

THE NEUROPHYSIOLOGY OF AUDITION IN BATS: DIRECTIONAL LOCALIZATION AND BINAURAL INTERACTION

By A. D. GRINNELL*

*From the Biological Laboratories, Harvard University,
Cambridge, Massachusetts, U.S.A.*

(Received 24 October 1962)

This is the third in a series of papers on the neurophysiological correlates of echolocation in the bats *Myotis l. lucifugus* and *Plecotus townsendii*. Previous papers (Grinnell, 1963*a, b*) have reported that sensitivity throughout the range of emitted frequencies, differential thresholds for frequency and intensity, and especially the ability to resolve two stimuli presented close together in time, are well adapted for gaining information from faint high-frequency echoes occurring within a few milliseconds of a much louder emitted cry. These findings provide some clues to the neural mechanisms involved in detection of an object, determination of its distance, and possibly even details of its size and structure, but there still remains the highly important question: where is the object?

A bat's livelihood depends on its ability to use sound as a substitute for light in locating objects in three-dimensional space. It is not known how accurately bats can do this, but there is some evidence that, even at a distance of 1–2 m and immediately after initial detection they can select the flight path which most effectively intercepts a flying insect 1–3 mm in diameter (Griffin, Webster & Michael, 1960). Moreover, as few as 4 or 5 pulses appear to be sufficient for the successful detection and avoidance of small wires (Grinnell & Griffin, 1958). These, with a variety of other considerations (Grinnell, 1962), strongly suggest that acoustic localization by bats is fully as accurate as that of human beings, and very likely more accurate, especially in the vertical plane.

Since accurate localization is so important to bats, problems of 'directionality' (directional sensitivity) and binaural interaction have been pursued at some length. These investigations reveal interesting features, which, if not unique to bats, are at least exaggerations of what is known in other mammals.

* Present address: Department of Biophysics, University College London.

METHODS

Bats were prepared and their responses studied in the way described in a preceding paper (Grinnell, 1963*a*). Gross electrodes were used to study evoked potentials at the level of the auditory nerve (N_1), and at the posterior colliculi (N_4). Micro-electrodes were also used to record evoked potentials and the responses of single units at the same levels. For the present experiments the loudspeaker was mounted so that it could be moved in the 180° horizontal arc from side to side equidistant (34 or 68 cm) from the bat's head. The 'directionality', or angular sensitivity, of the recorded potential was usually judged by measurement of the change in threshold to a sound coming from the loudspeaker as it moved through the 13 positions 15° apart in the 180° azimuth around the bat's head in the horizontal plane. Stainless-steel concentric electrodes were used in most cases to reduce the error introduced by electrical spread of a potential from the corresponding nucleus on the other side of the brain, although results were not found to differ significantly when uninsulated electrodes were used. Just-visible responses on the oscilloscope screen were chosen as the most easily determined and reproducible criteria of threshold. This method has the advantage of comparing sensitivity in terms of decibels rather than percentage of maximal response. Occasionally a criterion response or amplitude between threshold and maximal was used, and the intensity necessary to maintain this response was measured. These two methods showed no significant differences. When response amplitude was measured as a function of angle of incidence, however, it was found that the indicated directionality differed very markedly with different signal intensities, a result of the non-linearity between signal intensity and response amplitude (Grinnell, 1963*a*). A typical experiment showed the greatest reduction in response amplitude between the angle of maximal sensitivity and the angle of minimal sensitivity to be 29% for 100 db signals, 50% at 90 db, 70% at 80 db, 81% at 70 db and, 91% at 60 db (all sound levels mentioned in this paper are expressed in decibels relative to 0.0002 dyne/cm²). The resulting threefold ambiguity makes the reproducible determination of angular sensitivity very difficult if amplitude of evoked potential is used as an index.

RESULTS

Evoked potential recordings

Directional sensitivity. When the signal necessary to evoke a constant collicular response was determined for different angles relative to the bat's head, results such as are shown in Fig. 1 were obtained. These are the results of a single but typical experiment. The intensity necessary to elicit a just detectable N_4 response is plotted against angle of incidence of the sound. The electrode in this case was in the right posterior colliculus, where sensitivity was greatest to signals coming from 15 to 45° on the contralateral side, falling off regularly on both sides of this and reaching a minimum at 60 – 90° ipsilateral. In all of several experiments involving simultaneous recording from the two colliculi the resulting curves were nearly mirror images of each other.

It is clear from Fig. 1 that change in sensitivity with change in direction is highly dependent on frequency. There are two closely related measures of the magnitude of directionality: the absolute difference in threshold between most-sensitive and least-sensitive directions and the rate of

change of sensitivity over the steepest part of the curve. These two measurements have been made in the experiment shown and are plotted in the lower graph of Fig. 1. In both respects directionality nearly triples as frequency rises from 20 to 60 kc/s, with most of the change coming in one large step between 30 and 40 kc/s. At 20 kc/s the angle to which the response is most sensitive is only 19 db more effective than the angle of

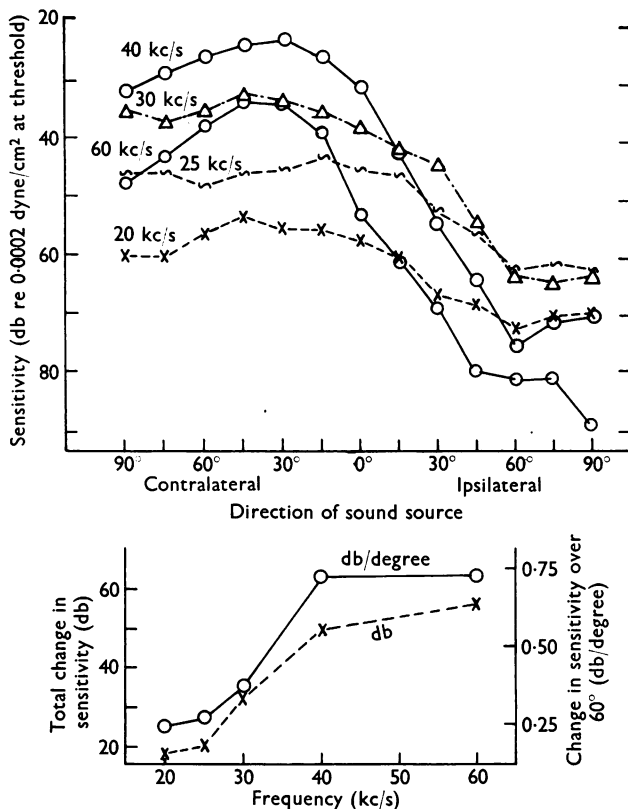


Fig. 1. *Myotis*. Above; directionality as a function of frequency. A single experiment showing the sensitivity of N_4 at different frequencies as a function of angle relative to the bat's head on the horizontal plane. Below: the total difference in sensitivity between angles of minimal and maximal sensitivity is shown for each frequency, as is the rate of change in sensitivity with angle over the 60° of arc in which sensitivity changed most rapidly at each frequency.

the bat's lowest sensitivity, with an average of only 0.2 db change in threshold per degree over the steepest 60° of the curve. At 40–60 kc/s, however, the total difference in threshold is of the order of 50–60 db, and the average change per degree is 0.7–0.75 db. This is typical of results from *Myotis*. Those from the long-eared bat *Plecotus* are very similar,

except that the break between low and high frequencies, slight and great directionality, comes between 40 and 50 kc/s rather than between 25 and 40 kc/s, as is observed in *Myotis*. Averages of all experiments in which this behaviour of N_4 was specifically studied in either species are shown in Fig. 2.

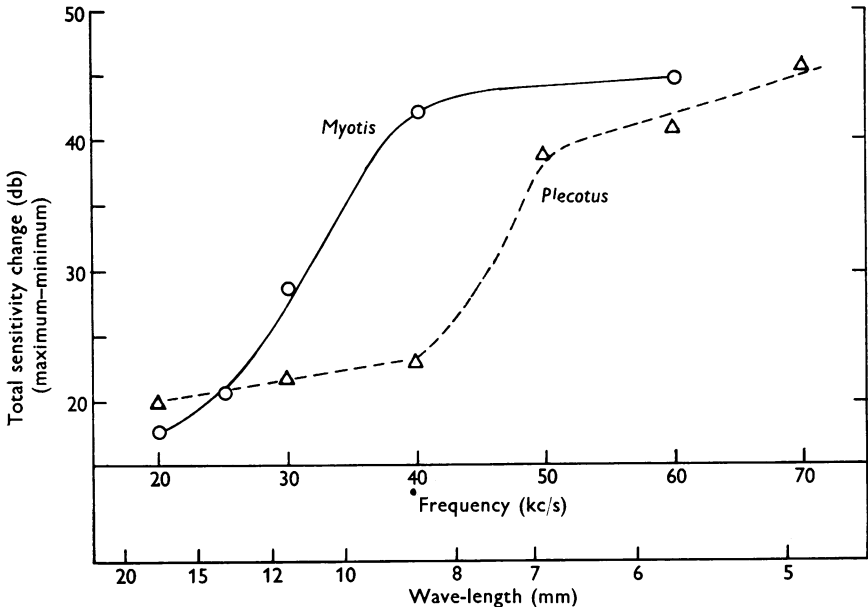


Fig. 2. Averages of all relevant experiments showing the total difference in sensitivity between angles of maximal and minimal sensitivity at different frequencies.

Table 1 summarizes directionality results for the two species at N_1 (recorded in the region of the cochlear nucleus) and N_4 (recorded in the colliculus). All measurements shown are the average of 10 or more records, and in each case for which sufficient data are available the difference between tone pips of high frequency and those of low frequency or clicks (which give results almost identical to those for low-frequency tone pips) have been shown. In both species the angle of greatest sensitivity changes from approximately 15° ipsilateral for N_1 to 30° contralateral for N_4 , reflecting the crossing of afferent auditory fibres from the ipsilateral ear to the contralateral colliculus, and vice versa.

N_1 in both species exhibits almost exactly the same (33 db) average difference in threshold between the angles of greatest and least sensitivity at high frequencies. However, in *Myotis* there is a distinct tendency for minimal sensitivity to be reached nearer the mid line, with the result that

70° contralateral is the average angle of minimal sensitivity, with very little change between 45 and 90°. Since the total change in sensitivity is approximately the same, the rate of change over the steepest 45–60° is greater in *Myotis* (0.48 db/degree averaged over this interval) than in *Plecotus* (0.38 db/degree).

N_4 has been extensively explored, with a total of more than 150 records. As is obvious from Table 1 N_4 is more directional than N_1 . Figure 3 compares the average directionality curves for N_4 in *Myotis* and *Plecotus*,

TABLE 1. Average angular sensitivity characteristics of N_1 and N_4 in *Plecotus* and *Myotis*

	Stimulus frequency (kc/s)	Angle of maximal sensitivity	Angle of minimal sensitivity	Maximal difference in sensitivity (db), with range	Average change in sensitivity over steepest 45–60°, with range (db/degree)
<i>Plecotus</i>					
N_1	20	15–30° i	90° c	20 (15–25)	0.26 (0.11–0.35)
	55–60	15–30° i	90° c	34 (32–38)	0.38 (0.28–0.48)
N_4	20–40	50° c	83° i	23 (6–35)	0.20 (0.05–0.42)
	50–70	27° c	88° i	38 (25–68)	0.43 (0.27–0.73)
<i>Myotis</i>					
N_1	40–60	35° i	70° c	33 (24–52)	0.48 (0.23–0.60)
N_4	Monaural	40° i	75° c	35 (24–43)	0.48 (0.28–0.53)
		to good ear	to good ear		
Binaural	20–30	35° c	70° i	21 (0–39)	0.27 (0–0.42)
	40–60	35° c	75° i	39 (20–68)	0.52 (0.23–0.80)

* i = ipsilateral, c = contralateral.

equated at 0°. Only 'high-frequency' data were used in these average curves, records employing 40 kc/s and higher frequency stimuli in *Myotis*, 50 kc/s and higher in *Plecotus*. Also included in Fig. 3 is the constructed mirror image of each curve, representing sensitivity in the opposite colliculus.

In *Plecotus* maximal sensitivity is at about 30° contralateral for high frequencies and, in what is the first really clear case of frequency-dependency of this feature, at an average 50° contralateral for low frequencies. The point of minimal sensitivity is again near 90° ipsilateral, but is brought to an average of slightly less than this by occasional minima at 60–75°. Most interesting is the total change in sensitivity. Here the average (38 db) is considerably greater than the extremes for man or cats and as great as the most extreme value observed for N_1 . In *Myotis* the direction of maximal sensitivity is further lateral, between 30 and 45° contralateral, and most of the loss in sensitivity to sound arriving ipsilaterally has occurred by 60° ipsilateral. There tends to be less loss of sensitivity at far contralateral angles than in *Plecotus*. The difference in sensitivity, from most to least sensitive directions, is 39 db, essentially the same as in

Plecotus, but again the rate of change over the steepest 60° of the curve is greater, about 0.5 db/degree as compared with just over 0.4 db/degree.

In fourteen experiments the directionality of N_4 was measured with micro-electrodes. Being the sign of activity of a relatively small number of elements, these potentials tended to be somewhat more variable than the N_4 measured with gross electrodes. In no respect, however, did they show qualitative differences. All were most sensitive contralaterally, and the average difference between the angles of greatest and least sensitivity was 37 db. More peripheral evoked potentials (N_1 – N_3) were not studied systematically in this respect.

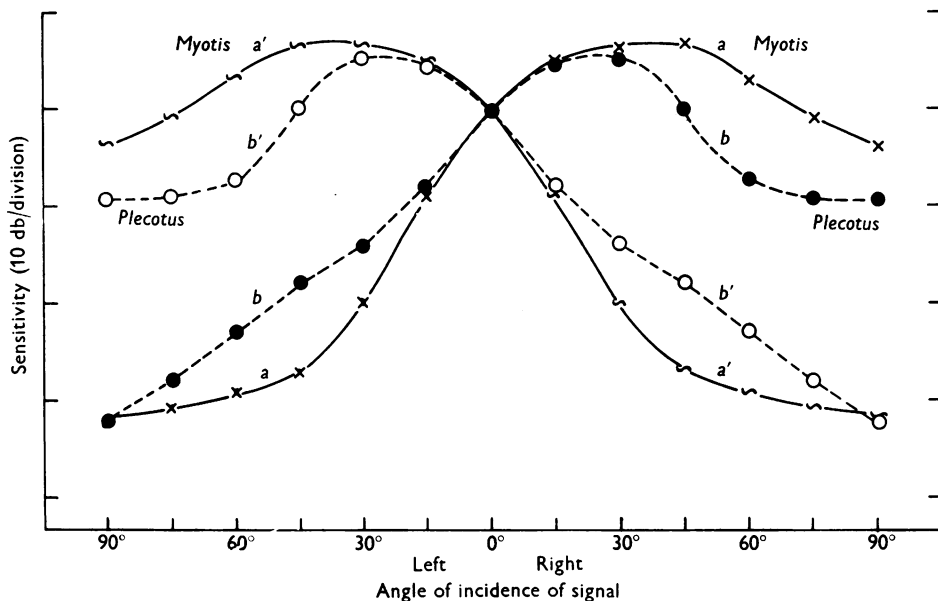


Fig. 3. Average 'directionality' curves for *Myotis* and *Plecotus*, showing relative sensitivity of N_4 as a function of angle of incidence of a signal on the horizontal plane. Only signals of 40 kc/s or higher frequency were used in determining the *Myotis* curve, only signals of 50 kc/s or higher frequency in determining the *Plecotus* curve. *a*, *b* = average, shown for left colliculus; *a'*, *b'* = right colliculus, constructed mirror-image of *a*, *b*. Left half, *a*, *b* degrees ipsilateral, *a'*, *b'* degrees contralateral: right half, *a*, *b* degrees contralateral, *a'*, *b'* degrees ipsilateral.

Individuals of both species have exhibited differences in sensitivity as great as 60–70 db, corresponding to rates of change as high as 0.8 db/degree averaged over 60°, while approximately 15% (12 of 85) show a 50 db or greater angular difference in threshold. (In the light of these findings it is puzzling to read in recent work of Wever & Vernon (1961) the report that the *Myotis* cochlear microphonic is only slightly directional, showing

a 5–7 db loss in sensitivity with 60° displacement of a sound source on either side of the most sensitive angle, and only about 23 db loss when the sound came from behind the bat. Clearly the behaviour of the microphonic must be further pursued.)

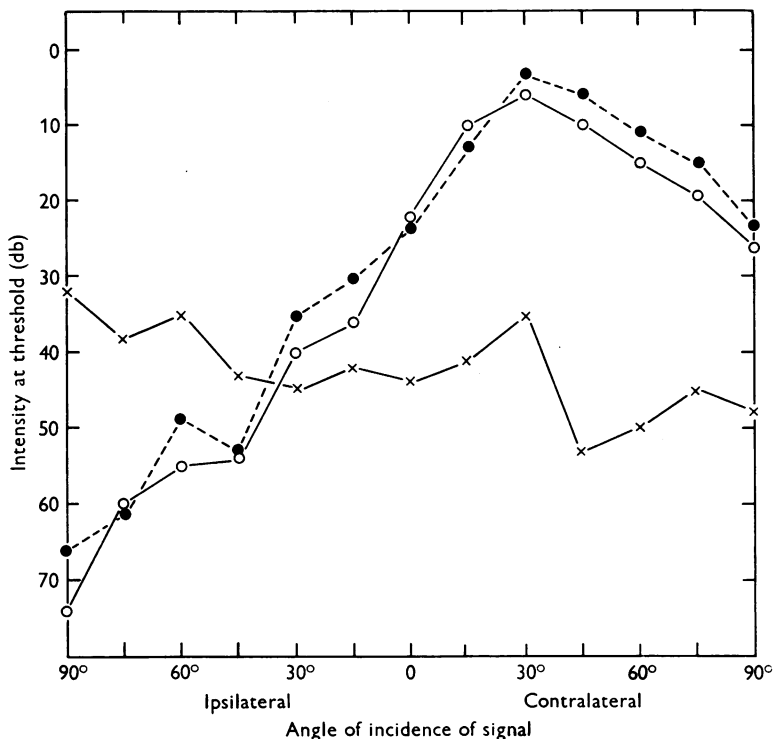


Fig. 4. An individual experiment with an unusually 'directional' N_4 response in *Plecotus* (left colliculus), showing the effect of shielding the contralateral ear with a tightly fitted piece of Plasticene. Although sensitivity to sound arriving contralaterally was much reduced, ipsilateral sensitivity was enhanced by as much as 30 or 40 db. ○ normal; ● control; × right ear 'shielded'.

Binaural interactions. The fact that N_4 is more sensitive than N_1 to change in stimulus angle suggests considerable binaural interaction. As a control, experiments were done to determine how N_4 behaves in a monaural preparation. The first and easiest approach to this was to shield the sound from one ear by surrounding the pinna with a heavy sheet of Plasticene or by enclosing it in a tightly fitting paper cup. When this was done in *Plecotus*, and less extensively in *Myotis*, the results were remarkably uniform and clear-cut (see Fig. 4). If the ipsilateral ear was thus shielded, there was no significant change in directionality. When the contralateral ear was acoustically blocked in this way, the response, as expected, was

much depressed for sound arriving from that side (20–30 db on the average). But in the latter case, when the sound source was shifted to the ipsilateral side, sensitivity was *enhanced*: the sensitivity to sounds from the ipsilateral side increased when the contralateral ear was shielded. In *Plecotus* this increase ranged from 11 to 40 db (average 19 db) at 50 kc/s and higher frequencies and from 7 to 19 db at lower frequencies (average 10 db). The first sign of increased sensitivity appeared, usually, at about 45° ipsilateral.

It is conceivable that the shield, as a physical change in the environment, was somehow causing an increase in sound intensity to one of the ears when sound came from an ipsilateral position. To examine this possibility several procedures were employed. Plugging the contralateral ear with dry or water-saturated cotton-wool produced similar but smaller changes in ipsilateral sensitivity. When more thorough but less easily reversible ear plugging with parlodion was tried, or when the middle ear ossicles were destroyed, sensitivity on the contralateral (deafened) side was sharply reduced (40–50 db), and the preparation was most sensitive on the ipsilateral side. Furthermore, the resulting curve had approximately the same shape as the normal directionality curve but was reversed and lowered in sensitivity. It is apparent that the electrode was in this case recording the comparatively minor part of the input of the colliculus which originated ipsilaterally and which would be mixed with contralateral input from the other ear in the normal, binaural preparation. What is most interesting is that this ipsilateral sensitivity was greater, at the angles 30–90° ipsilateral, than was observed in the binaural animal, a discrepancy which could be verified before deafening or after ‘unplugging’ the ear, and which agreed quantitatively with the measurements made of shielded ears. A characteristic example of these relationships in *Myotis* is shown in Fig. 5. At N_1 , which was quite carefully examined, no such phenomenon was observed. Thus by some neural interaction in the normal binaural animal, the ipsilateral component of the input to a colliculus is inhibited to the point of being undetectable. The fact that the extent of ‘disinhibition’ due to ‘complete’ plugging, or destruction of the middle ear apparatus, is apparently no greater than that measured in the ‘shielded’ preparations suggests that only partial reduction in sound pressure at the contralateral ear is sufficient.

One additional feature that has emerged from experiments with ‘one-eared’ preparations is that the monaural N_4 is apparently little if any more directional than N_1 , and is therefore 5–10 db less directional than the binaural N_4 . Thus, if a sound is arriving from an angle ipsilateral to the colliculus in which the recording is being done, the sensitivity is slightly greater if only one ear is intact than if both ears are intact. Apparently when both ears send afferents to the colliculus under these stimulus con-

ditions, i.e. when most of the sound energy is going to the ipsilateral ear, not only does the contralateral ear inhibit the ipsilateral ear as shown above, but also the ipsilateral ear must somewhat reduce the input from the contralateral ear. Both forms of interaction result in 'sharper' directionality at either colliculus, and increase the difference in relative excitation levels of the two. Figure 6 compares the average directionality curves of N_1 and monaural N_4 with that of the binaural N_4 in all *Myotis* tested at frequencies of 40 kc/s or higher. Both N_1 and monaural N_4 are arbitrarily equated with the binaural N_4 at its most sensitive angle.

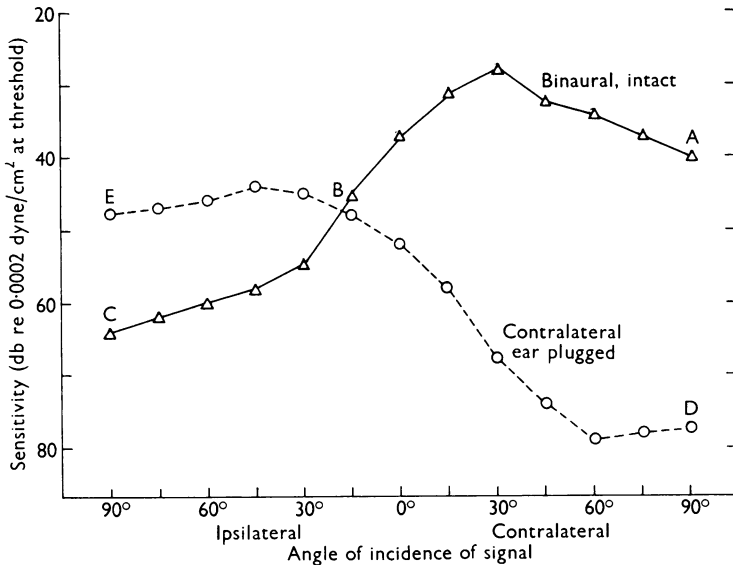


Fig. 5. *Myotis*. N_4 directionality; left posterior colliculus, 50 kc/s. An individual experiment demonstrating the effects of binaural interaction in the binaural preparation. Curve ABC was observed in the binaural animal. When the contralateral ear was plugged (with cotton and parlodion) curve DBE was observed. This apparently represents input to the left colliculus from the ipsilateral (left) cochlea. If this were simply added to input from the contralateral cochlea in the two-eared preparation, directionality of the form ABE would be expected. Since ABC was observed, the ipsilateral input represented by the area EBC must somehow have been inhibited by the contralateral input.

Single-unit recordings

A small number of single units were tested for angular sensitivity. The directionality curves of some of these are included in Fig. 7. Several closely resembled the evoked potential curve. Unit 16, located in the superior olive, was such an example. Others showed total differences in sensitivity of up to 75 db. Most of the units shown in this figure clearly

reflected neural interactions limiting sensitivity to sounds coming from a very restricted direction. Units 5.5, 7.7, and 8.7 all showed unusual reduction in sensitivity to sounds coming from contralateral angles, and, especially in unit 8.7, a very sharp loss in sensitivity between 0° and 45° ipsilateral. Units such as these, favouring sounds near 0° , were relatively numerous.

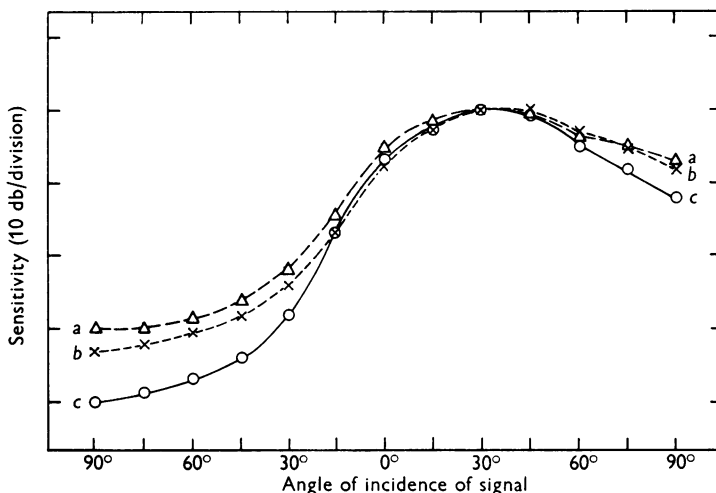


Fig. 6. Averages of *Myotis* directionality curves made with high-frequency signals at the levels of N_1 , N_4 in the normal binaural preparation, and N_4 when one ear was plugged. $a = N_1$; $b = \text{monaural } N_4$; $c = \text{binaural } N_4$.

Most sharply restricted, however, were units such as unit 4.3 and unit 8 of Fig. 7. Unit 4.3 responded only at angles between 10° ipsilateral and 55° contralateral; a 15–20 db more intense stimulus (the maximal intensity available), arriving from 5° further lateral in either direction, was ineffective. Over these 5° arcs, therefore, the drop in sensitivity was a minimum of 3 db/degree. Unit 8 was lost in the course of making its curve, but the contralateral angles were carefully measured and re-measured, particularly the remarkable disappearance of all sensitivity between 68 and 75° . The rise in threshold over this small arc was a minimum of 62 db/ 7° , or approximately 9 db/degree. All the collicular units tested were more sensitive to contralateral signals than to ipsilateral ones; but one unit just below the colliculus (2100μ) responded best to sounds arriving from ipsilateral angles. Six cells recorded at greater depth were all contralateral.

Erulkar (1959) found, in cells of the cat's posterior colliculus, that changes in signal direction resulted in changes in latency of firing of the unit. This is found to be true in the present experiments only if the signal intensity

is kept constant, in which case latency changes with change in sensitivity. If latency is determined for *threshold* responses to sound from different angles, the latency is normally constant.

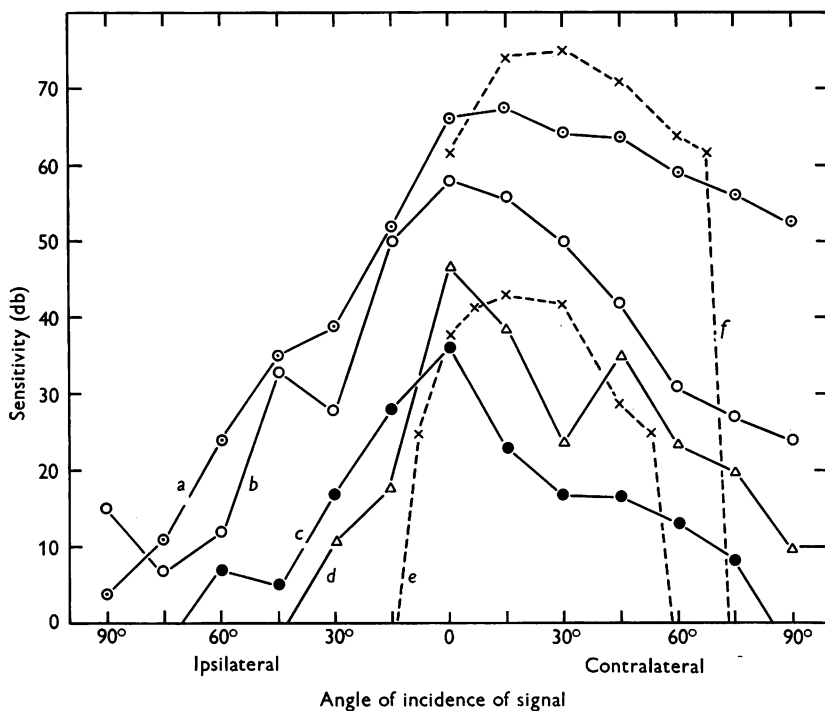


Fig. 7. Directionality curves of single units in *Myotis*

	Unit	Depth (μ)	kc/s
a	16	3200	55
b	5.7	1140	65
c	7.7	1540	110
d	8.7	1740	100
e	4.3	860	55
f	8	1600	59

DISCUSSION

Theoretically at a bat's disposal for location there are four types of binaural comparison: differences in phase, arrival time and intensity, and, because of the frequency-modulated nature of the orientation cries, a difference in simultaneously measured frequency at the two ears. In human beings the first three of these may all be used under certain conditions. Phase is operative as a source of information at frequencies up to about 1500 or 3000 c/s, above which the auditory nerve cells can no longer fire in synchrony, and wave-lengths become so small that a given phase

difference could represent more than one direction (Licklider, 1951; von Békésy, 1960). Differences in arrival time of a sound of any frequency can be used for location if greater than about 10 μ sec (Klumpp & Eady, 1956; Mills, 1958, 1960), at which point the deviation from the mid line is first detectable. As the arrival time difference is increased to about 2 msec the sound subjectively appears to move gradually to 90° on the side of the leading sound. These effects can be duplicated or counteracted by producing a difference in intensity at the two ears, when the sound appears to come from the side of the louder stimulus, with the degree of 'lateralization' a function of the difference in intensity (Fedderson, Sandel, Teas & Jeffress, 1957; David, Guttman & von Bergeijk, 1959; Deatherage & Hirsch, 1959; Moushegian & Jeffress, 1959; Harris, 1960). For fairly loud simultaneous stimuli, 1 db is found to be the intensity difference resulting in the first clear-cut deviation from the mid line, while larger differences are necessary at lower intensities (cf. Licklider, 1951). A difference of 15 db is cited by Wallach, Newman & Rosenzweig (1949) as being sufficient to overcome the precedence effect of a maximally effective arrival-time difference, though under ideal conditions (very high frequencies and particular angles of incidence to the head) physical sound shadows of up to 30 db may be created in man. At frequencies above about 3 kc/s, man appears to rely predominantly on binaural differences in intensity for localization.

Neural correlates of these binaural comparisons have been studied extensively in cats. Galambos, Schwartzkopff & Rupert (1959) have described single cells in the superior olive that were excited or depressed, depending on the arrival time of a sound at the two ears. Rosenzweig (1951) found that the cortical evoked potential response to a monaural contralateral click was usually larger than that to an identical ipsilateral click. If the ipsilateral click was increased 10 db in intensity, in one experiment cited, the responses became roughly equivalent. Wigand (1960) found certain cats for which a 30 db decrease in intensity of a contralateral sound was necessary for equality with an ipsilateral sound. Keidel, Keidel & Wigand (1961), on the other hand, reported that the contralateral input to the cortex is dominant only at intermediate intensities (20–50 db above threshold), while nearer threshold and at very high intensities the discrepancy vanished.

In bats phase differences at the two ears probably become ambiguous at frequencies well below those of the orientation sounds and their echoes. One-to-one volleying of auditory cells to every cycle of a sound probably fails above 2–5 kc/s, even in the bat. Pure tones of this frequency range elicit only an onset response, although synchronized N_1 responses are seen to clicks at repetition rates up to 2500/sec (Grinnell, 1963*b*). If phase

shifts greater than one wave-length must be avoided, frequencies above 20–30 kc/s would theoretically not serve the bat. On the other hand, the bat brain could perhaps overcome ambiguities due to the presence of several interference nulls by comparing the patterns for several different frequencies. The operation then comes to be the comparison of relative intensities of different frequencies at the two ears.

It seems improbable that difference in arrival time of the pulse envelope is useful for localization. In the species studied, with approximate interaural distances of 1.5 cm, 10 μ sec accuracy would correspond to a minimal detectable change of angle of about 20° , which is entirely insufficient to explain localization. If bats were of an order of magnitude more accurate than man, capable of resolving 1 μ sec time differences, they would theoretically be able to distinguish a 1.5° deviation from the mid line at a distance much greater than the interaural distance. This would probably give sufficient accuracy to explain localization in the horizontal plane. There is no evidence, however, that a bat can detect so small a time difference.

The instantaneous frequency difference at the two ears might be thought to provide its information about signal direction in one of two ways. It might be heard as a difference tone, which, since the cry is sweeping at rates up to 50 kc/msec, would reach frequencies as high as 1 kc/s for the most lateral angles. Since the echo is only approximately one msec long, such a difference tone could manifest itself only as one cycle of a 1 kc/s tone. This would be mixed with the original amplitude modulation of the emitted cry, and the distortions of this modulation due to selective reflexion of certain frequencies in the cry. The second possible type of comparison is literally the simultaneous measurement of frequency at the two ears, perhaps by populations of cells having bilateral input from the parts of both cochleas responding to exactly the same frequency. This is actually very similar to, if not identical with, the detection of an arrival time difference.

A difference in intensity at the two ears is the fourth possible source of information concerning signal angle and one which is probably of great, if not greatest, importance. In the experiments described above, the sound source, as it moved around the bat's head, produced signals which changed both in arrival time and intensity at the two ears. The net result was a very directional sensitivity pattern as measured at either posterior colliculus. Most of this difference in threshold was shown to be due to intensity, since N_1 , before any sort of time comparison could be performed, was nearly as directional. Moreover, the observed depression of ipsilateral input to a given colliculus took place despite the fact that a sound arriving from the ipsilateral side reached the ipsilateral ear at higher amplitude and up to 40 or 50 μ sec earlier than the contralateral ear. For the contra-

lateral input to inhibit the ipsilateral, this interval must be overcome; but it is short enough, compared with synaptic delay or even conduction time, so that this requires no great stretch of the imagination. Indeed, recently Wigand (1960) has reported a very similar phenomenon of *Einhölung*, or overtaking, over much larger time intervals in the auditory cortex of cats.

Whatever the cellular mechanism, it is clear that by means of binaural interaction the considerable directionality of either auditory nerve response in the bat is made greater still at the level of the posterior colliculus. Not only does contralateral input inhibit ipsilateral input, but it also appears that when the signal arrives from an ipsilateral angle the input from the strongly activated ipsilateral cochlea slightly inhibits contralateral input. The net result of this heightened directional sensitivity is the average directionality curve shown in Fig. 3. Reference to Table 1 shows that for 45–60° across the mid line and toward 90° ipsilateral, N_4 in the two colliculi was rising or dropping in sensitivity at an average of about 0.5 db/degree, and up to 0.8 db/degree in certain preparations. Within either colliculus there is doubtless a population of cells which, seen alone, would behave like that of the other colliculus, so that a full analysis could be made within a single colliculus. But it is reasonable to assume that a bat can compare the excitation levels of the two colliculi (or the equivalent operation at some different neural level). The angle of incidence could theoretically be very easily calculated from the difference between the two. This would both obviate the necessity of knowing the absolute intensity of a signal and would sharpen the discriminations twofold. Thus a change of 2°, where the average slope between 15° contralateral and 30–45° ipsilateral is 0.5 db/degree, would increase the excitation of one colliculus by 1 db and decrease the other by the same amount, at least in the 30° sector straight ahead. The result would be a 2 db change from the original condition. In cases of maximal recorded change of N_4 with angle, a 2° change could create a relative difference of more than 3 db. Consequently, if, as seems true (Grinnell, 1963*a*), the N_4 response is sensitive to changes of 0.5 db, a 1–2° change in direction of a sound should be easily detectable. Very accurate location in the horizontal plane may thus be postulated on the basis of the evoked potential data already on hand.

Single units frequently show even sharper dependence on angle of incidence of a sound (Fig. 7). Some of these provide the clearest examples seen of interaction. Since few cells were tested for directionality the few that have been found must be regarded as samples of larger populations. Some of these were capable of angular discriminations much finer than that indicated by the evoked potentials. It seems not unlikely, in fact, that there exist separate populations with sensitivity changes as great as that of unit 8 of Fig. 7 over small arcs in all directions. If a bat is able to use

the information present in such populations, sensitivity changes as great as 5–10 db/degree would be expected. This acuity, coupled with the probable ability to discriminate intensity changes of 0.5 db or less, indicates sensitivity to angular changes of less than 0.5 degree.

There are two major differences in directionality between *Myotis* and *Plecotus*: (1) Either ear (or colliculus) sharply increases in directionality between 25 and 40 kc/s in *Myotis*, but between 40 and 50 kc/s in *Plecotus*; and (2) most of the loss of sensitivity with changes in angle of incidence of the signal occurs between 30° contralateral and 60–75° ipsilateral in *Myotis*, whereas it continues smoothly to 90° ipsilateral in *Plecotus*. These differences have been observed at the level of N_1 as well as at higher centres, so they probably reflect either the performance of the cochlea or, more likely, differences in the external ear structure of the two species. If the latter, it is puzzling that the large pinnae of *Plecotus* are not more directional at lower frequencies than are the smaller ears of *Myotis*. It may well be that *Plecotus* get most of their location information from the frequencies of the second harmonic, which are more affected by change in angle of incidence than any frequencies in the fundamental. *Myotis*, on the other hand, are very directional throughout the frequency range of their cruising pulses, but during pursuit the 'buzz' comes to sweep from frequencies at which it is much less directional (20–25 kc/s). The resulting loss of localization acuity may well be counteracted by the larger angle subtended by the target at close range.

Localization in the vertical plane, a much more difficult task for human beings using sound, is fully as important to bats as localization in the horizontal plane. Investigations of possible neural mechanisms of vertical localization will be discussed in a later paper, along with studies of the role played by structures of the external ear in creating differences in sensitivity at different angles.

SUMMARY

1. The effects of angle of incidence of a signal on evoked potential and single unit responses were studied in the auditory nerve (N_1) and the posterior colliculus (N_4) of *Myotis l. lucifugus* and *Plecotus townsendii*. In certain preparations at high frequencies one colliculus was observed to respond to a signal 60–70 db fainter than was necessary to stimulate the other from the same angle of incidence.

2. The 'directionality', or change of threshold with change in angle of incidence of the evoked potentials is dependent on signal frequency. It increases sharply with increase in frequency. *Myotis* are about 15–18 db more directional at 40 kc/s and higher frequencies than at 30 kc/s or below, while *Plecotus* become about 15 db more directional between 40 and 50 kc/s.

3. *Plecotus* tends to lose sensitivity more uniformly than does *Myotis* from the angle of greatest sensitivity, 30° on the contralateral side, to the angle of least sensitivity, 90° on the ipsilateral side. Hence the latter averages over 0.5 db/degree change in threshold with change in angle over the $45\text{--}60^\circ$ of steepest slope, whereas *Plecotus* averages only slightly over 0.4 db/degree.

4. Despite the mixing of input from both ears to the colliculus, N_4 is more 'directional' than N_1 . The average difference in threshold for N_1 between angles of greatest and least sensitivity is about 34 db in both species; for N_4 the average difference is 38–40 db with extremes up to 68 db.

5. Two forms of binaural interaction appear to be causing this enhancement of angular sensitivity:

(a) In one type the contralateral afferent input inhibits the ipsilateral, reducing sensitivity of N_4 to sound coming from the ipsilateral side by an average of nearly 20 db at $75\text{--}90^\circ$ ipsilateral.

(b) The second type manifests itself in greater directionality for the binaural N_4 than for a monaural N_4 or N_1 . This suggests that in the binaural condition in which a sound is arriving ipsilaterally, the large signal from the ipsilateral cochlea, although it does not increase the evoked potential in the colliculus under study, somehow inhibits simultaneous input from the contralateral cochlea to this colliculus by an average of 5–10 db.

6. These 'sharpened' directionality curves, taken with the apparent ability to detect intensity differences of 0.5 db or less, would theoretically permit localization to within 1 or 2° in the horizontal plane.

7. Single units are frequently extremely sensitive to small changes in signal angle (changes in threshold of up to 9 db/degree have been observed) and may be restricted to very small sectors from which they can be successfully stimulated. Populations of cells with such extreme angular sensitivity may make directional localization even more accurate than is indicated by the evoked potentials.

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