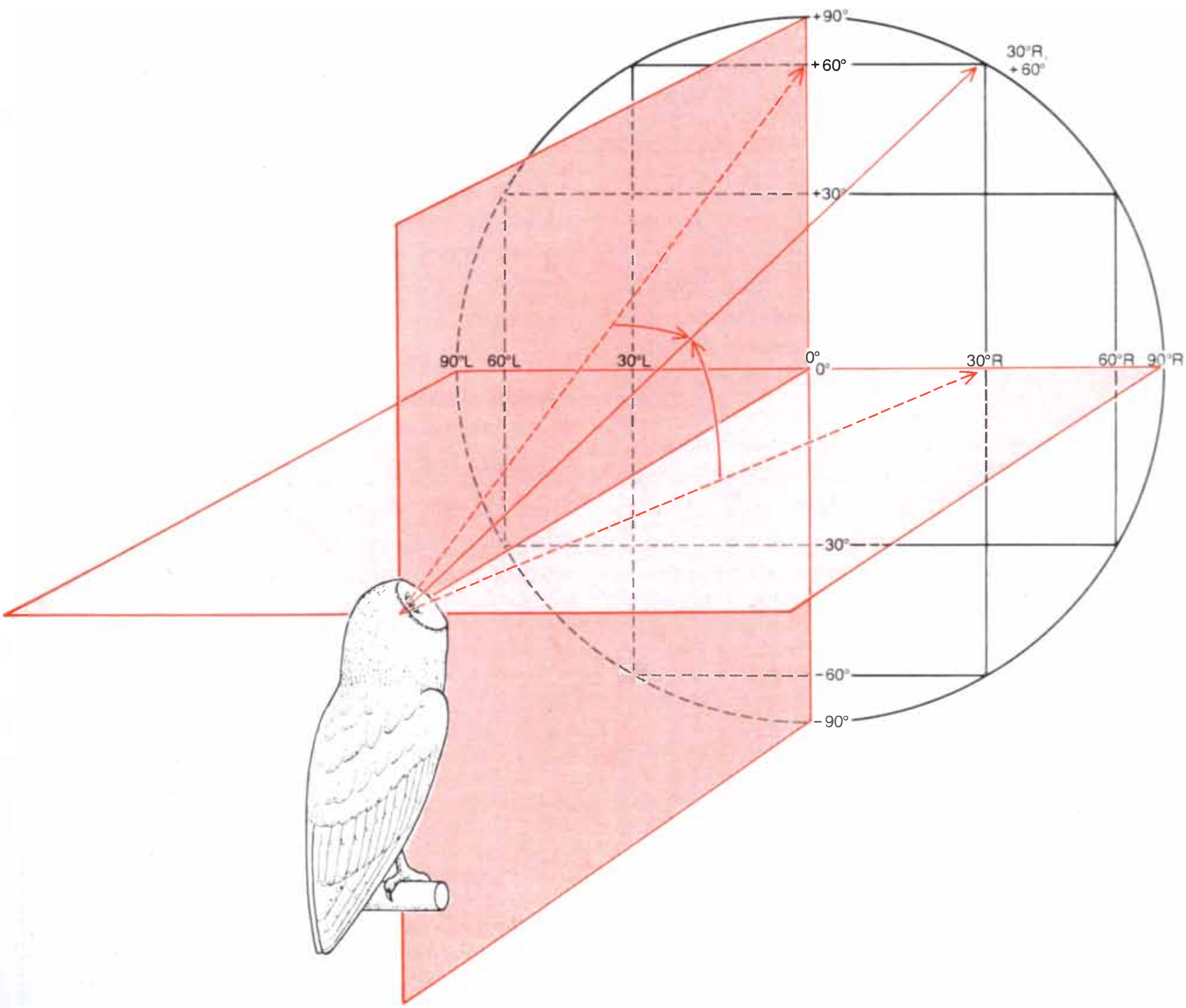
sound in the horizontal plane. The time delay can therefore yield information about the azimuth of the sound. This is not sufficient for the bird to locate the sound exactly, because sounds from several directions can give rise to the same difference in time. In three-dimensional space these directions form a cone around the axis between the owl's ears.

This is an example of the inadequacy of any one cue to provide information about both the horizontal and the vertical angle of a source of sound. To specify a location in both dimensions two independent cues are needed. In the owl's case the additional information is provided by differences in the directional sensitivity of the ears.

Directional sensitivity is provided by the facial ruff. Like a hand cupped behind the ear, the troughs of the ruff amplify the sound and make the ear more sensitive to sounds from certain directions. The amount of amplification and directional sensitivity imparted by the feathers of the facial ruff varies dramatically with the frequency of the sound. This is owing to one of the properties of the sound waves themselves. When sound waves encounter an object, they can bend around it or be reflected back from it. Which of these happens depends on the wavelength of the sound and the size of the object. If the wavelength is long compared with the object, the waves tend to propagate around the object; if the wavelength is short, the waves tend to be reflected back in the direction from which they came.

As a result of this phenomenon frequencies of less than 3,000 hertz are not efficiently reflected by the ruff. Because the funneling action of the ear depends on its capacity to reflect sound its directional sensitivity at low frequencies is relatively poor. At 3,000 hertz, for example, the left ear is only slightly more sensitive to sounds coming from an area between 20 and 40 degrees to the left than it is to sounds coming from other directions. The right ear has a similar degree of sensitivity to the right. Since the sensitivity of each ear at low frequencies changes only gradually with direction, the comparison of sound intensities at low frequencies can provide only a coarse spatial cue. Moreover, this difference yields no clue to the elevation of the sound.

With higher-frequency sound waves the situation is quite different. Each ear is much more sensitive to the direction of the sound; a small change in sound direction gives rise to a large change in perceived intensity. In addition, instead of being more sensitive to the right or to the left, the right ear is more sensitive above the horizontal plane and the left



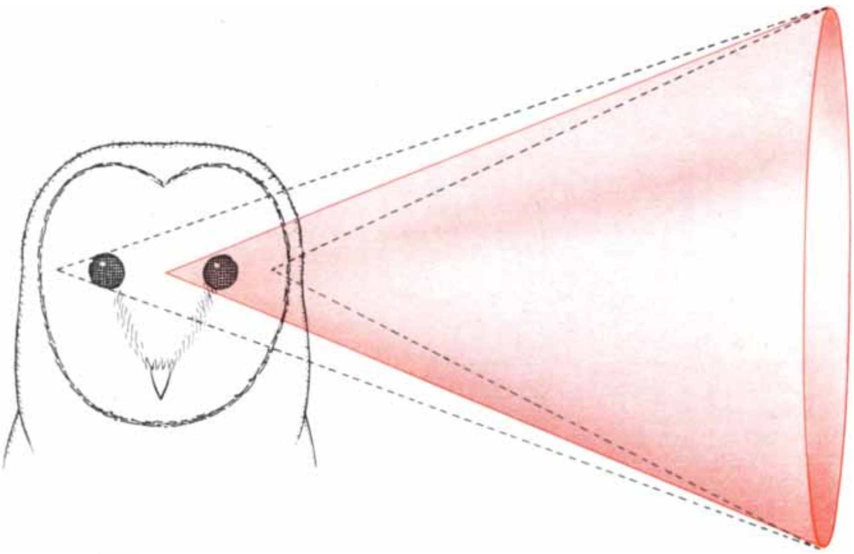
DOUBLE-POLE COORDINATE SYSTEM serves to map the positions of the owl's head in head-orientation tests. Each direction is specified by two measurements: the angle from the horizontal and that from the vertical through which the owl must turn its head to face that way. Facing forward, as the bird normally perches, the orientation is 0 degrees (horizontal) and 0 degrees (vertical). The map represents the 180 degrees of space in front of the bird. The other maps accompanying this article have the same coordinate system.

ear is more sensitive below it. This sensitivity is the result of an unusual anatomical asymmetry. The ruff on the left is directed slightly downward, and the ear opening and the preaural flap are higher in the ruff on the left side. On the right side the reverse is the case. Accordingly as the source of the sound moves up the high-frequency components of a natural sound become louder in the right ear and softer in the left. As the source of the sound moves down the sounds become louder in the left ear. Since at high frequencies the perceived loudness changes rapidly with elevation, this cue offers information that is very precise.

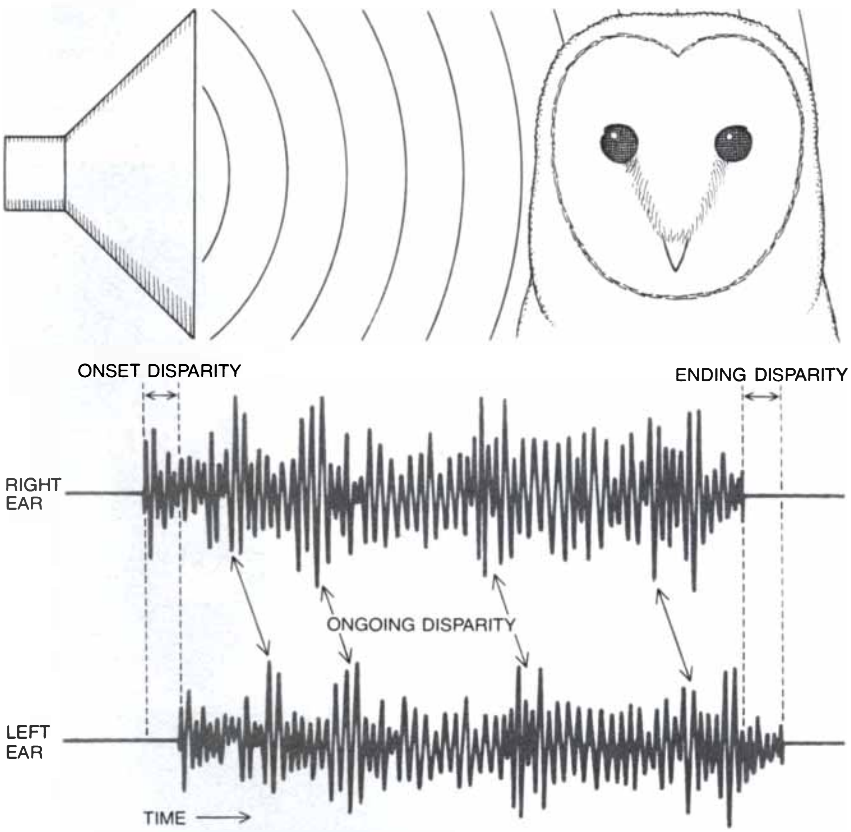
Although that information is valuable to the barn owl, it is also complex. The magnitude of the difference in intensity varies according to the frequency of the sound, because of the greater capacity of the ruff to reflect sounds at higher frequencies. The direction indicated also varies with frequency, since horizontal location is given by low frequencies and vertical location by high ones. The owl's auditory system must therefore compare the intensities detected at each ear for each frequency. A comparison of intensities made frequency by frequency is called an interaural spectrum.

Since low-frequency sounds yield clues to azimuth and those of high frequency yield clues to elevation, the interaural spectrum could by itself provide enough information for the owl to locate prey. Much evidence supports the hypothesis that owls use this spectrum. The strike accuracy of the bird increases sharply as the bandwidth (the number of frequencies contained in a sound) is increased. From differences in the intensity of a single tone (a sound of only a single frequency) the owl can determine direction in only one dimension; as the spectrum broadens more intensity differences are available, and their values indicate the angle of the source in more than one plane. Experiments in which one of the owl's ears is plugged show more directly that the owl compares intensities. A trained owl with its right ear plugged strikes to the left and short of the target; one with its left ear plugged strikes to the right and beyond the target. That the errors have components of both elevation and azimuth implies that the owl gains both types of information from comparisons of intensity.

Further confirmation has been obtained by removing the owl's facial ruff. When the ruff is removed, the owl is able to locate the azimuth of a sound quite well but cannot identify its vertical location: the bird consistently orients to a point on the horizontal, regardless of the elevation of the target. This accords with our hypothesis: the sound-reflecting properties of the ruff underlie directional sensitivity at high frequencies, which enables the owl to identify the



CONE OF CONFUSION (*color*) **is formed by the directions among which the barn owl cannot distinguish on the basis of time delay alone. Time delay can provide information about the horizontal angle of a sound source. Since the left and right ears are generally at slightly different distances from the source of a sound, sound waves reach them at slightly different times. The greater the angle of a sound source from the bird's frontal plane, the greater the time delay. There are many directions, however, that give rise to the same path lengths (*broken lines*) and hence to the same time delay; other cues are required for the bird to tell them apart. In three-dimensional space these directions form a cone whose peak is between the two ears.**



SOUND TRACE shows two kinds of differences in the timing of the sound between the barn owl's left and right ears. In this schematization the height of the trace indicates the pressure caused by the sound waves in each ear. When a sound comes from the right, the waves begin and end earlier in the right ear; major changes in intensity also occur slightly earlier there. These differences are collectively known as transient disparity. In addition, throughout the duration of the sound the waveforms are slightly advanced in the right ear; this is called ongoing disparity. Man relies on both differences to find the source of a sound. The barn owl relies heavily on ongoing disparity, but there is no evidence that the bird exploits the transient difference.

vertical angle of the source. Removal of the ruff eliminates the ability to discriminate among elevations. Some disparity in intensities is retained because the ear openings and preaural flaps are placed asymmetrically in the fold of skin supporting the feathers of the ruff, but this is not enough to make it possible to identify the elevation of the sound.

That barn owls rely on the interaural spectrum to locate sounds in both azimuth and elevation has thus been amply confirmed by the results gathered from the head-orientation tests. It is clear from other findings, however, that the bird also makes some use of timing differences in locating its invisible prey. The timing delay is manifested in two aspects of the binaural signal. First, the sound begins and ends sooner in the ear closer to the source; the timing of major discontinuities in intensity in the sound is also slightly different in each ear. These differences are known collectively as transient disparity. Second, throughout the duration of the sound the sound waves reaching the far ear will be slightly delayed. With a single frequency this difference in the timing of the waveforms is known as phase delay; with more complex natural sounds, made up of many frequencies, it is called ongoing time disparity.

In nature the ongoing and the transient disparities are of about equal magnitude; they vary with changes in the azimuth of the source of sound. They do, however, have different advantages for locating sounds. The ongoing time disparity can be measured repeatedly while the sound lasts. Transient disparity, on the other hand, can be monitored only intermittently, but it is less likely than the ongoing disparity to be confused by echoes.

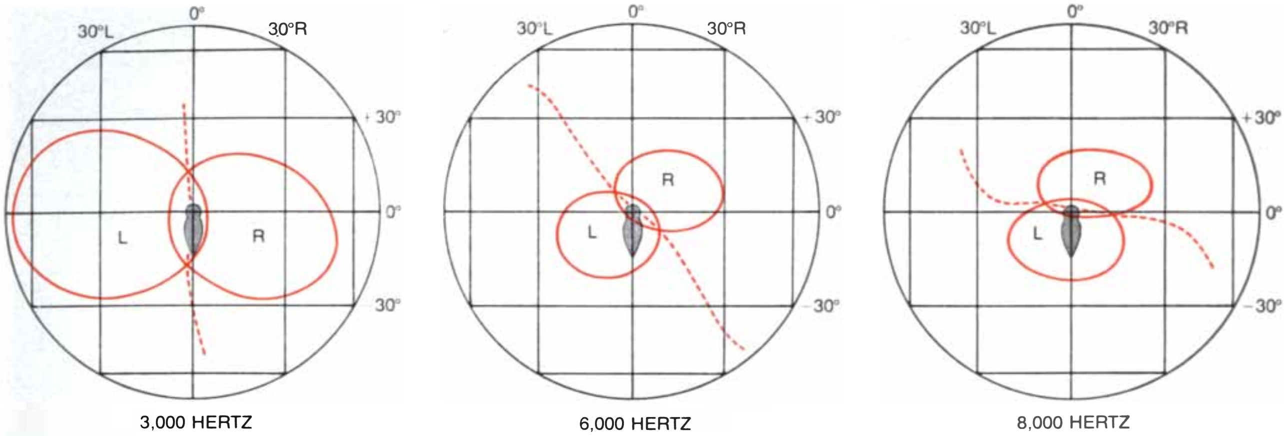
Human beings rely on both transient and ongoing disparity to determine the source of a sound. Owls appear to rely on only the ongoing difference. Like other kinds of spatial information, the ongoing disparity has a major ambiguity. It may be best understood in the case of a tone coming directly from the side. The signals detected by the owl's ears are sinusoidal (regular) waves; because of the different distances to the ears the waves will be slightly out of phase with each other. The magnitude of the phase delay so created will depend both on the frequency of the tone and on the distance between the ears. As the frequency of the wave or the distance between the ears increases, the wave passes through more of its cycle as it travels around the head to reach the far ear; hence the phase delay is greater.

When the frequency of the tone is so high that the wave passes through exactly half of its cycle before it reaches the far ear, the phase delay corresponds to half of the wavelength. Such a delay could be caused by a sound coming directly from the owl's left or directly from its right, since the difference in path lengths is the same for these two directions. It is therefore impossible for the bird's auditory system to determine the direction of the sound on the basis of ongoing disparity alone. At higher frequencies the situation is worse still. When the wavelength is equal to the distance between the ears, for example, there is no phase delay, since the wave travels through its entire cycle while passing around the head. This relation could correspond to a sound coming from the right, from the left or from directly ahead; on the basis of phase delay alone the bird has no way of determining which is the case.

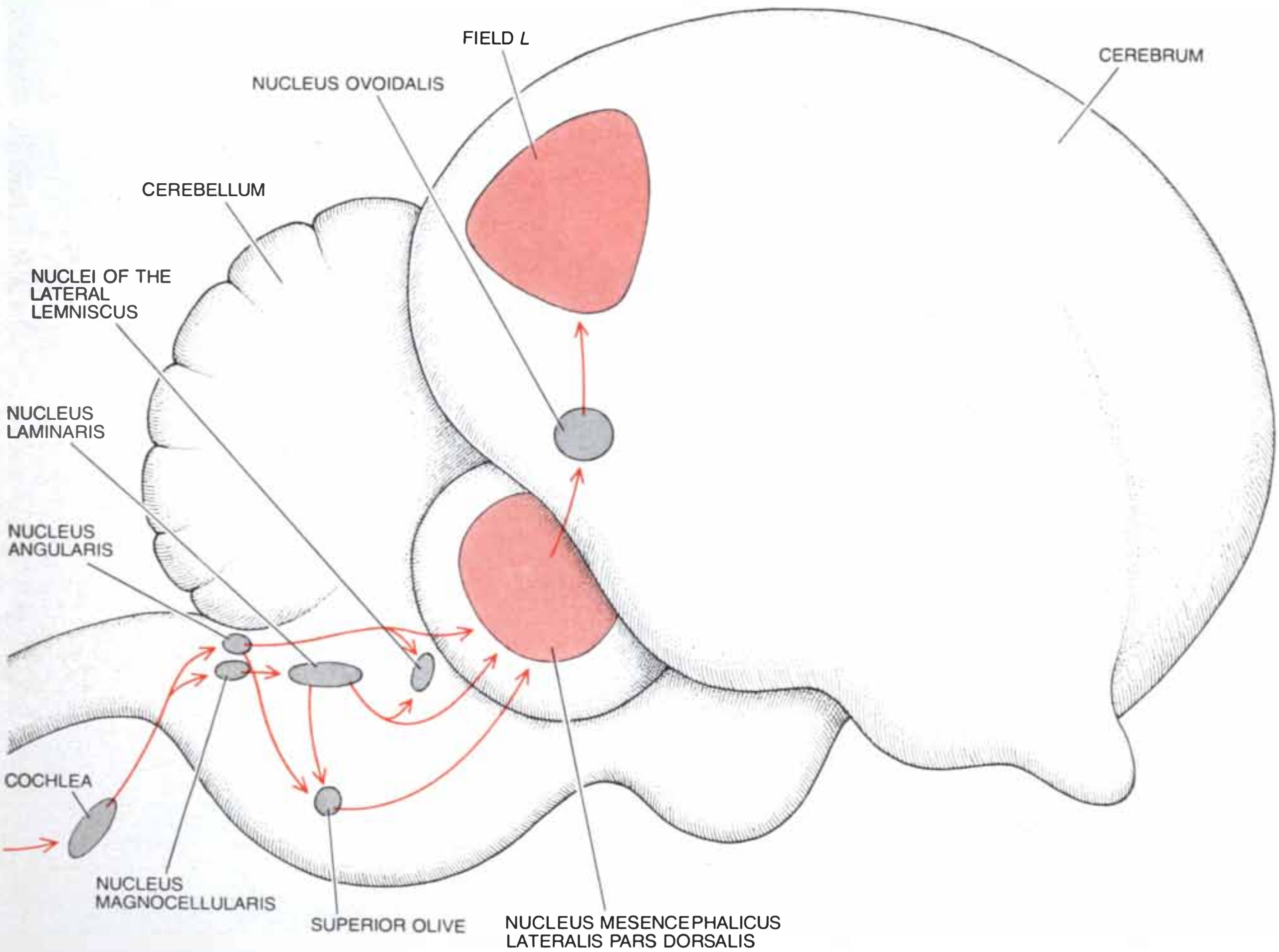
The wavelengths at which such ambiguities arise depend on the distance between the ears. The barn owl's ears are about five centimeters apart; phase ambiguity will therefore arise at a wavelength of 10 centimeters or less, which corresponds to frequencies of 3,000 hertz or more. Since the barn owl has no difficulty determining the azimuth of even high-frequency tones, Konishi and I assumed that at high frequencies the bird must rely on some source of information other than the ongoing time disparity. A likely candidate for the additional cue was transient disparity, because it is not affected by changes in frequency and because other species, including man, are known to depend on it at high frequencies.

How wrong this conclusion was has been demonstrated conclusively by Andrew Moiseff and Konishi in a further head-orientation experiment with the barn owl. They presented sound directly and independently to both ears by means of small speakers implanted in the owl's ear canals. This technique enabled them to eliminate transient disparities and differences in intensity between the ears as they varied the ongoing time disparity. The delay between the waveforms of the sound in the two ears could be adjusted in steps as small as one microsecond. In response to ongoing disparities of as little as 10 microseconds or as much as 80 microseconds the owl made quick horizontal turns of the head that corresponded approximately to the angle implied in the ongoing difference. This response suggests, in the absence of other interaural cues, that the owl continues to make use of the phase delay, or ongoing disparity, even at high frequencies.

The finding was startling because it implied that the barn owl has some means of overcoming the phase ambiguity. Furthermore, for the owl's auditory system to sense such small differences in the timing of the waveforms in the two ears it must receive specific information about acoustic signals occurring at 7,000 hertz, or once every 143 microseconds. This is remarkable, because the nerve impulses that convey this infor-



DIRECTIONAL SENSITIVITY of the ears of the barn owl changes with the frequency of sound waves. The funneling action of the troughs in the facial ruff makes the ears more sensitive to sounds from some directions than to sounds from others. At low frequency the area of maximum sensitivity of the left ear is to the left and that of the right ear is to the right. Waves with higher frequencies are more efficiently reflected by the ruff. Since the left trough is tilted down and the right trough up, as the frequency increases the areas of greatest sensitivity move toward vertical alignment: the right ear is more sensitive upward and the left ear downward. At 8,000 hertz (cycles per second) the regions of most sensitive hearing are almost directly above and below the bird. Because natural sound usually has many frequencies, the owl can exploit differences in loudness to identify both the horizontal and the vertical direction of a sound source.



AUDITORY PATHWAY of the central nervous system of the barn owl leads from the cochlea to an area of the forebrain known as Field *L*. Along this route the nerve impulses undergo considerable processing: data about the timing and frequency of sound are converted into information about the location of the sound source. Much processing takes place in various centers of the lower brain. By the time the impulses have reached the nucleus of the midbrain that is called the mesencephalicus lateralis pars dorsalis (MLD) they are directed into a network of neurons that respond to sounds from specific areas; the distribution of those areas forms a two-dimensional map of the space in front of the bird. Information about a sound's location then passes to Field *L*, corresponding to the auditory cortex of mammals.

mation from the cochlea to the brain last for more than 1,000 microseconds.

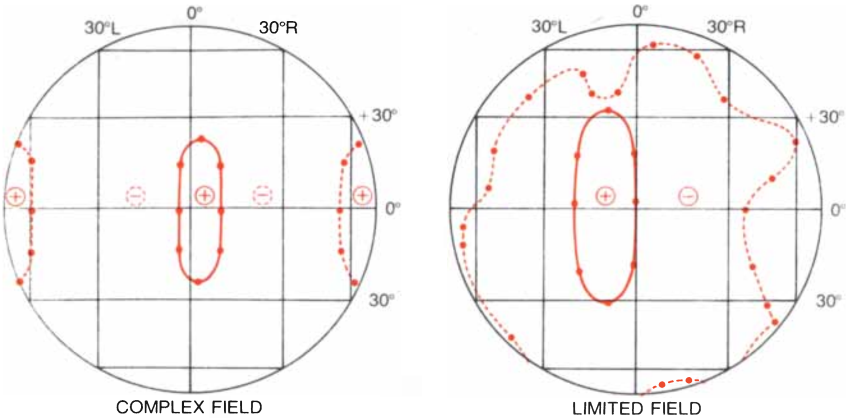
Ongoing time disparity is very useful to the barn owl; by itself, however, the cue does not have the precision the owl needs in order to hunt. With speakers implanted in the ear canals the owl responded to a given ongoing time disparity with turns that varied in magnitude by up to 15 degrees in either direction. In contrast, the largest standard deviation of error for owls responding to external targets is only 2.5 degrees in either direction, and the error is usually less than 1.5 degrees. Other cues must therefore be combined with the ongoing disparity. It is known that differences in intensity help to specify location, but we also tried to discover whether the bird employs transient disparities.

Our original hypothesis, that the owl relies on transient disparity to compensate for phase ambiguity at high frequencies, has clearly been invalidated. The owl's performance in determining the azimuth of a tone suggests that transient disparities are not relied on at all. In head-orientation trials the owl was presented with tones of 7,000 and 8,000 hertz. The speaker was sometimes at 30 degrees to the right and sometimes at 30 degrees to the left. In these situations a curious kind of behavior was observed: with the target at 30 degrees to the right the owl sometimes turned 30 degrees to the left, and vice versa.

This confusion is clearly a manifestation of phase ambiguity. The cycle period of a 7,000-hertz tone is 143 microseconds and that of an 8,000-hertz tone is 125 microseconds. With a source of sound at 30 degrees to the right or the left these tones pass through about half a cycle in traveling over the difference between the path lengths to the ears. Therefore a tone coming from 30 degrees to the right yields the same phase delay as one coming from 30 degrees to the left. The ambiguity is present only in the ongoing disparity; if the owl had been relying on transient disparity, it would immediately have picked out the correct location.

This result confirms that the owl continues to rely on phase-delay information, even at high frequencies, in spite of its ambiguity, and apparently does not rely on transient disparity. Since the wavelength of low-frequency sounds is considerably greater than the distance between the ears, phase ambiguity does not exist at low frequencies. Moreover, the presence of a number of frequencies in natural sounds helps the owl to resolve phase ambiguities. When many different pairs of directions arise from different frequencies, the owl selects the one direction in space that is consistent with one member of each pair.

Head-orientation trials clearly show that the barn owl relies on two kinds of information to determine the origin of



TWO TYPES OF NEURONS in the brain of the barn owl are sensitive to sounds from specific directions. Shown here are maps of the receptive fields of the two cell types. Receptive fields are the regions of space within which sounds will produce an excitatory response in the neuron. Complex-field neurons, found in the MLD, have several such areas. A typical complex-field receptive pattern is shown at the left. The receptive areas correspond to the directions that give rise to identical ongoing disparities in the timing of sound waves. Between those regions sounds produce an inhibitory response. Limited-field neurons are found in both the MLD and Field *L*. A typical limited-field receptive pattern is shown at the right. Limited-field cells have a single receptive area. Sounds from outside this area produce a strong inhibitory response. Each limited-field cell responds to a specific difference between the ears in sound timing and intensity.

a sound: the interaural spectrum and the ongoing time difference. The latter yields clues to the azimuth of the sound source. The differences in intensity between the ears yield clues to both the azimuth and the elevation. To learn how the auditory system transforms these cues into a neural image of sound location calls for a different experimental approach.

The technique I resorted to, first with Konishi and later in independent experiments, is that of inserting a microelectrode into the brain of an anesthetized owl and searching for sites of neuronal activity while sounds are presented to the bird's ears. Konishi and I began the experiments with the same apparatus we had used in the head-orientation trials. After the owl was anesthetized its head was held rigidly in a special stereotaxic frame. A microelectrode was lowered into the brain until nerve impulses from a single neuron could be recorded. By moving the target speaker around the owl it was possible to map the regions of space to which the neuron responded.

Since the source of a sound in space is determined only after considerable neural processing, we began our study by exploring structures fairly far along the auditory pathway: in the midbrain and forebrain. The main auditory center in the midbrain of birds is called the nucleus mesencephalicus lateralis pars dorsalis (MLD). (It corresponds to the structure in the brain of mammals called the inferior colliculus.) Nerve impulses reaching this center have already been processed in one or more nuclei farther down the auditory pathway. Farther up the pathway an area designated Field *L* is the primary receiving center in the forebrain for auditory impulses. (This structure corresponds to the auditory cortex in mammals; birds have no exact analogue to the auditory cortex.)

In both the MLD and Field *L* the large majority of neurons do not respond precisely to spatial cues. Some of the neurons show their highest level of activity in response to sounds from a certain region of space, but the borders of the region are not sharp, and they vary greatly with the intensity of a sound. Other neurons are even less specific in their response, being excited by sounds from virtually all directions. These neurons probably contribute not to specifying location but to the detection or identification of sounds.

Two types of neuron found in the MLD and Field *L*, however, are highly sensitive to sound location. The first of them, called the complex-field neuron, is found in large numbers in the MLD, usually in clusters scattered among other kinds of neurons. The activity of complex-field neurons is stimulated by sounds coming from several separate regions of space, called excitatory fields. The neurons are much less excited, or are even inhibited, by sounds arising in the regions of space between the excitatory fields.

When the location of the centers of the excitatory fields in space are calculated for an individual complex-field neuron, an interesting correspondence is observed. The excitatory fields are the same as the regions of space the owl confuses under conditions of phase ambiguity. The multiple excitatory fields represent the regions from which sounds reaching the ears will generate phase delays of equivalent magnitude. Each complex-field neuron therefore seems to be sensitive to a particular phase delay at a particular frequency. The presence of several excitatory fields for each neuron would appear to be the physical correlate of spatial confusion due to phase ambiguity.

The second type of neuron, called the limited-field neuron, which is found in both the MLD and Field *L*, responds in an even more specific way. Limited-field cells are excited only by sounds coming from a single region of space. The regions to which limited-field neurons respond are typically elliptical. Their size varies in azimuth from seven degrees to 42 degrees and in elevation from 23 degrees to an entire band in front of the bird. Unlike other neurons in the auditory pathway, the limited-field neurons are extremely selective, responding only to changes in location; large changes in sound intensity cause little if any alteration in the sharp borders of the receptive region.

Some of the sharpness of the borders of the limited-field-neuron receptive regions is due to the fact that sounds coming from outside the excitatory region inhibit the cell's response. The inhibitory effect becomes stronger as the location of the sound approaches the border of the excitatory region, at which point the inhibiting effect changes to one of excitation. Although the spatial regions that give rise to an excitatory response are fairly large, within them there is a smaller region of the best response. These "best regions" vary in size from 2.5 to 15 degrees in azimuth and from five to 45 degrees in elevation.

Limited-field units are found in both the MLD and Field *L*. Their distribution in the two centers is, however, fundamentally different. In Field *L* limited-field neurons make up only about 15 percent of the total population of nerve cells, and they are often found scattered among other types. In the MLD, on the other hand, these cells are concentrated on the side and front margins of the nucleus, interspersed only with a few neurons of the complex-field type. After we had intensively explored and mapped the MLD it became apparent to us that the arrangement of limited-field neurons in that nucleus constitutes a map of two-dimensional space, with the distribution of the receptive areas of the neurons following the contours of space.

The map is distorted, however: the area in front of the bird, the region of maximum auditory acuity, is represented disproportionately. Sound azimuths are arrayed in the horizontal plane. On the right side of the structure representing the map are neurons that are excited by sounds originating between 15 degrees to the right and 60 degrees to the left. On the opposite side are neurons stimulated by sounds between 15 degrees to the left and 60 degrees to the right. This arrangement means that the 30 degrees of space in front of the bird is represented on both sides of the map and therefore by two sets of neurons. In addition the map is arranged so that on both sides the population of neurons that represent the 30 degrees in front is disproportionately large. As a result of the double representation and the large number of neurons on each side the 30 degrees in front is analyzed with great precision, a fact that may explain the owl's particular accuracy in locating sounds in this area.

Sound elevations are arrayed transversely on the map. The "best regions" of the limited-field neurons range from 40 degrees upward to 80 degrees downward. The upper fields are at the top of the curved surface of the map and the lower fields are at the bottom.

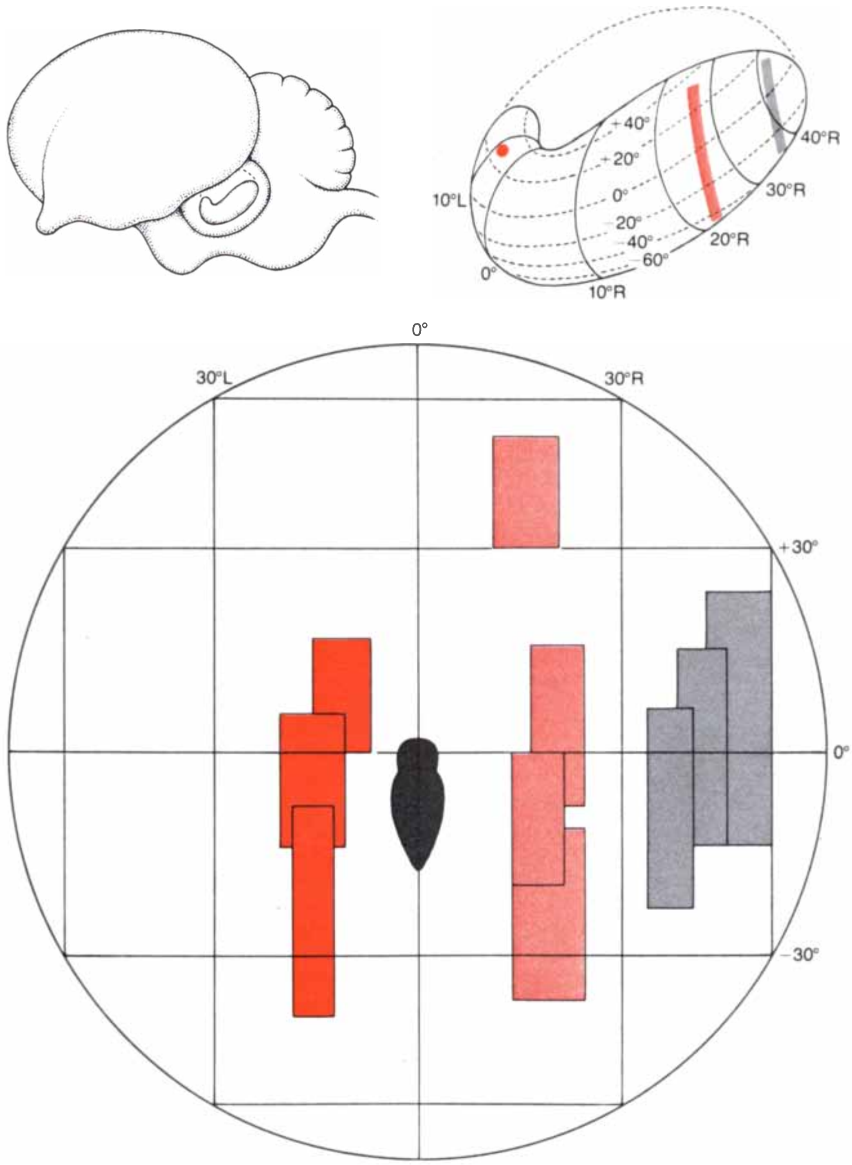
How does the nervous system of the barn owl construct this remarkable map? Substantial understanding of the process has come from experiments by Moiseff and Konishi. In these tests speakers were placed in the ear canals of anesthetized owls. When sound was delivered separately to the two ears, the timing and intensity differences required to elicit a response in each neuron could be observed. These values were then correlated with the areas of space known to excite each set of neurons. The results of the investigations show that the limited-field units in the map are quite sensitive to ongoing differences in timing. This observation corresponds nicely to the bird's dependence on ongoing disparities demonstrated in head-orientation experiments.

Limited-field neurons respond only to an extremely narrow band of ongoing time delays: the size of the band ranges from 40 to 100 microseconds. Even within this minute range one particular delay always elicited the greatest response. Changing the ongoing difference by as little as 10 microseconds could change the strength of the neuron's response by as much as 75 percent. This degree of sensitivity complements (and helps to explain) the owl's precision in aerial hunting.

The ongoing disparity that gives rise to the greatest response also corresponds to the region of space to which the cell responds. Neurons that respond to sounds coming from the front are maximally excited by small ongoing disparities. Neurons that respond to sounds at greater angles require larger disparities. These results confirm at the level of individual cells the conclusion drawn from behavioral tests: that the owl relies heavily on the ongoing difference in timing between the ears to determine location in the horizontal plane.

Such experiments have also helped to confirm and explain the owl's reliance on differences in sound intensity. By varying the relative intensity of sounds presented independently to the ears of an anesthetized owl it was found that for each limited-field neuron there is one difference in intensity that evokes the maximum response. Changing the difference away from this value causes the response to decrease and finally to cease. The pattern is not affected by the changes in the average sound level; it depends only on the difference in intensity between the ears.

The evidence derived from probing the brain of the barn owl shows that the map of space in the MLD is created by the same cues the owl was known to rely on in finding the azimuth and elevation of a sound: ongoing time disparities and the interaural spectrum. By means of an exquisitely precise transformation the auditory system converts these cues into spatial information. The arrangement of the cells of the map implies that neighboring neurons respond to cues that are only very slightly different. Moreover, the order of the excitatory fields in the map follows the continuity of space. How the brain of the owl is able to achieve such precise connections presents an intriguing problem for further investigation.



TWO-DIMENSIONAL MAP of frontal space is found in the MLD of the barn owl. The map is made up of limited-field neurons. Each cell responds to sounds from a specific region of space. The arrangement of the receptive areas of the neurons follows spatial contours. Shown above is the region on the left side of the brain that responds to sounds from the right. Neurons in this region are sensitive to sounds in an area from 15 degrees on the left to 60 degrees on the right, and from 40 degrees upward to 80 degrees downward. Electrode traces through the structure will thus correspond to a set of regions of space aligned vertically; a set of three such traces and the spatial regions they correspond to are shown. A corresponding structure on the right side of the owl's brain consists of the neurons that respond to sounds originating from the left. The region from 15 degrees on the left to 15 degrees on the right is thus represented on both sides of the brain and is mapped on each side by a disproportionately large number of neurons; this is the area of the barn owl's greatest acuity in locating a sound source.