CODING OF DIRECTIONAL INFORMATION BY SINGLE NEURONES IN THE S-SEGMENT OF THE FM BAT, *MYOTIS LUCIFUGUS*

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SUMMARY

1. Response parameters of S-segment neurones of the FM bat *Myotis lucifugus* were measured as a sound was delivered from different azimuthal angles around the animal's head.

2. The response parameters investigated were the amplitude and threshold of the evoked potential (N_3) of the S-segment, together with the threshold, latency and number of impulses (per stimulus pulse) of single units.

3. All the neurones studied had their lowest thresholds either at 20–40° contralateral, or 20–40° ipsilateral or at the front (0°).

4. The amplitude of the sound affected the relationship between stimulus direction and the amplitude of a non-monotonic N_3, and the relationship between stimulus direction and the number of impulses of a non-monotonic single unit. It had no such effects with a monotonic N_3 and a monotonic single unit.

5. From a study of N_3 amplitudes and numbers of impulses of single neurones, it appeared that an azimuthal difference as small as 3° could be easily coded at a 95% correct level with stimuli presented at around 20° ipsilateral, 20° contralateral, and at the front.

6. The inter-aural pressure difference (IPD), which is considered an essential cue for echolocation in *Myotis* (Shimozawa *et al.* 1974), changed linearly with angle from 0 to 40° lateral at a rate of 0·4 dB/degree for sounds between 33·5 and 49·0 kHz.

7. Assuming the just-detectable IPD to be 0·5 dB (as in man), the minimum detectable azimuthal difference of *Myotis* around the median plane would be 1·25°.

INTRODUCTION

Most mammals obtain spatial information about the environment through their sense of vision. Bats of the suborder Microchiroptera, in contrast, obtain this information through their sense of hearing. As originally shown by Griffin and his co-workers (1941, 1958), bats can detect, track and evaluate targets in their acoustic space by

emitting sounds and listening to the returning echoes. Griffin (1944) called this process echolocation.

Bats locate the source of an echo in the way that all vertebrates locate the source of a sound: by binaural comparison. The interaural time and pressure differences are the two main cues in sound localization (van Bergeijk, 1962). The classical view is that interaural times are important for localizing low-frequency sounds whereas interaural pressure differences are utilized for localizing sounds above 3 kHz (Stevens & Newman, 1936).

Since bats have a very small interaural distance and use ultrasonic signals in echolocation, most investigators believe that interaural pressures are the main cues which bats use for sound localization. Indeed, this is indicated by the relative sizes of the nuclear regions in the superior olivary complex (SOC), which is the first region in the brain where the inputs from the two ears converge (Papez, 1930; Rasmussen, 1946; Stotler, 1953). The S-segment (lateral superior olive), which has been shown to be sensitive to the interaural pressure difference, is very prominent in *Myotis lucifugus*, but the accessory nucleus (medial superior olive) which processes interaural time differences is very small or absent (Irving & Harrison, 1967; Masterton & Diamond, 1967; Masterton, 1974). The proportion of the SOC occupied by these nuclei (and others) is different in bats than in cats or dogs (Irving & Harrison, 1967; Goldberg & Brown, 1968; Harrison & Feldman, 1970).

Over the past decade there have been a number of studies concerned with the directionality of single units and evoked potentials in the cochlear nucleus and inferior colliculus of bats (Grinnell, 1963b; Suga, 1964; Grinnell & Grinnell, 1965; Neuweiler, 1970; Grinnell & Hagiwara, 1972; Shimozawa *et al.* 1974; Schlegel, 1977). However, there have been no studies dealing with the directional properties of neurones in the S-segment. The purpose of this study is to investigate the directional sensitivity of S-segment neurones in order to better understand how the auditory system of a bat processes directional information.

MATERIALS AND METHODS

Twenty-eight *Myotis lucifugus* (weighing 7–12 g) were anaesthetized for surgery with Nembutal (45 mg/kg of body weight). Using a method described previously (Jen, 1978), the flat head of a 1·8 cm nail was glued onto the bat's exposed skull with Eastman 910 and dental cement. The animal was then secured onto a small cross-like metal plate and its head was immobilized by fixing the shank of the nail into a metal rod with a set screw. After a tracheotomy was performed, those parts of the basioccipital and basisphenoid bones which overlay the ventral aspect of the brain stem were exposed. A small opening was made in the bone, then a 3 M-KCl micro-pipette electrode or a tungsten wire electrode was inserted into the brain through the opening.

After the location of the S-segment had been identified by histological examination, it was possible to insert an electrode in this segment by noting the position of the electrode relative to landmarks on the basioccipital bone, and the angle and depth to which the electrode was inserted. The S-segment measures about $370 \times 520 \times 730 \ \mu m^3$ as estimated from stained sections.
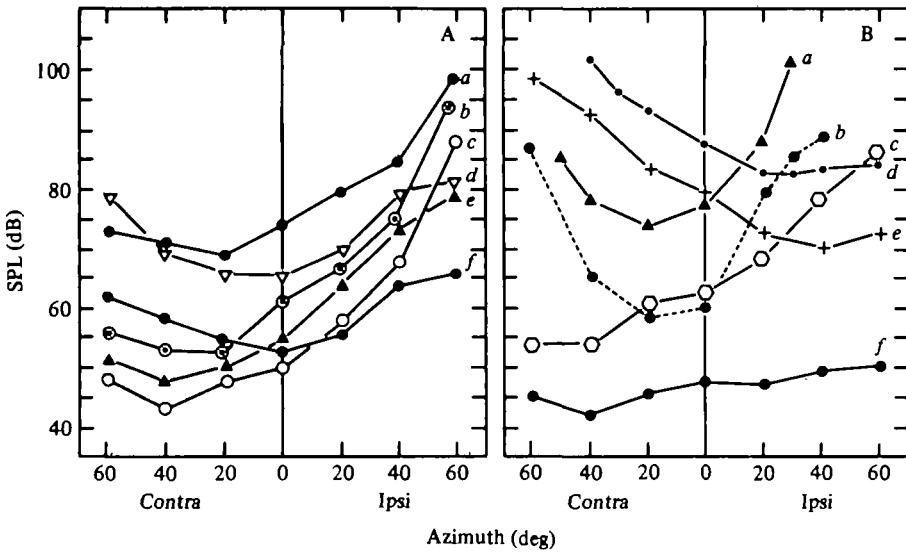
Fig. 1. Relationship between stimulus direction and threshold of (A) six N_3 potentials and (B) six single units. Best frequencies (kHz) in A were 53·6 (*a*), 48·2 (*b*), 41·0 (*c*), 34·0 (*d*), 41·5 (*e*), 44·8 (*f*). In B they were 80·8 (*a*), 37·5 (*b*), 76·2 (*c*), 73·4 (*d*), 37·5 (*e*), 65·6 (*f*). Contra = contralateral; Ipsi = ipsilateral.

A condenser loudspeaker (38 mm in diameter) was mounted on the top of a wooden bar that could be moved around the bat's head. The distance between the loudspeaker and the animal's ears was 62 cm. Neural responses were recorded in an electrically shielded chamber, the inner walls and ceiling of which were covered with convoluted polyurethane foam to reduce echoes. The temperature of the chamber was kept between 35 and 38 °C. The stimulus was a tone burst of 40 ms duration and 0·5 ms rise and decay times. Tone frequency was chosen to be that frequency which, when delivered at 0° (in front of the bat's head), resulted in the lowest threshold for the measured response. It is here termed the best frequency, BF.

Coding of stimulus direction by the S-segment was studied by delivering the stimulus at different angles around the bat's head while measuring the threshold, latency and amplitude of the evoked potential of the S-segment, N_3 (Grinnell & Hagiwara, 1972; Suga & Shimozawa, 1974; Jen, 1978), and the threshold, latency and number of impulses of single unit activity. Unless otherwise stated, the stimulus was presented from 60°, 40° and 20° contralateral, 0° (in front of the bat), and 20°, 40° and 60° ipsilateral.

RESULTS

Directional sensitivity of S-segment neurones

(*a*) *Effect of stimulus direction upon N_3 threshold.* The threshold of the N_3 response was defined as the minimum stimulus level which evoked 15 μV peak response amplitude. In these experiments, BF's ranged from 38 to 50 kHz.

Among 31 impalements, 28 (90%) showed the lowest thresholds at 20–40° contralateral (Fig. 1 A, *a–c, e*) and the remaining 3 (10%) exhibited the lowest threshold when the sound was delivered in front of the bat's head (Fig. 1 A, *d, f*). For convenience,
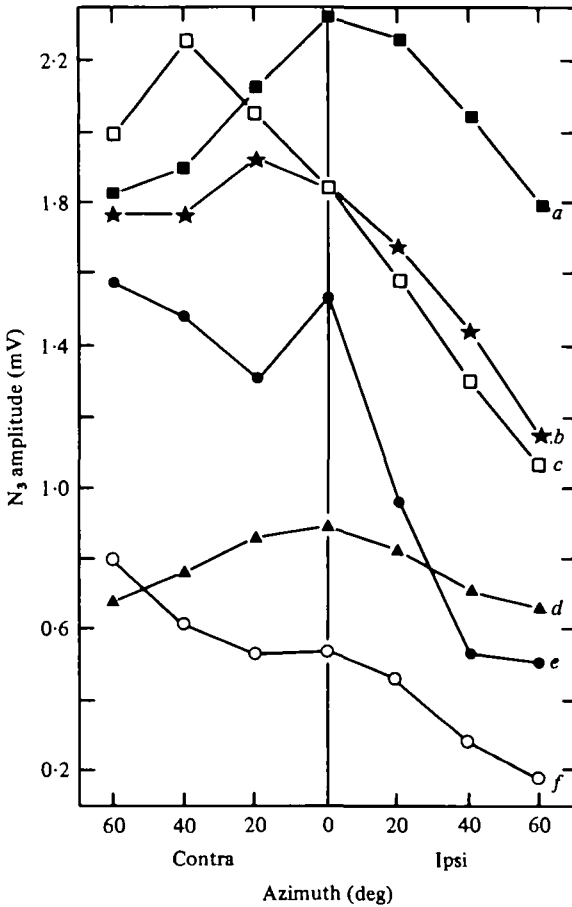
Fig. 2. Relationship between stimulus direction and the amplitude of six representative N_3 potentials (a–f). The best frequency (kHz) and stimulus level (dB SPL) used to obtain these plots were: (a) 33·5, 91; (b) 45, 95; (c) 41, 95; (d) 44·8, 92; (e) 44·1, 94; (f) 41·5, 84.

the azimuthal angle at which the lowest threshold was obtained is called the best angle. Similarly, the angle at which the highest threshold was obtained is called the worst angle. The difference in threshold between the best and worst angles ranged from 16 to 34 dB with an average of 25 dB.

For the group with a best angle between 20° and 40° contralateral, the worst angle was 60° ipsilateral. The rate of change of threshold between best and worst angles was 0·15–0·5 dB/degree with an average of 0·3 dB/degree. This value is greater than that for cochlear nuclear neurones but smaller than that for inferior collicular neurones (Grinnell, 1963b; Suga, 1964). For the front-sensitive group, the average rate of change in the threshold between the front (0°) and the worst angle (60° contralateral or 60° ipsilateral) was 0·22 dB/degree.

(b) *Effect of stimulus direction upon N_3 amplitude.* In these experiments, the BF's of N_3 ranged between 34 and 70 kHz but the majority (75%) were between 38 and 45 kHz. The stimulus amplitude was between 49 and 95 dB SPL which was always more than 10 or 20 dB above the threshold of each investigated N_3 potential.
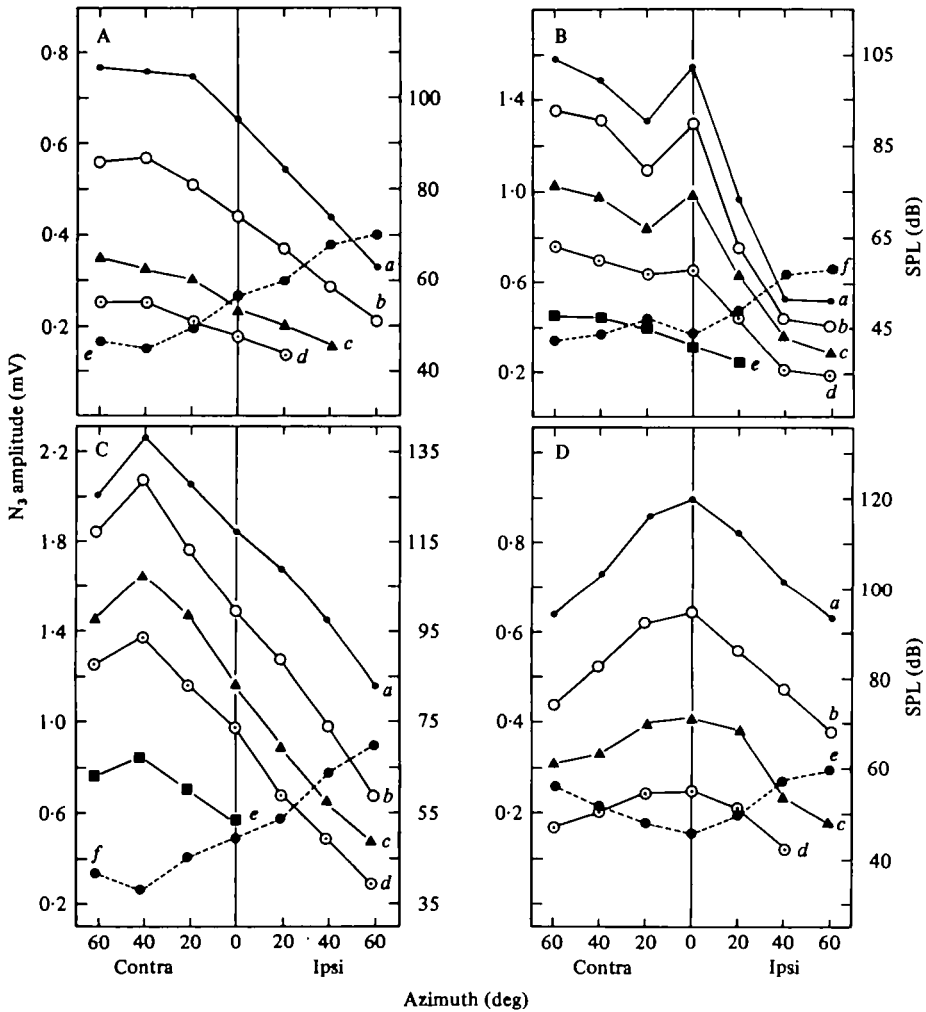
Fig. 3. Relationship of stimulus direction to amplitude (solid lines) and to threshold (dashed lines) for four monotonic N₃ potentials (A–D). For (A), best frequency was 45 kHz, and to study effect on amplitude, stimulus level was 95 (*a*), 85 (*b*), 75 (*c*) and 65 (*d*) dB SPL. For (B), BF was 42 kHz and stimulus level was 94 (*a*) 84 (*b*), 74 (*c*), 64 (*d*), and 54 (*e*) dB SPL. For (C), BF was 41 kHz, stimulus level was 95 (*a*), 85 (*b*), 77 (*c*), 70 (*d*) and 59 (*e*) dB SPL. For (D), BF was 47·7 kHz and stimulus level was 92 (*a*), (*b*), 73 (*c*) and 63 (*d*) dB SPL.

The N₃ potentials fell into three categories. In one, maximum amplitude was observed with contralateral stimulation (89 impalements; 78%) (Fig. 2*b*, *c*, *f*). In the second, the maximum was found with stimulation at the front (20 impalements; 18%) (Fig. 2*a*, *d*). In the third group (5 impalements; 4%), maximum amplitude occurred at two stimulus angles – one contralateral and the other either ipsilateral or at the front (Fig. 2*e*).

Whether stimulus level affected the relationship between stimulus direction and N₃ amplitude depended upon whether amplitude increased monotonically with stimulus level. When there was a monotonic response, stimulus level did not alter the angle at which maximum amplitude was obtained (Fig. 3), and this angle was the same as that
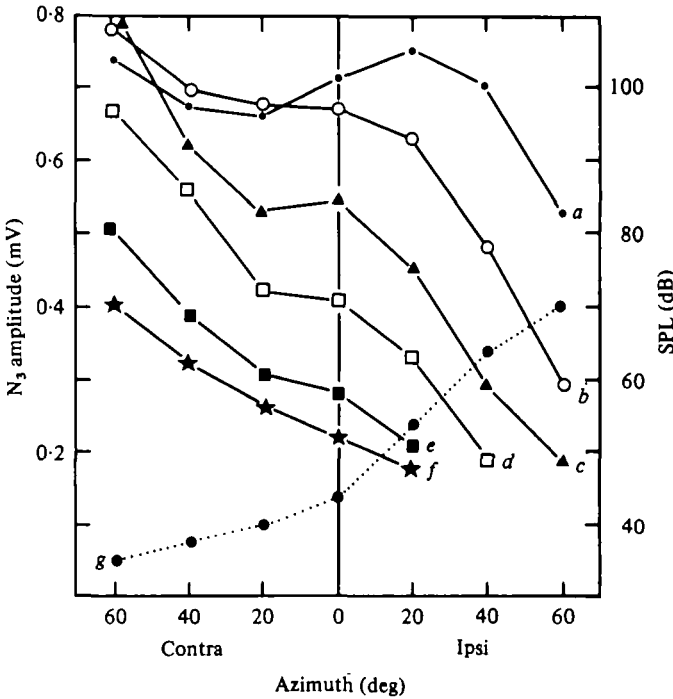
Fig. 4. Relationship of stimulus direction to amplitude (solid lines) and to threshold (dashed lines) for one non-monotonic N_3. BF was 41·5 kHz and stimulus level was 94 (a), 84 (b), 74 (c), 64 (d), 59 (e) and 54 (f) dB SPL.

at which there was the lowest stimulus threshold (Fig. 3, dashed lines). When there was a non-monotonic response, the angle of maximum amplitude was altered by stimulus level (Fig. 4), and this angle was not always the same as the angle with the lowest threshold (Fig. 4, dashed lines).

The shape of the direction:amplitude plots did not show any significant correlation with the value of the BF, unlike in previous studies (Grinnell, 1963b; Shimozawa et al. 1974).

(c) *Effect of stimulus direction upon the threshold of S-segment units.* The threshold of the units was defined as the minimum stimulus level which evoked 0·1–0·2 impulses per stimulus. Among 19 neurones whose BF's were between 40 and 80 kHz, 12 (63%) had their best angles at 20–60° contralateral (Fig. 1B, a–c, f), and 7 (37%) had their best angles at 20–40° ipsilateral (Fig. 1B, d, e). These results are very similar to those obtained from inferior collicular neurones (Grinnell, 1963b).

The difference in threshold between the best and worst angles was 15–35 dB with an average of 25·2 dB. The rate of change in threshold over this range was 0·15–0·56 dB/degree with an average of 0·32 dB/degree.

(d) *Effect of stimulus direction upon latency of S-segment units.* The latency of single units is known to be affected by a change in stimulus amplitude (Grinnell, 1963a; Jen, 1978). Since the amplitude of sound reaching the cochlea varies with the direction of the sound source, the response latency might change as a function of the sound location. To investigate this, sound was delivered from different directions, at th◀
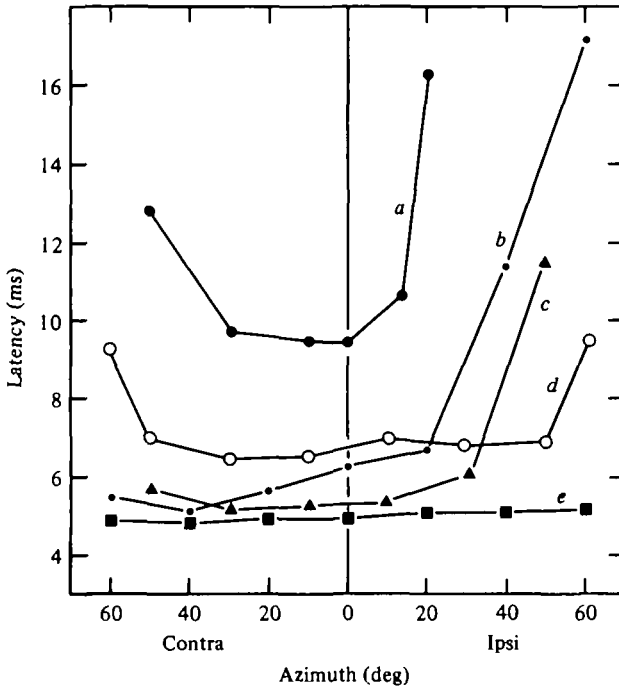
Fig. 5. Relationship between stimulus direction and latency for five representative single units. The frequency (kHz) and stimulus level (dB SPL) used for each measurement were 42·0, 92 (*a*); 61·0, 91 (*b*); 65·6, 95 (*c*); 45·5, 92 (*d*); and 47·5, 92 (*e*).

unit's BF, at the loudest available level, 85–100 dB SPL (depending upon the BF of each investigated unit).

Among the 10 units studied, 2 exhibited their shortest latencies when the sound was presented directly in front of the bat (Fig. 5*a*). Their latencies became very long when measured beyond 10° and 20° ipsilateral or 30° and 40° contralateral. One unit (Fig. 5*e*) maintained almost a constant latency regardless of the position of the loudspeaker. The latency of another unit (Fig. 5*d*) fluctuated only slightly within the range of 50° contralateral and 50° ipsilateral. Beyond that, its latency sharply increased by more than 2 ms. The remaining six units (Fig. 5*b*, *c*) had their shortest latencies increased sharply when the sound was delivered beyond 20° ipsilateral.

Comparable results have been obtained from inferior collicular neurones of a cat (Erulkar, 1959) and a bat (Grinnell, 1963*b*).

(*e*) *Effect of stimulus direction upon the number of impulses of S-segment units.* The stimulus amplitude was always 10–20 dB above the threshold when measured at the front. Among 45 units, the mean number of impulses per stimulus pulse was greatest when stimulation was: (*a*) contralateral (*n* = 15; 33%) (Fig. 6*d*, *e*); (*b*) ipsilateral (*n* = 5; 11%) (Fig. 6*c*); (*c*) at the center (*n* = 10; 22%) (Fig. 6*b*, *g*); (*d*) at two angles (*n* = 11; 25%) (Fig. 6*f*, *h*); (*e*) over a wide range of angles (*n* = 4; 9%) (Fig. 6*a*).

For a monotonic neurone, the angle obtaining maximum discharge was also the angle at which the lowest threshold was observed. For a non-monotonic neurone, the angle of maximum discharge depended on stimulus level. For example, with one non-monotonic neurone (BF = 49·5 kHz), least threshold was obtained at 40°
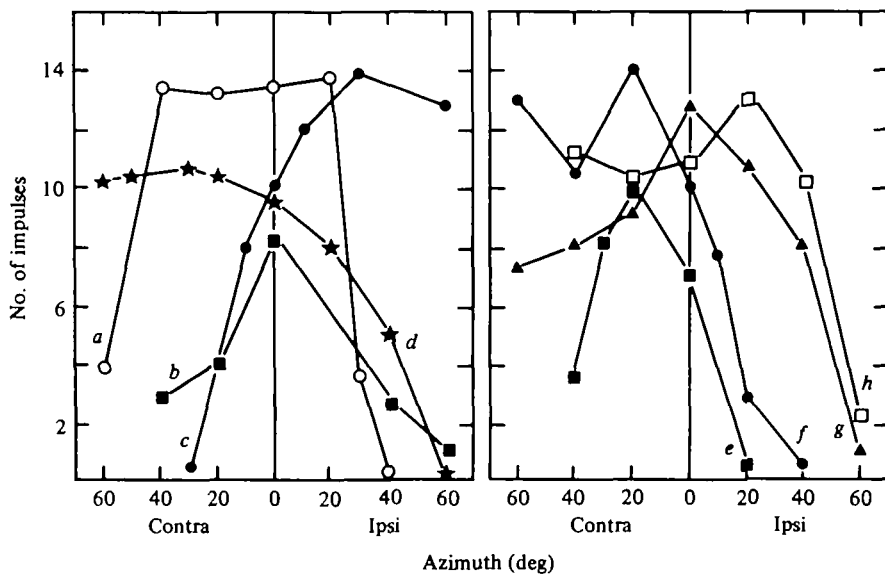
Fig. 6. Relationship between stimulus direction and the number of impulses per stimulus pulse for eight single units. The frequency (kHz) and stimulus amplitude (dB SPL) used for each measurement were: 72·0, 90 (a); 75·0, 91 (b); 80·0, 91 (c); 80·8, 91 (d); 72·4, 90 (e); 60·2, 89 (f); 58·8, 91 (g); and 65·2, 90 (h).
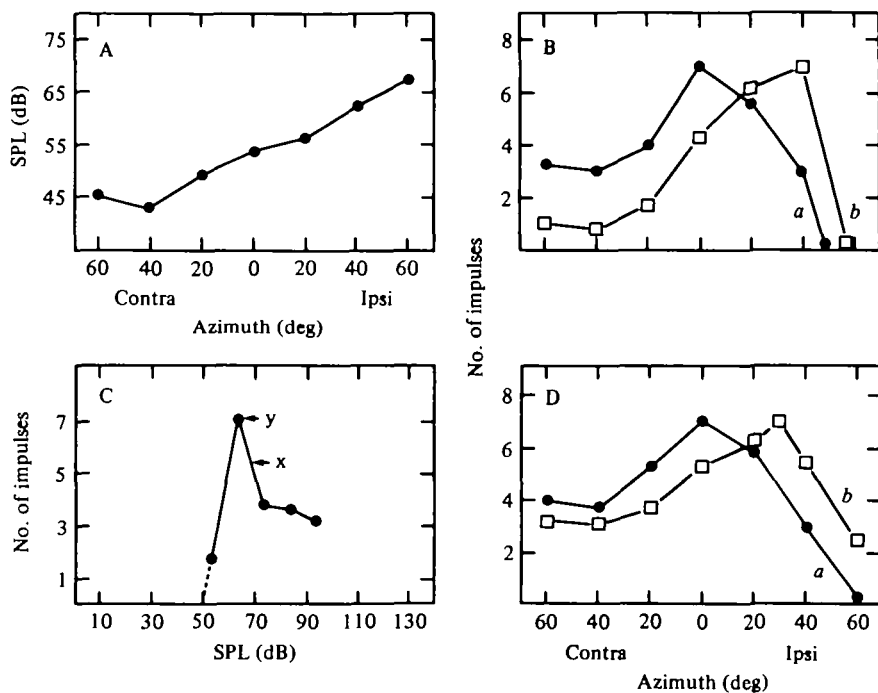

Fig. 7. For one non-monotonic unit (BF = 49·5 kHz), observation was made of relationships between: (A) stimulus direction and threshold; (B) stimulus direction and number of impulses per stimulus pulse at (a) 64 dB; (b) 69 dB; (C) stimulus level and impulse number – (x) ordinates level at 69 dB and (y) level at 64 dB. From (A) and (C) prediction can be made of the relationship between stimulus direction and impulse number (D) at (a) 64 dB and (b) 69 dB. See text.
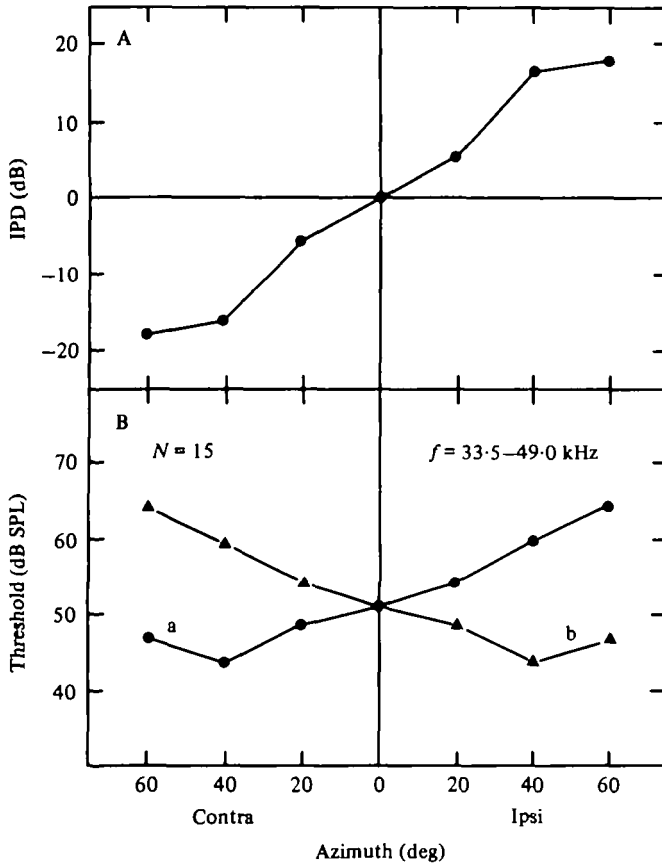
Fig. 8. (A) Relationship between stimulus direction and interaural pressure difference (IPD) was calculated from the mean values of observed thresholds for 15 N_a potentials (B, a) by subtracting 'mirror-image' values (B, b). See text.

contralateral (Fig. 7A). With stimulus strength at 64–10 dB higher than the threshold at 0° (Fig. 7A) – the angle for maximum discharge was 0° (Fig. 7B, *a*); with stimulus strength at 69 dB, the angle was 40° ipsilateral (Fig. 7B, *b*).

The observed effects of stimulus strength upon the angle for maximum discharge (Fig. 7B) can be predicted on the basis of the direction:threshold plot (Fig. 7A) and the number of impulses obtained at different signal levels (at the BF) delivered at 0° (Fig. 7C). For a signal strength of 69 dB, a mean value of 5·3 impulses per stimulus pulse was observed (Fig. 7C, *x*). From 7A it can be predicted that such a stimulus would produce the same effect as a stimulus 5 dB lower, at 20° contralateral. Such a level, 64 dB, produces 7·0 impulses per stimulus pulse at 0° (Fig. 7C, *y*). Hence a 64 dB pulse at 20° contralateral can be predicted to produce 5·3 impulses on average. By this procedure, the points of Fig. 7D (*a*) were calculated for a 64 dB stimulus level, and those of Fig. 7D (*b*) for 69 dB. These plots are similar to the experimental results (Fig. B).

(*f*) *Effect of stimulus direction upon interaural pressure difference (IPD)*. IPD values at different angles (Fig. 8A) were obtained from a plot of mean thresholds for 15 N_3
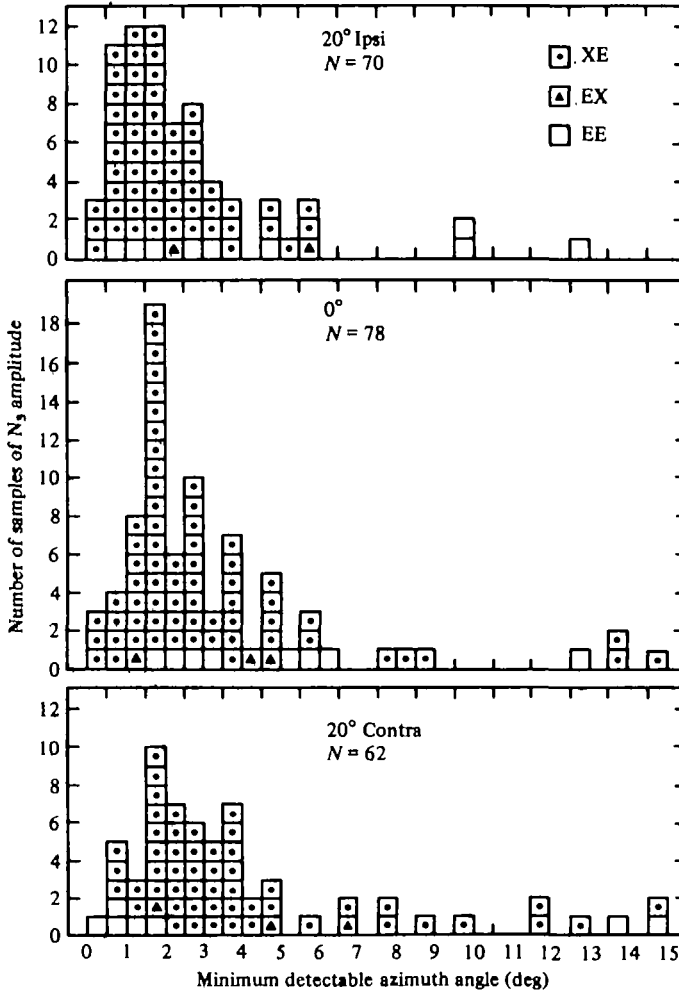
Fig. 9. Distributions of the minimum detectable change in stimulus direction as determined by variation in N_3 amplitude. XE, EX and EE represent those N_3 potentials whose maximum amplitude appeared at 20–40° contralateral, 20–40° ipsilateral and at the front, respectively.

potentials with their best angles at 40° contralateral, and BF's ranging from 33·5 to 49·0 kHz (Fig. 8B, a). Assuming sagittal symmetry of the auditory system, the IPD plot was obtained by a subtraction of the values of Fig. 8B (a) from their 'mirror-image' values (Fig. 8B, b). The IPD changed linearly with azimuth between 0° and 40° at a rate of 0·4 dB/degree.

Coding of the minimum detectable change in stimulus direction

To determine the minimum angle that could be detected by S-segment neurones, statistical comparison (t test, $P < 0.05$) was made between N_3 amplitudes, and between the number of impulses of single units, that were recorded with a change in stimulus direction at around 20° contralateral, 0°, and 20° ipsilateral. These angles were chosen because the main energy of the orientation signals of *Myotis* is emitted within right 30° to left 30° of the bat's eye–nostril line (Shimozawa *et al.* 1974) an◼
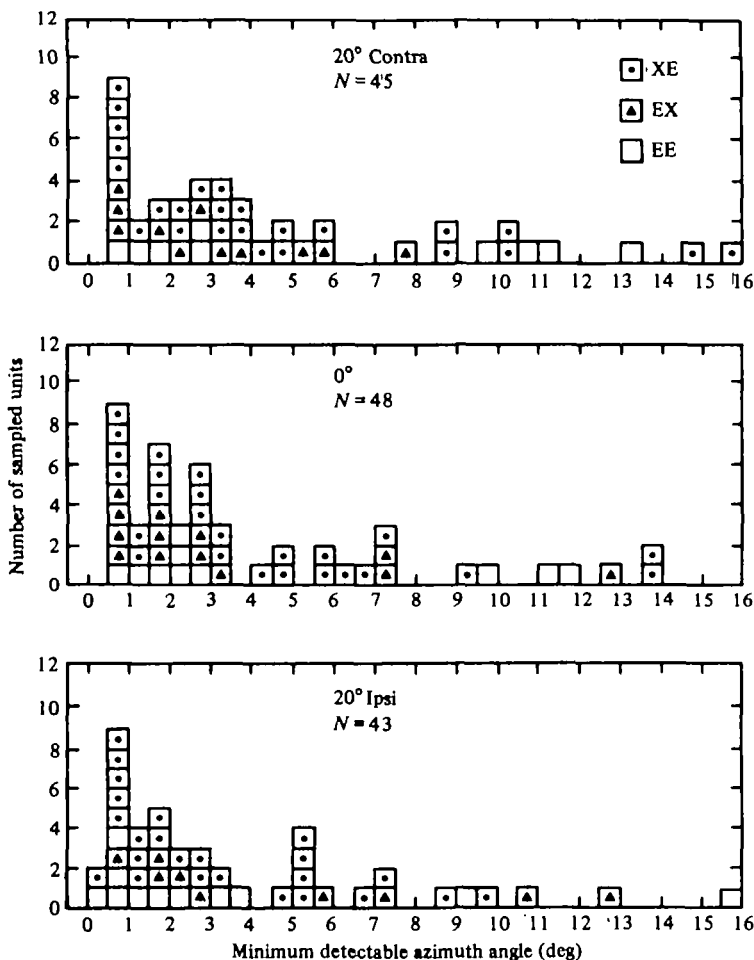
Fig. 10. Distributions of the minimum detectable change in stimulus direction as determined by variation in the mean discharge rate of single units. XE, EX and EE represent those units whose maximum discharge rates appeared at 20–40° contralateral, 20–40° ipsilateral and at the front.

the animal is apparently interested in processing echoes returning within this range owing to the forward position of its ears. Sound stimuli, 10–20 dB above the thresholds of investigated N_3 potentials or single units, were swung through these three angles in such directions that the stimulus effects on thresholds were similar in all measurements.

Data were obtained from 78 N_3 potentials and 48 single units. The standard deviations of each mean recorded value were always less than 10% of the mean.

At each of the three angles studied, percentages of the N_3 potentials which could code an azimuthal difference of less than 5° are 90% at 20° ipsilateral, 84·5% at 0° and 79% at 20° contralateral. Those which could code an azimuthal difference of less than 3° are 75·7% at 20° ipsilateral, 64·1% at 0° and 51·6% at 20° contralateral (Fig. 9).

In the single units study, 69·8% of the units could detect an azimuthal difference of

less than 5° at 20° ipsilateral, 70·8% at 0° and 69% at 20° contralateral. Furthermore,
percentages of single units which could code an azimuthal difference of less than 3°
are 60·5% at 20° ipsilateral, 58·3% at 0° and 47% at 20° contralateral (Fig. 10).

<div align="center">DISCUSSION</div>

Binaural neurones of S-segment

The majority of the recordings from the S-segment showed neural responses that
were most sensitive to stimuli at 20–40° ipsilateral or contralateral. The neurones
underlying these responses may be comparable to the EI neurones of *Rhinolophus
ferrumequinum*, which receive excitation inputs from one ear and inhibitory inputs
from the other (Schlegel, 1977). The responses with a best angle of 0° would appear to
indicate neurones excited by both ears, like the EE neurones of *R. ferrumequinum*
(Schlegel, 1977).

Directional sensitivity of S-segment

When a sound source is moved around the head of an animal, there is a change in
both the interaural pressure difference (IPD) and interaural time difference (ITD)
because of the proportional change in the amount of head shadowing and the change
in the lengths of the pathways along which the sound waves must travel before arriving
at the two ears. In terms of variations in threshold of cochlear nuclear neurones, the
amplitude of a sound of 40–60 kHz is attenuated by about 20 dB when it is moved
from ipsilateral to 40° contralateral (Grinnell, 1963*b*; Suga, 1964).

If binaural interaction were to occur in the S-segment, one would expect a difference
in threshold of N_3 potentials or S-segment units between the best and worst angles to
be larger than that of the primary auditory neurones. This was demonstrated in the
present study, for a sound of 38–50 kHz at 40° contralateral became 25 dB weaker
when measured at 40° ipsilateral. Lowering the sound amplitude by 25 dB would
change the latency of response and discharge rate of single unit activity (Jen, 1978).
Furthermore, as the sound is moved around the animal's head, the proportional
change in IPD would cause bilateral differences in the population and number of
impulses of activated neurones. All these anticipated changes in neural responses are
reflected by the results of the present study (Fig. 1–6) in which the amplitude and
threshold of N_3 as well as threshold, latency and discharge rate of single units did
change with the movement of the sound source.

The mean discharge rates of single units changed as a function of sound location
(Fig. 6). This may be due to changes in IPD or ITD as the sound moves from one
location to another. A similar effect has been found with cat collicular neurones
(Leiman & Hafter, 1972; Bock & Webster, 1974).

An effect of stimulus level upon the relationship between stimulus angle and impulse
number in non-monotonic units (Fig. 7C) has also been found in the brainstem of
Rhinolophus ferrumequinum (Schlegel, 1977).

Coding of directional information

The minimum detectable azimuthal angle which could be significantly coded at a 95% correct level was less than 5° in about 70% of the S-segment neurones studied. About two-thirds of that 70% could even code an azimuthal difference of as small as 3°.

For each neurone in the right S-segment of a given capacity to code a difference in stimulus angle, there must be a neurone in the left S-segment with a corresponding coding capacity. If the outputs from corresponding EI neurones receiving inhibitory signals from the contralateral ear and excitatory inputs from the ipsilateral ear are compared by some higher-order neurones (von Békésy, 1930, 1960; van Bergeijk, 1962), the coding capacity should be theoretically doubled. Thus based on the present data, a bat could easily detect an azimuthal difference as small as 1·5°. Furthermore, the detection of a difference in stimulus direction even as small as 0·25° by a bat should be possible.

If one assumes the minimum detectable IPD of a *Myotis* bat is 0·5 dB (Shimozawa *et al.* 1974), then, based on the present data, the bat should be able to detect a 1·25° azimuthal difference around the median plane because the slope of the IPD curve around the midline was 0·4 dB/degree for a 33·5–49·0 kHz sound (Fig. 8). A similar value has been suggested by others (Grinnell, 1963b; Shimozawa *et al.* 1974; Schlegel, 1977) and calculated for *Phyllostomus hastatus* (Harrison & Downey, 1970).

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