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NEUROPHYSIOLOGICAL STUDIES OF THE RESPONSE CHARACTERISTICS OF AUDITORY FIBERS IN THE CRICKET (GRYLLIDAE ORTHOPTERA) WITH PARTICULAR REFERENCE TO TELEOGRYLLUS OCEANICUS, (LE GUILLOU).

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the City of London Polytechnic, London, CNAA Board.

February, 1981.

TABLE OF CONTENTS.

I hereby declare that this Thesis is my own work, except where the contrary is specifically indicated. No other registration for an award of either the CNAA or any University occured during the period of this research programme.

M. Hutchings.

February, 1981

Mary Elizabeth Hutchings.

Advanced studies undertaken in connection with this programme of research included attending the M.Sc. course, Neurophysiological Basis of Behaviour at the City of London Polytechnic. In addition I visited Marburg University, West Germany to learn further techniques applicable to the study of insect nervous systems; this work was supported by a grant from the European Training Foundation.

Chapter III forms the basis of a paper which has been accepted for publication in the Journal of Comparative Physiology A. Investigations with other workers led to co-authorship of two papers on directional hearing in the Japanese Quail.

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Coles, R.B., Lewis, D.B., Hill, K.G., Hutchings, M.E., Gower, D.M.: Directional hearing in the Japanese Quail (Coturnix coturnix japonica). II.Cochlear physiology. J. exp. Biol. 86,153-170 (1980)

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ABSTRACT.

Single unit recordings of primary and central auditory fibers of the cricket Teleogryllus oceanicus show responses to frequencies over the range 1kHz to at least 42kHz. The characteristic frequencies, (ChFs) of units were distributed over most of the bandwidth investigated although few units were recorded with ChFs below 4kHz or in the region 7kHz to 10kHz. Some units showed more than one peak of sensitivity and others were broad-banded with no tuning to a particular frequency. Primary units whose ChFs approximated to the carrier frequency (C.F.) of the species proclamation song were the most highly tuned.

The derived threshold curves for all primary and central threshold data had major peaks of sensitivity at 4.8kHz and 22kHz. The majority of primary units were not spontaneously active and had tonic response patterns but phasic responses were occasionally observed. Some central units have highly complex response patterns involving correlated spiking responses, silent periods and rebound activity. The response pattern of a single unit may vary with both the intensity and frequency of the stimulus. The implications of these findings are discussed.

Abbreviations.

The terminology of Broughton, (1964) has been adopted therefore the term proclamation song rather than calling song is used throughout this thesis. When reference is made to published work, the terms used by the authors are adhered to.

The abbreviation C.F. is used to denote carrier frequency and the term characteristic frequency, (ChF) has been used rather than best frequency for the frequency at which maximum unit sensitivity occurs.

CHAPTER I.

General Introduction.

Introduction.

A. Sound emission mechanisms.

a) Strigilation and rate multiplication.

The Orthoptera produce several types of song, and show highly evolved and sophisticated acoustic behaviour, (Alexander, 1962). The songs are normally produced by the interaction of tooth and file systems which are moved against each other as a result of muscle contraction. While some crickets have no strigilatory ability i.e. Phaeophilacris spectrum, (Kämper and Dambach, 1979), most crickets produce sound by rubbing their tegmina together. The exoskeleton on the inner edge of each tegmen is modified to form a plectrum (Nocke, 1972 and Michelsen and Nocke, 1974) which moves over the file on the ventral side of vein V7 of the opposite tegmen. Both tegmina possess a perfect file and plectrum but the right wing usually overlaps the left so that only the left plectrum and right file are used. Although the rate of muscle contraction does not exceed 200/s during sound production, frequencies in the kHz range are emitted. Each movement of the wings causes the file to pass over the plectrum thereby converting the single muscle twitch into a number of tooth-impacts, (rate-multiplication). Sound is usually produced only during the closing strokes of the

wings, (Pierce, 1948 and Davis, 1968). As the plectrum strikes each tooth in the file it produces a "click". A train of clicks is produced during wing closure and has a fundamental frequency (equivalent to that at which the plectrum strikes the teeth), and a Fourier series of harmonics. Each time a tooth is dropped by the plectrum the resulting vibration is transmitted to other parts of the wing and the spectrum of the emitted sound is modified by the frequency response of systems whose natural frequency may or may not be different from the tooth-impact rate. If the tooth-impact rate equals the natural frequency of the sound radiator a state of resonance occurs and the fundamental of the tooth-impact rate is emphasised relative to the harmonics. But if the tooth-impact rate is dissimilar to the natural frequency of the resonator, the harmonic of the tooth-impact rate most similar to the resonance frequency of the resonator will be emphasised.

b) <u>The sound radiator and carrier frequency</u>.

The maximum amplitude of vibration of the resonator will occur when energy is fed into it at a rate corresponding to the resonance frequency, (i.e. when the tooth-impact rate equals the resonance frequency). At resonance the system is self-

sustaining except for frictional losses due to contact with the surrounding medium, (Bennet-Clark, 1971). At the beginning of each emission, energy is required to overcome the resistive forces on the resonator. If the system is lightly damped (i.e. has a high Q-value) the buildup is long-lasting and the resulting signal is sharply tuned and the harmonics are of low intensity. The radiator system or "harp" in the crickets has a high Q-value so that rise and decay times are long and the resulting emission is relatively pure tone with narrow, low-energy side-bands. The remainder of the wing acts as a baffle, increasing the effective air load on the harp. Although the load is small it increases the damping of the system, reducing the Q-value, but facilitating the acoustic coupling with the air and thus increasing the efficiency of propagation.

In the male cricket there are two regions of thin cuticle on each tegmen, (Dumortier, 1963); the harp and the "mirror". The harp is bordered in the midline of the tegmen by V5, posteriorly by V6 and anteriorly by V7. Pierce, (1948) suggested that the cricket harp was a resonant system, the mode of vibration of the harp depending on the thickness, size and

elasticity of the cuticle. The spectrograms of the proclamation and "rivalry" songs of Gryllus campestris show characteristic main peaks at 4kHz, (Lottermoser,-1952; Huber, 1960; Dumortier, 1963 and Nocke, 1972). The carrier frequency of these songs (C.F. 4kHz) is equal to the tooth-impact rate which also coincides with the resonance frequency of the harp. Nocke, (1971) removed the harps and showed that the sound level was reduced by 46dB. The court-ship song has a main peak at 14kHz although components up to 100kHz are present, (Lottermoser, 1952); but the relative intensity of the ultrasonic components varies greatly between individuals, (Nocke, 1972). The 14kHz C.F. of the courtship song agrees well with the tooth-impact rate for this song but the radiator is unknown. Nocke, (1971) found that the mirror was tuned to 7.2kHz and the 14kHz component may be the second harmonic of the 7.2kHz fundamental.

In contrast, some bush-crickets (e.g. Platycleis affinis, Broughton, 1954; P. intermedia, Broughton et al., 1975 and Metrioptera brachyptera, Lewis et al., 1971) use systems with low Q-values and rapid decay following each tooth-impact. This heavy damping results in the introduction of numerous side-bands; the frequency spectrum will also contain a dominant frequency and

the fundamental frequency of the tooth-impact rate.

II. Song types and the effects of frequency and temporal patterning on the behavioural response.

a) Categorisation of three song types.

Insect songs are intermittent and side-bands are introduced because of amplitude modulation. Amplitude modulation of the songs results in patterns which differ in their temporal sequences and complexity. Alexander, (1960) observed the behavioural context within which crickets produced different songs and categorised the signals according to their inferred function. The acoustical repertoire of Teleogryllus oceanicus comprises three distinctive song types; proclamation (or calling), aggressive and courtship, (Alexander, 1961); for a detailed description of the song types see Bentley, (1977). Proclamation songs are associated with the occupation of a territory and appear to function in attracting a mate; aggressive songs occur when males are unacceptably close to each other, (Broughton, personal communication).

Courtship song is elicited in the close presence of a female and is a "softer" song with a much broader frequency band than the proclamation or aggressive songs. In some species the courtship song consists of long chirps ending in a rapid "tick", (Alexander,

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1975). Ticks with an energy peak at 14kHz have been reported in G. campestris, (Huber, 1963, 1970; Nocke, 1972) and Lewis (personal communication) has shown loud ticks in the courtship song of Acheta domesticus with frequency components up to at least 30kHz. During courtship the wings are lowered from 45° to the body to 20° and the closing movement of the wings is about three times faster than during the proclamation song. These differences may give rise to the relatively broad-band courtship song as opposed to the narrow band emissions of the proclamation and aggressive songs.

b) Phonotaxis and carrier frequency.

Female crickets show positive phonotaxis to the proclamation song of the conspecific male, (Regen, 1913). However the response is dependent upon the phase of the female's reproductive cycle, (Busnel and Busnel, 1954). Many workers have tried to ascertain what part of the song is species-specific . But as Popov and Shuvalov, (1977) commented, the methods and species used have been so different that the results obtained by different authors are contradictory in many respects.

Young female Acheta domesticus demonstrate negative

phonotaxis to frequencies in the range 2.5kHz to 45kHz but with maturation, the escape reaction to frequencies around the carrier frequency, (C.F.) of the conspecific calling song is replaced by positive phonotaxis, (Shuvalov and Popov, 1971). Popov and Shuvalov, (1977) observed similar responses in G. bimaculatus. Moiseff et al., (1978) used models of the conspecific calling song of T. oceanicus (natural C.F.; 4-5.4kHz) to test the effect of altering the C.F. on phonotactic behaviour. They found that females showed positive phonotaxis to models whose C.Fs ranged from 3kHz to 9kHz but negative phonotaxis to models with C.Fs ranging from 30kHz to 70kHz. Popov and Shuvalov, (1977) found that only the fundamental frequency of the proclamation song was important in the phonotaxis of G. bimaculatus, but Zaretsky, (1972) found that female Scapsipedus marginatus reacted positively to models of the calling song temporal pattern that had a C.F. of 18kHz, (the fundamental frequency of the natural calling song being 5kHz). Although the C.F. of the proclamation song is important for eliciting phonotaxis it is unlikely that it is a basic cue for the recognition of the species song since the spectra of C.Fs of symmpatric crickets overlap, (e.g. Alexander, 1957;

Walker, 1957, 1969; Popov, 1972 and Popov et al., 1974).

c) Temporal patterning and species-specificity.

Orthopteran songs with the most complex temporal patterns occur in regions where there are many species and Alexander, (1961) stresses that species which do not live together sometimes have identical calling songs and repertoires. T. oceanicus and T. commodus have overlapping geographic distributions, (Hill et al., 1972) but hybrids are not found although there are no anatomical barriers to prevent interbreeding, (e.g. Leroy, 1966; Hogan, 1967 and Bentley, 1971). The two species have distinctive calling songs which differ in both C.F., (T.oceanicus, 4.5-5.4kHz; T. commodus, 3.5-4.5kHz; Hill, 1974) and temporal pattern. Hill, (1974) showed that presentation of the heterospecific song in a one-way trial elicited positive phonotaxis, but specificity occured in the response to two-choice trials when both the conspecific and heterospecific songs were presented. Pollack and Hoy, (1979) presented models of the calling songs of both T. oceanicus and T. commodus in which the C.Fs were identical and found that T. oceanicus could recognize the conspecific calling song from its temporal pattern alone.

The temporal pattern of a song is less likely to undergo modification during transmission through the biotope than is the frequency spectrum since it is dependent on the lowest frequency present. High frequencies are particularly susceptible to environmental modification (see below) and are therefore less likely to encode species-specific information than is the temporal patterning. It appears that different parameters of the calling song confer recognition of the signal as species-specific to those that elicit the orientation response. The combination of these factors, together with the motivational state of the female, interact as a releasing mechanism and determine her response.

C. Sound transmission.

a) Geometric spreading.

Sound waves radiated from a point source have two components; medium displacement and pressure. Utilisation of medium displacement only occurs in the near-field since the oscillation velocity of the molecules decreases by 12dB per distance doubled, (dd). The arista of Drosophila detects medium displacement and is used in near-field communication, (Bennet-Clark, 1971 and Burnet et al., 1971). Most animals communicate in the far-field and utilize the pressure component of sound waves

which decreases by 6dB/dd. However the intensity and spectral content of the signal may be changed by environmental factors.

b) Reflection and diffraction.

Reflections occur where there are discontinuities in the impedance of the medium and where the objects exceed the wavelength of the sound. If the emitter is located on the ground the signal may be reflected from the ground producing a sound-shadow. The sound pressure at a point is the resultant of both the progressive and reflected waves reaching that point at a given time. Therefore the reflected waves reaching that point may interfere with the direct wave either constructively , (such that the intensity is enhanced) or destructively (resulting in a reduction of the sound pressure) depending on the wavelengths and the phase angles involved.

Objects which are similar in size to the wavelength of sound cause diffraction of the sound in all directions which will interfere with the surrounding sound pressures either constructively or destructively. High frequencies have relatively small wavelengths and are therefore attenuated faster than low frequencies during propagation through a complex

environment.

c) <u>The efficiency of insect sound radiators</u>.

To increase the distance over which communication can occur it is advantageous to use low-frequencies, in which case a larger emitter is required for efficient radiation. Most insects are unable to produce much sound below a few kHz, (Michelsen and Nocke, 1974). The efficiency of sound emission increases as the diameter of the sound source approaches the wavelength of the sound, (Beranek, 1954). To efficiently radiate a frequency of 5kHz, (about the C.F. of most cricket calling songs) a source 70mm in diameter is required, (Bennet-Clark, 1975) but the wings of most insects are far smaller than this. The radiations from a freely suspended membrane are equal and opposite in phase i.e. when the membrane on one side produces a compression the opposite side undergoes a rarefaction. At high frequencies the radiation from the front of the membrane is mainly transmitted forwards. At low frequencies the radiation distribution becomes more spherical and front to back cancellations occur with a cut-off at a frequency whose wavelength equals the distance from the front

to the back of the membrane, (Broughton et al., 1975). Front to back cancellations can be prevented by mounting the membrane in an infinite baffle. An approximation of an infinite baffle can be achieved by mounting the membrane in a wall which is backed by an air-filled enclosure, (i.e. a closed-box), however the air will effect the membrane compliance and a resonance will be imposed which will be a function of the dimensions of the enclosure. In practice a baffle which is one-quarter the wavelength of the lowest frequency to be transmitted approximates to a closed-box. Although the cricket harp is set in the wing which acts as a baffle the anatomical dimensions of the wing do not allow efficient transmission of low frequency sounds. The harps of G. campestris are situated in the dorsal field of a "box" formed from the tegmina and dorsal surface of the insect body. Nocke, (1971) determined that the box acted as a baffle but its dimensions are approximately one-eighth of the wavelength of the calling song C.F.; emission is therefore inefficient. The harp vibrates as a unit and Nocke, (1971) suggested that the veins V1-V4 traversing the harp, function to increase the stiffness of the harp (therfore increasing the natural frequency) without raising the harp mass (the "studding"

principle). This will also increase the coupling efficiency, Nocke, (1971, 1972) showed that in Gryllus sound is produced as a doublet source, the sound pressure being maximal on the axis of vibration with a minimum at right angles to the sagittal plane. The emission of Gryllus is directional, sound being directed backwards by holding the two fore-wings at 90° to each other and at about 45° to the substrate. The sound pressure behind the animal exceeds that in front and at the sides by 6dB, (Nocke, 1971).

d) The effects of temperature, humidity and vegetation on the effective propagation distance.

The velocity of sound in air is dependent on temperature; heating of the earth's surface during the day results in sound waves travelling faster and being bent away from the surface creating a sound-shadow. At night the reverse phenomemon occurs. To compensate for these variations in the effective propagation distance, strategies of climbing to higher positions in the vegetation during the day and returning to the surface at night may be employed.

With increasing humidity the dissipation maximum of sound in air will shift from low to high frequencies, (Michelsen, 1978). Vegetation affects the microclimate in terms of temperature, humidity and air turbulence. Many animals inhabit zones of dense vegetation

where multiple scattering of sound by leaves can result in an excess 6dB attenuation per dd, (Meister and Ruhrberg, 1959 and Meister, 1960). Absorption of sound by leaves and stems can amount to an extra 6dB attenuation per meter. Attenuation of the high frequency components of signals by vegetation is such that ultrasonic frequencies although highly directional can only be used over distances of a few meters, (e.g. Silver et al., 1980). Zhantiev and Dubrovin, (1968) divided 11 species of tettigoniids into two groups on the basis of the C.F. of the calling songs; the first group had sonic C.Fs in the range 8-15kHz, the second group had ultrasonic C.Fs ranging from 20-40kHz. Field observations indicated that the first group had a lower mean population density than the second. Electrophysiological experiments demonstrated that the insects using sonic C.Fs could perceive natural sounds from distances of more than 9m. Zhantiev and Dubrovin concluded that the difference was due to attenuation by vegetation.

D. Frequency discrimination by insects.

Katsuki and Suga, (1958, 1960) demonstrated that insects could discriminate frequencies. Nocke, (1972) showed

that the whole nerve threshold curve for G. campestris had at least two optima; one near 4kHz and a second near 14kHz. These are the frequencies at which the calling and rivalry songs show main and secondary peaks. Esch et al., (1980) demonstrated the presence of clusters of tuned primary units in G. campestris and G. bimaculatus in the range 2kHz to 20kHz. Rheinlaender, (1975) and Kalmring et al., (1978) showed that primary units in the tettigoniid Decticus verrucivorus were tuned to frequencies across the whole of the bandwidth investigated, (2kHz to 40kHz). The retention of frequency information in general may be important for directionality, (Colès et al., 1980 and Hill et al., 1980) and ultrasonics may be important in predator-prey interactions. Behavioural studies, (Popov et al., 1975 and Moiseff et al., 1978) indicate broad-band reception in crickets.

E. Strategies for directional hearing.

a) Binaural time difference.

Directional cues can be determined from the arrival time of sound at each ear and are dependent on the effective inter-aural separation. In vertebrates the pinnae may affect time of arrival cues by causing complex reflections which alter the path length of the sound to the tympana. In crickets the tympana are

directly exposed and the interaural distance in T. commodus is about 1.6cm, (Boyan, 1978). Since sound travels at 344m/s in air, the interaural time difference experienced by the tympana for sound incident at 90° is about 50μs. Bailey and Thomson, (1977) have demonstrated that T. commodus can resolve sounds incident from 10° to the longitudinal body axis, at this angle of incidence the theoretical interaural time difference is only 8μs. Reliable coding of such short time periods would require accurately balanced receivers.

b) Sound shadow effects.

In the cricket, sense organs responsive to sound are situated on the proximal part of the prothoracic tibiae. Interposed between the ears are the head and prothorax which constitute a potential barrier to sound waves reaching the contralateral ear. Hill and Boyan, (1977) tested frequencies up to 5kHz in T. commodus and demonstrated that there was no appreciable attenuation of the sound at the contralateral ear. The C.F. of the proclamation song of T. commodus is about 3.7kHz and the body does not produce a sound-shadow since its dimensions are small relative to the wavelength. Therefore the sound pressures acting on the external

surfaces of the tympana are similar in amplitude when the wavelengths used are long with respect to the dimensions of the interposed anatomy.

c) Binaural phase comparison.

Binaural phase comparison could be used to localize a sound source but the receivers must be separated by at ~~least~~ most half a wavelength since with shorter wavelengths it is not possible to determine which ear is in the leading phase, (Konishi, 1977). Theoretically the upper limit for phase comparison by T. commodus is about 11kHz but even at 4kHz (the C.F. of the calling song) the oscillations are too close together for the receptors to discriminate phase, (Boyan, 1978).

d) The pressure gradient mechanism.

Hill and Boyan, (1977) presented a 4kHz sound to T. commodus and demonstrated that the effective sound pressure at the contralateral ear was reduced by about 20dB relative to that at the ipsilateral ear. In crickets the prothoracic leg trachea originates at the spiracle and descends in the leg behind the tympana, (Zeuner, 1936). In the prothorax a branch of the trachea runs ventrally to abutt the symmetrical element from the opposite

side forming a connection between the tympana of opposite legs. Hill and Boyan,(1977) showed that sound was transmitted in the trachea from the ipsilateral to the contralateral ear. When the component waves were of similar phase and amplitude destructive interference between the internal and external sound pressures occured. Therefore the effective sound pressure results from the pressure gradient across each of the membranes, (Michelsen, 1971; Lewis, 1974 and Michelsen and Nocke, 1974). The system is inherently directional since the relative phase of the sound pressures acting on the front and back of each membrane is a function of the angle of incidence. Maximal augmentation (+6dB) of the response can also occur when the two waves are of similar amplitude and phase. The dimensions of the leg trachea in T. commodus are such as to enable efficient transmission of sound at frequencies approximating the fundamental frequency of the proclamation song. Frogs, small reptiles and birds which also communicate using wavelengths that are long relative to the interaural separation also have patent connections between the tympana, (Strother, 1959; Wever and Vernon, 1957; Schwartzkopff, 1952; Coles et al., 1980 and Hill et al., 1980). Coles et al., (1980) and Hill et al.,(1980) have shown that the quail ear functions

as a pressure gradient receiver.

E. Aim of the investigation.

As shown above the majority of studies on gryllids have concentrated on responses to frequencies lower than 20kHz. The question arises whether crickets, with their relatively narrow-band emission (at least of the proclamation and aggressive songs) also show broad-band reception and tuned units in the ultrasonic range. The following experiments were designed to look at the frequency range over which responses could be elicited, (within the limits of the experimental equipment) and to provide a detailed characterisation of the responses of single units. Recordings of primary units were undertaken to investigate the input to the central nervous system. Comparison of the primary and central responses may help in understanding the information processing that occurs in the central nervous system.

CHAPTER II.

Materials and Methods

Experimental techniques.

A) The crickets.

Crickets, Teleogryllus oceanicus, were cultured in the laboratory from eggs originally provided by Dr. R. Dawkins (Oxford). The animals were fed on rat cubes (Dixons FFG(M)), a wheatgerm cereal (Bemax) and occasionally slices of apples and orange, and they had continual access to water. The crickets were kept in a separate insect room in perspex tanks at 23°C and 30% relative humidity on a 12hr light/dark cycle. Eggs were collected in Petri dishes filled with moist sand and the young emerged approximately three weeks after the eggs had been laid.

The juveniles were segregated at the 5th instar and males and females reared separately. Selected males and females formed the breeding colony. The culture has been maintained for a three-year period.

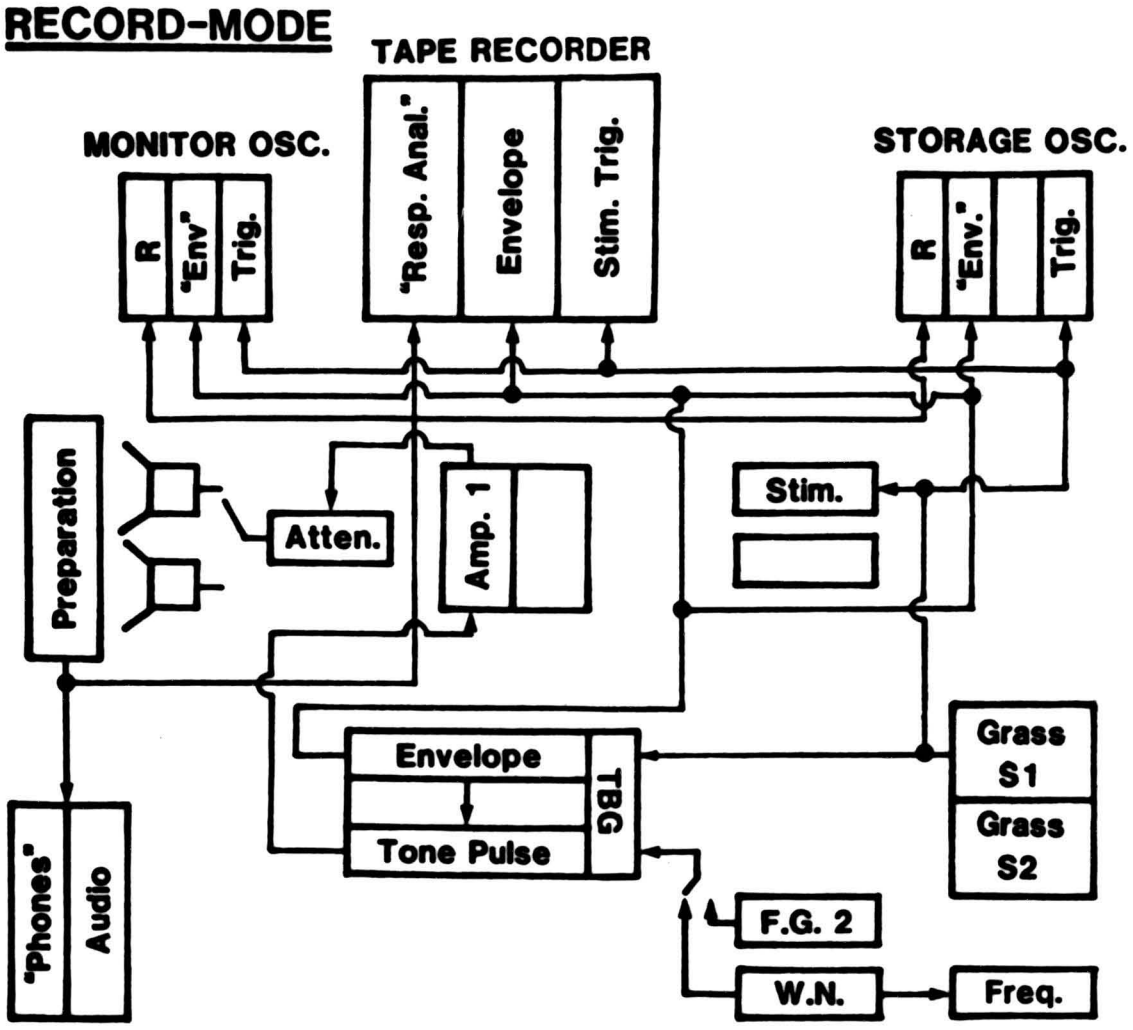
B) The generation of the stimulus.

Pure tones were produced using a function generator (Farnell FG2), and the frequency of the waveform was monitored using a counter, (Heathkit 1M-4100). Alternatively, white noise based on the output of a noisy resistor could also be switched into the

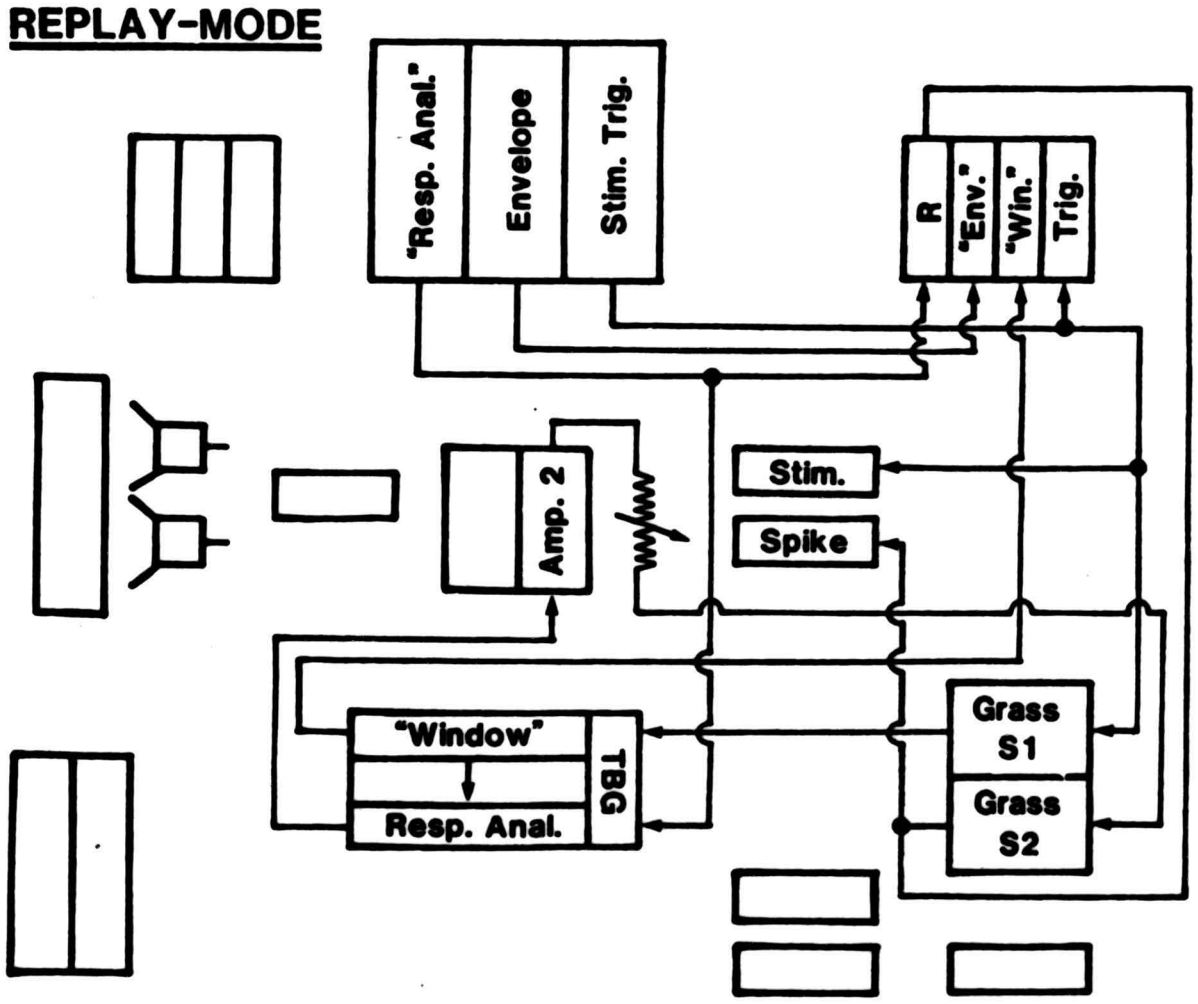
circuit. The continous waveform (pure tone or white noise), provided the input to a Tone Burst Generator, (TBG) which was built in the laboratory, Taylor, (1978a,b), Fig.1 Record-Mode. The S1 channel of a Grass S88 Stimulator was used to provide a trigger which gated the output of the TBG enabling stimulus repetition rates to be modified by the manipulation of the S1 channel. By this means stimulus trains of 10 stimuli/s could also be generated thus approximating the syllable rate of chirps in the song of T. oceanicus. A series of fixed stimulus durations (25, 50, 100, 200, 300, 400 and 600ms) could be selected with an alternative facility for the continous variation of the stimulus duration, (see section H). The TBG also had independently variable rise-fall times but, during the experiment only symmetrical rise-fall times (5ms) were used. The gated signal was amplified (Xelex Power Amplifier DD8) and then attenuated in 1dB steps using a Hatfield Attenuator 2125. The output of the attenuator could be switched to one of two loudspeakers, (Fig.1 Record-Mode). Low frequency stimuli (below 5kHz), were emitted using a Kef B200 loudspeaker (specified frequency range 25Hz to 3.5kHz). An Audax TW8B loudspeaker (specified frequency range 1Hz to 40kHz) was used to emit frequencies exceeding 5kHz up to a maximum of 42kHz.

Fig.1 Block diagrams of experimental apparatus used in Record and Replay-Modes, arrows indicate signal movements. Amp; amplifier: Atten; attenuator: "Env"; stimulus envelope: F.G.2; Function Generator: Freq.; frequency of stimulus: Osc.; oscilloscope: "Phones"; monitor headphones: R/Resp Anal.; response analog: Spike; discriminated spikes: Stim; stimulus: Stim. Trig.; stimulus trigger: TBG; Tone Burst Generator: Trig.; Trigger: W.N.; white noise; Win.; window. For further details see text.

RECORD-MODE



REPLAY-MODE

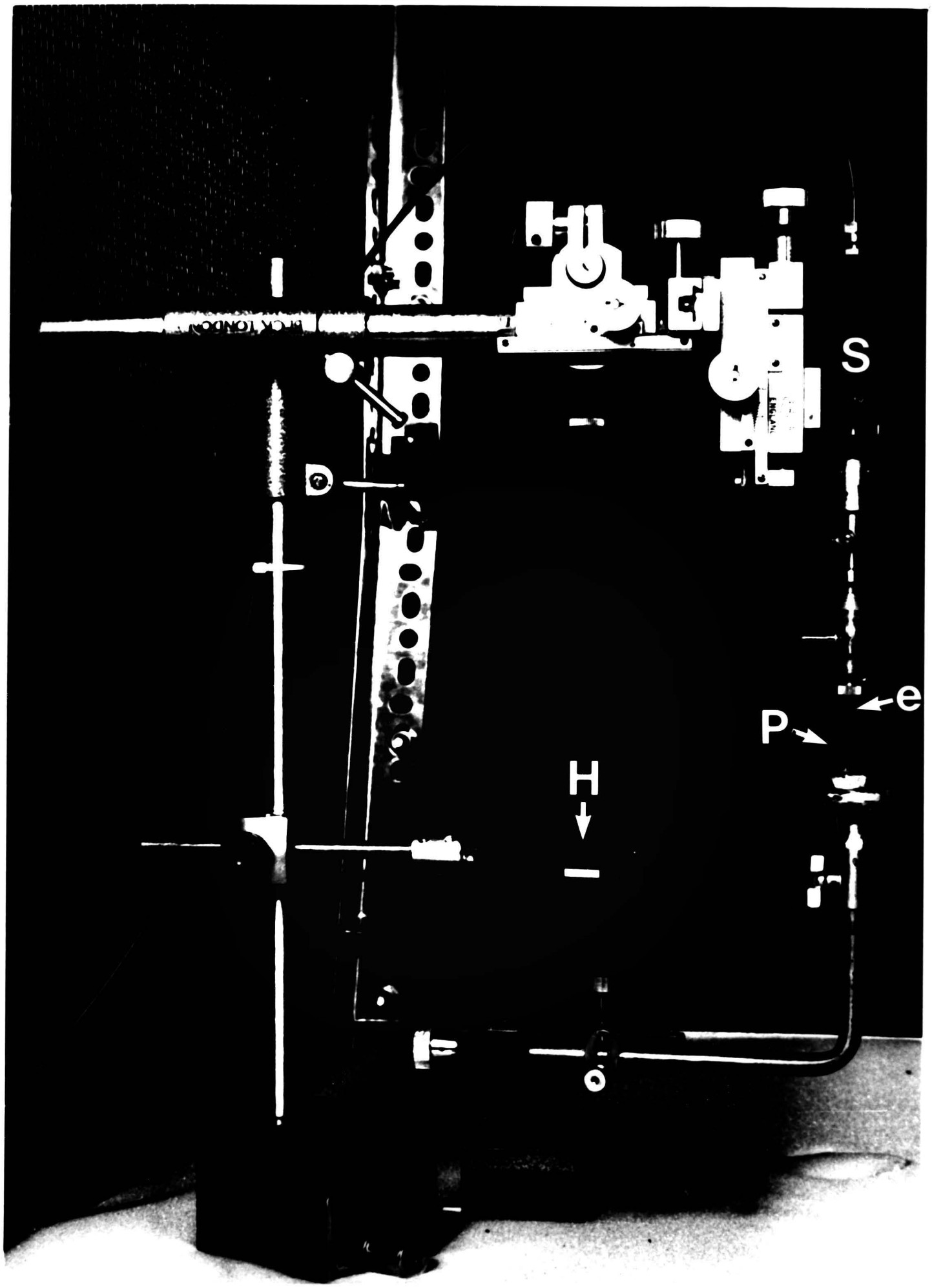


C) The experimental room.

The experimental room was approximately 3.0x2.5x2.5m and was situated in a basement. A chipboard channel, square in cross-section and closed at one end (1.0x1.0x1.3m) ran diagonally across the room. The channel was lined on all sides with mineral-wool wedges, (Rockwool slab insulation, density; 100kg/cubic meter, thickness; 60mm) calculated lower cut-off frequency 212Hz, (calculated using the equation for a conical horn with non-absorptive surface; Beranek, 1954). The loudspeakers (Audax TW8B and Kef B200) were mounted on a removable piece of chipboard which fitted flush in the plane of the closed end of the channel.

A magnetic stainless-steel baseplate was sited at the open end of the channel. The upper surface of the baseplate was covered with foam rubber and was below the level of the mineral-wool wedges in the channel. On the baseplate a micromanipulator (Prior) was used to support a right-angled copper tube ($\frac{1}{4}$" diameter), which carried an adjustable plate on which the preparation was positioned, (Fig. 2). The plate consisted of a perspex sheet (0.1x1.8x3.8cm), supported on thin metal rods (0.2cm diameter, 2.0cm long) and served to minimize sound-field disturbance in the

Fig.2 Photograph of the preparation during recording from central units. e; electrode: H; headstage: P;preparation: S; slave cylinder of microdrive.


S
e
P
H

vicinity of the preparation which was placed 21cm above the level of the baseplate. A second micromanipulator was mounted on a vertical post and enabled coarse adjustment of the position of the micro-electrode. The post was 2cms thick and was placed beyond the preparation. The headstage (Neurolog 100) was attached to the vertical post at a height of 18cm above the baseplate, (Fig. 2). The whole table was enclosed by a Faraday cage (mesh diameter 1.5cm) to reduce electrical interference.

i) D) Calibration of the sound-field.

1) Anechoic conditions.

Since the sound pressure at a given point consists of both the original progressive wave and the reflected waves reaching the point, investigations of the effect of stimulus intensity on a response must be performed under either anechoic or free-field conditions. To demonstrate the efficiency of sound absorption by the Rockwool wedges, a microphone (Bruel and Kjaer ½" Type 4134) was mounted in the position normally occupied by the preparation; the diaphragm of the microphone was parallel to the baseplate.

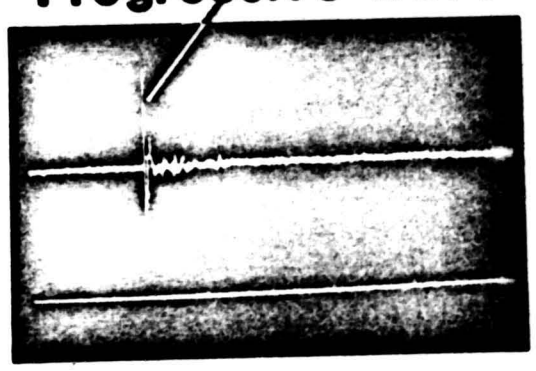
The condenser microphone provided the input to a Frequency Analyser (Bruel and Kjaer Type 2107) and the analog signal

was displayed on one channel of an oscilloscope, (Tektronix D13), Fig. 3. The S1 channel of a Grass S88 Stimulator was used to produce square waves ("clicks"), duration 0.1ms which were switched into the sound production circuit prior to amplification by the Xelex DD8 Amplifier, (Fig. 1 Record-Mode). The square waves were displayed on the second channel of the oscilloscope, (Fig. 3) The signal was emitted by the Audax TW8B loudspeaker.

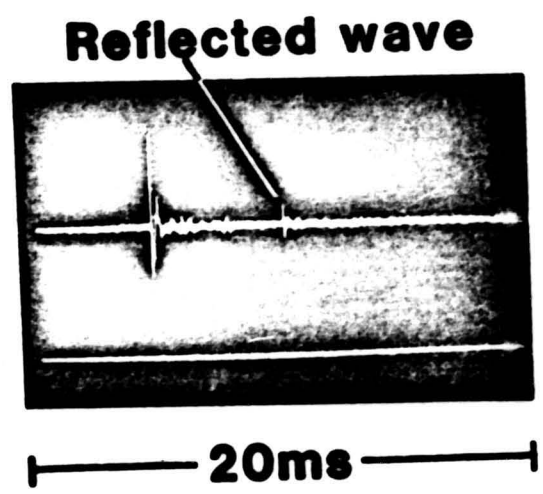
The emission of a "click" resulted in a significant disturbance of the sound pressure level, (SPL) at the microphone (Fig. 3 upper). Transduction of the signal and the time taken for the sound pressure wave to travel from the loudspeaker to the microphone resulted in a delay in the microphone response relative to the stimulus trigger. The delay (approximately 4ms) constitutes a correction factor used in the determination of latency measurements.

Echoes were produced when a sheet of reflective material (cardboard) was placed in front of the wedges, (Fig. 3 lower). The voltage change produced by the echo was 1/6th that of the original progressive wave. On removal of the cardboard to expose the wedges an echo occurred 6ms after the trigger but its amplitude was barely discernible above the background noise level, indicating that the

Fig.3 Analog signals from a condenser microphone photographed from the oscilloscope. Upper; microphone response to a "click" emitted under experimental conditions. Lower; echo produced when a sheet of card was lowered in front of the Rockwool wedges, (for details see text).



Card absent



Card present

Reflected wave 12dB/SPL lower than Progressive wave

wedges are highly absorptive, (Fig.3 above).

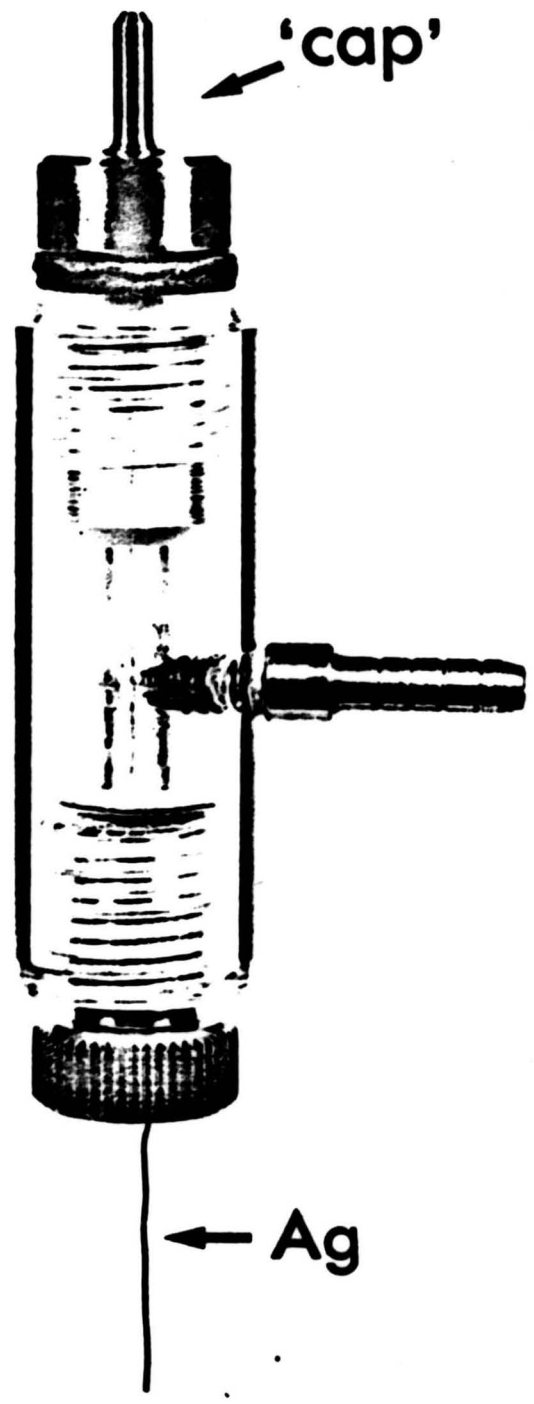
2. Sound intensities.

To calibrate speaker outputs a ¼" microphone (Bruel and Kjaer Type 4135) was placed horixontally in the sound field with the diaphragm facing the sound source. The microphone was positioned above a preparation so that the diaphragm approximated to the position of the ipsilateral organ. Sound pressure levels were measured at 1kHz steps over the experimental frequency range (Bruel and Kjaer Frequency Analyser Type 2107) and are everywhere expressed in dB SPL relative to $0.00002 N/m^2$. Further tests indicated that the sound field was within $\pm$1.25dB at a distance of 4cm about the preparation. Calibrations were repeated every 2 months and following the replacement of a loudspeaker. The output of the Audax TW8B loudspeaker fell rapidly above 35kHz restricting the range of stimulus intensities that could be investigated.

E) Microelectrodes.

Microelectrodes were pulled from 1.5mm diameter capillary glass (Clarke Electromedical GC 150F), using a vertical microelectrode puller (Scientific Research Instruments). The electrodes were filled with either potassium acetate (3M) or potassium chloride (3M) immediately prior to use. Electrode resistances were measured using a

Fig.4 Microelectrode holder. A silver wire (Ag) was soldered to the "cap" and inserted into the electrolyte of the glass electrode. The "cap" made electrical contact with a brass fitting from which the signal was taken to the headstage.


'cap'
Ag
1cm

DC Amplifier (Neurolog 102) and ranged from 20 to 40MOhm. The electrodes were held in an electrode holder (manufactured in the workshop, Fig.4). The electrolyte contacted a silver wire soldered to the "cap" of the holder. During the experiment the electrode holder was inserted via the "cap" into a small brass fitting from which a lead connected to the "A" terminal of the headstage, (Fig.2).

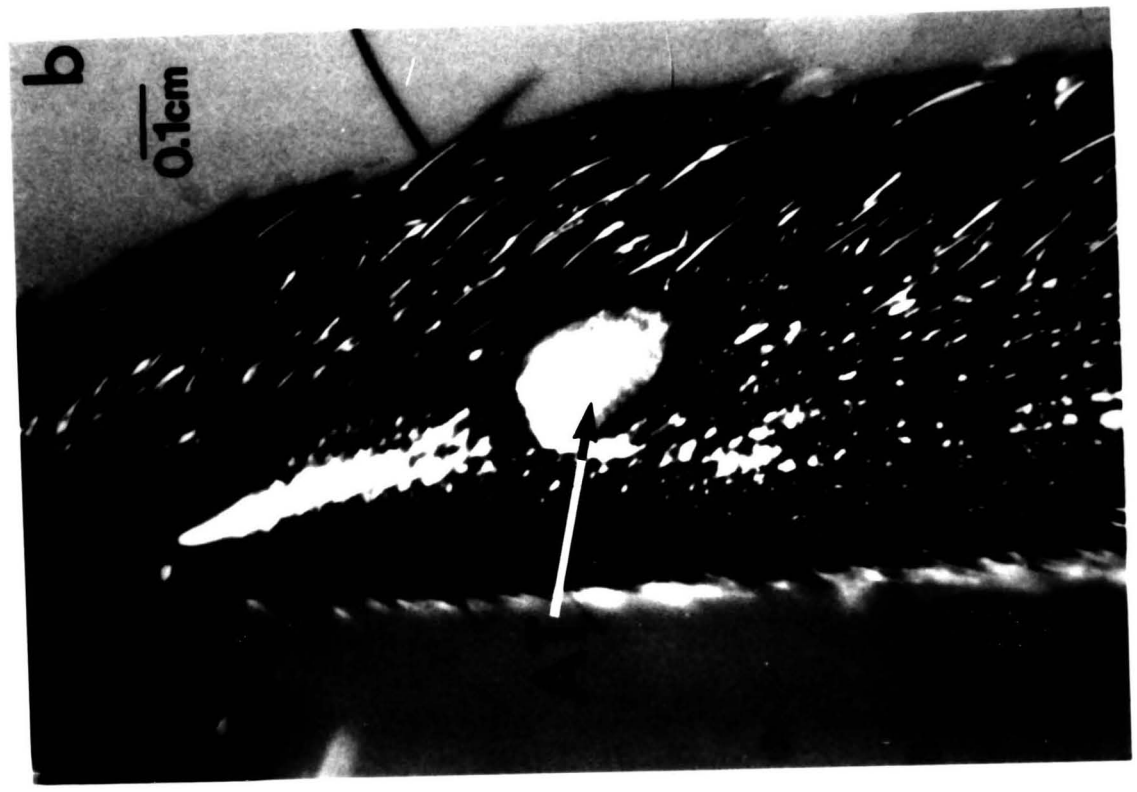
F) <u>The preparation</u>.

Adult crickets were anaethetized with carbon-dioxide gas and the antennae, metathoracic and mesothoracic legs removed. Both pairs of wings were also cut off. The insect was waxed with its ventral surface uppermost to a perspex holder, (5.0x1.5x0.2cm thick) which also carried a 1mm socket into which was soldered a length of silver wire (the indifferent electrode), which was inserted into the abdomen. The prothoracic legs were waxed at the tarsae and femora to thin right-angled wires attached to the stand. Care was taken to ensure that the position of the legs approximated the normal stance. The head was pulled back to expose the thin neck cuticle and waxed in place. The maxillae and mandibles were removed and the labium lifted to expose the pharynx. Connective tissue was cut to free the oesophagus and the fore and midgut removed via a slit made in the abdomen. The cavity was packed

with tissue soaked in Clarke's Ringer. The labrum and labium were then removed. When recording from the central nervous system the neck cuticle was cut away to reveal the ventral neck connectives between the sub-oesophageal ganglion (SOG) and the prothoracic ganglion (Th1). Care was taken to minimize damage to the tracheae and the acoustic tracheae were left intact. A small piece of blue tissue paper moistened with ringer was inserted beneath the connectives, (Fig.5c). When recording from primary units the soft cuticle between the presternal process, presternum and prothoracic coxa was removed to reveal Th1 and the leg nerve, (Fig. 5d).

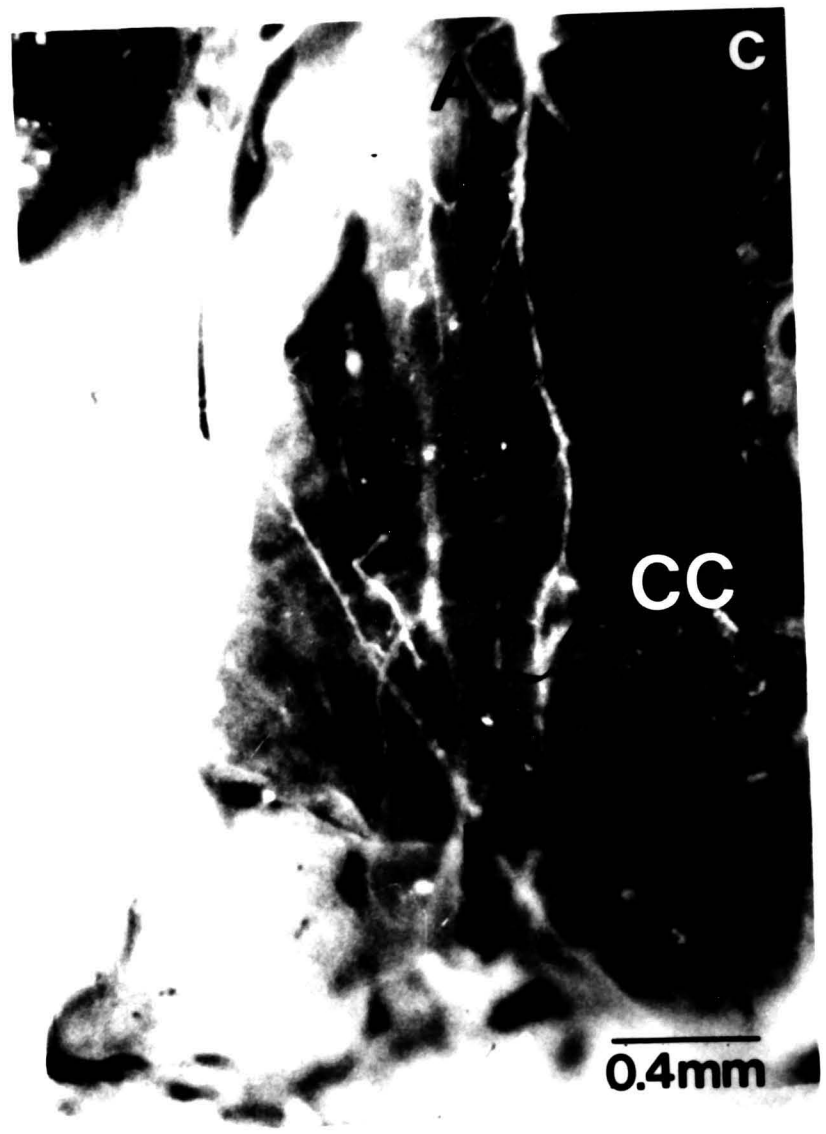
No contralateral recordings were made, the animal being rotated through 180° to enable both right and left connectives and leg nerves to be examined using an ipsilateral sound source. The connective responses were recorded with the longitudinal axis of the animal perpendicular to the loudspeaker. Primary units were recorded with the longitudinal axis of the cricket in line with the loudspeaker. The preparation was illuminated by a cold light source (Schott KL150B), and the electrode lowered under visual guidance (Bausch and Lomb microscope). When the electrode was located above the site of penetration, the microscope and light source were removed from the sound field and the electrode further advanced using a hydraulic microdrive (Clarke HMD-1M). Early

Fig.5a Caudal view of left prothoracic tibia to show large posterior tympanum (PT). b. Frontal view of the left prothoracic ~~tympanum~~ tibia to show the small anterior tympanum (AT).


b
0.1cm


a
0.2cm
PT

Fig.5c Dissection to expose the cervical connectives (CC) between the suboesophageal and prothoracic ganglia. A; anterior: P; posterior: * recording position for the majority of central units. d. Dissection to enable primary unit recording showing the leg nerve (LN) running to the coxa (right upper). A; anterior: P; posterior.

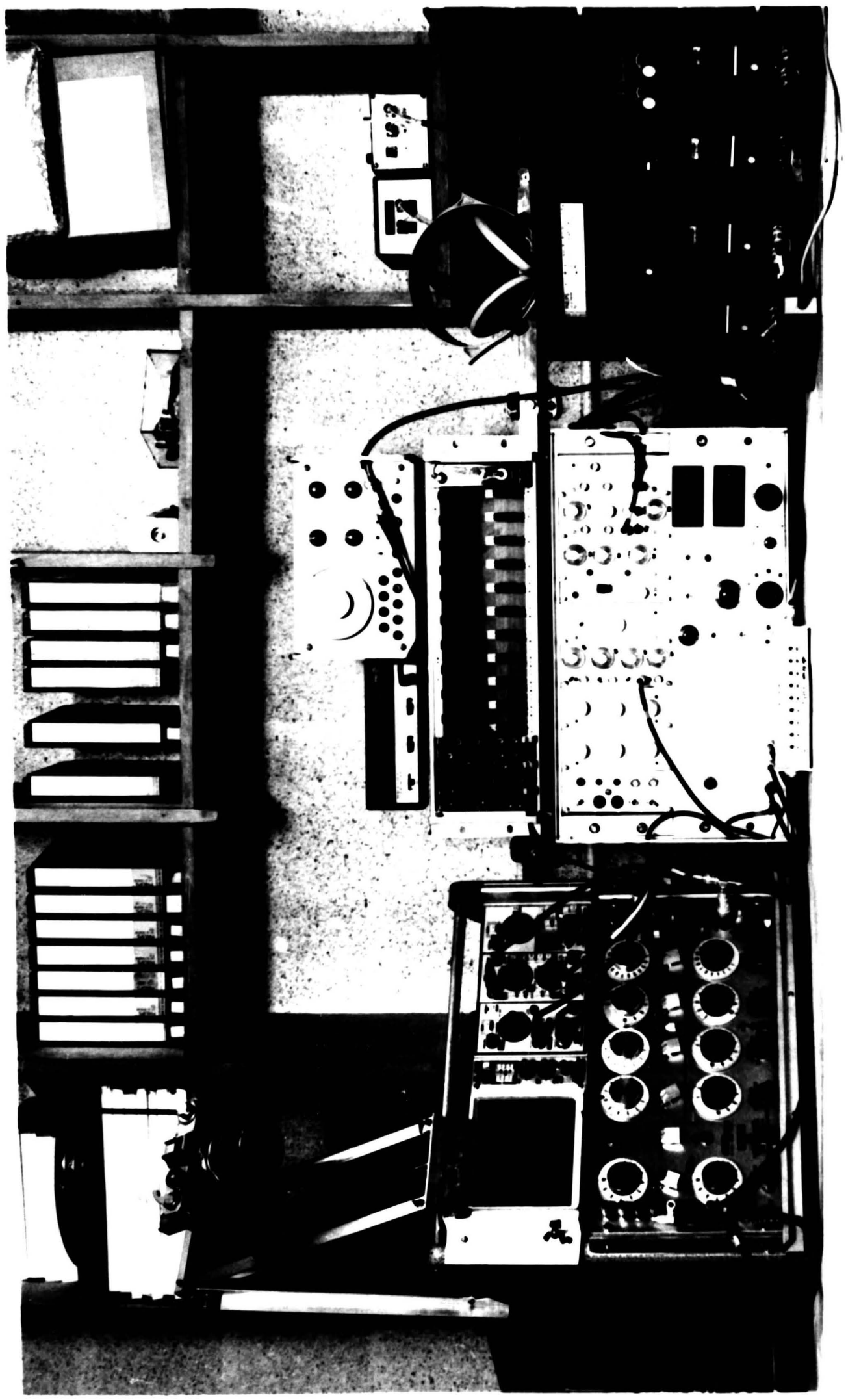

C
CC
0.4mm


d
LN
0.2mm

experiments indicated that few units responded well to white-noise but a response could usually be elicited by either a 5kHz or a 12kHz tone. The search stimulus consisted of the output of two oscillators set at 5kHz and 12kHz respectively, The sine waves were mixed (TBG) and the resultant search stimulus emitted using the Audax TW8B loud-speaker. A series of penetrations was made until a stimulus-locked response was detected. The neural response was monitored on an oscillo-scope in the experimental room and via headphones, (Danasound), Fig.1 Record-Mode. The stimulus "envelope"was monitored on the second channel of the oscilloscope. The response analog and stimulus "envelope" were also passed to a storage oscilloscope, (Tektronix D13) outside the room, (Fig.6). The neural response was taken to the headstage from where it was taken to a preamplifier, (Neurolog 103) and was further amplified using an A.C. amplifier (Neurolog 105). Filters removed frequencies above 10kHz and below 100Hz and a 50Hz notch filter was also incorporated to reduce mains interference.

The stimulus (or Grass S1) trigger, TBG "envelope" and response analog were recorded on magnetic tape (Phillips portable instrumentation recorded Ana-log 7) at a speed of 15ips (frequency response 0Hz to 5kHz on DR). The stimulus "envelope" rather than

Fig.6 View of apparatus outside the experimental room which was used in recording and analysis of data and in the generation of the stimulus.



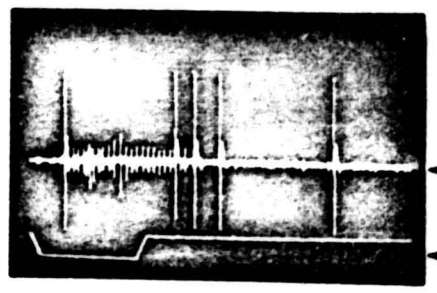
the pulsed tone was recorded on tape because, at high frequencies, the response of the tape recorder degraded the signal, (Figs.1 Record-Mode and 7).

Ten stimuli were presented for each test frequency, intensity and duration. Test experiments indicated some adaptation to stimulus repetition rates of 2 stimuli per second and unless stated otherwise a stimulus repetition rate of 1 stimulus every 1.5 seconds was used. Response intensity curves were determined by attenuating the stimulus in 5dB steps except near threshold where 1dB steps were investigated. During recording the stimulus intensity was reduced to determine the threshold level of the response. The lowest intensity at which a unit responded to two out of five successive stimuli was defined as the threshold level. Threshold curves were drawn indicating the range and sensitivity of units to the frequencies tested.

G) <u>Replay of data</u>.

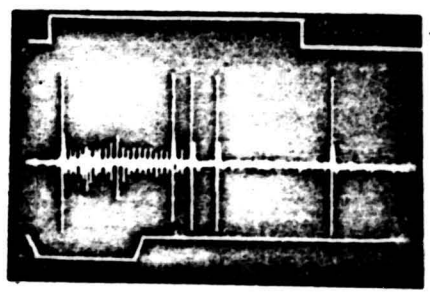
During replay the taped stimulus trigger was used to trigger the storage oscilloscope, (Tektronix D13) which displayed the response analog and stimulus "envelope", (Figs.1 Replay-Mode and 7). The stimulus trigger was also amplified (Xelex DD8) and used to gate

Fig.7 Diagram of the steps in the analysis of data and the generation of dot-displays, (for details see text).

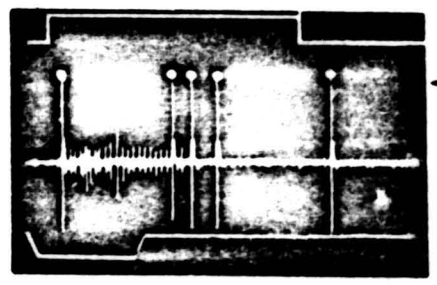


Response Analog

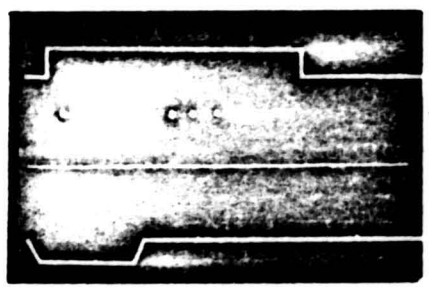
Stimulus



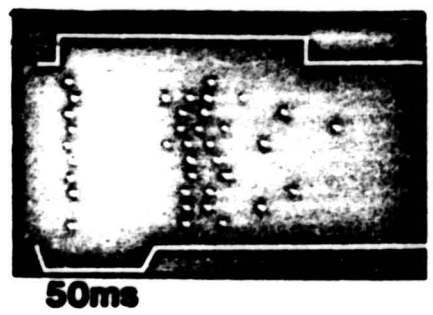
Window



Z-modulated bright-up of discriminated spikes



Triggers to counter



50ms

Dot-display of ten responses

the S1 channel output of the Grass S88 Stimulator which in turn triggered the TBG, (Fig.1 Replay-Mode). During analysis the TBG was used to produce and "envelope" (termed "window" during replay to distinguish from record-mode stimulus "envelope"), which had transient rise-fall times (less than 1μs), Fig.7. Whereas in the record-mode, the TBG gated a sine wave or white noise input, in the replay-mode the TBG was used to gate the response analog. Thus the TBG only passed the section of the response analog that occured in the "window",(Fig. 7). The position of the "window" in time (relative to the stimulus trigger pulse), could be moved by varying the "Delay Function" of the S1 channel of the Grass S88 Stimulator. The onset of the "window" could therefore be set for any point between the first trigger pulse (zero delay) and the succeeding trigger pulse, (maximum delay). The duration of the "window" could be changed by varying the "Continuously Variable Flat Top Duration" function of the TBG. By these means the entire stimulus-evoked response could be encompassed, whatever its latency or duration. For units with discrete "on" responses followed by silent periods and rebound excitation, the data were re-run to enable to enable different windows to be examined. The "windowed" analog signal was then

amplified (amplifier built in the department, frequency response 20Hz to 20kHz) and the output of this amplifier was then attenuated using a continously variable potentiometer. The signal provided the input to the S2 delay function of the stimulator and gated the S2 output. Since S2 delay requires a minimum of 6V input, adjustment of the potentiometer enabled the circuit to act as a Schmitt Trigger discriminator, a 13V square wave pulse being produced at the main S2 output for each discriminated spike regardless of the original spike amplitude. The S2 output was used to produce Z-modulation of the response analog fed directly to the left vertical amplifier of the Tektronix D13 oscilloscope via the External Intensity Input. This resulted in the brightening of the response analog at the voltage where S2 output was initiated, (Fig.7). The discriminator was set and maintained for each unit. The S2 output was also counted (Radio Spares counter 258-798) giving a digital record of spike number. Stimulus triggers were also counted in both replay and record modes, (Fig. 1).

Dot-displays were produced by reducing the intensity of the left vertical (response analog) oscilloscope beam until only Z-modulation brightened dots were visible, (Fig. 7). With the

oscilloscope in the storage mode, dot data could be displayed and the responses to successive stimuli moved down the screen using a D.C. resistor-division circuit. Each dot-display was photographed (Canon F.P. camera; Kodak Recording Film 2475, 12mm extension ring), and summarized the data obtained for either 5 or 10 successive presentations of any stimulus, (Fig. 7). A photographic record of the response analogs for selected stimuli were also taken. In most cases this was the approximate "mean" response for any stimulus. This mean value was determined from the pulses counted by the Radio Spares counter. From counts of spike numbers, means, standard-deviations and variances were calculated.

CHAPTER III.

Response Properties of Primary Auditory Fibers in the Cricket

Teleogryllus oceanicus (Le Guillou).

Summary:

Single unit recordings of primary auditory fibers of Teleogryllus oceanicus show responses to frequencies over the range 0.5kHz to 42kHz. The characteristic frequencies, (ChFs) of units were distributed over most of the bandwidth investigated although few units were recorded with ChFs below 4kHz or in the region 7kHz to 10kHz. Some units showed more than one peak of sensitivity and others were broad-banded with no tuning to a particular frequency. Units whose ChFs approximated to the carrier frequency of the proclamation song were the most highly tuned. The majority of units had a tonic response pattern and were not spontaneously active. The implications of these findings are discussed.

Introduction.

In the cricket, sense organs responsive to substrate and airborne vibration are situated in the proximal part of the tibia. The subgenual organs respond to low frequency airborne sound (below 3kHz) and substrate vibration, and are present in all three pairs of legs, (Dambach, 1972,1976). Only the anterior tibiae possess tympana and complete tympanal organs, the morphology of which is well documented, (Young and Ball, 1974; Eibl, 1978). Previous physiological studies at the level of the tympanal nerve have shown a correlation between the carrier frequency (C.F.) of the conspecific songs and the tuning of the tympanal organs in a variety of crickets (e.g. Nocke, 1972 and Hill and Boyan, 1977). Nocke, (1972) showed that the threshold curve for the tympanal organ of Gryllus campestris had at least two optima; one near 4kHz and a second at 14kHz. These were the frequencies at which the spectrograms of the calling and rivalry songs show main and secondary peaks; the courtship song shows a single peak at 14kHz. Zhantiev and Tshukanov, (1972) also showed two response peaks in G. bimaculatus. Further, by destruction of the branches of the tympanal nerve, they showed that the low frequency peak (optimum

4-5kHz; range 1-15kHz) could be ascribed to the proximal part of the tympanal organ, while the high frequency peak (optimum 16kHz; range 10-50kHz) originated from the distal portion. Anatomical studies also suggest a subdivision of the receptor cells into at least a proximal and a distal group, (Young and Ball, 1974; Eibl, 1978) but the morphological basis of any frequency discrimination is still problematical. The evidence may be indicative of frequency discrimination by a minimum of two groups of cells in the cricket ear but the extent of the frequency resolution cannot be ascertained using gross recording techniques since only the more accessible axons may be recorded. At the single unit level Esch et al., (1980) suggest that in G. campestris and G. bimaculatus, fibres tuned to the C.F. of the calling song predominate. Within the frequency range investigated, (2kHz to 20kHz) 22 out of 34 units were most sensitive to 4-5kHz (the C.F. of the calling songs). In addition two fibres responding to higher frequencies (best frequencies/characteristic frequency (ChF), 12kHz and 17kHz) were recorded and, in four animals, fibres which were maximally responsive below 2kHz. This paper presents the results of an investigation, at the single unit level, of primary fibres of Teleogryllus oceanicus over the frequency range 500Hz to 42kHz.

Materials and Methods.

The crickets were obtained from a culture held in the laboratory. Both male and female crickets were used two to six weeks after the final moult; successful recordings were made in 30 animals.

The crickets were anaesthetised with carbon-dioxide gas and the antennae, mesothoracic, metathoracic legs and both pairs of wings removed. The insect was waxed with its ventral surface uppermost to a thin perspex holder and a silver wire serving as the indifferent electrode, inserted into the abdomen. The prothoracic legs were waxed at the femora and tibiae to thin, right-angled wires attached to the stand. The gut was removed and the cavity plugged with paper tissue soaked in insect ringer, (Clark's). A small piece of soft cuticle was removed between the prothoracic sternellum and the base of the coxa to give access to the leg nerve, (LN). Neither the prothoracic ganglion nor the acoustic tracheae were exposed during the dissection.

The preparation was positioned 21cm above the experimental baseplate with the head towards the loudspeaker for the initial recording. Rotation through 180° enabled the other

LN to be examined. This procedure resulted in the original recordings being made with the anterior tympana facing the sound source; following rotation the posterior tympana faced the source.

The experimental room was approximately 3.0 x 2.5 x 2.5m and was situated in a basement. A chipboard channel, square in cross-section (1.0 x 1.0 x 1.3,), and closed at one end ran diagonally across the room. The channel was lined with mineral-wool wedges (Rockwool) which were also used to cover the walls opposite the open end of the channel. The loudspeakers were sited at the closed end of the channel. An Audax TW8B, (specified frequency range 1Hz to 40kHz), was used to emit frequencies exceeding 5kHz up to a maximum of 42kHz. Low frequency stimuli (below 5kHz) were emitted using a Kef B200 loudspeaker, (specified frequency range 25Hz to 3.5kHz). The preparation was situated on a base-plate below the open end of the channel and the sound-field intensity was uniform within 1dB at a radius of 4cm from the insect. Echoes were not detected on either the Bruel and Kjaer equipment or on the oscilloscope at the frequencies investigated. All dB values are given with reference to $0.00002 N/m^2$.

Glass microelectrodes filled with 3M potassium

chloride (20 to 40MOhm), were used for recording and were advanced using a remote hydraulic microdrive (Clarke HMD-1M). Responses were monitored both visually and on headphones.

The search stimulus (50ms duration, 5ms rise-fall time, one stimulus every 1.5s) consisted of the mixed output of two oscillators set at 5 and 12kHz, (Taylor, 1978a,b). When a single unit was obtained the 5 and 12kHz components of the search stimulus were tested individually to ascertain if the unit was "low" or "high" frequency responsive. During experiments these oscillators were switched off and the output of a more accurate Farnell FG2 continously variable oscillator was used as the stimulus. The output frequency was monitored using a Heathkit counter. Sound intensities were changed using a Hatfield 2125 Attenuator which could be varied in 1dB steps over 100dB. The rise-fall time of the stimulus was always 5ms and the 50ms stimulus duration was chosen to approximate to the syllable duration of the conspecific song. However a variety of fixed stimulus durations could also be selected; "continous" tones (exceeding 600ms duration) were occasionally used. The effect of a stimulus repetition rate of 10 stimuli/s was also investigated. This rate approximates to

the syllable repetition rate in the proclamation song of T. oceanicus.

Due to the instability of the unit recordings (see also Esch et al., 1980) only 5 stimuli were usually presented at each frequency, intensity and duration. Further, it was not always possible to collect complete response-intensity data. Threshold curves were collected for each unit, the threshold level being defined as the lowest sound intensity which elicited a response to at least two out of five successive stimuli.

The stimulus trigger, stimulus "envelope" (defined as the D.C. gate for the tone pulse) and the response analog were recorded on magnetic tape (Philips instrumentation recorder Ana-log 7, frequency response 1Hz to 5kHz on DR at 15ips). Spikes were discriminated off-line using the Schmitt trigger of a Grass S88 delay function. The TTL-compatible S2 output pulses were then counted (Radio Spares Counter 258-798). Means, standard-deviations, variances and cumulative counts of spike number were calculated. The approximate mean response analog for selected stimuli together with dot-displays summarising the responses to five identical stimuli were photographed. Latencies were determined and defined as the time between the onset of the stimulus and the first spike of the response.

Results.

A. Characterisation of units by their Threshold Curves.

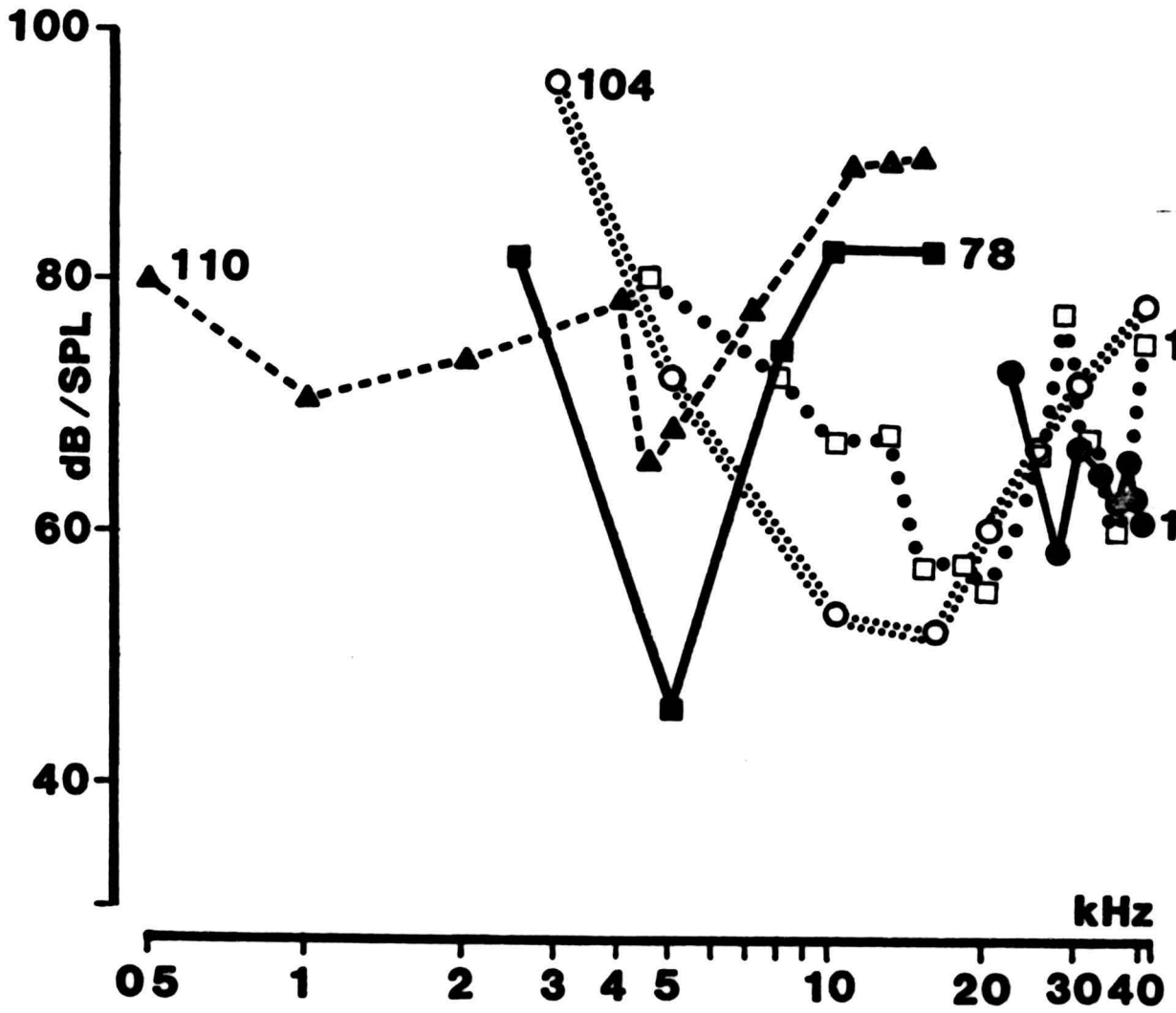
a) 15 recorded units (36%) were maximally sensitive to frequencies in the range 4 to 5kHz, (Fig.8 e.g.78) and are therefore tuned to the C.F. of the proclamation song, (4.5kHz, Hill, 1974). The threshold curves of these units were sharply tuned and the roll-off values on either side of the ChF were between 35 and 107dB/octave, (see also Fig.10). The maximum sensitivity at the ChF of these units ranged from 46 to 69dB. If the dynamic range of a single unit is considered to be 30dB, these units could potentially code intensities from 46 to 100dB; i.e. intensity coding may be extended by range fractionation (Rheinlaender, 1975).

The majority of the units with ChFs approximating the C.F. of the proclamation song did not respond to frequencies in excess of 20kHz.

b) 10 units, (24%) had threshold curves which were broad-banded with no tuning to a specific frequency, Fig.8 e.g.110. Such units were relatively insensitive and did not respond to frequencies above 30kHz.

c) Threshold curves of 10 units (24%) showed maximum sensitivity to

Fig.8. Representative threshold curves of single primary units showing the distribution of characteristic frequencies over the range 0.5kHz to 42kHz. (Animal Nos. 78, 104, 107, 110 and 111).


100
80
60
40
dB/SPL
104
110
78
107
111
kHz
05
1
2
3
4
5
10
20
30
40

frequencies in excess of 10kHz, (Fig.8 e.g. 104). They were more broadly tuned than units with ChFs in the range 4kHz to 5kHz.

d) 3 units, (7%) were recorded with threshold curves which were incomplete but which indicated probable maximum sensitivity to frequencies in excess of 40kHz, (Fig.8 e.g. 111).

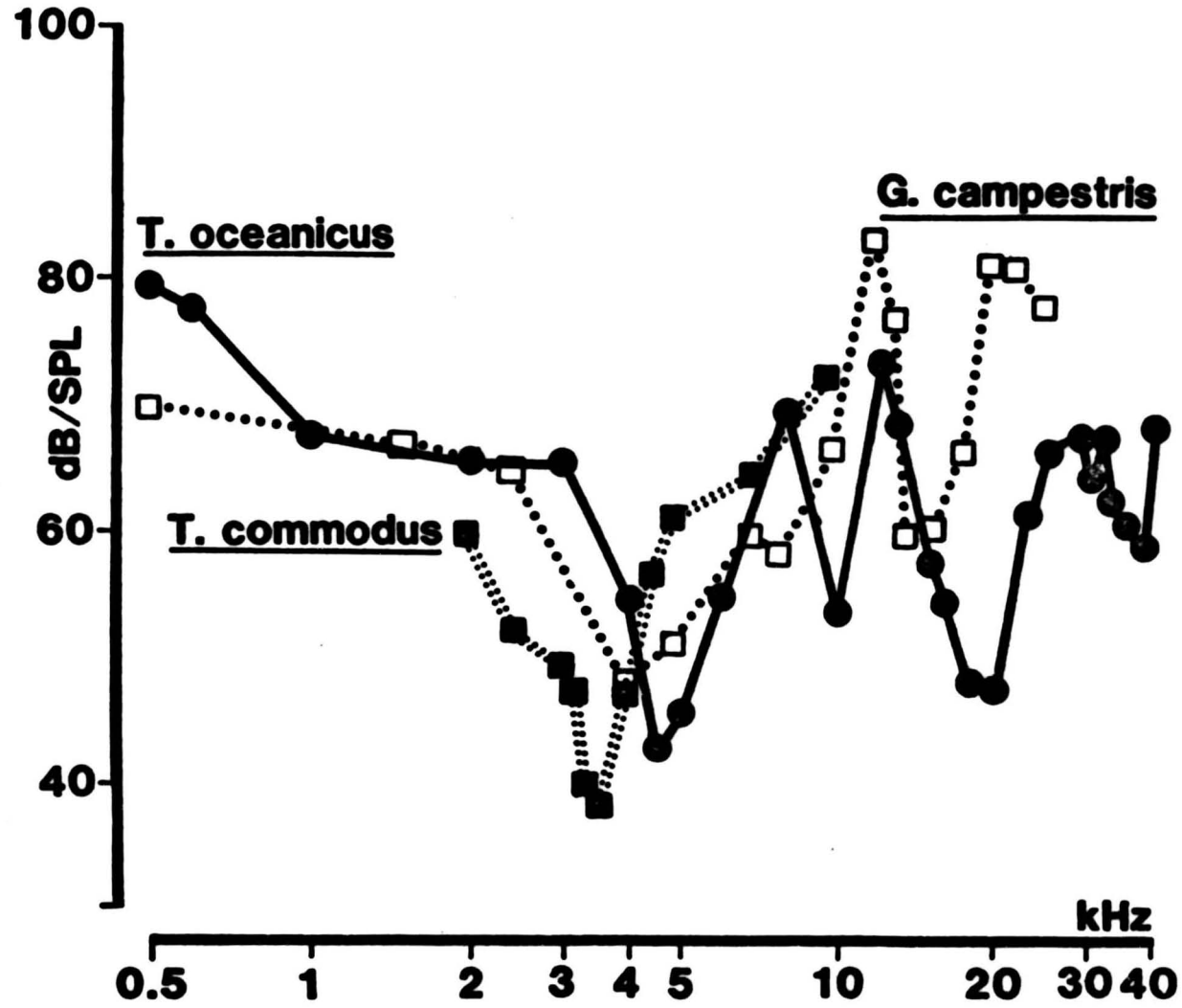
e) 4 units, (10%) were recorded which showed two distinct peaks of sensitivity, Fig.8 e.g. 107; this unit had optima at 20 and 30kHz, (c.f. Esch et al., 1980).

This data shows that primary units can code frequencies over the range 0.5kHz to 42kHz although there are frequency gaps in which no tuned units are found.

B. Derived Tympanal Nerve Threshold Curve.

The lowest intensity required to elicit a response in any unit to each of the test frequencies was determined and on the basis of all primary data a threshold curve for the tympanal organ was derived, (Fig.9). High intensities (79dB) were required to elicit a response to airborne sound at 0.5kHz and may indicate that these units are preferentially responsive to substrate vibration, (see Kalmring et al., 1978). Above 1kHz the threshold curve shows four peaks of sensitivity at what may be harmonically related

Fig.9 Derived threshold curve for T. oceanicus (for details see text) and the comparable threshold curves obtained for T. commodus (after Hill and Boyan, 1977) and G. campestris (after Nocke, 1972).

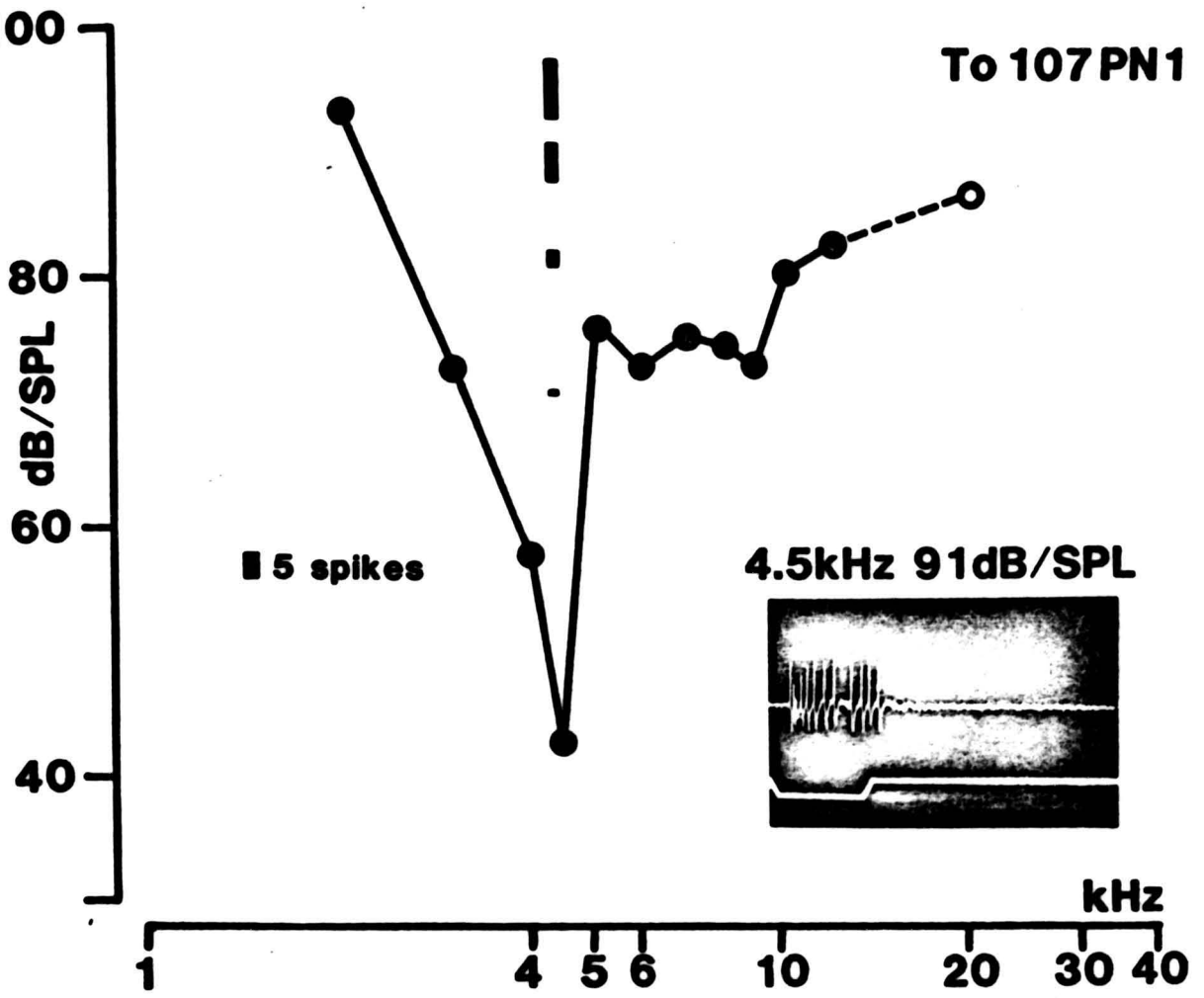

100
80
60
40
dB/SPL
T. oceanicus
G. campestris
T. commodus
kHz
0.5
1
2
3
4
5
10
20
30
40

frequencies. The curves obtained for tympanal nerve recordings in G. campestris, (Nocke, 1972) and T. commodus, (Hill and Boyan, 1977) are also shown. The threshold curve of T. commodus has an optimum at the C.F. of the proclamation song (3.8kHz) but the range of frequencies investigated was limited. The threshold curve for G. campestris has two distinct optima at 4 and 14kHz which coincide with peaks in the spectrograms of the conspecific songs, (Nocke, 1972). The derived curve for T. oceanicus is more sensitive than that for G. campestris to frequencies in excess of 4.5kHz and the frequency range investigated extends beyond that used by Nocke.

C. Representative Units of Differing Response Types.

To107PN1: The threshold curve of this unit was highly tuned, (lower roll-off; 45dB/octave, upper roll-off; 107dB/octave), and centered on the C.F. of the proclamation song, (Fig.10). At the ChF the unit responded with only a single spike at intensities from threshold to Th+30dB. At higher intensities the response consisted of a volley of spikes. The dynamic range within which spike number increased linearly with logarithm of stimulus intensity at the ChF was approximately 20dB, (Th+30dB to Th+50dB). The unit responded

Fig.10 Threshold curve for unit To107PN1 with ChF at 4.8kHz. Bars represent mean spike number in response to a 50ms stimulus at 4.8kHz; stimulus intensities represented by the baseline of each bar. Inset; response analog to the stimulus parameters shown.


100
80
60
40
dB/SPL
To 107PN1
5 spikes
4.5kHz 91dB/SPL
kHz
1
4
5
6
10
20
30
40

tonically at Th+50dB with a mean response latency of 10ms, (Fig.10 insert). At 4.5kHz at an intensity of 86dB, spike number increased linearly with stimulus duration over the range 25 to 100ms; the unit was not spontaneously active.

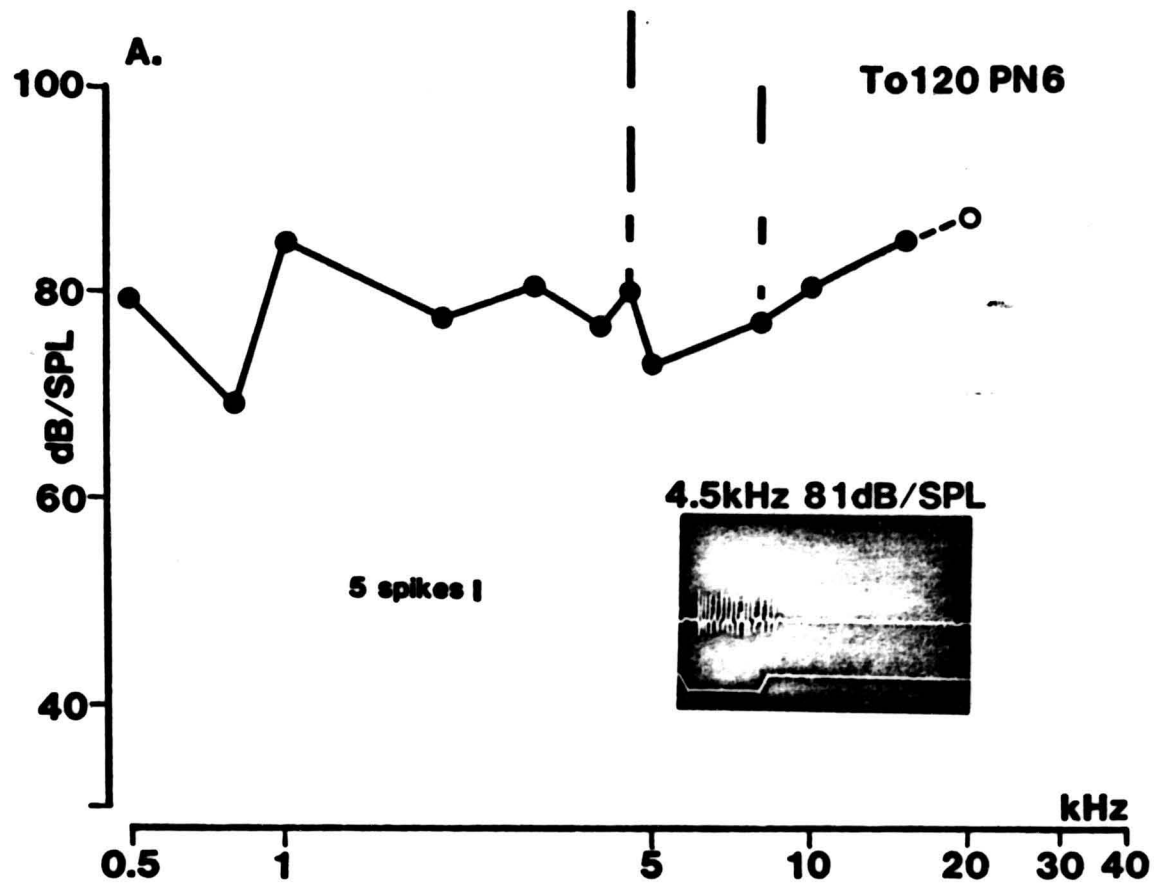
To120PN6: The threshold curve of this unit was broad-banded; it was relatively insensitive,,(maximum sensitivity 69dB at 0.8kHz)and was not spontaneously active, (Fig.11 A).

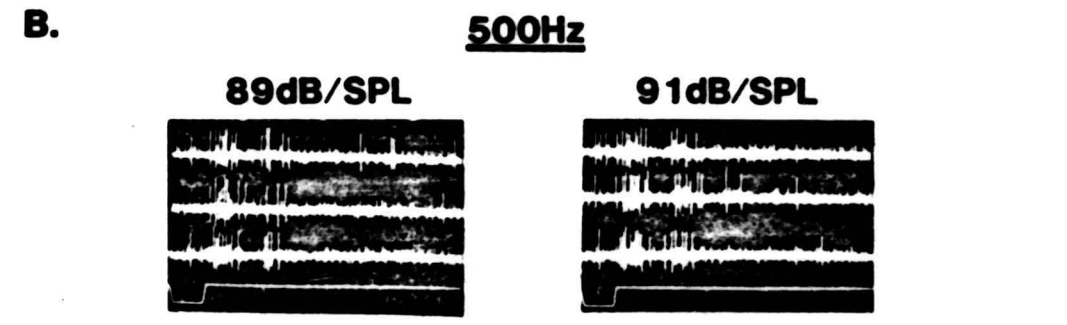
At 4.5kHz and 8kHz the response was "simple" consisting of a tonic discharge during the stimulus presentation; no rebound activity was observed, (Fig.11A insert). Spike number increased with stimulus intensity for at least 15dB above threshold and was mirrored by a decrease in the latency of response.

At 0.5kHz the response pattern of the unit was atypical, spikes only occuring at the termination of the stimulus. At higher intensities the response consisted of tonic firing followed by a silent period and "rebound" activity. The signal to noise ratio at this point in the experiment was not high enough to permit quantitative analysis but analogs of responses to three successive stimulus presentations are shown, (Fig.11B).

To105PN1: This threshold curve shows two distinct peaks of sensitivity

Fig.11A Threshold curve for unit To120PN6. Bars as in Fig.10. Inset; response analog for a 50ms stimulus. B. Response of unit To120PN6 to a 500Hz stimulus at two intensities.


A.
100
80
60
40
dB/SPL
To120 PN6
4.5kHz 81dB/SPL
5 spikes I
kHz
0.5
1
5
10
20
30
40


B.
500Hz
89dB/SPL
91dB/SPL

at 6kHz and 20kHz, and responses were elicited over the entire range from 2 to 40kHz, (Fig. 12A). The response pattern was tonic. At 4.5kHz the mean spike number increased linearly over the range Th+8 to Th+23dB and was related to a decrease in the latency to first spike. Responses to five successive stimuli showed no adaptation.

At 35kHz the mean spike number increased with intensity up to Th+10dB after which the response decreased and then plateaued at Th+20dB (Fig.12B). This decrease in response is due to a reduction in the spike number per response rather than to adaptation to successive stimuli. The mean latency of the first spike decreased with intensities up to Th+10dB, then remained constant. At 4.5kHz the mean spike number increased with stimulus durations up to 400ms. Stimulus duration was also coded at 35kHz, although some adaptation to successive stimuli was evident with durations in excess of 400ms.

To 111PN7 and PN8: Units N7 and N8 were recorded simultaneously. The threshold curve of N7 was broad-band extending from 10 to 40kHz and was relatively insensitive, (Fig.13). Spike number increased gradually with intensity at 22,27 and 35kHz; at 38kHz a high spike number was elicited at Th+3dB. At frequencies lower than 22kHz the response of N7 masked that of N8. N8 was more sensitive than

Fig.12A Threshold curve for unit To105PN1. Bars as in Fig.10.

Inset; response analog to a 50ms stimulus.

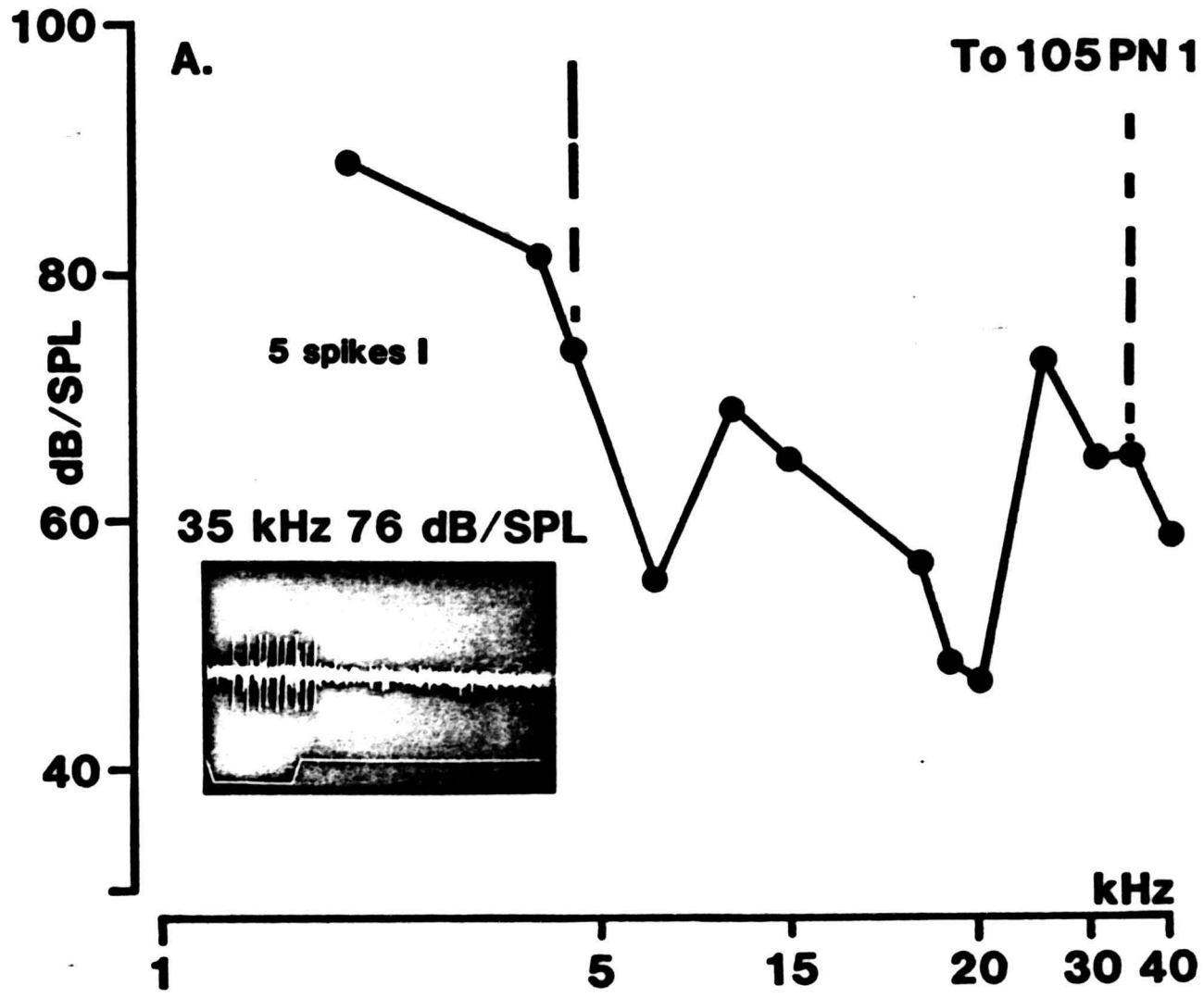

100
80
60
40
dB/SPL
A.
To 105 PN 1
5 spikes I
35 kHz 76 dB/SPL
kHz
1
5
15
20
30
40

Fig.12B. Left upper:mean spike response per stimulus to 4.5kHz and 35kHz versus intensity above threshold. Left lower: mean latency in ms against dB above threshold for these two frequencies, (Error bars are not shown since the variance was less than 2.4 spikes/stimulus). Right upper: Cumulative spike number at 35kHz for six intensities above threshold. At each intensity the increase in spike number with successive stimuli is similar. Right.lower: as right upper but at 4.5kHz, four intensities tested, (for details see text).

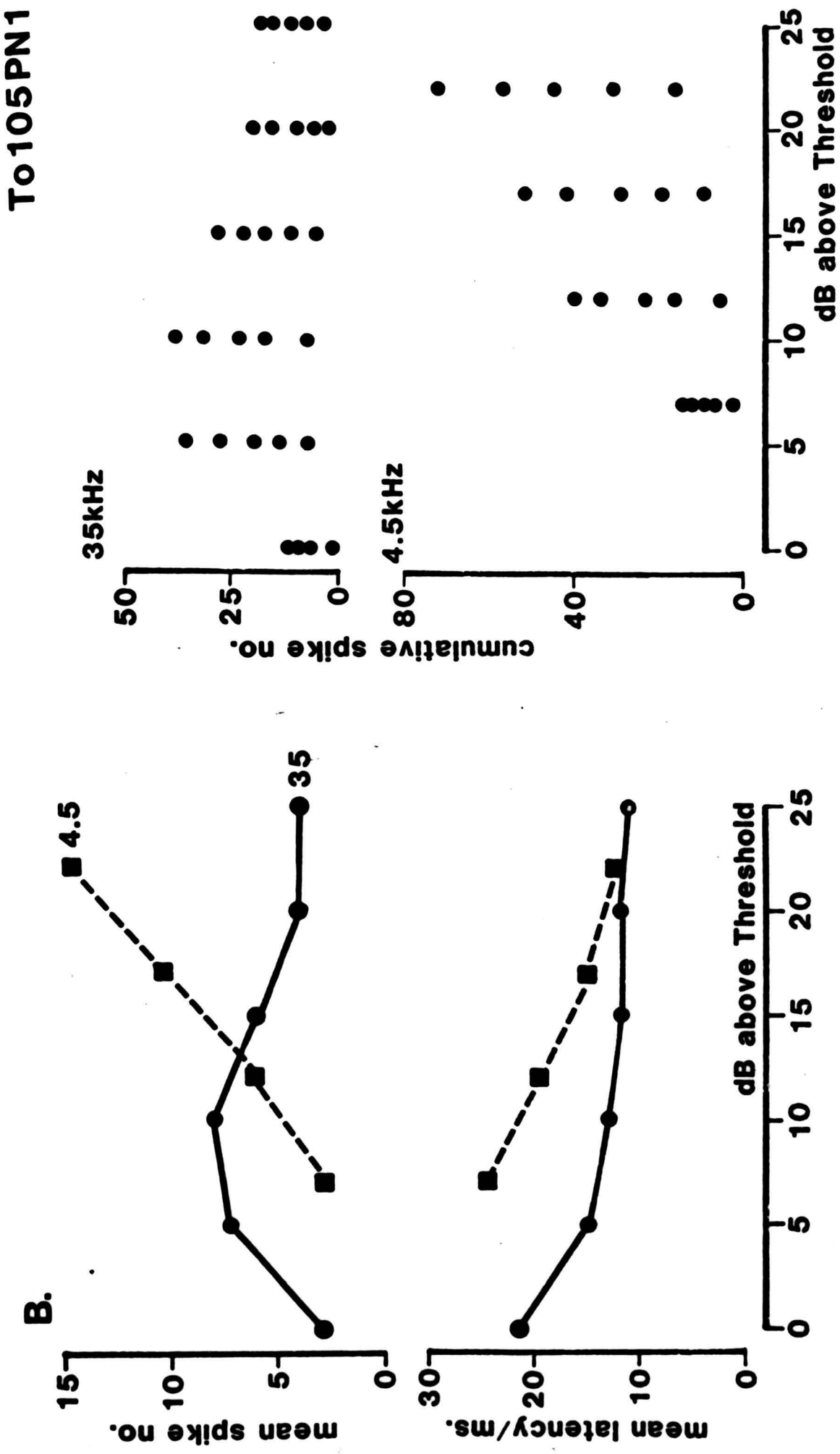
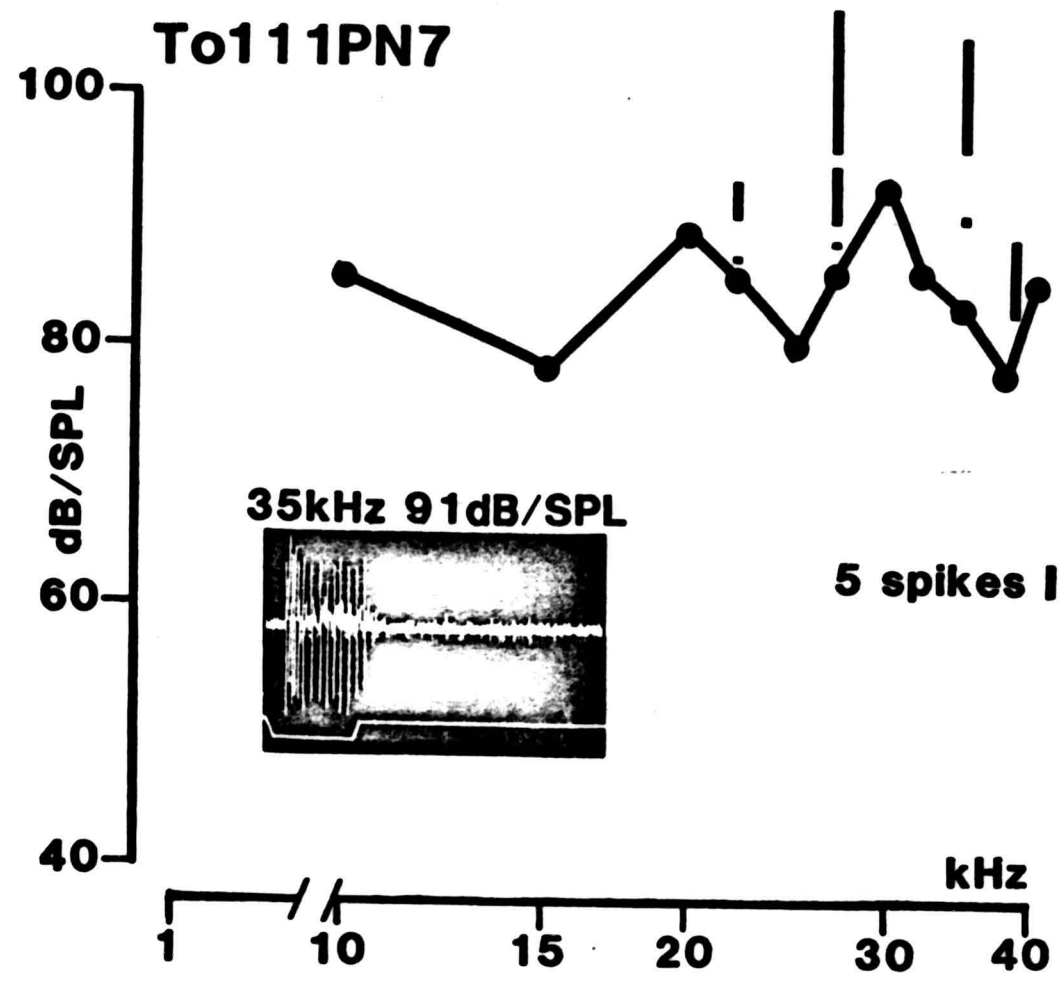
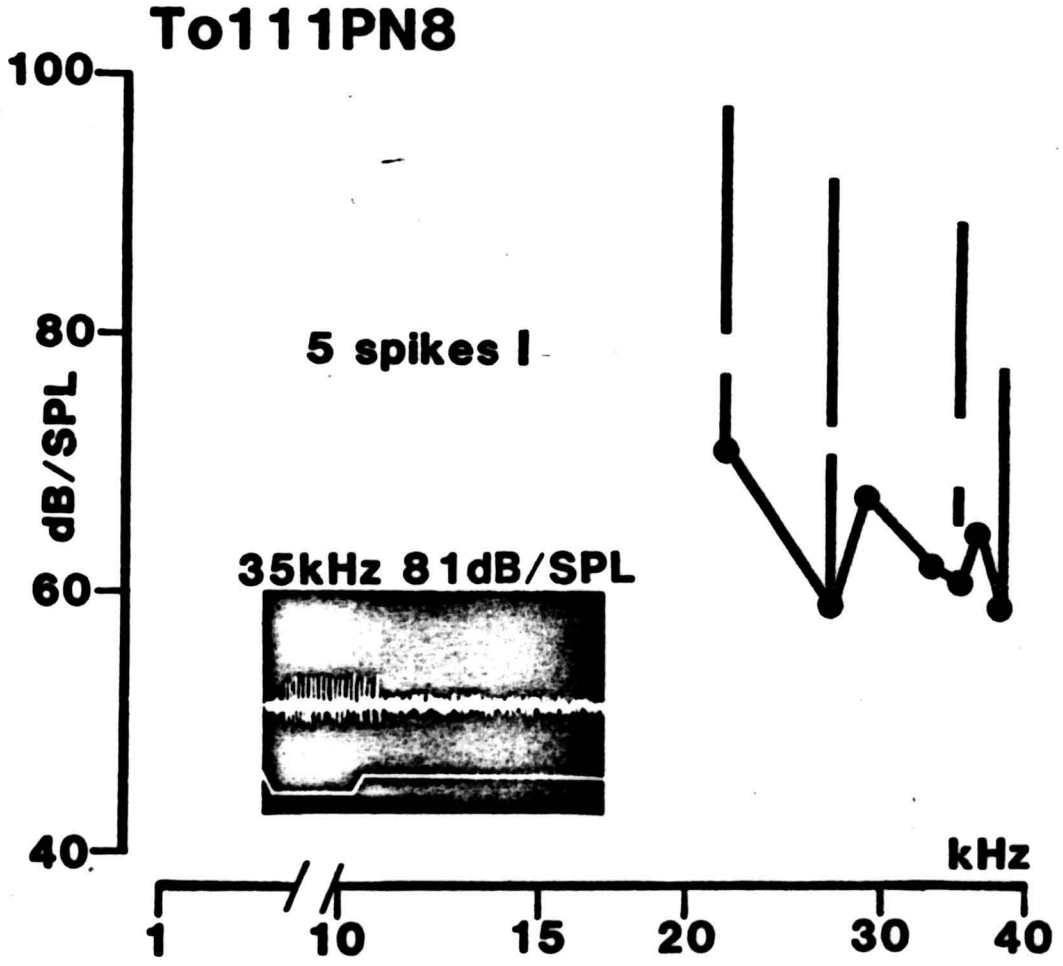

To105PN1
35kHz
4.5kHz
50
25
0
80
40
0
cumulative spike no.
0
5
10
15
20
25
dB above Threshold
B.
4.5
35
15
10
5
0
mean spike no.
30
20
10
0
mean latency/ms.

Fig.13 Threshold curves for two units recorded simultaneously

Response bars as in Fig.10. Insets show response analogs to 50ms stimuli.


To111PN7
100
80
60
40
dB/SPL
35kHz 91dB/SPL
5 spikes I
kHz
1
10
15
20
30
40


To111PN8
100
80
60
40
dB/SPL
5 spikes I
35kHz 81dB/SPL
kHz
1
10
15
20
30
40

N7 to frequencies in excess of 22kHz and responded up to at least 42kHz. The amplitude of the response of N8 was insufficient for electronic counting but the signal to noise ratio enabled the unit to be counted by eye. Unlike N7, N8 responded with a volley of spikes even at threshold; maximum response was reached at approximately Th+10dB.

D. Response Patterns of Primary Units.

The majority of primary units responded with a tonic discharge at suprathreshold intensities. With increasing intensity the latency of response decreased to a minimum of 6ms, (Fig.14a,f). At the C.F. of the proclamation song (appro imately 4.5kHz) the typical discharge pattern was elicited, although in Fig.14b the after-discharge is more pronounced. Primary units responding phasically with a single spike were recorded in four experiments, (Fig.14c). Response patterns consisting of an initial volley of spikes, a"silent" period, and a second volley of spikes were observed in some units in response to 0.5kHz, 27kHz and 35kHz, (Fig.14d,e; c.f. Nocke, 1972). At o.5kHz the initial volley of spikes only occured on termination of the stimulus. In contrast at 35kHz the entire response occured during the stimulus period.

Fig.14 Response analogs showing the range of response patterns obtained for units from the tympanal nerves of T. oceanicus. Stimulus parameters as given; stimulus durations, 50ms.

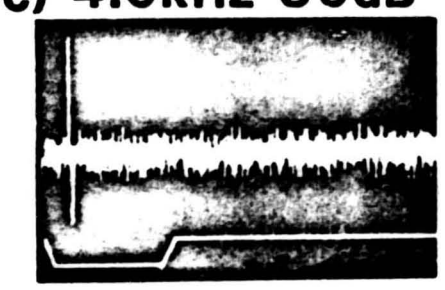
us.

1 stimulus/1.5s

a) 4.8kHz 91dB

b) 5kHz 91dB

c) 4.6kHz 86dB



d) 500Hz 91dB

e) 27kHz 94dB

f) 30kHz 87dB

Discussion.

Previous studies of the cricket auditory system have concentrated on those frequencies that are characteristic of the almost pure-tone species songs; little attention has been paid to frequencies outside this range. The tympanal whole nerve threshold curves obtained for G. campestris, (Nocke, 1972) and Scapsipedus marginatus, (Zaretsky, 1972) show two threshold minima, one at the C,F, of the proclamation song and one at the third harmonic. Zaretsky and Eibl, (1978) using suction electrodes on S. marginatus showed that different groups of units responded to the C.F. of the proclamation song and to its third harmonic. They concluded that their results indicated a lack of uniformity in the size and distribution of tympanal receptor axons of S.marginatus. Esch et al., (1980) reported a clustering of single unit threshold curves at 4, 10 and 15kHz in G. campestris. On this basis they suggested a separation of acridid grasshoppers, bush-crickets and gryllids based on the degree of grouping of receptor threshold curves. They concluded that the difference might reflect the constraints of auditory behaviour in these species; crickets produce narrow-banded songs whereas those of bush-crickets and acridid grasshoppers are

broad-banded. However the apparent grouping of threshold curves at the C.F. of the species songs may be due to bias in the recording techniques employed by these studies. The frequency ranges investigated extended only from 2kHz to 20kHz. Thus while the proportion of recorded units with characteristic frequencies (ChFs) similar to the carrier frequency (C.F.) of the songs appears high, units with ChFs above 20kHz and below 2kHz may have been missed, perhaps entirely: no statement as to their prevalence can therefore be made. The search-stimulus used by Esch et al., (1980) was a synthesised proclamation song with a C.F. of 4-5kHz; this may have resulted in a "preferential" recording of units with ChFs at this frequency. Kalmring et al., (1978) showed that the primary units of the tettigoniid Decticus verrucivorus were tuned to frequencies across the whole of the bandwidth investigated, (2kHz to 40kHz) and in this study a determined attempt was made, using a high frequency stimulus to search for ultrasound units. Although the threshold curves for units in T. oceanicus are less tuned than those in D. verrucivorus the ChFs do range over most of the bandwidth investigated, (0.5kHz to 42kHz). Few units were recorded with ChFs below 4kHz or in the region 7 to 10kHz but units were recorded whose ChFs are

likely to be above 42kHz, (Fig.8). This study suggests that the primary units of the cricket are more similar to those of tettigoniids and acridid grasshoppers than had been previously thought. Therefore the separation suggested by Esch et al. appears premature. Broad-band reception and frequency analysis may be important when both interspecific interactions and conspecific communication are considered. Behavioural studies have indicated broad-band reception by gryllids. Popov et al., (1975) found that tethered G. bimaculatus tended to move away from a loudspeaker emitting high frequencies. Moiseff et al., (1978) presented a synthesised conspecific song (C.F. 3kHz to 100kHz) to adult female T. oceanicus and studied the steering responses of the tethered cricket. Their results indicated positive phonotaxis to stimuli with C.Fs from 3kHz to 9kHz but negative phonotaxis when the C.Fs ranged from 30kHz to 70kHz. The ability to analyse broad-band sounds means that more potential information is available to the animal in terms of frequency, intensity and direction. At higher frequencies the acuity of localization should improve as shown by Hill et al., (1980); Coles et al., (1980) in the quail. This possibility must be tested behaviourally for the cricket but it may prove difficult to demonstrate if the

response is one of negative phonotaxis as suggested by Hill, 1974; Popov et al., 1975 and Popov and Shuvalov, 1976.

CHAPTER IV.

Response Properties of Central Auditory Fibers in the Cricket Teleogryllus oceanicus (Le Guillou).

Summary:

Single unit recordings of central auditory fibers of Teleogryllus oceanicus show responses to frequencies over the range 1kHz to at least 40kHz. Approximately 50% of units had broad-band threshold curves with indistinct peaks of sensitivity. Some broad-band units had secondary peaks of sensitivity near the carrier frequency of the proclamation song. Only 10% of units were tuned to frequencies below 10kHz, while 40% of units were tuned to frequencies in excess of 10kHz. The derived threshold curve for all central unit data had two major peaks of sensitivity at 4.8kHz and 22kHz. Some units have highly complex response patterns involving correlated spiking responses, silent periods and rebound activity and the response pattern of a single unit may vary with both intensity and frequency of the stimulus. The implications of these findings are discussed.

Introduction.

The ventral nerve cord of insects contains both ascending and descending auditory neurons as well as T-shaped neurons which connect both rostral and caudal parts of the central nervous system, (Suga and Katsuki, 1961a,b; Zhantiev and Tschukanov, 1972). Ventral cord neurons in the acridid Locusta migratoria (Kalmring, 1975; Cökl, 1977) and in tettigoniids, (Khüne et al., 1980) have been shown to respond to both vibrational and airborne sound stimuli. The primary neurons are thought to project to the ventral cord neurons either directly or via interneurons and the combination of inputs to each ventral cord neuron will determine its response characteristics.

Most neurophysiological studies in crickets have concentrated on the responses to the frequencies typical of intra-specific communication and few have looked at the effects of frequencies in excess of 20kHz. Rheinlaender et al., (1976) reported a ventral cord unit in Gryllus bimaculatus responding to frequencies ranging from 3kHz to 50kHz and suggested that it might be used in predator avoidance behaviour. Popov et al., (1975) found that G. bimaculatus tended to move away from high frequency stimuli and Moiseff et al., (1978) demonstrated negative phonotaxis by Teleogryllus oceanicus

to stimuli with carrier frequencies ranging from 30kHz to 70kHz. Earlier work (Hutchings and Lewis, in press) demonstrated that primary units in the leg nerve of T. oceanicus responded to frequencies over the range 500Hz to at least 42kHz. In this study of ventral cord units, frequencies in the range 1kHz to 40kHz were investigated Each unit was tested with a wide range of artificial stimuli throughout its frequency range to enable a more complete characterisation of its responses.

Materials and Methods.

The crickets were obtained from a culture held in the laboratory. Both male and female crickets were used two to six weeks after the final moult; successful recordings were made in 38 animals.

The crickets were anaesthetised with carbon-dioxide gas and the antennae, mesothoracic, metathoracic legs and both pairs of wings removed. The insect was waxed with its ventral surface uppermost to a thin perspex holder and a silver wire, serving as the indifferent electrode, inserted into the abdomen. The prothoracic legs were waxed to thin right-angled wires attached to the stand.

The gut was removed and the cavity plugged with tissue soaked in Clarke's insect ringer. The neck cuticle was cut away to reveal the ventral neck connectives between the suboesophageal and the prothoracic ganglia. Care was taken to minimize damage to tracheae and the acoustic tracheae were left intact. A small piece of moistened blue tissue paper was inserted beneath the connectives.

The preparation was placed in a Faraday cage in anechoic conditions:the temperature of the experimental room was maintained at 23°C ± 2°C. Details of the recording apparatus and stimulus production have been described elsewhere, (Hutchings and Lewis, in press 1981 p40). Glass microelectrodes were used to record the activity of single units in the ipsilateral connective. The electrodes were filled with 3M potassium chloride; the measured resistances ranged between 20MOhm and 40MOhm.

At least ten stimuli were presented at each frequency, intensity and duration, and the response analog, stimulus trigger and stimulus "envelope" (defined as the D.C. gate for the tone pulse) recorded on magnetic tape (Philips instrumentation recorder Ana-log 7, frequency response 1Hz to 5kHz on DR at 15ips). Data was analysed off-line as described elsewhere, (Hutchings and Lewis, in press 1981 p43).

Results.

A. Characterisation of Units by their Threshold Curves.

a) 5 units, (13.2%) had characteristic frequencies (ChFs) approximating the carrier frequency, (C.F.) of the proclamation song, (4.5kHz) Fig.15a, unit 22. A further 9 units showed secondary peaks of sensitivity in this region, (Fig.15a, units 29 and 24). The minimum intensity required to elicit a response from any unit to a 4.5kHz tone was 36dB.

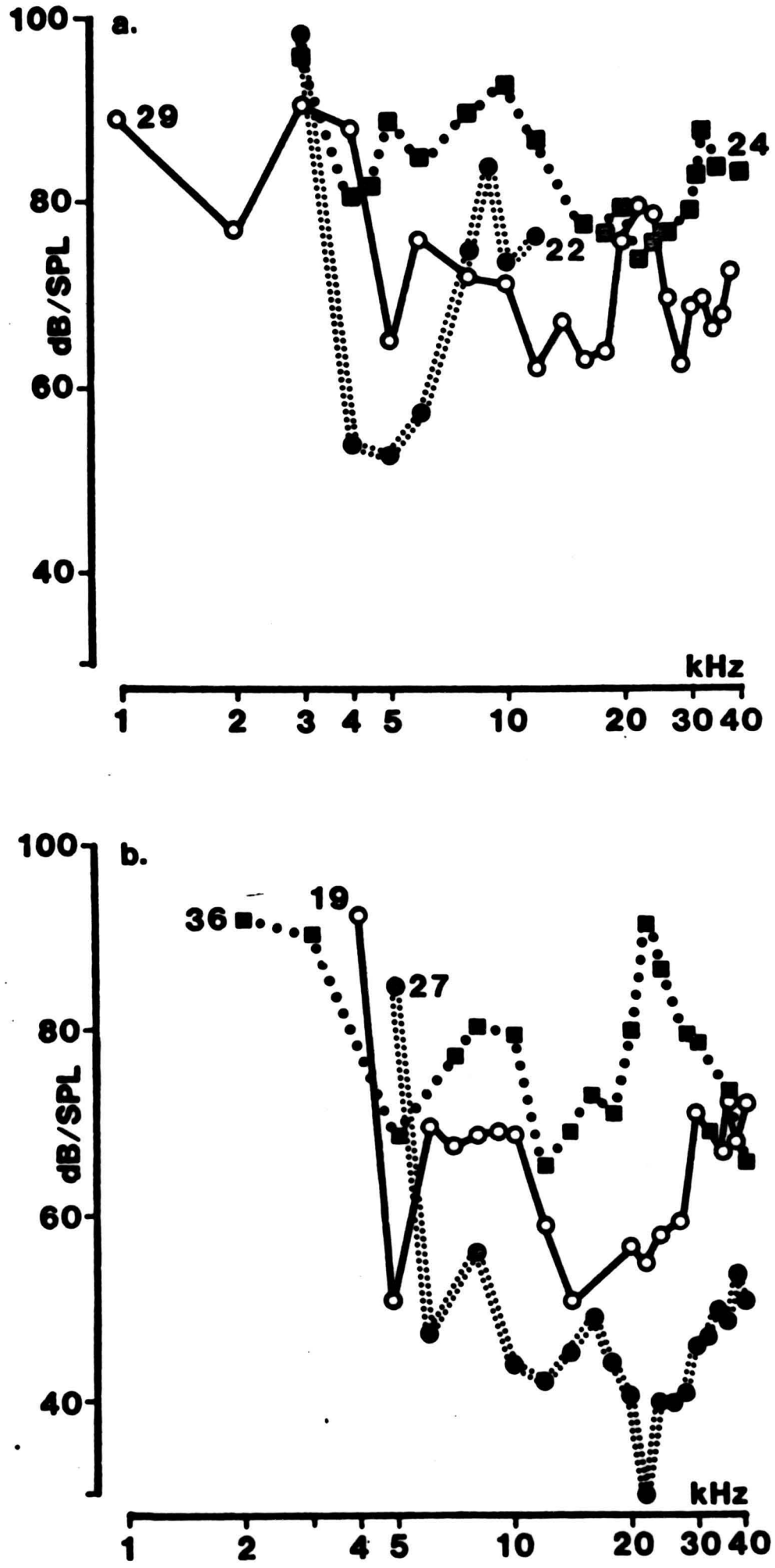
b) Threshold curves of 18 units, (47.4%) were broad-banded with indistinct peaks of sensitivity. Many of these units responded to frequencies over the range 1kHz to at least 40kHz, (Fig.15a, unit 29). The threshold curves of some other broad-band units showed more than one defined peak of sensitivity, (Fig.15b, unit 36).

c) 15 units, (39.5%) had ChFs in excess of 10kHz, (Fig.15b, unit 27). Unit 27 was the most sensitive unit recorded, responding to 22kHz at 30dB. If the dynamic range of a unit is considered to be 30dB range fractionation at 22kHz by units in Fig.15b could enable coding of intensity over the range 30dB to 120dB.

B. Derived Threshold Curve for Units in the Cervical Connectives.

The lowest intensity required to elicit a response

Fig.15a,b; Representative threshold curves of single central units showing units with clear LF and HF characteristic frequencies e.g. units 22 and 27 (see text for details) and broad-band threshold curves e.g. units 29, 24 and 26.


a.
100
80
60
40
dB/SPL
29
22
24
kHz
1
2
3
4
5
10
20
30
40
b.
100
80
60
40
dB/SPL
36
19
27
kHz
1
2
4
5
10
20
30
40

in any unit to each of the test frequencies was determined and on the basis of all central unit data a threshold curve for the central neurons was derived, (Fig.16). Intensities in excess of 80dB were required to elicit a response at 1kHz. The derived curve had two major peaks of sensitivity at 4.8kHz and 22kHz. Above 22kHz the threshold levels increased although there was a slight improvement in sensitivity at 38kHz.

The derived curve for primary units recorded in T. oceanicus, (shown 20dB less sensitive than the real values to aid clarity) is presented for comparison, (Fig.16). Both curves have peaks of sensitivity at the C.F. of the proclamation song and at 22kHz and 38kHz. No units were recorded that were tuned to frequencies in the range 7kHz to 10kHz; this frequency band apparently constitutes a relatively insensitive region in the derived threshold curves of both central and primary units. Few individual primary and central unit threshold curves could be directly compared but primary unit 107 and central unit 38, recorded in different animals, had strikingly similar curves both in respect of their ChFs, (4.8kHz) and their $Q_{10}{}^{dB}$ values on either side of the C.F., (Fig,17). However there are differences, notably the peak in unit 38 at 6kHz.

Fig.16 Derived threshold curve for T. oceanicus central (C) units. The comparable threshold curve for T. oceanicus primary (P) units is shown 20dB less sensitive than the real values to aid clarity, (for details see text).

TableI Numbers and percentages of recorded central and primary units with broad-band, (Broad); low frequency, (L.F.) and high frequency, (H.F.) characteristic frequencies, (ChF). Units with more than oneChF are combined with the broad-band numbers, (see text for further details).

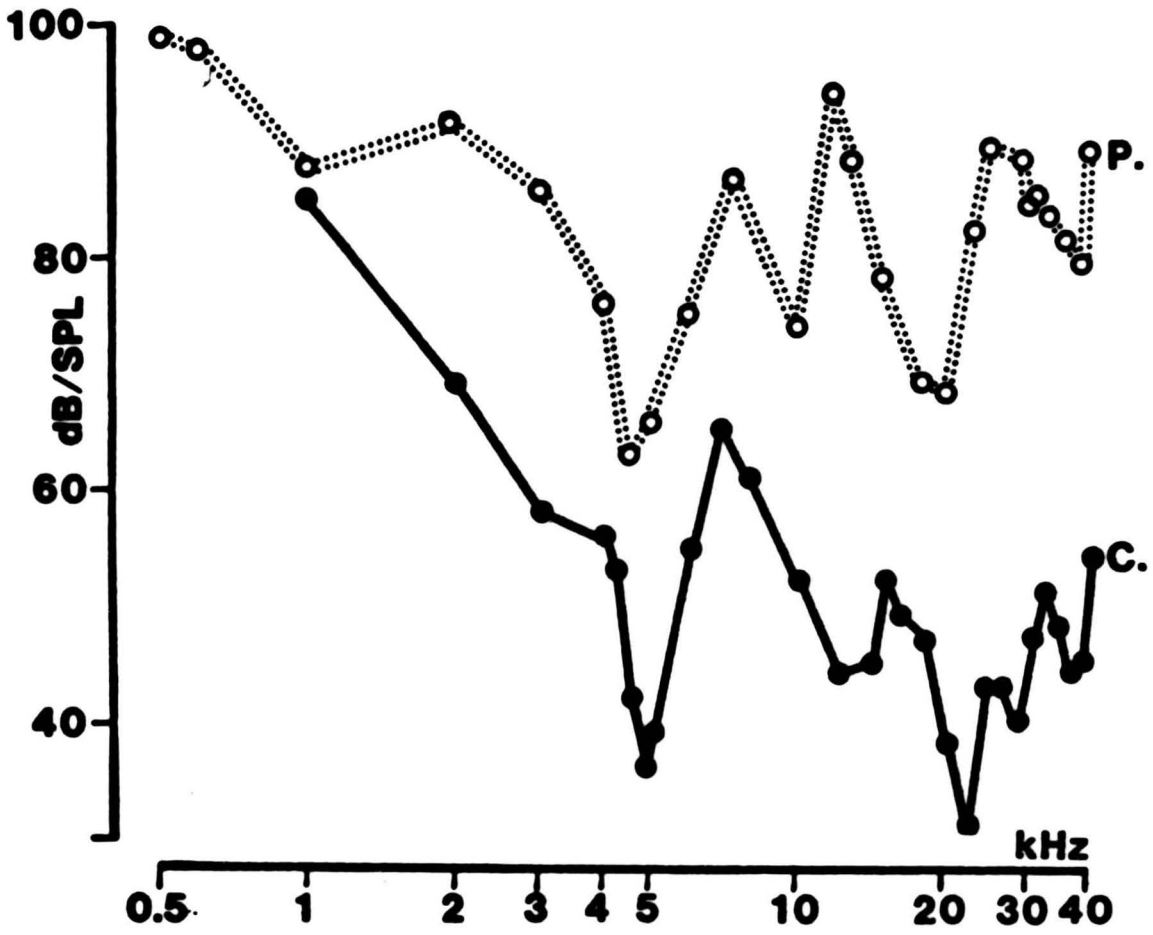
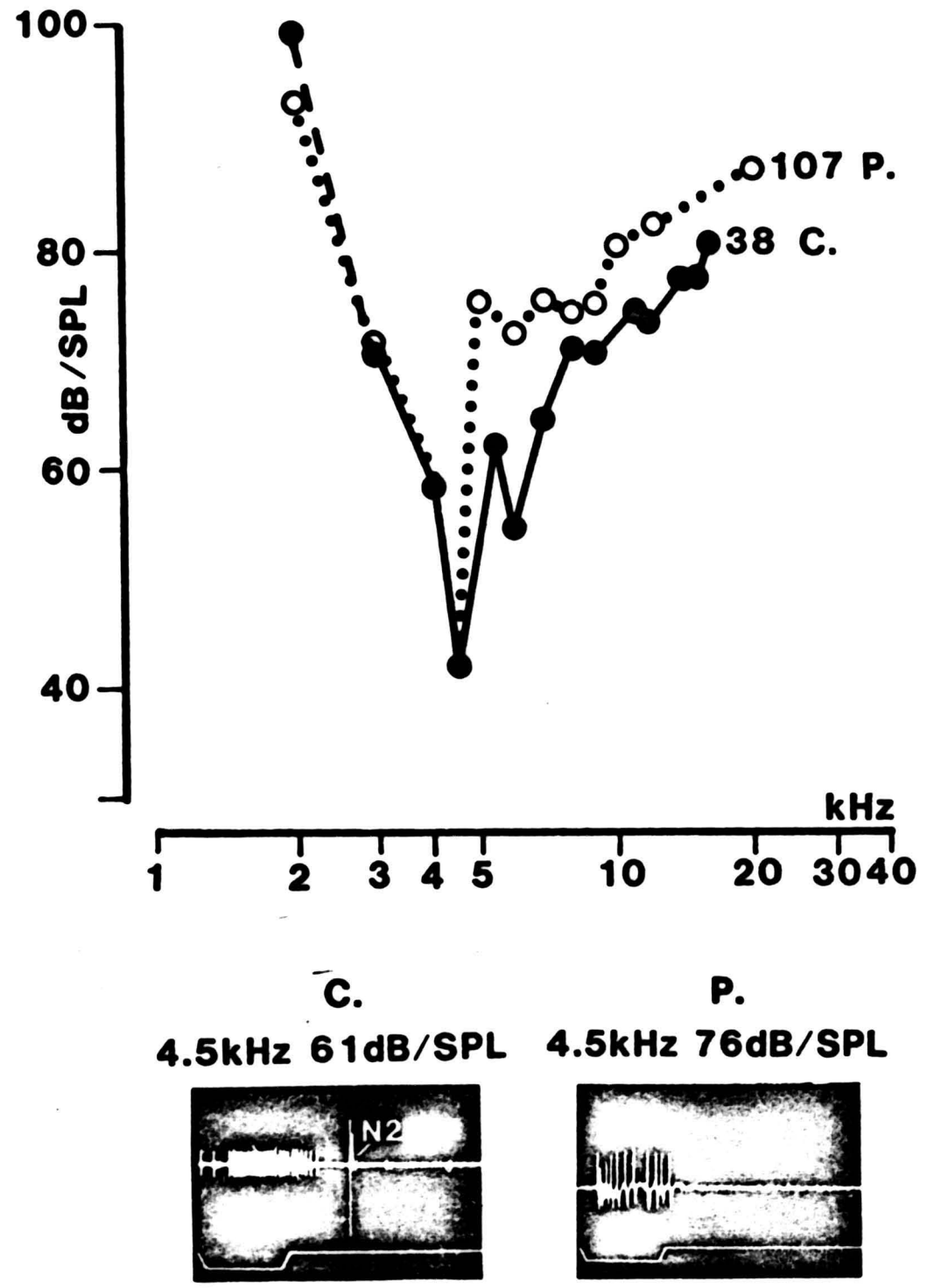


Table I. **CRITERION: ChF**

	BROAD	L.F.	H.F.	TOTAL
CENTRAL UNITS	18 (47.4%)	5 (13.2%)	15 (39.5%)	38
PRIMARY UNITS	14 (33.3%)	15 (35.7%)	13 (31.0%)	42

Fig.17 Threshold curves for a single central unit, (C 38)small spikes and a single primary unit, (P 107) recorded in different animals. Insets; response analogs to the parameters shown. The ChFs and lower roll-off values for both units are similar.


100
80
60
40
dB/SPL
107 P.
38 C.
kHz
1
2
3
4
5
10
20
30
40
C.
4.5kHz 61dB/SPL
N2
P.
4.5kHz 76dB/SPL

C. Central Units with "Simple" Response Patterns.

To24AN4: This unit responded tonically and had a broad-band threshold curve extending from 5kHz to 30kHz, (Fig.18). It was relatively insensitive, with lowest threshold in the range 18kHz to 24kHz. Dot-displays of responses to two intensities presented at 14kHz show an increase in spike number at the higher intensity and a reduction in the latency of response. At 24kHz, (86dB) the response was similar to that at 14kHz, (85dB). Trains of 5kHz were coded and little adaptation of the response occured during 6s of the trained stimulus. The unit did not respond to white noise and it was not spontaneously active.

To27AN1: This unit responded to frequencies in the range 5kHz to 40kHz, (Fig.19a) with a pronounced peak of sensitivity at 22kHz. The unit responded tonically during the stimulus with some after-discharge, (e.g. Fig.19a inset) and was not spontaneously active. At 10dB above threshold, (Th+10dB) intensity coding was clear for white noise, (W.N.), 10kHz and 20kHz and no adaptation was apparent in the responses to 10 successive stimuli, (Fig.19b). Increases in intensity at 5kHz, 28kHz and W.N. resulted in only a slight increase in mean spike number followed by inhibition at high intensities, (Fig.

Fig.18a Threshold curve for unit To24AN4. Bars represent mean spike number in response to 50ms stimuli; stimulus intensities represented by the baseline of each bar. Inset; response analog to parameters shown.
b. Dot-displays of the responses to 10 successive 50ms stimulus presentations for the parameters given. Stimulus repetition rate; 1 stimulus/1.5s. For this and future Figs. open circles represent frequencies at which no response could be elicited to the maximum experimental stimulus intensity.

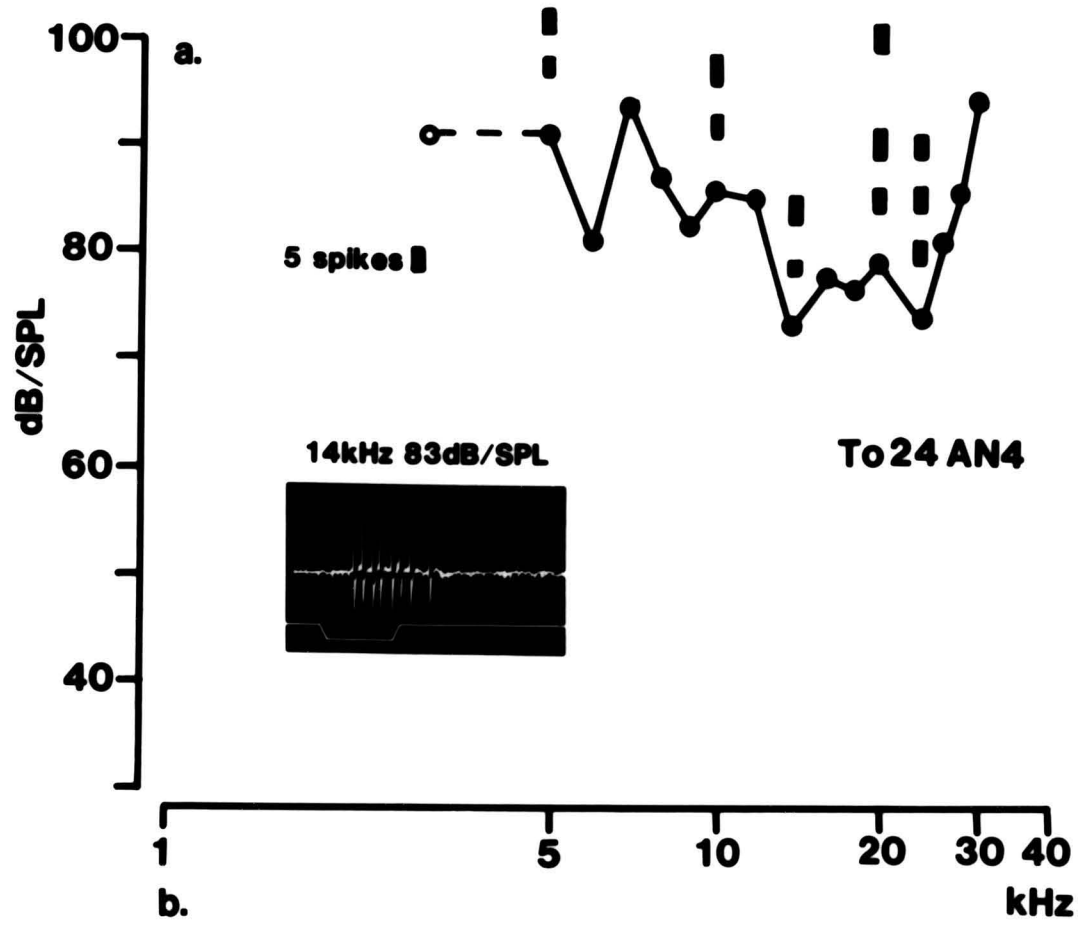
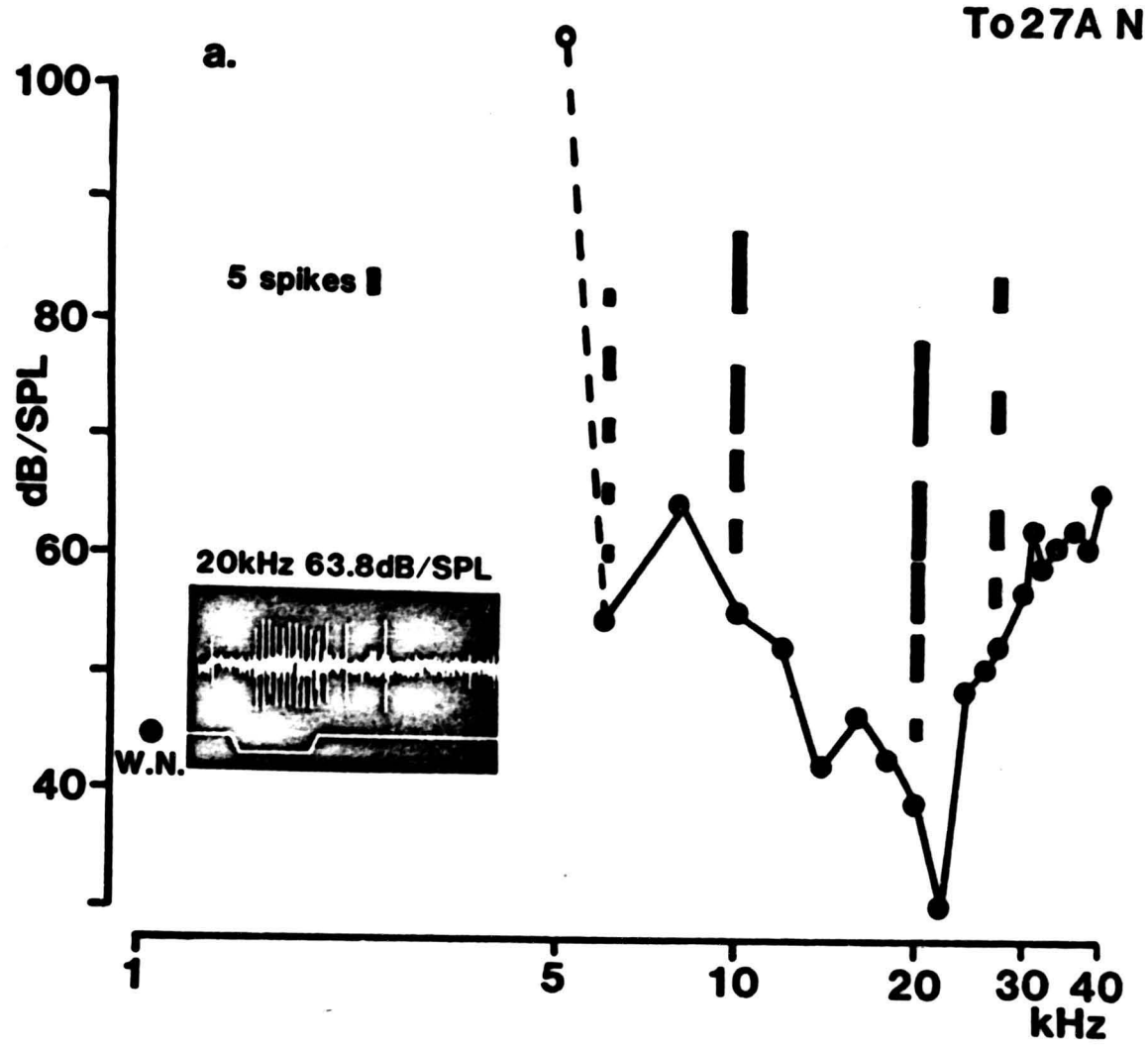

a.
100
80
60
40
dB/SPL
5 spikes
14kHz 83dB/SPL
To 24 AN4
1
5
10
20
30
40
kHz
b.
14kHz 80dB/SPL
14kHz 85dB/SPL
24kHz 86dB/SPL
5kHz 100dB SPL

Fig.19a Threshold curve for unit To27AN1 with ChF at 22kHz. Bars as in Fig.18. Inset; response analog to the stimulus parameters shown. b. Cumulative spike numbers against stimulus number at Th+10dB for 5kHz, 20kHz and W.N., (white noise). The gradients indicate no adaptation to successive stimuli. c.Mean spike number against stimulus intensity. At high intensities inhibition of the response to 5kHz, 28kHz and W.N. stimuli is evident;no inhibition ofthe response to 20kHz stimuli up to Th+32dB occured.



10dB above Threshold

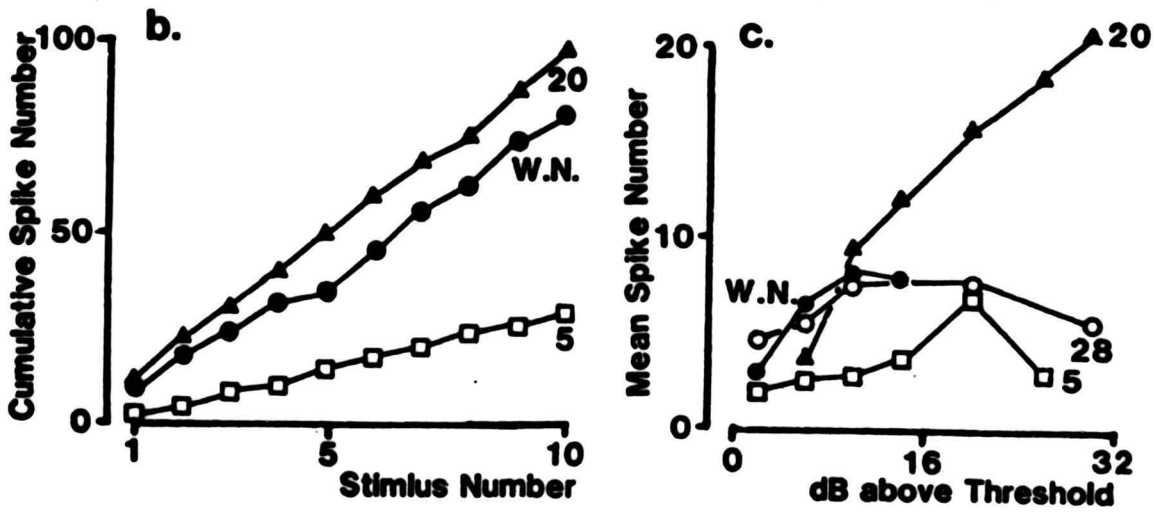


Fig.20a Threshold curve for unit To31AN1B. Bars as in Fig.18.

Inset; response analog to the stimulus parameters shown.

b, Dot-displays of the response to ten successive stimuli.

Stimulus duration; 50ms. Stimulus repetition rate;

1 stimulus/1.5s, except at 20kHz 63dB when the rate was

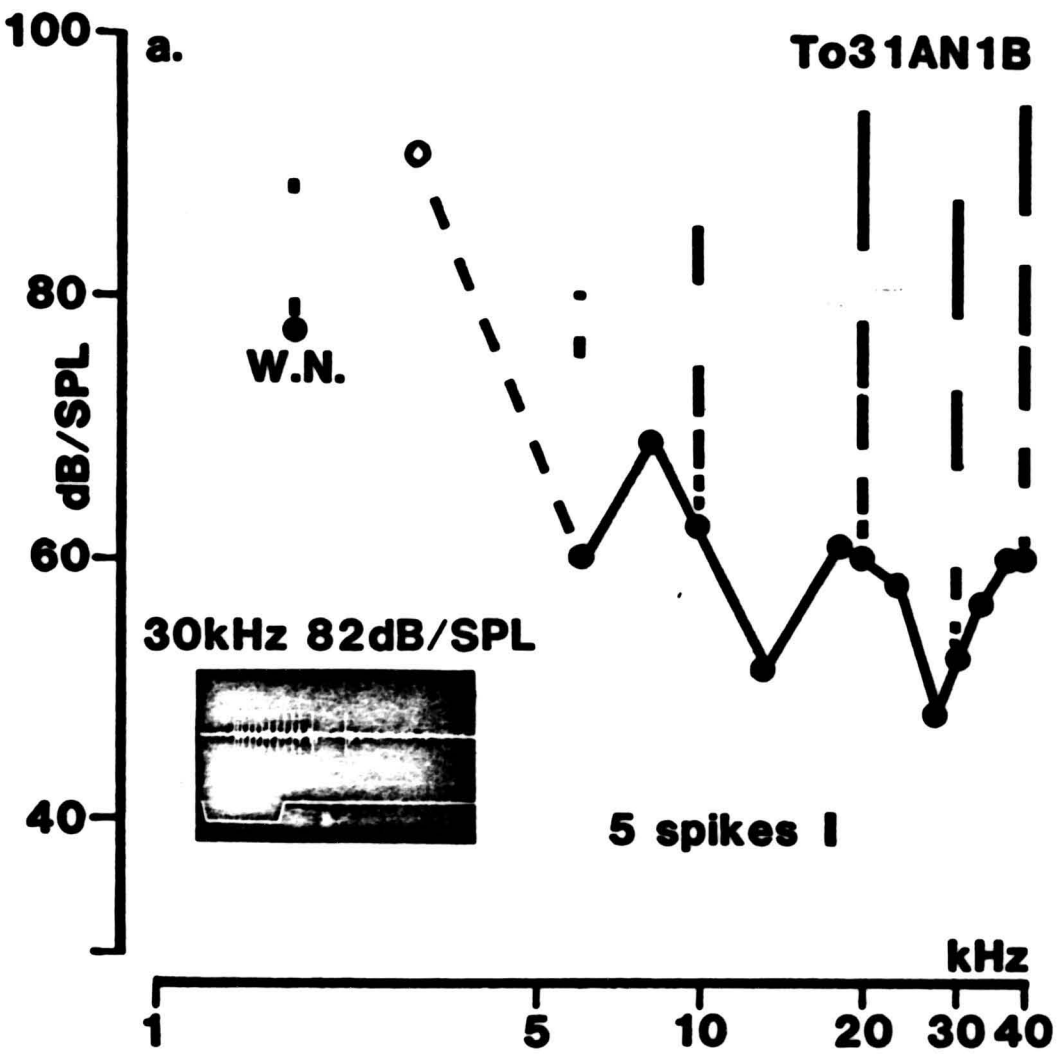
10 stimuli/s.

18.

own.

timuli.

was



19c). At 20kHz spike number increased with intensity up to Th+30dB.

To31AN1B: This unit responded to frequencies over the range 6kHz to at least 40kHz, (Fig.20a) and there were three regions in which sensitivity was relatively high, 6kHz, 13kHz and 27kHz. The response was tonic with some after-discharge and showed little habituation at stimulus repetion rates of 10 stimuli/s, (Fig.20a inset and b). Latency decreased with increasing stimulus intensities up to Th+8dB but further increases in intensity only slightly reduced the response latency, (Fig.21a) The latency of response was similar at all frequencies tested when stimuli of comparable intensity above threshold were presented. With pure-tones the mean spike number increased with intensity (up to Th+25dB) at the frequencies tested, (Figs.20a and b). No adaptation was shown on the responses to ten stimulus presentation (1 stimulus/1.5s, Fig.20b). At Th+10dB the responses to 10kHz, 20kHz and 40kHz were similar but at Th+20dB the gradients of the cumulative curves indicate a preferential response to high frequency stimuli, (Fig.21b,c).

D."Complex" Units.

To31AN1: This unit responded to frequencies ranging from 4kHz

Fig.21a To31AN1B, (as in Fig.20a,b) showing latency to the first spike of the response for three frequencies.

b. Cumulative spike number against stimulus number at Th+10dB. c. as b. at Th+20dB.

irst

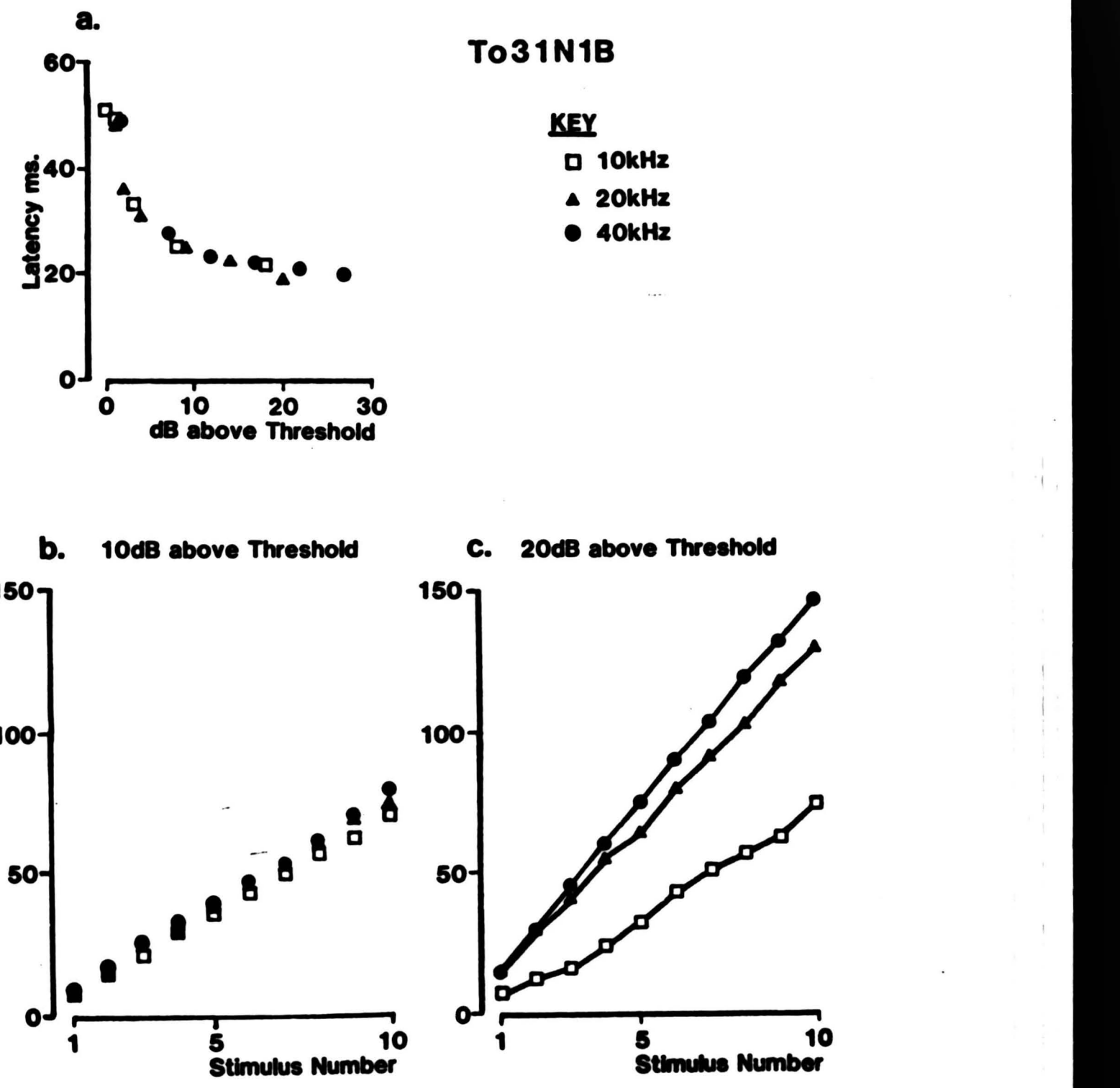

a.
To31N1B
KEY
10kHz
20kHz
40kHz
Latency ms.
60
40
20
0
0
10
20
30
dB above Threshold
b. 10dB above Threshold
Cumulative Spike Number
150
100
50
0
1
5
10
Stimulus Number
c. 20dB above Threshold
150
100
50
0
1
5
10
Stimulus Number

Fig.22 Threshold curve for To31AN1. Bars as in Fig.18. Inset; response analog to the stimulus parameters shown.

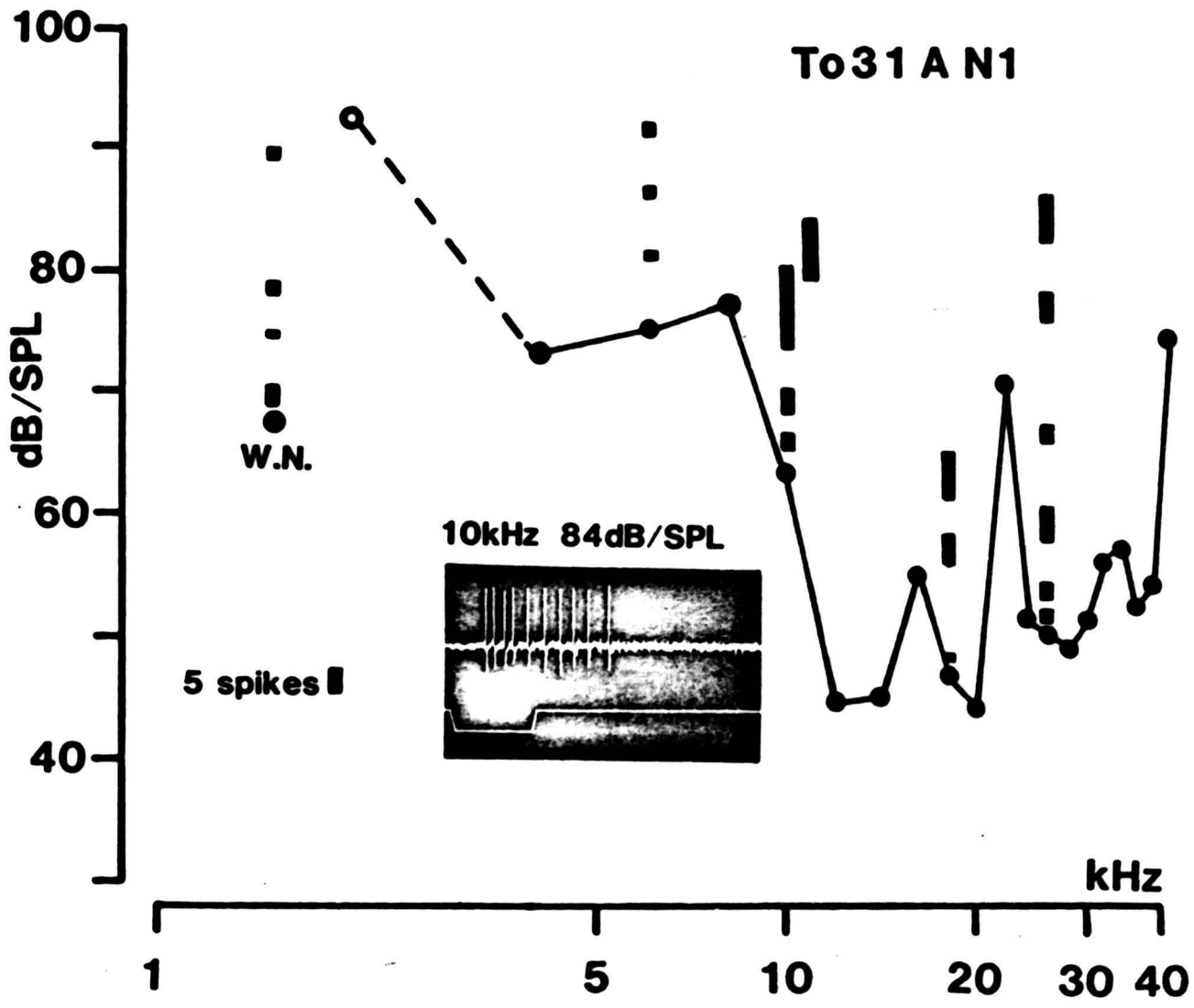
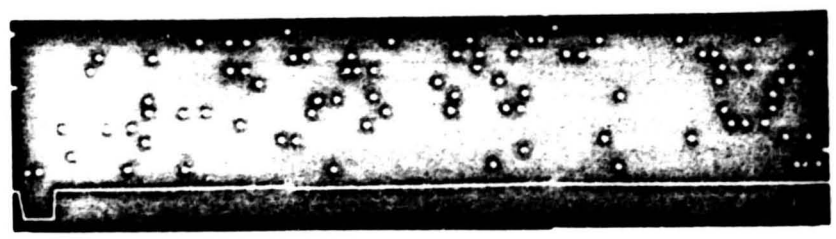
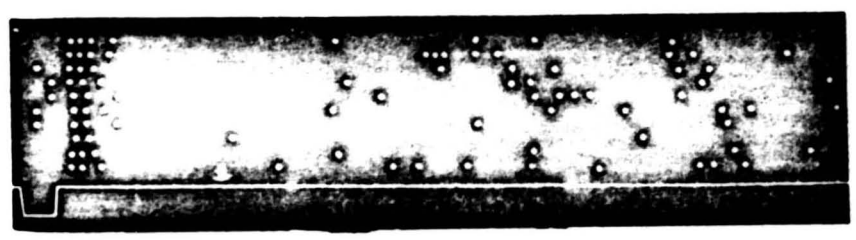

To31 A N1
100
80
60
40
dB/SPL
W.N.
10kHz 84dB/SPL
5 spikes
kHz
1
5
10
20
30
40

Fig.23 Dot-displays of spontaneous and stimulus-induced spiking activity by To31AN1, (as in Fig.22). All spikes throughout a 1.5s period following a stimulus trigger were discriminated. No sound was presented during the spontaneous activity recording although a stimulus "envelope" was generated.

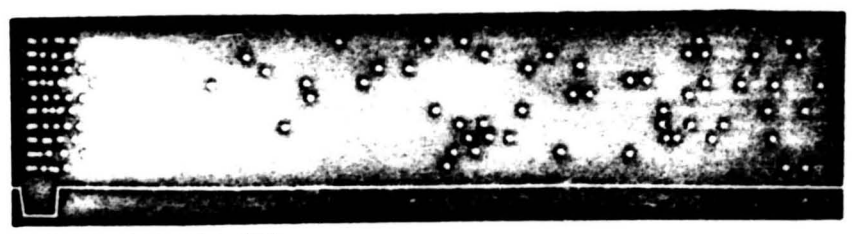
To31AN1



Spontaneous



W.N.70dB/SPL



26kHz 69dB/SPL

Total time span 1.5s.

to 40kHz; best sensitivities occured above 12kHz but were interspersed with regions of relative insensitivity, (Fig.22). Intensity coding was poor at the frequencies tested and the units showed a high degree of spontaneous activity, (8 to 9 spikes/s; Fig.23). Presentation of W.N. at 70dB resulted in a response (mean latency 64 ms) which occured after termination of the stimulus; spontaneous activity was suppressed for approximately 400ms after the spike burst. At 26kHz a short latency, (mean 16ms) tonic response was elicited and spontaneous activity was again depressed for approximately 400ms following the spike volley.

<u>To10AN1</u>: This unit responded to frequencies in the range 4.5kHz to 20kHz, (Fig.24) and was spontaneously active, (Fig.25). The response to low intensity, (less than 80dB) 5kHz stimuli consisted of 4 or 5 spikes occuring at least 40ms after the stimulus onset, (Fig.25a, b) and spontaneous activity was inhibited throughout the interval between stimuli, (1.1s). At higher intensities, (i.e. 85dB and 95dB) the duration of spontaneous activity suppression was reduced and rebound activity increased with successive stimuli, (Fig.25b). After presentation of ten stimuli the spike repetition rate remained elevated for approximately 600ms before spontaneous

Fig.24 Threshold curve for To10AN1. Inset; response analog to the parameters shown.

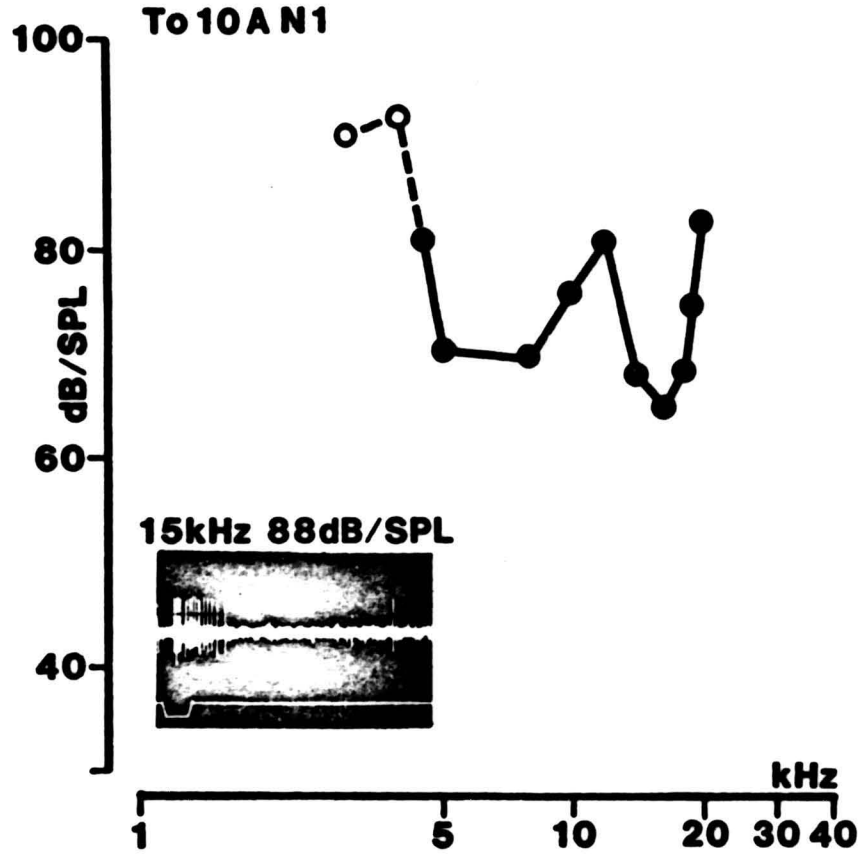
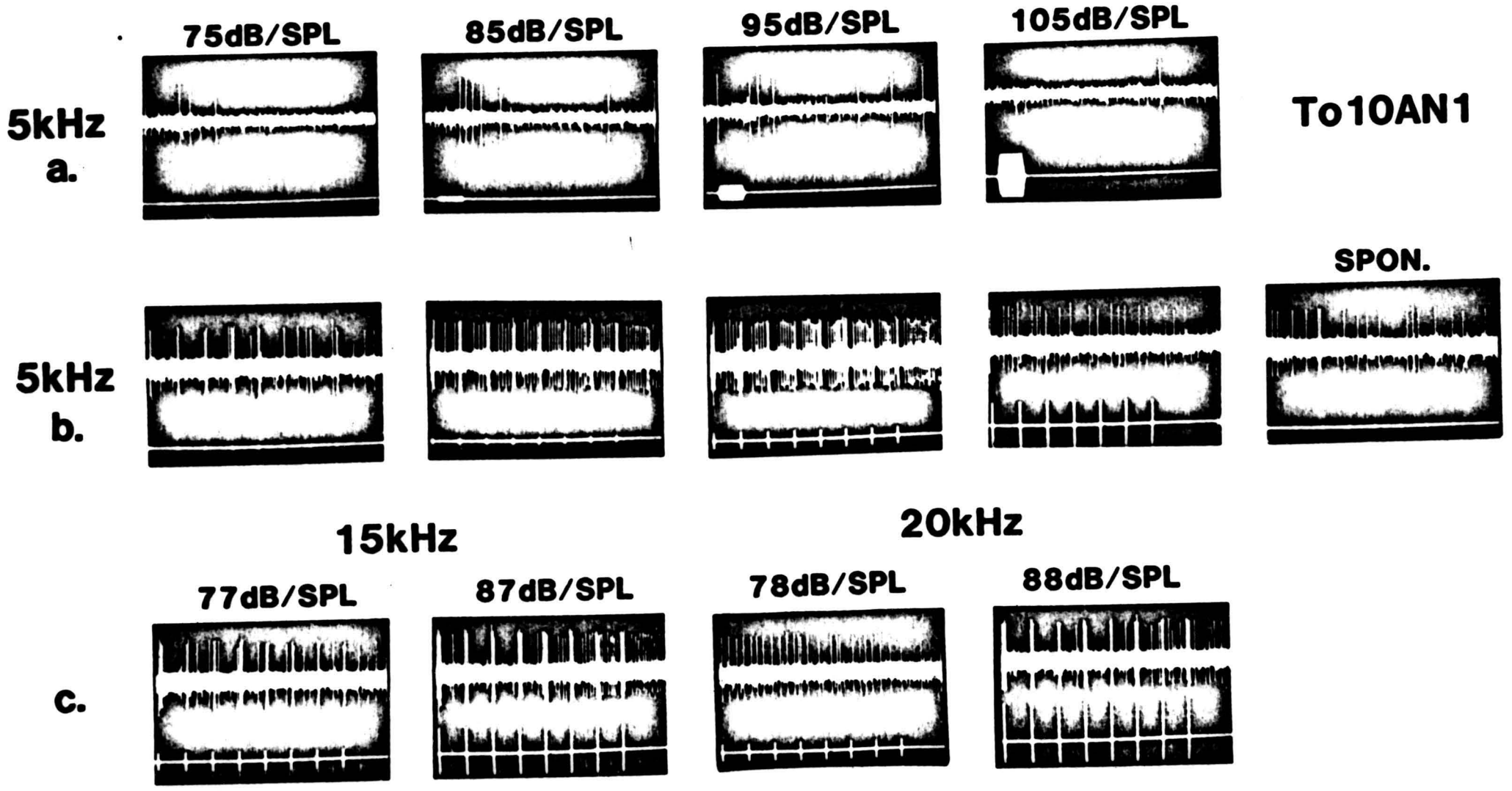

To 10A N1
100
80
60
40
dB/SPL
15kHz 88dB/SPL
kHz
1
5
10
20
30
40

Fig.25 Response analogs of To10AN1, (as in Fig.24). Row a. responses to a single 5kHz stimulus at the intensities shown. Row b. responses to a number of successive stimuli. Note the gradual increase in rebound activity with successive stimuli at 85dB and 95dB. Intensities identical with those above in Row a. Spon.; spontaneous activity over the same time period as preceding photographs in Row b. Row c. response analogs to 15kHz and 20kHz stimuli at the intensities given. Stimulus repetition rate in all cases; 1 stimulus/1.5s. Stimulus duration; 50ms in all cases.


75dB/SPL
85dB/SPL
95dB/SPL
105dB/SPL
5kHz
a.
To10AN1
SPON.
5kHz
b.
15kHz
20kHz
77dB/SPL
87dB/SPL
78dB/SPL
88dB/SPL
c.

levels of activity were regained. At still higher intensities (i.e. 105dB) the response was inhibited. The response patterns to 15kHz and 20kHz stimuli were similar to those to 5kHz stimulation.

To32AN1: This unit responded to frequencies above 6kHz up to at least 42kHz and was not spontaneously active, (Fig.26). The pattern of response varied with both intensity and frequency, (Fig.27). At 12kHz, (69dB) the response consisted of two groups of spikes; increasing the stimulus intensity resulted in a filling in of the silent period between the spike groups and at 83dB a tonic response pattern with after-discharge occured. Inhibition at high intensity resulted in a response pattern similar to that at 69dB. At 15kHz spike number increased with stimulus intensity becoming tonic with after-discharge at 68dB and above; no inhibition was shown at this frequency. The response to W.N. was similar to that produced at 12kHz to high intensty stimuli. When low frequency trains of stimuli were presented, (Fig.28) spikes occurred during both the period and interval although coding stabilized with successive stimuli. Clear coding of the stimulus period occurred to high frequency and W.N. trains of stimuli.

Fig.26 Threshold curve for unit To32AN1. Bars as in Fig.18.

Inset; response analog to the parameters shown.

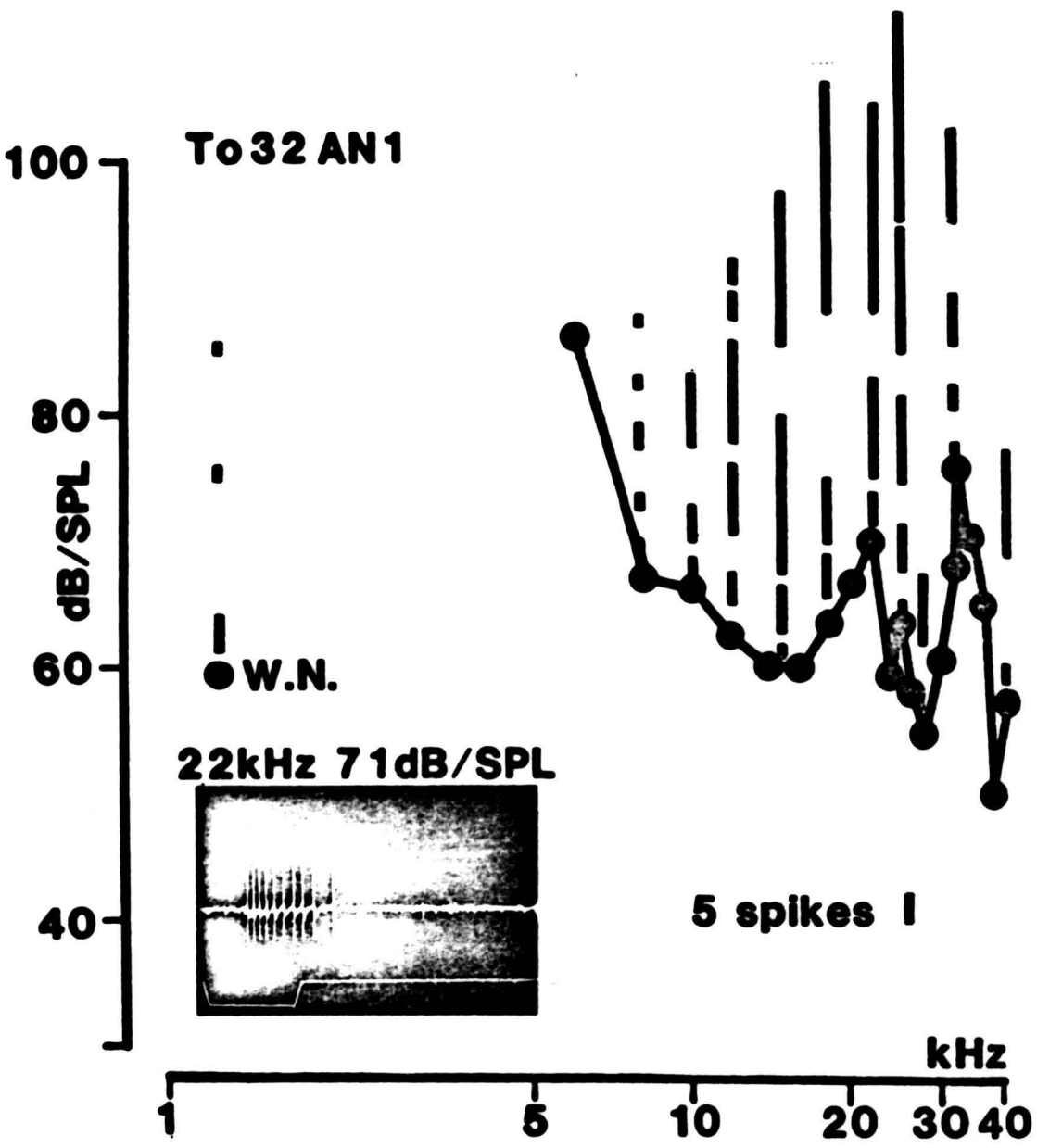
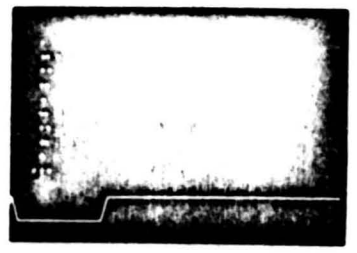

100
To 32 AN1
80
60
40
dB/SPL
W.N.
22kHz 71dB/SPL
5 spikes I
kHz
1
5
10
20
30
40

Fig.27 Dot-displays of the responses of unit To32AN1 (as in Fig 26) to ten successive 50ms stimulus presentations at the frequencies and intensities shown. Numbers in brackets give the threshold intensity (dB) for the unit at the above frequency. Stimulus repetition rate; 1 stimulus/1.5s.

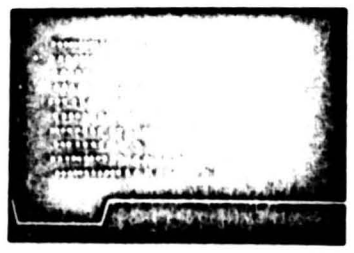
12kHz
(62)

69dB/SPL

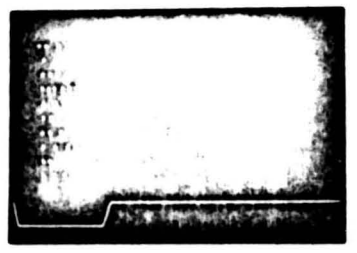


76dB/SPL

83dB/SPL



86dB/SPL



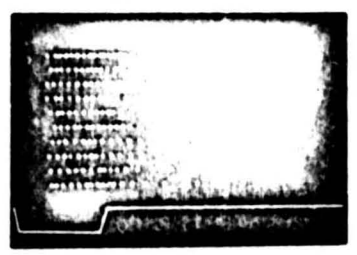
88dB/SPL

15kHz
(57)

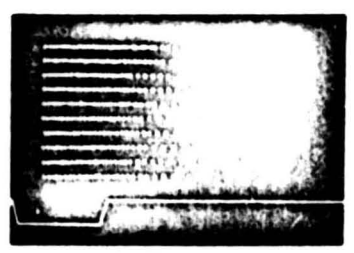
58dB/SPL

60dB/SPL

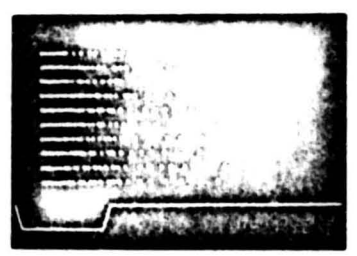
68dB/SPL



78dB/SPL



88dB/SPL

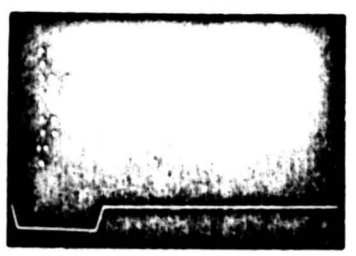


W.N.
(59)

60dB/SPL

70dB/SPL

80dB/SPL



90dB/SPL

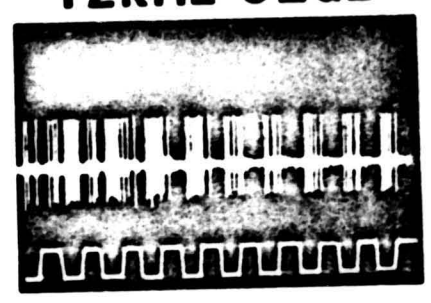
To32AN1

Fig.28 Response analogs and dot-displays of the responses of unit To32AN1, (as in Figs 26 and 27) to the parameters shown. Stimulus repetition rate; 10 stimuli/s.

To32AN1

8kHz 85dB

12kHz 92dB



25kHz 85dB

40kHz 79dB

W.N.69dB/SPL

Ten 50ms stim./s

To38AN1 and N2: These units were recorded simultaneously but could be clearly distinguished from each other as single , discrete units, (Figs.29a and b insets).

The threshold curve for N1 was sharply tuned to the C.F. of the species proclamation song, (4.5kHz) and the unit responded to frequencies in the range 3kHz to 20kHz, (Fig.29a). The response pattern of N1 was tonic with a high spike repetition rate (approximately 460 spikes/s) and spike number did not increase with increased stimulus intensities, (Figs.29 and 30).

The threshold curve for N2 extended from 3kHz to 40kHz, (Fig.29b) but no response was obtained to maximum stimulus intensities at either 27kHz or 37kHz; the unit was most sensitive to W.N., responding to 52dB stimuli. The response pattern of N2 was highly complex; intensity coding occured at some frequencies with inhibition at high intensities.

i) Response intensity characteristics at different frequencies.

At 4.5kHz, 48dB, (Th+3dB) the response of N1 was tonic and suppression of spontaneous activity was apparent for 50ms following the stimulus, (Fig.30). At 61dB, the spike repetition rate increased and spontaneous activity was inhibited for about 250ms.

Fig.29a Threshold curve for unit To38AN1 with ChF at 4.5kHz. Bars as in Fig.18. Inset; response analog to the parameters shown. b. Threshold curve for unit To38AN2. Bars as in Fig.18. Inset; response analog to the parameters shown.

8AN2.

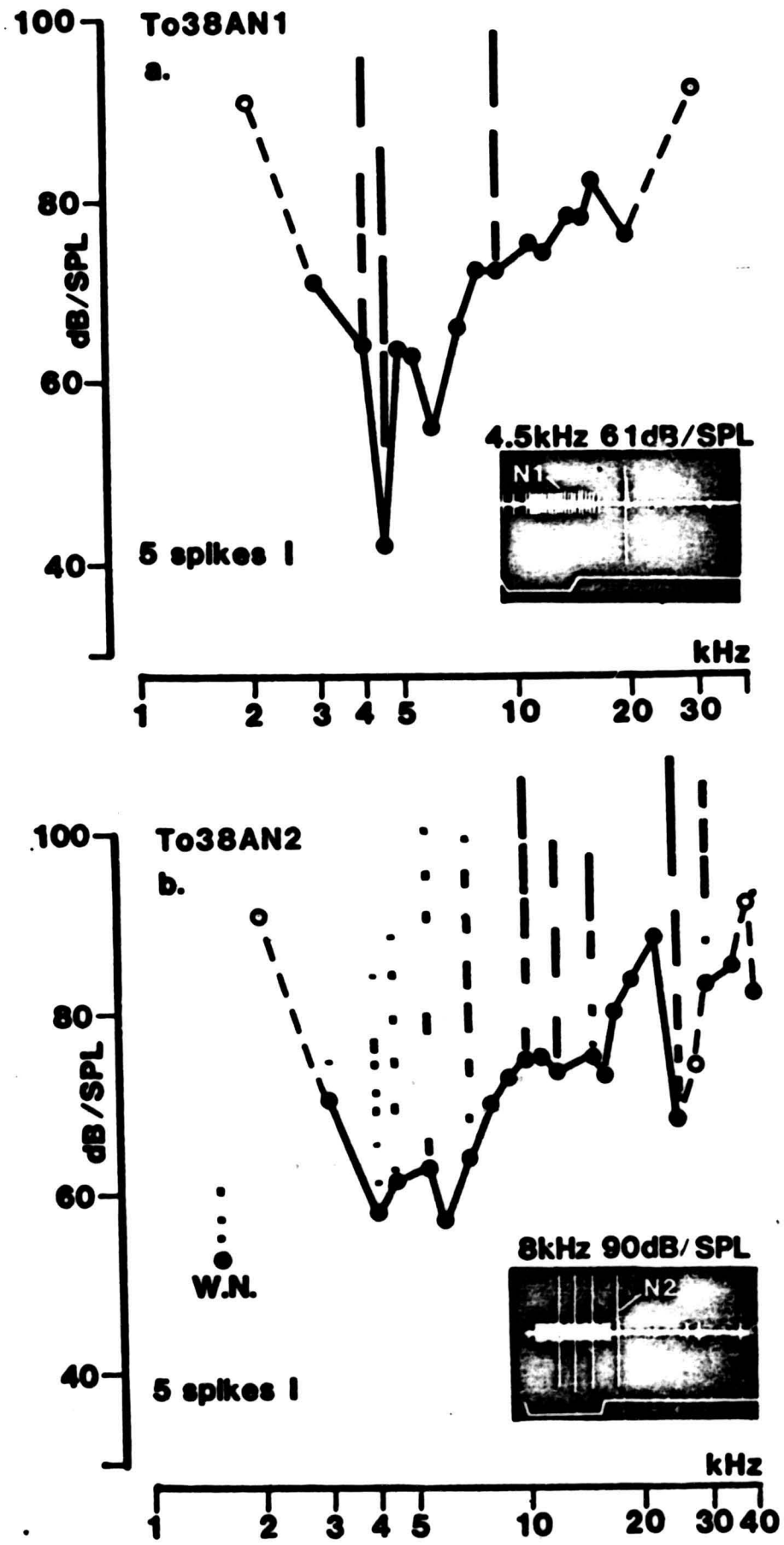
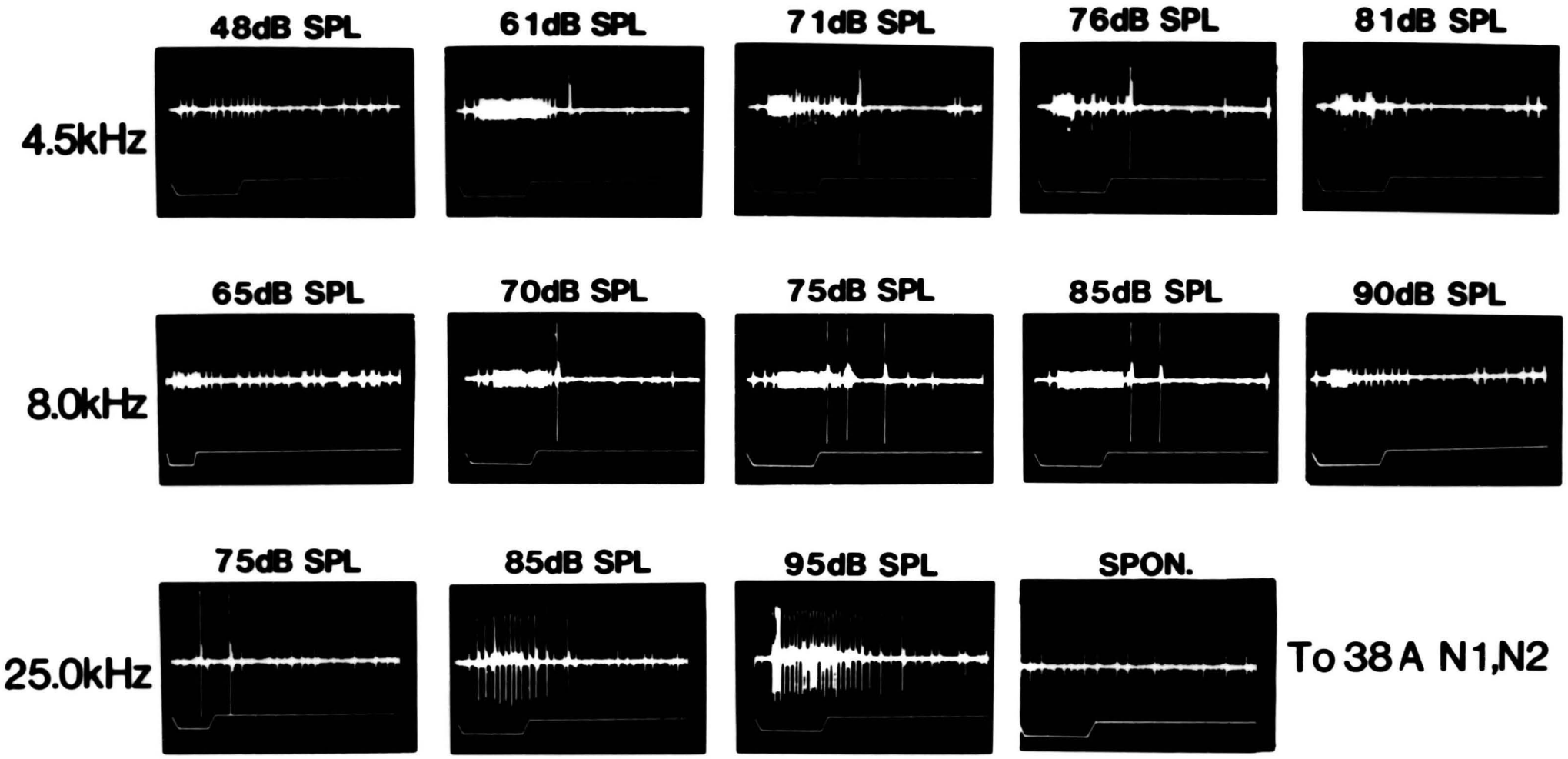

100
80
60
40
dB/SPL
To38AN1
a.
4.5kHz 61dB/SPL
N1
5 spikes I
kHz
1
2
3
4
5
10
20
30
To38AN2
b.
W.N.
8kHz 90dB/SPL
N2
5 spikes I
kHz
1
2
3
4
5
10
20
30
40

Fig.30 Response analogs for To38AN1 and N2 (as in Fig 29) to 4.5kHz, 8kHz and 25kHz stimuli at the intensities shown. For details see text. Spon.; spontaneous activity, (no sound was produced during recordings of spontaneous activity although a stimulus "envelope" was generated). Stimulus repetition rate; 1 stimulus/ 1.5s: stimulus duration; 50ms.


48dB SPL
61dB SPL
71dB SPL
76dB SPL
81dB SPL
4.5kHz
65dB SPL
70dB SPL
75dB SPL
85dB SPL
90dB SPL
8.0kHz
75dB SPL
85dB SPL
95dB SPL
SPON.
25.0kHz
To 38A N1,N2

Partial inhibition of the response occured at higher intensities and was associated with an earlier recovery of spontaneous activity levels. A similar pattern of response occured at 8kHz; N1 did not respond to 25kHz.

N2 responded to 4.5kHz with a single spike which occured after termination of the stimulus. The latency decreased with intenstiy and the response was totally inhibited at 81dB. More than one spike was produced in response to 75dB and 85dB, 8kHz stimuli; inhibition of the response occured at 90dB. The latency of the N2 response at 25kHz was reduced to about 30ms and at higher intensities the response pattern was tonic. Spike number increased with intensity and after-discharge occured at 95dB. At 25kHz no inhibition was apparent at the intensities tested.

ii) <u>Effect of stimulus duration</u>.

N1 coded stimulus durations up to at least 6s and the response showed little adaptation after the initial 30ms. The period of spontaneous activity suppression was related to the duration of stimulus-locked activity, (Fig.31a,b). When 400ms stimuli were presented spontaneous activity was inhibited throughout the entire stimulus interval, (1.1s)

Fig.31a Response analogs of units To38AN 1 and N2 (as in Figs 29 and 30), to stimuli of varying durations at the frequencies and intensities shown.

a.

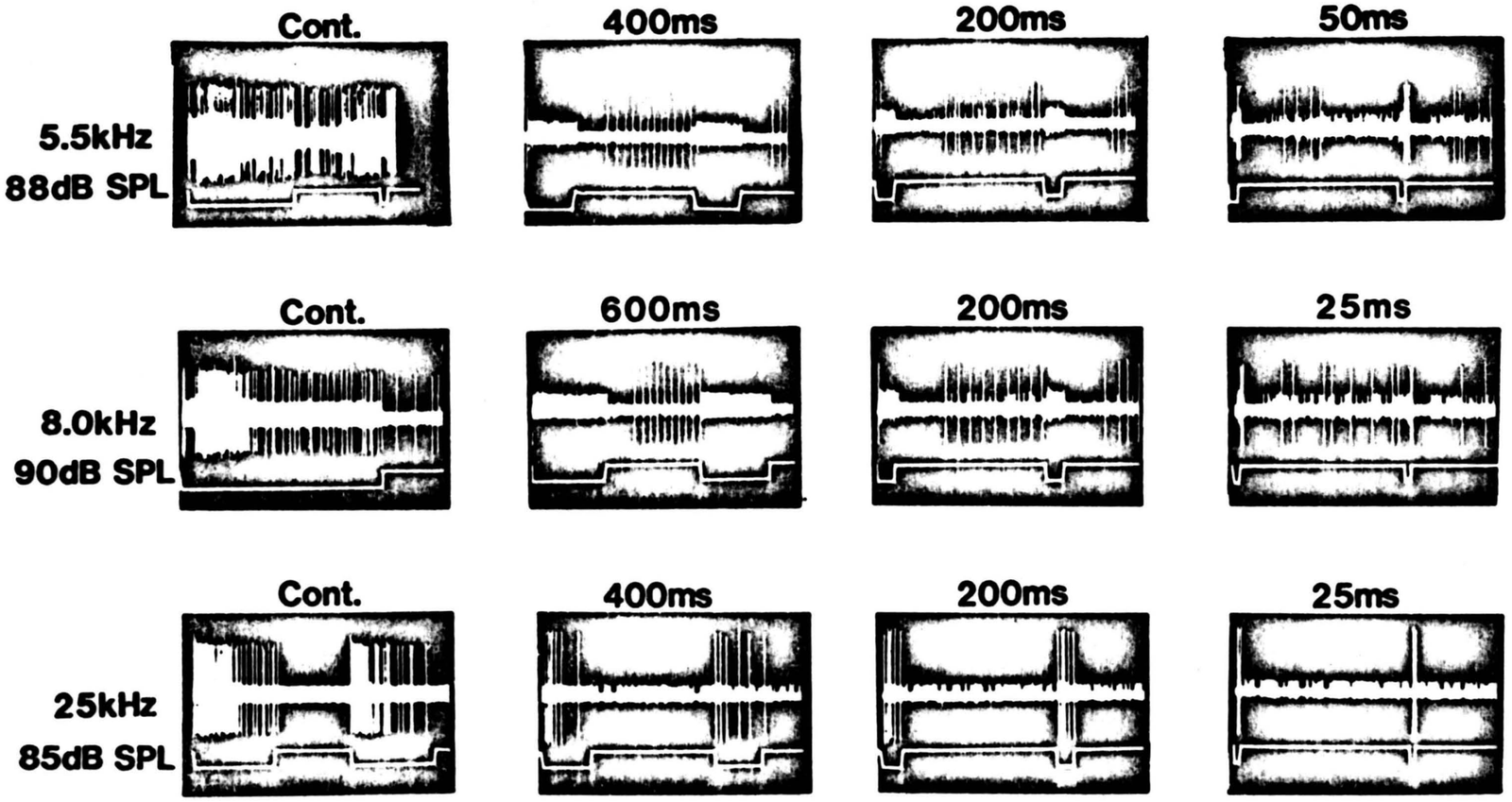
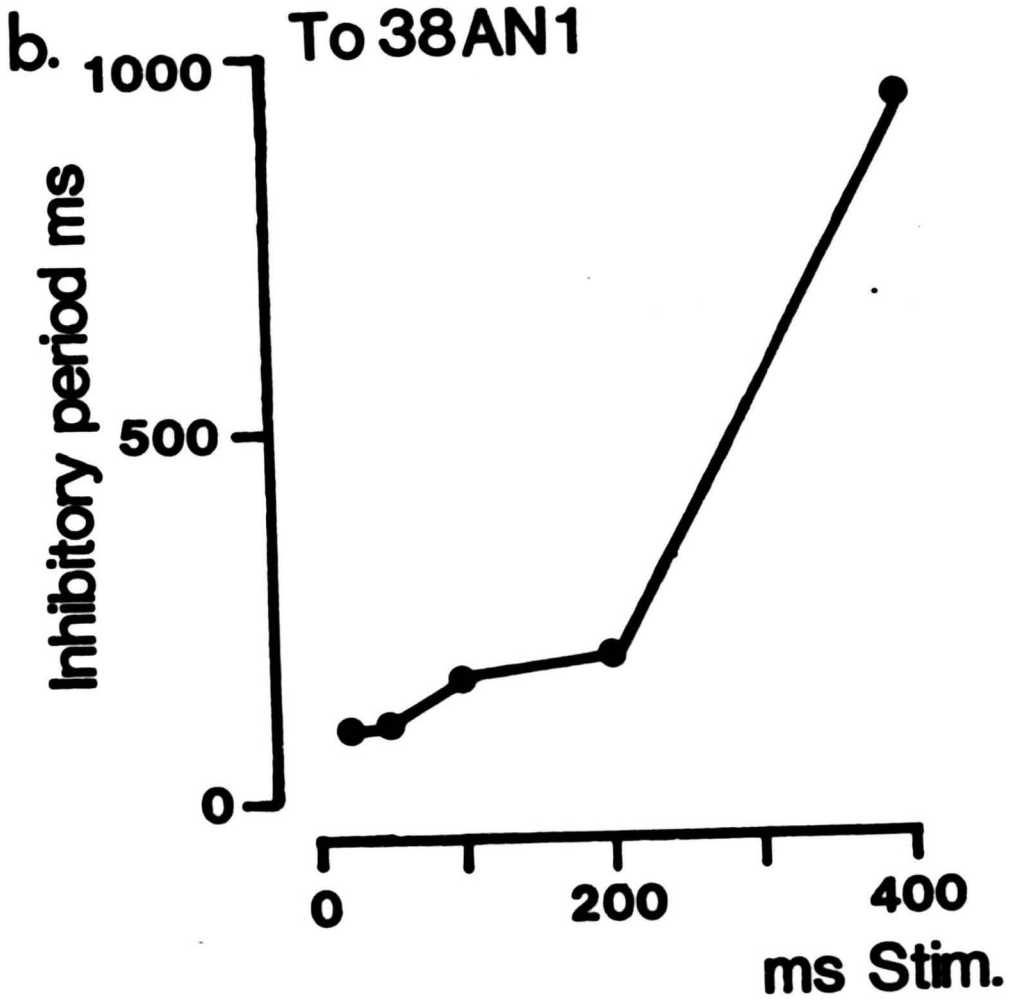

To 38 AN1,N2
Cont.
400ms
200ms
50ms
5.5kHz
88dB SPL
Cont.
600ms
200ms
25ms
8.0kHz
90dB SPL
Cont.
400ms
200ms
25ms
25kHz
85dB SPL

Fig.31b Period of post-stimulus inhibition for unit To38AN1 (as shown in Figs. 29a, 30 and 31) versus stimulus duration (ms).


b.
To 38AN1
1000
500
0
Inhibitory period ms
0
200
400
ms Stim.

N2 responded to a 50ms 5.5kHz stimulus with a burst of spikes (mean latency 50ms), followed by a silent interval prior to a second low repetition rate period of spike activity, (Fig.31a). Presentation of a 100 ms stimulus resulted in N2 activity 50ms after stimulus onset, a silent period and more spikes some 350ms after the stimulus onset; these continued at a low repetition rate (12 spikes/s) until the onset of the subsequent stimulus. Similar patterns of response resulted from stimulation with 200ms and 400ms tones, the latency of the initial response being 50ms. At 8kHz the response was limited to 1 to 3 spikes (latency approximately 60ms) irrespective of stimulus duration. Rebound activity occured after termination of the stimulus. At frequencies above 10kHz the latency of response was reduced and at 25kHz the latency was about 30ms. N2 responded tonically with rapid adaptation to long tones.

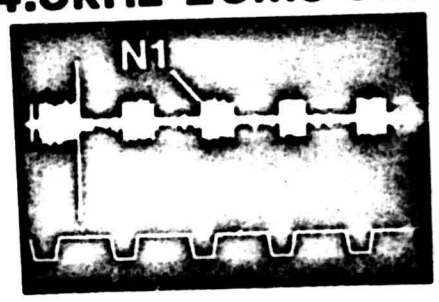
iii) <u>Effect of stimulus repetition rate</u>.

N1 responded to both 25ms and 50ms trains of stimuli, (10 stimuli/s) with a burst of spikes coding stimulus period and suppression of spontaneous activity in the intervals, (Fig32). At 5kHz, 12kHz and 25kHz the response to 50ms trains of stimuli adapted out after presentation of 4 or 5 stimuli. At 4.5kHz

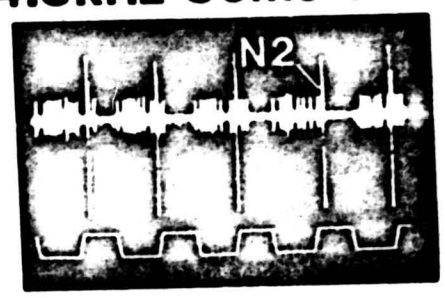
Fig.32 Response analogs for units To38AN1 and N2 (as in Figs. 29, 30 and 31) to stimuli with the parameters shown. Stimulus repetition rate; 10 stimuli/s.

To38AN1,N2

4.5kHz 25ms stim

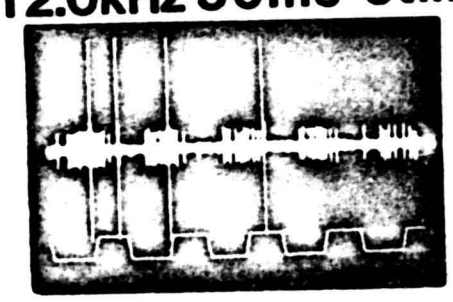


4.5kHz 50ms stim.

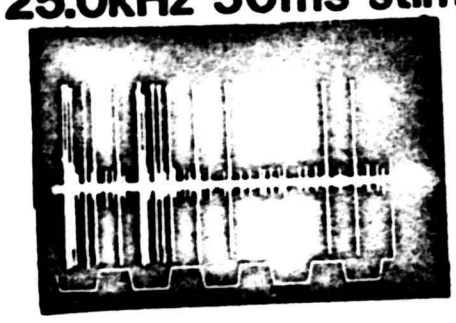


5.0kHz 50ms stim.

12.0kHz 50ms stim.



25.0kHz 50ms stim.



N2 reliably coded trains of 50ms stimuli with a single spike per stimulus but only responded to the first presentation of a train of 25ms stimuli.

To35AN1: This unit responded to frequencies in the range 8kHz to 40kHz and was most sensitive to 12kHz, (Fig. 33). The unit responded to W.N. and was not spontaneously active. Little coding of stimulus intensity occured at any frequency, (Fig. 34). At intensities higher than Th+20dB the responses usually consisted of a single spike of uniform latency, e.g. Fig. 34, 12kHz. In cases where a second spike occured it appeared to be associated with the termination of the stimulus e.g. 16kHz, 80dB. However the response pattern to both 50ms and 300ms, 16kHz stimuli was similar, indicating that the second spike is not an "off" response.

Discussion.

Ventral cord units of Teleogryllus oceanicus respond to frequencies over the bandwidth 1kHz to at least 40kHz. The relative insensitivity of the threshold curves from our cultured animals in comparison to those obtained from wild animals may reflect altered selection pressures in the laboratory, (see e.g.

Fig.33Threshold curve for To35AN1, ChF 12kHz. Bars as in Fig.18. Inset; response analog to the parameters shown.

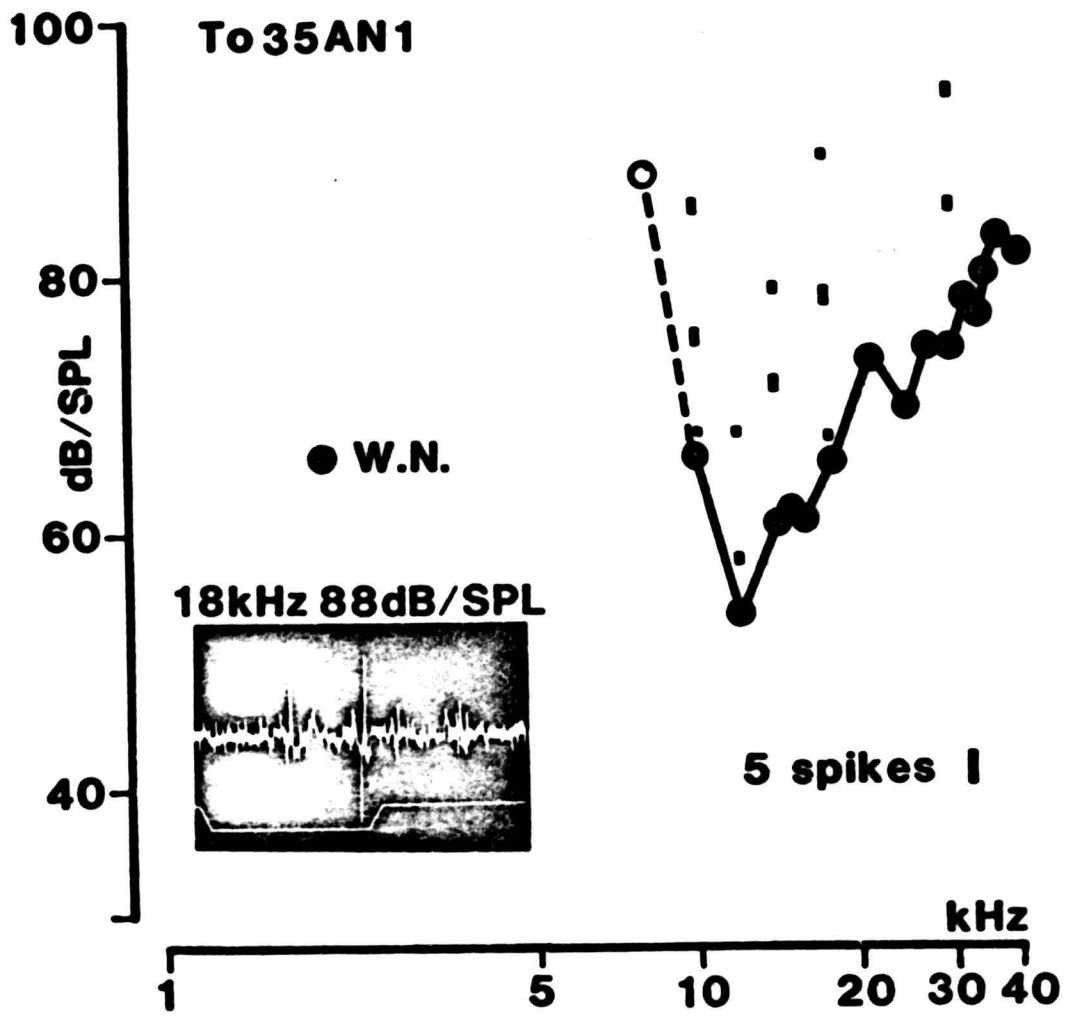
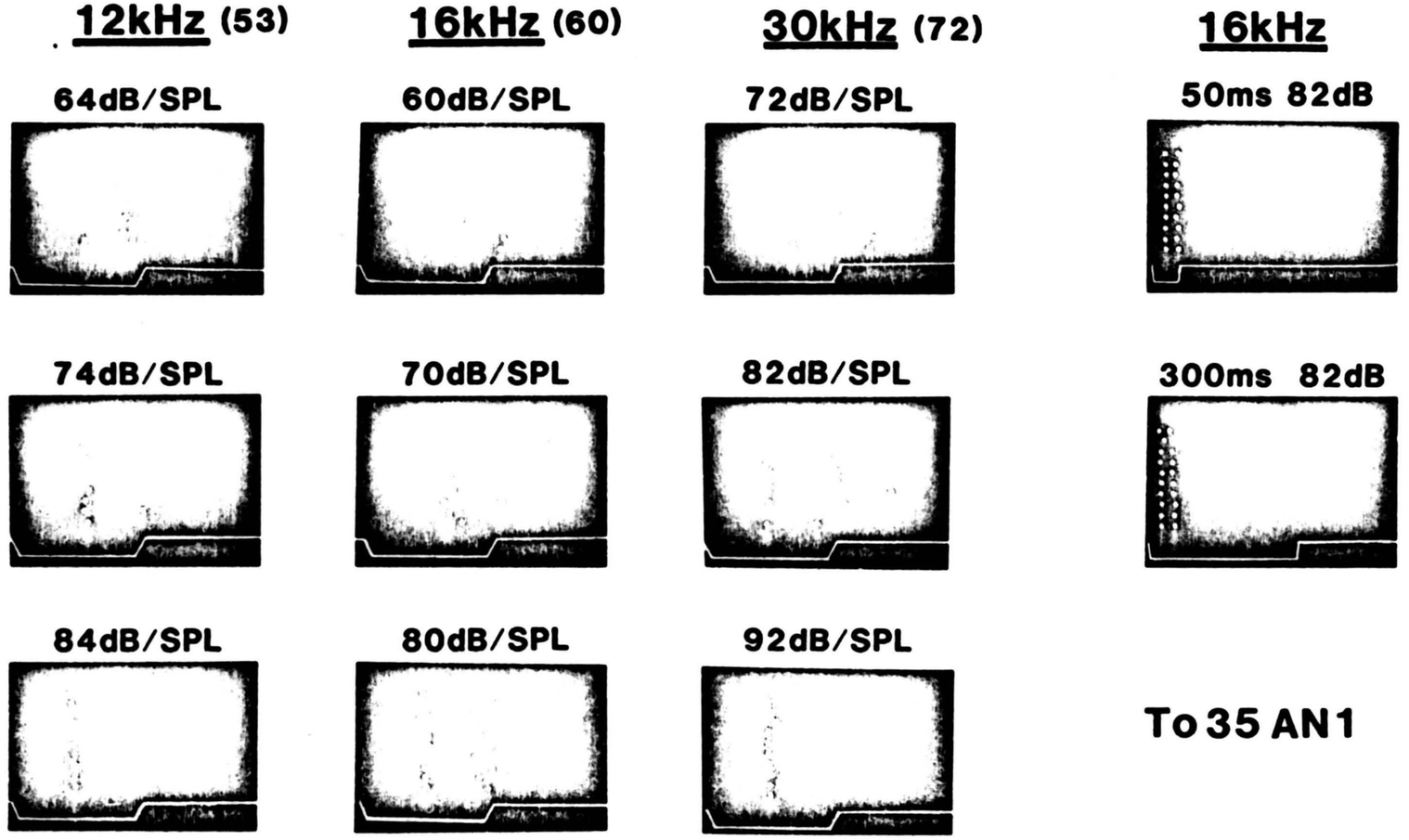

100
To 35AN1
80
dB/SPL
60
● W.N.
18kHz 88dB/SPL
40
5 spikes I
kHz
1
5
10
20
30
40

Fig.34 Dot-displays of the responses of unit To35AN1 (as in Fig. 33) to ten successive stimuli at the parameters shown. Numbers in brackets refer to the threshold level at that frequency. Stimulus duration 50ms unless stated otherwise: stimulus repetition rate; 1 stimulus /1.5s.

n Fig.
wn.
that
ther-



To 35 AN1

Ball and Hill, 1978 and Goodman et al., 1979). 50% of ventral cord units exhibit either more than one ChF e.g. Fig.15B, unit 36 or enhanced sensitivity to a broad range of frequencies e.g. Fig. unit 29. Rheinlaender, (1975) reported a similar percentage of broad-band units in the tettigoniid Decticus verrucivorus. In the present study, highly tuned units with clear, single ChFs, (e.g.To27AN1 and To38AN1), were divided into low-frequency (ChFs less than or equal to 10kHz) and high-frequency, (ChFs in excess of 10kHz)groups, Table I, (Fig.16). On the basis of this division nearly 13% of threshold curves were low-frequency whereas 40% were tuned to high-frequencies. These findings agree with those of Kalmring et al.(1972) and Kalmring, (1975) in Locusta and with Rheinlaender's, (1975) observations in D.verrucivorus. In addition many of the broad-band units had secondary peaks of sensitivity near 4.5kHz indicating that some information concerning carrier frequency (C.F.) may be integrated with that of other frequencies.

The large percentage of high-frequency units recorded in the ventral cord may be somewhat suprising but may indicate that detailed processing of high-frequency information occurs at a higher level. The retention of frequency information in general may be particularly

important for directionality, (Hill and Boyan, 1977; Hill et al,. 1980 Coles et al., 1980) and ultrasonics may be involved in predator-prey interactions, (Popov et al., 1975; Casaday and Hoy, 1977 and Moiseff et al., 1978). Primary threshold curve data for T. oceanicus have approximately equal percentages of low, high and broad-band units, (Table I Fig.16) although the number of high-frequency units may have been slightly over-estimated due to experimental procedure.

On the basis of all the data it appears unlikely that there is a simple 1:1 relationship between any primary and central unit in T. oceanicus. Rheinlaender, (1975) found that the responses of all ventral cord units of D. verrucivorus differed from those of the receptor units and this has been confirmed by Kühne et al., 1980 and Silver et al., 1980.

The responses of central units result from variations in the combinations of excitatory and inhibitory inputs which they receive and they are also likely to be influenced by the hormonal and motivational state of the animal. Some central units integrate information from both ipsilateral and contralateral receptors as well as interneurons, (Boyan, 1978). In the present study all inputs to the prothoracic ganglion remained intact, therefore reciprocal interactions

may be involved in the generation of response patterns, as has been clearly demonstrated for the omega-neuron, (Wohlers and Huber, 1978). In addition many central units are multimodal and their responses reflect the complexity of their synaptic inputs, (e.g. Kalmring et al., 1979 and Kühne et al., 1980)

Due to the complexity of central acoustic units it is difficult to find homologies with the data of other workers particularly since the majority of studies have tested only a limited set of stimulus parameters. Since the response pattern of a unit may vary with both frequency and intensity of stimulation (e.g. To38AN1 and also Kalmring, 1975), it is necessary to present a wide variety of stimuli to provide a detailed characterisation of a unit. A stimulus may cause a long-lasting reduction in the level of spontaneous activity as well as a direct spiking response, (Rheinlaender, 1975 and To31AN1, Fig.23). Such a long- term reduction in spontaneous activity may be a significant part of the response rather than a passive hyperpolarisation following the direct response. Rheinlaender, (1975) found that the durations of the direct discharge and suppression depended on stimulus intensity in different ways and neurons have been reported that respond to sound stimuli only

via suppression of spontaneous activity, (Rheinlaender and Kalmring, 1973, Casaday and Hoy, 1976). Changes in spontaneous activity levels may alter the state of post-synaptic neurons and their subsequent responses. Rheinlaender, (1975) also reported phasic units in D. verrucivorus whose responses were virtually independent of stimulus intensity, duration and frequency. Similar patterns of response have been seen in Locusta, (Kalmring, 1971) noctuid moths, (Roeder, 1966), and have now been recorded in T. oceanicus, (e.g. To35AN1 Fig.34).

Attempts have been made to classify central units into groups on the basis of physiological and anatomical characteristics, (Rehbein, 1974, 1976 and Kalmring et al., 1978 for Locusta migratoria: Rheinlaender et al., 1972 and Rheinlaender and Kalmring, 1973 for D. verrucivorus). In crickets few units have been characterised anatomically an physiologically. Casaday and Hoy, (1976) recorded and intraganglionic neuron, int-2 in T. oceanicus which appears to be homologous with the LSAN recorded by Popov et al., (1978) in Gryllus bimaculatus and the omega-neuron recorded in G. bimaculatus and G. campestris by Wohlers and Huber, (1978)

On the basis of the existing data from a variety of studies in different animals some attempt may be made to draw homologies for ventral

cord units. Units have been reported which are tuned to the C.F. of the proclamation songs. The characteristics of some of these units are summarised in Table II. These units had a relatively high level of spontaneous activity which was suppressed during sound presentation; they were non-habituating and duplicated the temporal structure of the proclamation song. Although little is known of the anatomy of these units they are described as producing small spikes and are often recorded simultaneously with a large amplitude spiking unit, (Hill,1974; To38AN1 and N2). The similarities in the physiological characteristics of units in Table II suggests that they are the same unit type in any one species or homologues in different species.

Table III summarizes the data on a number of units which respond to frequencies over the range 3kHz to at least 20kHz. These units are characterised by rapid adaptation to stimuli in excess of 10 stimuli/s. The response pattern of these units changed with frequency; below 10kHz the response had a long latency and a low-discharge rate; a short latency, tonic responses was elicited to frequencies in excess of 10kHz.

Despite some similarities between the other units

Table II Summary of ventral cord units from different Gryllids that show similar response characteristics. The units are tuned to the carrier frequency of the species proclamation song. ChF; characteristic frequency: S.A.; spontaneous activity levels.

AUTHOR	UNIT	SPECIES	FREQUENCY RANGE, ChF	S.A.	EFFECT OF DURATION, REPETITION RATE AND SONG TYPE.	ANATOMY AND OTHER DETAILS
Popov, 1971	L.F.	Gryllus bimaculatus	4-5kHz			Tonic response over whole intensity range. Marked after-discharge to high intensity 4kHz stimuli. Inhibition of S.A. for some time after stimulus ceases. Slow to adapt.
Stout and Huber, 1972	Pulse coder	Gryllus campestris	Responds to calling song.		Responds to calling song, codes pulse duration and rate.	Non-habituating.
Zhantiev and Tschukanov, 1972	C-neurons	Gryllus bimaculatus				
Popov et al., 1974	Type II	Gryllus bimaculatus	4-20kHz, ChFs4-5kHz 10-20kHz	Yes	Follows amplitude modulation of calling song, codes 100ms stimuli.	Spontaneous activity totally suppressed during response to calling song.
Rheinlaender et al., 1976	L.F.	Gryllus bimaculatus	3-10kHz, ChF: 5kHz	Yes (High)	Codes temporal pattern of calling song, codes pulse duration and repetition rates of pulses and chirps.	Axon runs to protocerebrum. Terminal branches go to the lateral region between the protocerebrum and deutocerebrum and to the frontal region of the protocerebrum.
Hill, 1974	STU	Teleogryllus commodus	2-16kHz, ChF:3.5-4kHz	Yes	Codes pulse train. Spike rate decreases during stimulus but codes duration.	Small amplitude spikes, non-habituating. Latency not closely correlated with intensity.
	STU	Teleogryllus oceanicus	ChF: 4.5kHz	Yes	Codes durations in excess of 200ms pulse number and repetition rate.	
Ball and Hill,	STU	Teleogryllus commodus	2-?kHz ChF:3.4-4kHz		Follows trains of stimuli with sustained spiking to long tones.	
Boyan, 1978	STU	Teleogryllus commodus	ChF:3.5-4kHz		As Hill,(1974).	Directional, cardioid directivity pattern, maxima at 90°
Elsner and Popov, 1978	L.F.	Gryllus bimaculatus	ChF:4.5-5kHz	Yes (High)	Codes calling and aggressive songs following chirp repetition rate. Poor coding of courtship song.	Soma contralateral to axon. One main dendritic branch restricted to anterior part of prothoracic neuropile. S.A suppressed when sound is presented. Duration of suppression related to intensity and duration of the stimulus.
Hutchings and Lewis, ~~1981~~ in press	To38AN1	Teleogryllus	3-10kHz ChF: 4.5kHz	Yes	Codes 6s stimulus with little adaptation. Follows repetion rates up to at least 10 stimuli/s.	Small amplitude spikes, recorded simultaneously with a large amplitude unit, (see Table III). S.A. suppressed by sound. Duration of suppression related to intensity, duration and direct spiking response.

Table III Summary of ventral cord units from different insects that show similar response characteristics. The units are responsive to a wide range of frequencies.

ChF; characteristic frequency; S.A. spontaneous activity levels.

AUTHOR	UNIT	SPECIES	FREQUENCY RANGE, ChF	S.A.	EFFECT OF DURATION, REPETITION RATE AND SONG TYPE	ANATOMY AND OTHER DETAILS
Kalmring, 1975	G1-neuron	Locusta migratoria	4-40kHz			Soma contralateral to the axon in the mesothoracic ganglion. High thresholds, response varies between phasic and tonic.
Casaday and Hoy, 1977	int-1	Teleogryllus oceanicus	No data	Yes	Did not reliably code the temporal of the calling song.	Axon terminates in the brain. Soma contralateral to the axon in the prothoracic ganglion.
Rheinlaender et al., 1976	H.F.	Gryllus bimaculatus	3-50kHz	No	Codes short duration stimuli. Follows courtship and aggressive songs.	Response may exceed stimulus duration and is partially inhibited to 5kHz stimuli. Possibly used to detect brief ultrasonic sounds of predators.
Hill, 1974	LAU LAU	Teleogryllus commodus Teleogryllus oceanicus	3.5-16kHz ChF:3.5-4kHz ChF: 4.5kHz		No consistent temporal coding.	Often recorded with a small amplitude unit, (see TableII). Sustained stimulation results in a decrease in the response within the first 200ms. Infrequently inhibition of the response occurs with an offOresponse on cessation of the stimulus.
Ball and Hill, 1978	LAU	Teleogryllus commodus	2-15kHz ChF:4-4.5kHz		LAU responds to repeated stimuli but the spike rate declines during extended stimuli.	
Boyan, 1978	L	Teleogryllus commodus	As for Hill, 1974			Directional, possibly used by female for locating a singing male.
Elsner and Popov, 1978	H.F.	Gryllus bimaculatus	3-40kHz Best above 10kHz	No	Fast adaptation to stimuli exceeding 100ms, then after-discharge. Only codes repetition rates up to 10 stimuli/s. Poor response to calling song.	Axon ascends to brain; terminal branches are limited to ipsilateral side and primarily to the protocerebrum. Most dendritic arborisations are contralateral to to the soma in the ganglion. Probably used in evasive behaviour.
Wohlers and Huber,	AIAA	Gryllus bimaculatus Gryllus campestris	Active range 12-20kHz Excited above 10kHz			Morphologically similar to H.F. unit of Elsner and Popov, (1978) and to int-1 of Casaday and Hoy, (1977). IPSP'S to the carrier frequency of the species calling songs. Latency suggests AIAA is a first-order neuron.
Hutchings, 1981	To38AN2	Teleogryllus oceanicus	4-40kHz ChF: 3.5kHz	No	Codes short duration stimuli accurately, reproduces high frequency 50ms stimuli at rates of 10 stimuli/s.	Recorded simultaneously with a small amplitude unit, (see Table II). Ultrasonic response poosibly used in predator-prey interactions.

recorded in this study and those reported by other workers there is insufficient information to justify further grouping. On the basis of the results in Tables II and III it does appear that there are homologous units in the different species of gryllids but it is difficult to draw strong comparisons with the acridids or tettigoniids. It is clear from this discussion that wherever possible a standard set of stimuli should be tested and supported with anatomical data; only then can conclusive comparisons be drawn.

CHAPTER V.

148-157

General Discussion.

Discussion.

The behavioural studies of Popov et al., (1975) and Moiseff et al., (1978) iniicated that crickets are capable of broad-band reception but the behavioural importance of ultrasound to crickets has received little attention except in these studies. Most workers have concentrated on the low frequencies typical of the proclamation and aggressive songs but the courtship songs of crickets are relatively broad-banded and ultrasonic components have been shown in the songs of G. campestris, (Lottermoser, 1952) Nemobius fasciatus, (Pielemeier, 1946) and Acheta domesticus, (Lewis , personal communication). The ultrasound in courtship songs may be of low intensity but these signals are usually produced when the male is very close to the female, ultrasound may therefore be used in intraspecific communication. Ultrasound signals may also be produced by predators either directly i.e. the squeaks of rodents and bat cries, (Sales and Pye, 1974) or spuriously during movement through the undergrowth. Rheinlaender et al., (1976) described a ventral cord unit(H.F. neuron) in G. bimaculatus which they suggested was suitable for the analysis of signals produced by rodents and bats. Broad-band noise can be produced in the biotope when vegetation is rustled in the wind or

moved by predators, and it may mask some animal calls. However few of the central units of Teleogryllus oceanicus respond to white noise and this may indicate the prescence of a filtering mechanism for "random" noise in the environment.

In this study both primary and central units have been recorded which are maximally sensitive to frequencies above 20kHz and some were recorded which are likely to have characteristic frequencies, (ChFs) in excess of 42kHz. Some units responded to a wide range of frequencies but were relatively insensitive, while others showed peak sensitivity at a particular frequency. Low frequency, (L.F.) primary units were more sharply tuned than high frequency, (H.F.) units. In addition both primary and central units were recorded that showed more than one ChF; (e.g. Figs 8,15, 8, unit 107; 15 unit 36). Although the primary threshold curves of T. oceanicus are less tuned than those recorded in Decticus verrucivorus, (Kalmring et al., 1978), it is likely that crickets , like bush-crickets are able to perform an approximation of a Fourier analysis rather than a simple frequency discrimination as suggested by Pumphrey, (1940).

The basis of frequency discrimination (and/or analysis) in insects has been a matter of considerable discussion. A number

of factors intervene between stimulus incidence and action potential production. One important stage is the membrane displacement. Johnstone et al., (1970) investigated the resonance properties of the tympanal membranes of T. commodus and T. oceanicus using the Mossbauer technique and concluded that the membranes were tuned to a narrow spectrum of frequencies with a peak sensitivity at 4kHz. They suggested that the tuning curves of single units could result from resonant properties of the membrane alone. Dragsten et al., (1974) used a laser technique to demonstrate that the posterior tympanic membrane of G. pennsylvanicus was mechanically tuned to 5.5kHz; the frequency at which the tympanal nerve threshold curve shows a sensitivity peak. Larsen and Michelsen, (1977) also used a laser technique and found that the velocity curves for the posterior tympanum of G. campestris did not show the fine tuning of the tympanal nerve threshold curve. Membrane resonances will contribute to the tuning of the receptor organ since the transfer of energy to the receptor will be maximised at the resonance frequency of the membrane. The resonant properties of the tympanic membranes may be due in part to the characteristics of the acoustic tracheae. Paton et al., (1977) found that the tympanic membrane did not seem to play an important role in the frequency

sensitivity of the tympanal organ in T. oceanicus, G. campestris or Acheta domesticus. The receptor cells are situated in a haemocoelic space with no direct attachment to the tympanal membranes but their tuning may be enhanced as a consequence of their anatomy. Zhantiev and Tschukanov, (1972) have suggested that both the anatomy and attachment of the receptor cells are involved in tuning. Young and Ball, (1974) were able to divide the scolopidia of T. commodus into 5 groups on the basis of anatomy. In this study 5 types of primary threshold curve were distinguished but it is not yet possible to correlate the anatomical and physiological results. Further experiments are required in which the recorded units are marked back to the cell bodies.

The derived threshold curves for primary and central unit data are similar both in terms of sensitivity and frequency range indicating that intensity and frequency information coded peripherally is retained at the level of the cervical connectives. Some units code stimulus intensity, the number of spikes produced usually increasing linearly with the logarithm of sound intensity. The accuracy of coding depends on the number of spikes produced per dB intensity change. Units may show prefered intensity ranges within which

intensity is accurately coded but the coding of intensities close to threshold level is often poor. At intensities in excess of 30dB above threshold, the majority of unit responses are saturated; the dynamic range of most units is about 30dB. Since the units responding to any one frequency have differing thresholds, then as the response of one unit saturates a second will reach threshold level and respond to higher intensities. Therefore intensity coding can be extended by range fractionation, (Rheinlaender, 1975). Some primary and central units show intensity coding only at certain frequencies within their frequency ranges. These units may be involved in direction and distance coding, (see below). Other units respond phasically or achieve maximal spike production within a few dB of threshold and maintain this output at higher intensities. Such units are unsuitable for intensity coding.

The majority of recorded units in T. oceanicus are tuned to the carrier frequency, (C.F.) of the proclamation song. Changes in the relative percentages of low and high frequency units recorded in the leg nerve and connectives indicate that some analysis of low frequency information occurs at the level of the prothoracic ganglion. Casaday and Hoy, (1977) recorded an intraganglionic neuron (int-2) in

T. oceanicus which was tonically excited by 5kHz tones and accurately coded the temporal pattern of the species song. This unit appears homologous to the LSAN, (Popov et al., 1978) and the omega cells recorded in G. campestris and G. bimaculatus by Wohlers and Huber, (1978). These cells are tuned to the C.F. of the species proclamation songs, (Elsner and Popov, 1978) but the tuning is no sharper than that of the primary units recorded in these species, (Esch et al., 1980).

The LSAN, int-2 and omega cells are thought to relay receptor signals to higher order interneurons without modifying the temporal pattern significantly. Interaction between the two omega cells is used in determining sound direction, (Wohlers and Huber, 1978) and may be important in localising singing conspecifics in the field.

Narrow-band or pure-tone calls which begin and end softly are difficult to localise,(Marler, 1955). The ability to analyse broad-band sounds means that more potential information is available to the animal in terms of frequency and intensity which may be used in localizing a sound-source. Directional cues are ultimately determined from differences in the effective intensity of sound registered by the two receivers, (Hill and Boyan, 1977), comparisons occuring within the central nervous system. However, distance is

also coded in terms of intensity functions. Despite the attenuation due to geometric spreading and environmental factors which may cause artifactual variations in the sound pressure, the intensity of a sound is still a reasonable parameter for judging the distance of an emitter. There are therfore many potential ambiguities in the information present at the primary level. Rheinlaender, (1975) and Lewis, (in prep,) propose that different forms of analysis must occur within the central nervous system and help to minimise ambiguity. Some central units receive both ipsilateral and contralateral input and crossed-inhibition enables large differences to be maintained whatever the incident sound intensity. The omega-cells, (Wohlers and Huber, 1978) receive auditory input entirely from the cell body side. Two such mirror-image cells exist in the protharacic ganglion and they mutually inhibit one another. Wohlers and Huber suggest that the omega cells may enhance the ipsilateral-contralateral differences arriving from the peripheral pressure-gradient system. In the avian auditory midbrain, the binaural EI cells may also be used to produce a response which reflects a differential input, (Coles and Aitkin, 1979 and Coles et al.,1980). Other insect central units occur whose responses are independent of direction, (Rheinlaender, 1975). Such cells may

reflect the overall intensity levels and be used in determining the distance of a sound-source. Units which code the effective intensity of sound at only one of the receivers may also provide a directional response. Lewis, (in prep.) suggests that a separation of direction and intensity parameters can be achieved by this form of analysis. This data must be analysed at a higher level but it is also likely to descend in the ventral cord in T-shaped fibers, (Rheinlaender et al., 1972) and descending neurons, (e.g. Zhantiev and Tschukanov, 1972; Rheinlaender and Kalmring, 1973; Zhantiev and Kalinkina, 1977 and Boyan, 1978). The destination of these fibers is not yet known.

When male crickets, bush-crickets and grasshoppers sing they produce both airborne sound and vibration which is transmitted to the substrate. Attenuation of the high frequency components is high but the lower frequencies important in amplitude modulation may be propagated via the substrate. Dambach, (1972) demonstrated that primary neurons in the three pairs of legs of G. campestris and G. bimaculatus were responsive to vibration and that each pair of legs showed maximum sensitivity at different frequencies. Many workers have shown that units in the ventral cord ot bush-crickets and acridids are responsive to both sound and vibration stimuli, (e.g. Čokl et al.,

1977 in Locusta migratoria; Kalmring et al., 1980 in Tettigonia cantans; Kühne et al., 1980 in D. verrucivorus and Silver et al., 1980 in D. verrucivorus and T. cantans). In this study primary units were recorded in T. oceanicus that were responsive to 500Hz airborne sound stimuli at high intensities. These units may be preferentially responsive to vibratory stimuli like the VS units of D. verrucivorus, Kalmring et al., (1978). The central acoustic neurons of D. verrucivorus are influenced by both airborne sound and vibration stimuli and the effect may be either inhibitory or excitatory, (Kühne et al., 1980). Many insects sing in dense vegetation and vibrations transmitted via the legs to stems and leaves may be propagated, carrying species-specific information associated with the amplitude modulation pattern of the song. Similarly predators may cause vibration during movements through the undergrowth; simultaneous processing of both sound and vibration stimuli may facilitate localisation of the emitter by the receiver at airborne sound intensities which produce saturation of acoustic receptors. Although the majority of acoustic ventral cord neurons tested with sound and vibration stimuli are effected by both modalities, Boyan, (1980) found units in the brain of G. bimaculatus which appear to be unimodal indicating that

some separate processing of data from the different modalities must occur.

The units recorded in T. oceanicus appear capable of performing broad-band frequency analysis although the degree of tuning of the primary units is not as sharp as that seen in the tettigoniid D. verrucivorus, (Kalmring et al., 1978). The sensitivity to ultrasound may reflect the importance of high frequencies in intraspecific communication but may also be involved in predator detection. The complexity of some central unit responses may reflect the results of binaural processing and the variation in response patterns with stimulus frequency, intensity and duration indicates that considerable integration occurs at the level of theventral cord.

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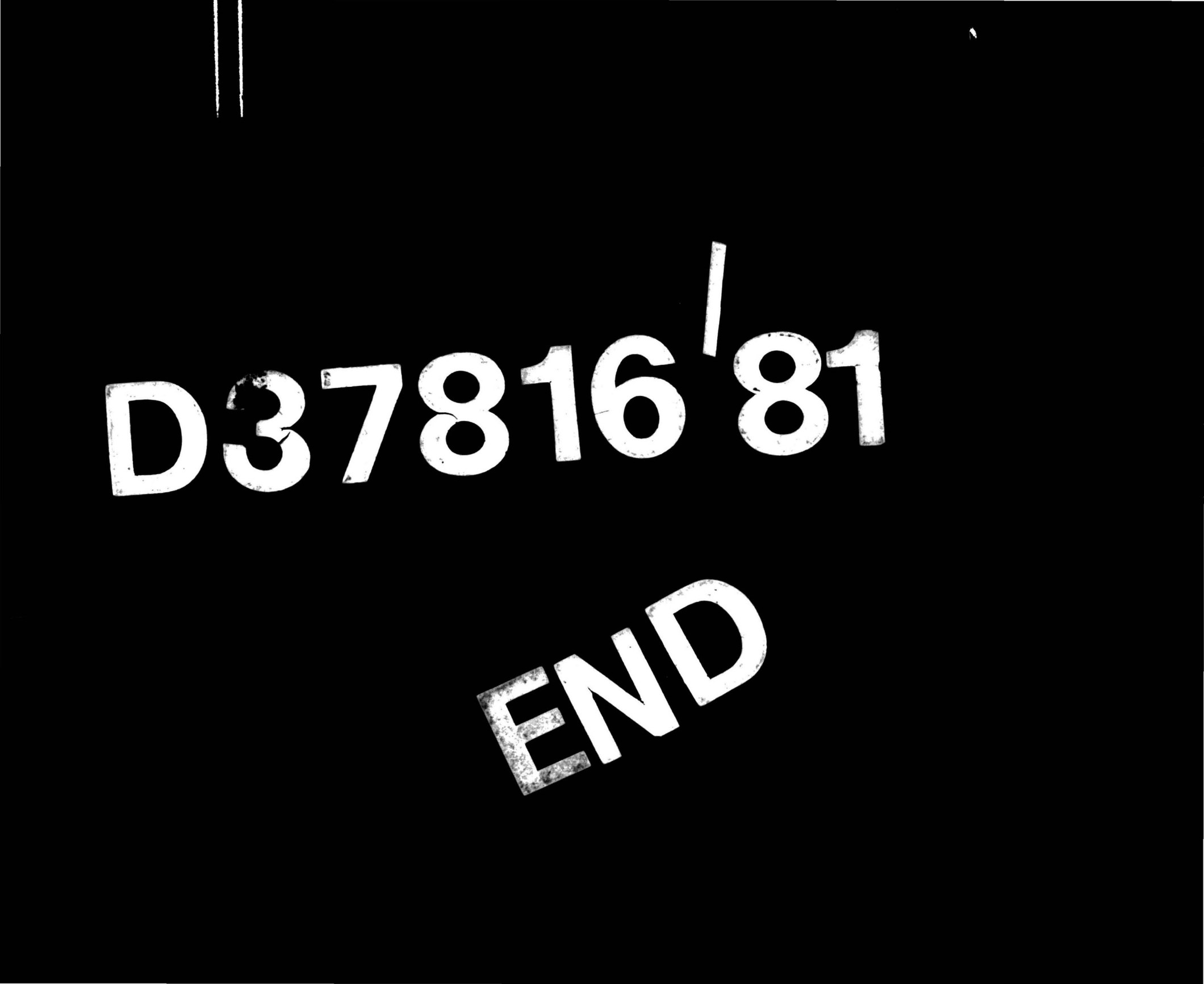
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