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THE CODING OF INTENSITY IN THE PERIPHERAL AUDITORY SYSTEM OF THE CAT

by

A. R. PALMER

Dissertation presented to the University of Keele for the degree of Doctor of Philosophy.

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Research Department of
Communication and Neuroscience,
University of Keele.

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Abstract

A discrepancy exists between the dynamic range of peripheral auditory neurones and the range over which the human ear maintains fine intensity discrimination. Psychophysical experiments, using simultaneous high and low pass (bandstop) masking noise, indicate that intensity discrimination at high intensities under these specific conditions is unlikely to be mediated by a spread of activity to neurones innervating neighbouring regions of the basilar membrane.

A conclusion from these psychophysical data is that neurones coming from a limited region of the basilar membrane must, at least under bandstop noise masking conditions, be capable of signalling small intensity differences over a wide dynamic range. It is the validity of this conclusion which the experiments reported in this dissertation have sought to test.

A related but separate problem is the way in which the absolute intensity of a signal is represented in the activity of the cochlear nerve. The encoding of absolute intensity is therefore considered and briefly discussed in relation to the results of the present study.

Microelectrode recordings from the cochlear nerve and nucleus of the anaesthetised cat led to the following conclusions:

1. The range of minimum thresholds of neurones in the cochlear nerve and nucleus of a single ear is limited, at any frequency, to 20-30 dB, which is consistent with the literature and probably excludes the possibility that a high threshold population of neurones had been previously overlooked.

2. The dynamic range of some monotonic cochlear nucleus neurones measured after adaptation is wider than that measured under unadapted conditions. However, the dynamic ranges of cochlear nerve fibres and

all monotonic cochlear nucleus neurones, even allowing for the extension afforded by the adaptation process, are still insufficient to account for the wide dynamic range shown psychophysically. Non-monotonic cochlear nucleus neurones have dynamic ranges of up to 100 dB, which may reflect inhibitory input to such cells from fibres of differing characteristic frequency.

3. Under conditions of bandstop noise masking, analogous to those used in the psychophysical studies, some two-thirds of the neurones in the dorsal cochlear nucleus (with characteristic frequencies from 0.7-29 kHz) have very wide dynamic ranges, some of which were up to 110 dB. In contrast, cochlear fibre dynamic ranges in response to tones are the same, whether or not the bandstop noise masker is present. The results of parametric studies of the responses of cochlear nucleus neurones are consistent with the suggestion that the wide dynamic range, under bandstop noise masking conditions, results from lateral inhibition induced by the masking noise.

4. Under conditions of bandstop noise masking, intensity differences at high intensity levels are not encoded in the cochlear nerve by <u>large</u> differences in the mean discharge rate of single fibres, but could possibly be encoded by <u>small</u> differences in the mean discharge of a minority of fibres. A second possibility for the encoding of intensity differences, under these conditions, is the fine time structure of the cochlear fibre discharge.

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CHAPTER ONE: GENERAL INTRODUCTION

1.1 Preface

In his natural environment man is exposed to an enormous range of sound intensities and, not surprisingly, the human ear has evolved to accommodate this range. The loudest sound which can be heard without immediate deleterious effects to the ear is some million, million times more intense than the weakest audible sound. This enormous range of intensities can be conveniently expressed on the decibel scale as 120 dB.

Over the whole of this range of stimulus intensities humans can accurately judge the loudness of a sound. Loudness is a subjective attribute of sound which, although primarily determined by its intensity, depends upon factors such as its duration, frequency, and spectral composition (the variation of loudness with changes in these parameters is described in detail in section 1.2). For a given stimulus the loudness varies monotonically with the stimulus intensity. Since humans are able to judge loudness over a wide range of intensity, the absolute intensity of the stimulus must be represented in the overall discharge pattern of the cochlear nerve over an equally wide range.

For the purposes of the present study, a more relevant observation is that over a substantial part (100 dB) of the ear's dynamic range, humans can detect very small differences in the intensity of a stimulus (of the order of 1 dB, see section 1.2 for details). Thus, small intensity differences must also be represented in the cochlear nerve discharge pattern over a wide dynamic range.

We have, therefore, two related observations; intensity and intensity differences are represented in the cochlear nerve discharge over a wide dynamic range. Clearly, the encoding of intensity and of intensity differences are not completely separable problems. A

single neurone whose discharge varies linearly with the intensity of the stimulus (measured in dB) over a sufficient range could perform both functions. Such neurones do not, according to presently available data, exist in the cochlear nerve of the cat.

The discharge rate of peripheral auditory neurones only varies as a function of intensity over a range of the order of 30-50 dB. This narrow 'dynamic range' of peripheral auditory neurones was first shown by Galambos and Davis (1943) in their pioneering recordings from the cochlear nucleus. However, since these same authors found a wide range of minimum thresholds of single neurones at any frequency, their limited dynamic range did not present any difficulties for the existing theories of the encoding of intensity or intensity differences over a wide range of stimulus intensity. (The combination of limited single fibre dynamic ranges and a wide range of minimum thresholds is considered in detail in section 1.7.)

More recently, redeterminations of the range of minimum thresholds, at any frequency, have revealed that in a single ear minimum thresholds are distributed over a range of only 20-30 dB (first shown by Kiang (1968)). There is, therefore, a considerable discrepancy between the intensity range over which single neurones can apparently signal intensity and intensity differences and the range over which humans can detect intensity differences or make judgements of the loudness of a sound.

Some recent data of Smith and Zwislocki (1971) did suggest, however, that some neurones in the cochlear nucleus might, as a result of adaptation, retain sensitivity to small intensity differences over a range of intensity wider than their dynamic range to stationary stimuli (discussed in detail in sections 1.8 and 4.1). Furthermore, recent psychophysical data (see section 1.7) imply that, under conditions of bandstop noise masking, neurones coming from a limited region of the

basilar membrane are apparently able to convey information concerning intensity differences over a wide dynamic range.

It was therefore decided to concentrate on the problem of the encoding of intensity differences. The prime aim of the present study was to determine whether single neurones coming from a limited region of the basilar membrane could signal small intensity differences over a range of intensity sufficient to account for the psychophysical intensity discrimination data.

The related problem of the representation of intensity *per se*, in the cochlear nerve activity has not been the major concern of these experiments. Thus it might seem unnecessary to include a review of current theories of the encoding of intensity (section 1.7). These theories do, however, suggest ways in which differential intensity sensitivity may be maintained over a wide dynamic range. Indeed, many of the psychophysical experiments crucial to the present study were performed to test theories of intensity encoding (and are therefore described in this review section). The implications of the present study for the encoding of the intensity of stimuli are discussed briefly in chapter six.

In this introductory chapter, several bodies of relevant literature are reviewed. The psychophysical experiments on loudness are reviewed in order to place the present study in context (section 1.2). In addition, since the present experimental data have been obtained from the cat, the animal behavioural literature is discussed (section 1.3), in order to evaluate the usefulness of the cat as an animal model for the investigation of intensity encoding.

The middle-ear structure and function is described in detail (section 1.4) since, in the view of several authors (Simmons, 1959;

Suga and Jen, 1974; Borg and Zakrisson, 1977), the effect of the acoustic middle-ear reflex is to extend the operating range of the ear.

Recordings were made initially from the cochlear nucleus, which is a second-order nucleus, and, as a result of the data obtained, recordings were made from the primary neurones of the cochlear nerve to determine the degree to which re-encoding of the stimulus related information had occurred. The anatomy and physiology of both cochlear nerve and nucleus are therefore reviewed. Detailed reviews of the physiological literature specifically relevant to the different types of experiments performed in the present study are deferred to the appropriate chapters (see note on page 84).

The experiments of this study were performed to test the validity of certain conclusions from previous psychophysical and physiological studies. These conclusions, and the way in which the present experiments sought to test them, are briefly described in the final section of this first chapter.

1.2 Psychophysical Experiments on Loudness

It is necessary at the outset to clearly distinguish between the terms loudness and intensity.

The term intensity is used to mean the power of a sound, which is expressed in physical terms as units of energy. The intensity of a sound is therefore a physical quantity which can, if necessary, be measured without reference to a human observer.

Loudness is a subjective attribute of the sound and as such can only be measured by evaluating the responses of normal human subjects.

It has long been known that the loudness of a sound depends upon its intensity. Helmholtz (1877) noted that both the amplitude and loudness of a sound decreased with distance but its pitch and spectral composition remained unchanged; he therefore concluded that

> '. . . loudness must depend on this amplitude and none other of the properties of sound do so'.

Certainly the loudness of a sound does depend on its intensity but also upon its frequency, duration and spectral composition. It is convenient therefore to divide the following review of the psychophysical experiments on loudness into sections according to which of these variables was studied.

1.2.1 Loudness as a Function of Intensity

One of the earliest attempts at quantifying the relation of the loudness of a sound to its intensity was that of Fletcher and Munson (1933). These authors measured the loudness-level of tones by comparing their loudness with that of a 1 kHz reference tone. Loudness-level of any sound is defined as the sound pressure level of the equally loud reference tone at the position where the listener's head is placed. The german word phon has been adopted as the unit on the

Figure 1

The loudness of a 1 kHz tone as a function of its intensity.

(From Churcher, 1935.)

Figure 2

Histogram of the decibel difference between two tones in the vicinity of 1 kHz, which produces a loudness ratio of 2:1, as determined by different investigators. N = 178.

(From Stevens, 1955.)

Figure 1

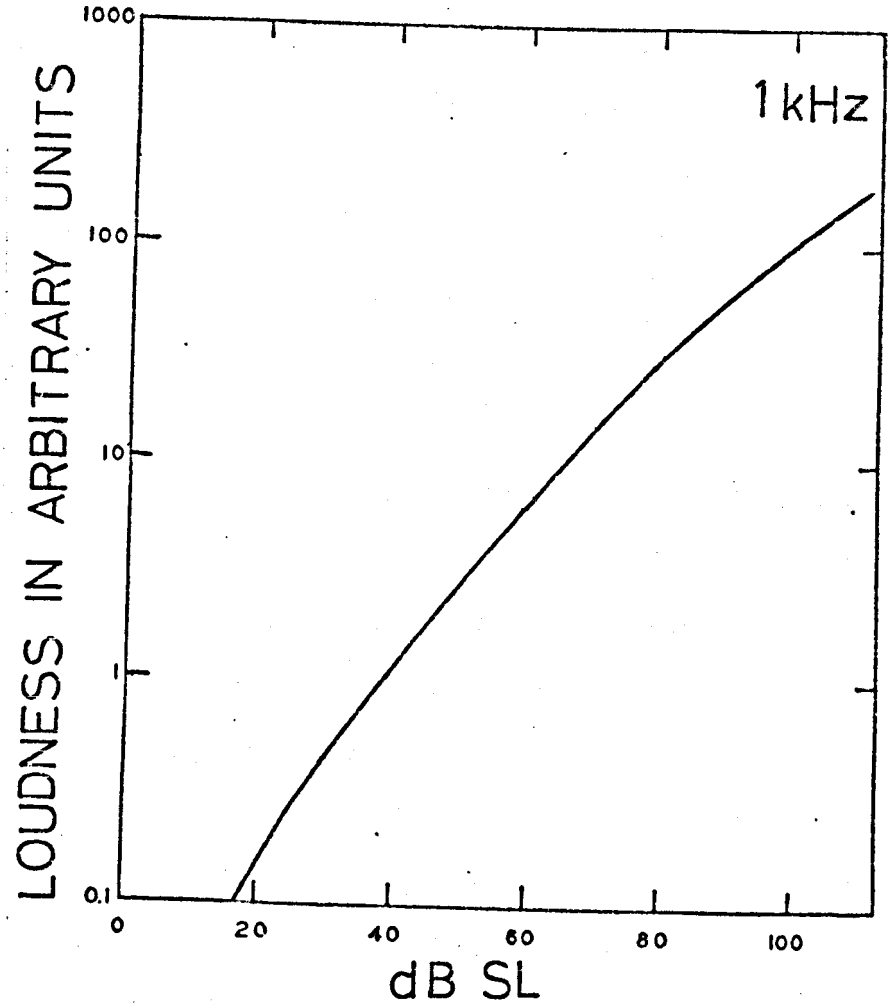
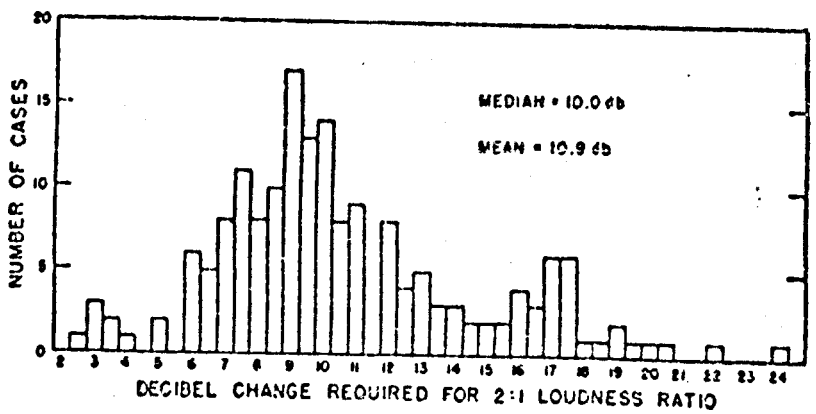


Figure 2



loudness-level scale. The phon is mathematically equivalent to the decibel and hence a sound of loudness-level 50 phons is equal in loudness to a 1 kHz tone of 50 dB SPL. The logarithmic phon scale, however, although covering a wide intensity range conveniently, does not fit a subjective loudness scale. A factor of two in loudness does not correspond to a halving or doubling of the number of phons. A more appropriate scale would be one on which the number N represents a loudness which does in fact appear to be half as great as that represented by the number 2N etc. A number of studies have attempted to determine such a subjective loudness scale (Bekesy, 1929; Ham and Parkinson, 1932; Geiger and Firestone, 1933; Churcher, King and Davis, 1934; Churcher, 1935; Stevens, 1936, 1955).

In the study of Churcher (1935), the loudness of a 1 kHz tone 100 dB above threshold was designated as 100 units, and subjects were asked to assign values of 50 and 10 units etc., to levels of tone sounding half and one tenth as loud accordingly. The loudness function devised from these experiments is shown in Fig. 1. In Fig. 1, between 1 and 10 loudness units on the ordinate, the dB difference required to achieve a doubling of the loudness is 8.6 dB, whereas between 10 and 100 loudness units the value is 10 dB. Stevens (1955) reviewing the extensive data then available, also obtained a median value of 10 dB for tones in the vicinity of 1 kHz. The 178 values from which the median value was computed are shown in histogram form in Fig. 2. It is clear from the scatter of values in this figure, that the choice of the median value of 10 dB is somewhat arbitrary for normal subjects. Stevens (1955) suggested that the greater slope below 40 dB in the older scales was consistent with the results of experiments in which subjects were asked to adjust a tone to half the loudness of a standard. The outcome of experiments in which subjects adjusted tones to double the loudness of the standard suggests that the slope becomes less steep below 40 dB. Since methods involving halving and doubling of the loudness appear to produce biassing of the data in

opposite directions, Stevens produced a compromise loudness scale by combining data from both sorts of experiment. The resulting loudness scale has a slope invariant of intensity indicating that loudness is a power function of stimulus intensity. The exponent of this power function was determined by Stevens to be $Log_{10}2$.

The term sone is used as the unit on the subjective loudness scale. It was first proposed by Stevens (1936) and defined as the loudness of a 1 kHz tone 40 dB above threshold, heard with both ears. A more useful definition which relates the phon and sone scales is that contained in ISO recommendation R131: one sone corresponds to a loudness-level of 40 phons, if for loudness-levels of 40 phons or greater, the relationship between the numerical values of loudness-level L_s (in phons) and loudness S (in sones) is given by

$$S = 2^{(L_s - 40)/10}$$

For white noise, at low levels of intensity, the loudness grows more rapidly as a function of intensity than the loudness of a 1kHz tone. Above approximately 50 dB SL the two loudnesses remain more nearly proportional (Stevens, 1955). Loudness remains an approximate power function of intensity (at least for 1 kHz tones) up to 140 dB above threshold (Stevens, 1955, is the only determination at such high levels). At levels of 140 dB above threshold the stimuli are extremely painful, in fact, the level of sounds causing discomfort ranges from 93-130 dB SPL depending on the criterion of discomfort employed (tickling feeling, etc.), the methods used and the spectral composition of the stimuli (Wegel, 1932; Bekesy, 1936b; Silverman et al., 1946; Stevens, 1970; Morgan et al., 1974).

The available data suggest therefore, that the best estimate of the difference in the level of two signals required to produce a loudness ratio of 2:1 is 10 decibels. When experimental biases are eliminated by combining results of different types of experiment this relation holds over the entire range of audible intensities, despite the fact that at the highest levels the signals are extremely painful.

1.2.2 Loudness as a Function of Frequency

When the intensity of a tone is held constant, loudness varies as a function of its frequency. By comparing the loudness of pairs of tones it is possible to determine the intensity levels of tones at various frequencies which are judged to be equally loud. A curve giving the relationship between different frequencies and intensities which are equally loud, is known as an equal loudness contour. Kingsbury (1927) was the first to make a series of measurements of equal loudness contours. Since this first study there have been several other studies (Fletcher and Munson, 1933; Churcher and King, 1937; Robinson and Dadson, 1956; Zwicker and Feldtkeller, 1967), and mean curves based on several studies have been included in an International Standards Organization recommendation (ISO R226) which is shown in Fig. 3.

At low loudness-levels the equal loudness contours follow the absolute threshold curve. Absolute threshold corresponds to the 3 phon loudness-level contour; this is because loudness-levels are defined relative to the sound pressure level of a 1 kHz tone the threshold of which is approximately 3 dB SPL (not 0 dB SPL as was earlier taken to be the case). It can be seen in Fig. 3 that with increasing level the equal loudness contours take an increasingly flatter course. At low frequencies the separation between the curves is not very great and only at levels above 50 phons are the curves more nearly parallel to each other. The decibel difference required for a loudness ratio of 2:1 which at 1 kHz is 10 decibels is clearly much less at low frequencies, indicating that either the exponent of the loudness function is much reduced or that the power law relation of loudness to intensity does not hold at these frequencies. That this is in fact the case is demonstrated by the actual determinations of loudness functions for low frequencies by Fletcher and Munson (1933) and Stevens and Davis (1938).

Figure 3

The loudness of pure tones as a function of frequency and intensity. Curves of equal loudness level for pure tones in frontal sound field.
(ISO Recommendation 226.)

Figure 4

Dependence of loudness on (a) the spacing of the components of a four tone complex centred at 500 Hz (upper curve) and (b) the bandwidth of a noise of constant SPL centred at 440 Hz (lower curve).

Loudness balances between a tone at the centre frequency and either the tone complex or noise were made.

For the upper curve T indicates adjustment of the comparison tone level and C adjustment of the tone complex level. The vertical bars on the lower curve show the interquartile ranges of adjustments. The straight lines through the data were drawn from predictions based on other measures of the critical band.

(From Zwicker, Flottorp and Stevens, 1957.)

Figure 3

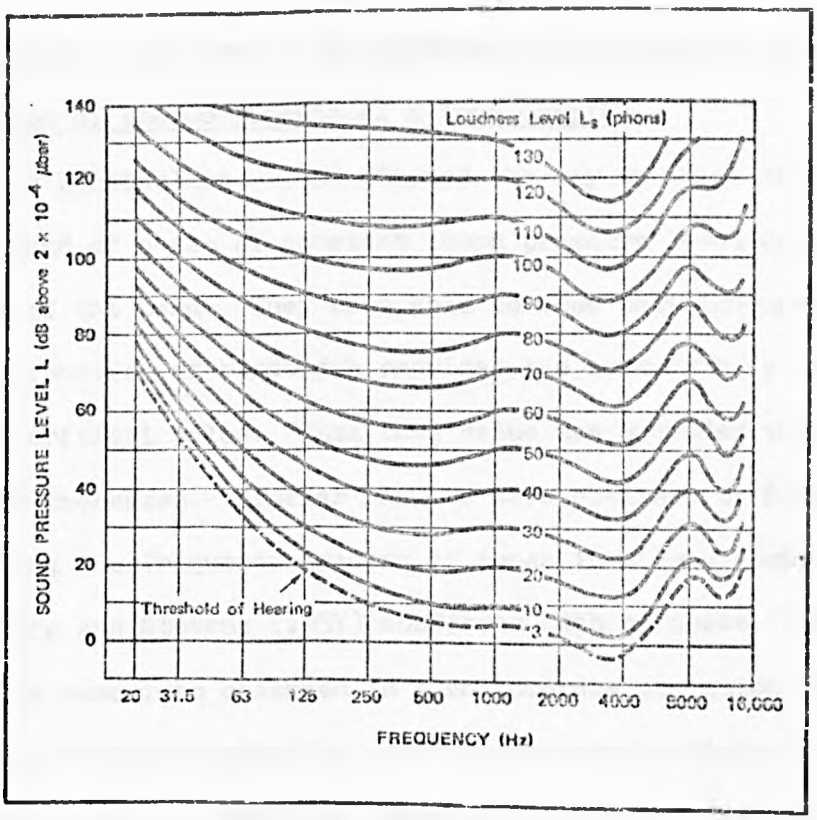
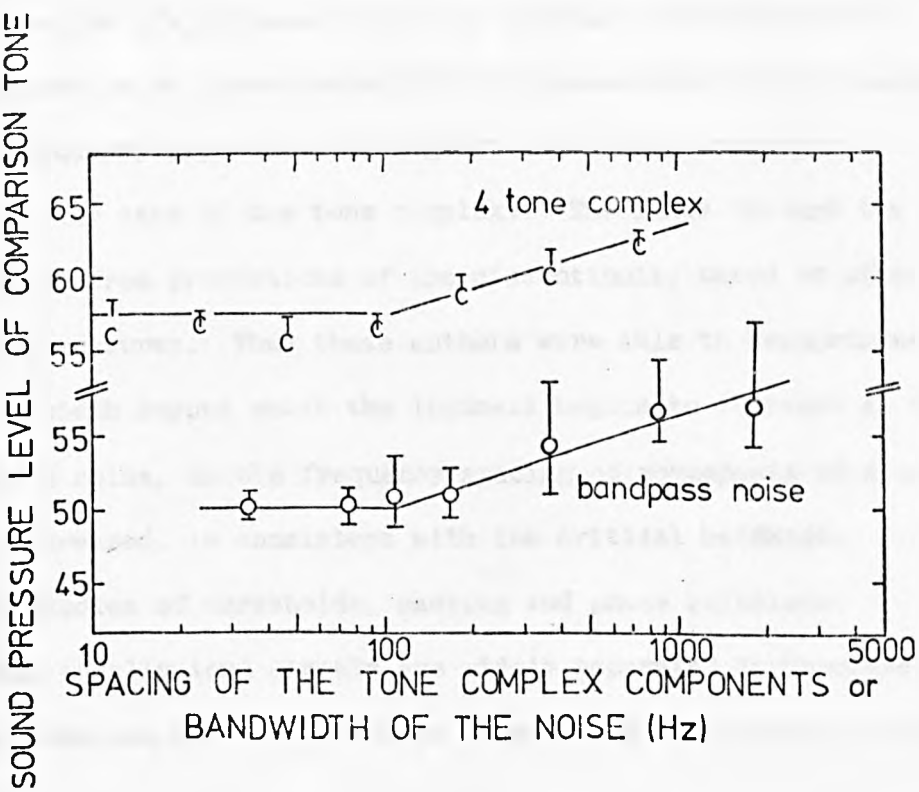


Figure 4



1.2.3 Loudness as a Function of the Bandwidth of Bandpass Noise and of the Separation of the Components of a Tone Complex

Zwicker and Feldtkeller (1955) studied the way in which the loudness of a band of noise of constant sound pressure level depended upon the width of the band. They were able to show that loudness was invariant as a function of bandwidth provided the bandwidth is smaller than a certain critical value. When this value was exceeded the perceived loudness increased. Similar results were obtained by Bauch (1956) by varying the frequency spacing of tones in a tone complex. Zwicker, Flottorp and Stevens (1957) confirmed both of these findings and compared the bandwidth observed in such loudness summation experiments with the critical bandwidths derived from observations of other phenomena, such as thresholds, masking and phase relations. Fig.4 (after Zwicker and Flottorp and Stevens) shows the way in which the loudness varied as a function of bandpass noise bandwidth (centre frequency 440 Hz) and the spacing of four tones in a tone complex centred at 500 Hz. The two functions are clearly comparable and the point at which the loudness begins to increase for both experimental paradigms is at approximately 100 Hz (bandwidth in the case of the noise, frequency separation of highest and lowest frequency components in the case of the tone complex). The lines through the data were drawn from predictions of the discontinuity based on other critical band measures. Thus these authors were able to demonstrate that the bandwidth beyond which the loudness begins to increase as the bandwidth of a noise, or the frequency spacing of components of a tone complex is increased, is consistent with the critical bandwidth observed in studies of thresholds, masking and phase relations.

When two equally loud signals are widely separated in frequency their loudnesses sum and the perceived loudness is twice that of either

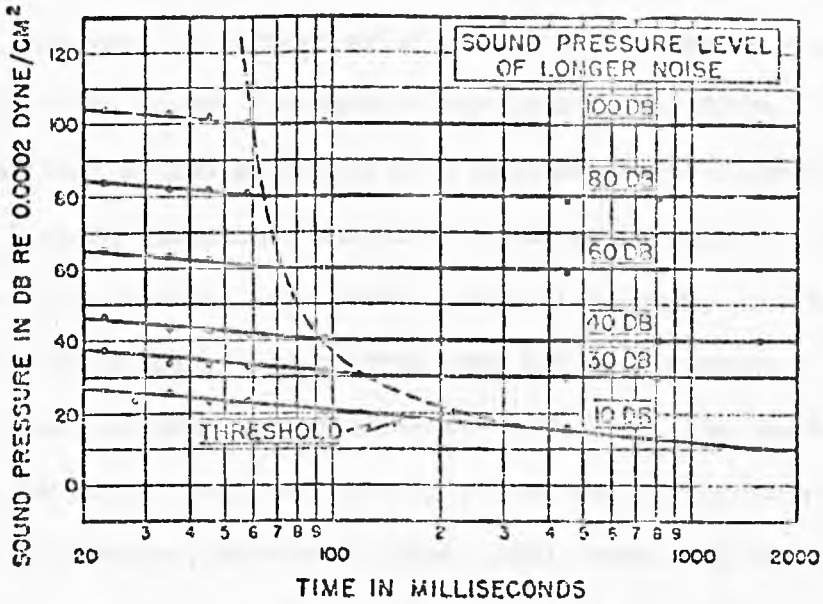
Figure 5

Dependence of the loudness of a broadband noise burst on its duration.

Equal loudness contours for noise as a function of duration. The sound pressure of the shorter burst of noise which sounded equal in loudness to the longer burst is plotted as a function of the shorter burst. Dashed curve indicates the shortest duration for which loudness is independent of duration.

(From Miller, 1948.)

Figure 5


SOUND PRESSURE LEVEL OF LONGER NOISE
100 DB
80 DB
60 DB
40 DB
30 DB
10 DB
THRESHOLD
SOUND PRESSURE IN DB RE 0.0002 DYNE/CM²
120
100
80
60
40
20
0
20
100
1000
2000
TIME IN MILLISECONDS

As level is increased the time constant falls progressively as shown by the dashed line in Fig. 5, reaching a value of only 60 msec at 100 dB SPL. It is generally agreed that as duration is increased by a factor of 10 the loudness level increases by about 10 phons.

There is, however, no indication of a temporal summation of acoustic energy of this order in the discharge of cochlear nerve fibres. The latency of the first action potential of a cochlear nerve fibre in response to a long duration near threshold stimulus is only of the order of a few milliseconds, not hundreds of milliseconds. Furthermore, the activity in the cochlear nerve does not show a gradual build up over time but does in fact decrease with time. On the basis of these data and of the high sensitivity of the auditory system to dichotic time differences, Zwislocki (1960, 1969) concluded that the locus of the temporal summation process was unlikely to be before the level at which signals from both ears are combined. Thus the process of temporal summation appears to operate on the neural activity evoked by a stimulus rather than directly on the acoustic energy (Zwislocki, 1960, 1969).

1.2.5 The Difference Limen for Intensity

In measuring the difference limen (DL or JND) for intensity, one measures the intensity difference required to produce a just detectable change in the perceived loudness. The variation of the DL with intensity has been studied by a number of investigators using a wide variety of different signals (tones, Knudsen, 1923; Reisz, 1928; Zwicker, 1956: random and square wave noise, Miller, 1947; pseudo-random noise, Raab and Goldberg, 1975). The data of three of these studies are shown in Fig. 6.

The DL near threshold is greater than 3.5 dB and falls with

Figure 6

Dependence of the just noticeable difference in the intensity of a variety of stimuli upon the sensation level of the stimulus.

(From Miller, 1947, with the addition of the data of Jesteadt, Wier and Green, 1977.)

Figure 7

Calculated (solid line) and measured values (open circles) of the just perceptible amplitude modulation depth of a 1 kHz tone as a function of its level; the dashed curve represents the function determined in the presence of a high pass masking noise.

(From Zwicker and Feldtkeller, 1967.)

Figure 6

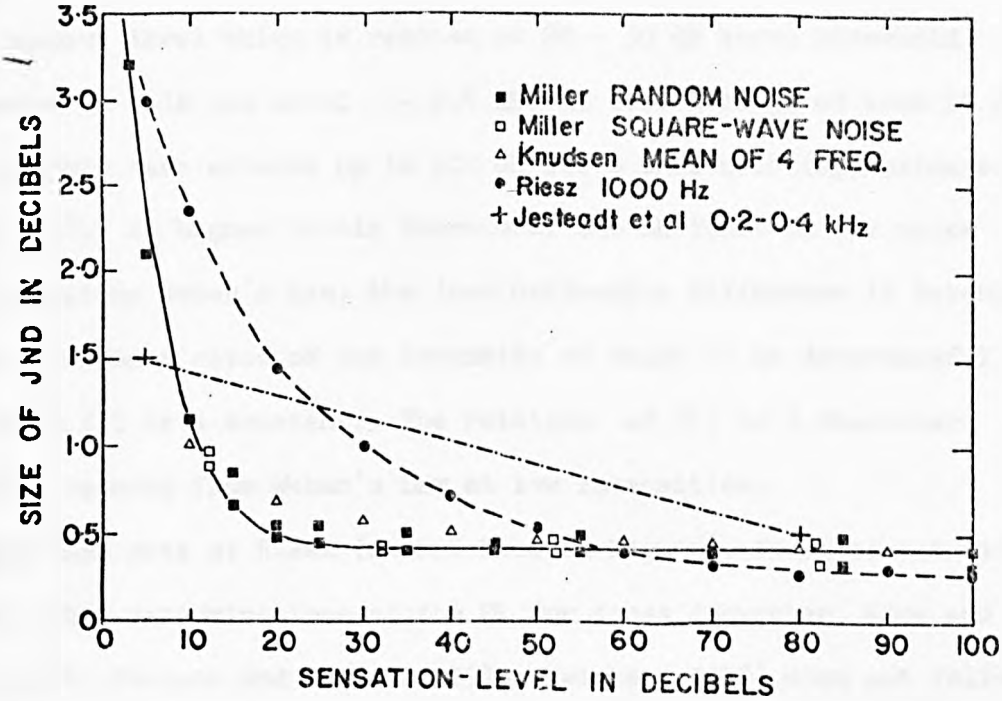
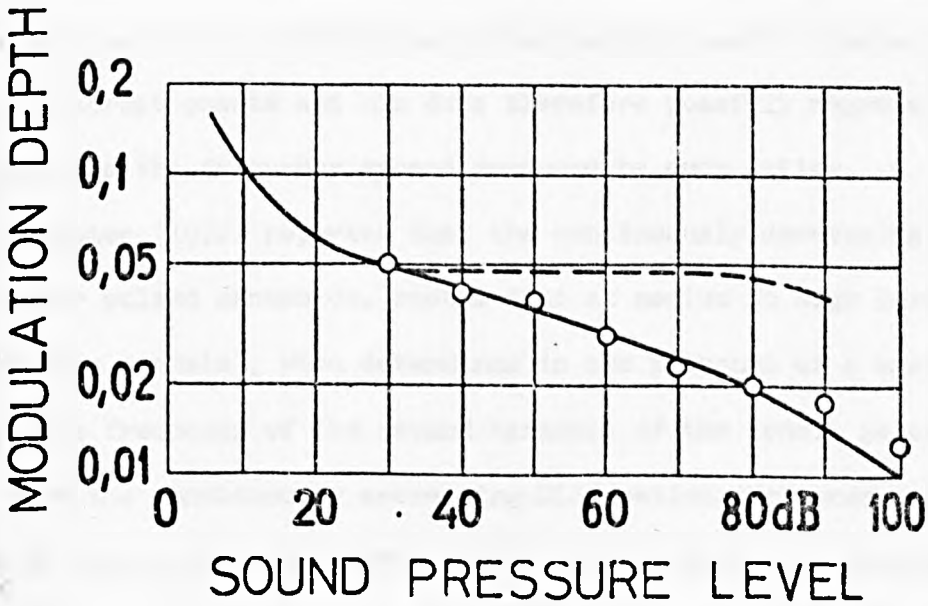


Figure 7



increasing stimulus level for all of the determinations in Fig. 6. For broadband noise signals (solid line in Fig. 6) the DL decreases to a constant level which is reached at 20 - 30 dB above threshold. It remains at this low level - 0.4 dB - over a range of some 80 dB which in this case extends up to 100 dB above threshold (approximately 110 dB SPL). At higher levels therefore, the DL function for noise signals follows Weber's Law; the just noticeable difference in intensity ΔI is a constant ratio of the intensity at which it is determined I, that is $\Delta I/I$ is a constant. The relation of ΔI to I characteristically departs from Weber's Law at low intensities.

The tone data of Riesz (dashed line in Fig. 6), in agreement with several other determinations of the DL for tones (Churcher, King and Davis, 1934; Stevens and Volkman, 1940; Zwicker, 1956) does not follow Weber's Law. The DL for tones continues to decrease with increasing intensity up to the maximum levels studied and has been commonly termed a 'near-miss' to Weber's Law. This is at variance with the tone data of Knudsen which follows closely the DL function for noise. The discrepancy between Knudsen's data for tones and the data of other workers is likely to be due to differences in the methods used. Knudsen used tones with abrupt onsets and his data therefore possibly represents sensitivity to the frequency spread produced by such gating.

Viemeister (1972) reported that the continuously decreasing DL function for pulsed sinusoids, became flat at medium to high levels (as for noise signals), when determined in the presence of a masking noise at the frequency of the second harmonic of the tone. He concluded that the continuously decreasing DL function for tones reflected the use by the subject of information at aural harmonics. Moore and Raab (1974) specifically tested this suggestion and found that information at aural harmonics was not essential in order to obtain a continuously decreasing DL function for pure tones.

Zwicker (1956) determined the just noticeable amplitude modulation for 1 kHz tones as a function of stimulus level. This is shown as the solid line in Fig. 7 which falls continuously as a function of intensity. When this function was redetermined in the presence of a high pass masking noise, it became flat at medium to high levels as indicated by the dashed line in Fig. 7. Zwicker concluded that when no masking noise was present the subjects were able to use information from frequencies above the stimulus frequency in making intensity discriminations.

The data from pure tone studies in which amplitude modulation was used to obtain small intensity changes, indicated that intensity discrimination varied with frequency, and that the DL increased as intensity decreased more rapidly near threshold than at medium and high levels. This is not the case in pure tone studies in which pulsed sinusoids and forced-choice techniques were used. The data of Jesteadt, Wier and Green (1977) (crosses and dot-dash line, Fig. 6) indicate that intensity discrimination under such conditions is not a function of frequency (at least for 0.2 - 8 kHz). They also found that the change in discrimination with level (the near-miss to Weber's Law) could be represented by a single function from which there were no systematic deviations from 5 - 80 dB SL. The DL for intensity fell continuously from 1.5 dB at 5 dB SL to 0.5 dB at 80 dB SL.

The ear maintains fine intensity discrimination (of the order of 0.5 dB) for white noise signals over a range of intensity of at least 80 dB (Fig. 6). For pure tone signals the DL for intensity as determined by using pulsed sinusoids is less than 1.5 dB over a 75 dB range (Jesteadt, Weir and Green, 1977). No deterioration in the intensity discrimination of white noise or pure tone signals is observed at the highest levels studied (100 dB SL, see Fig. 6). It appears,

however, that when subjects are deprived of information from frequency regions above the stimulus frequency, the intensity discrimination of pure tones is degraded (Zwicker, 1956; Viemeister, 1972; Moore and Raab, 1974). Even in the absence of such information, however, the DL for intensity for pure tones is still of the order of 1 dB even at high intensities (Zwicker, 1956).

Intensity discrimination in the presence of masking noise has been used to investigate the suggestion that intensity is encoded via spread of activity along the cochlear partition, and is further discussed in that context in Section 1.7.

1.3 Animal Behavioural Experiments

The purpose of the following review of some of the animal behavioural literature, is to assess whether the chosen experimental animal, the cat, is an appropriate animal model for determining the way in which intensity might be encoded in humans. Wherever possible, therefore, comparisons are drawn between measurements which have been obtained in both man and cat. Some necessary requirements of any animal model for intensity encoding are the following: 1) That the animal be sensitive to a wide range of frequencies; 2) that the absolute sensitivity of the animal be comparable with that of man; 3) that the animal be able to discriminate small intensity increments over a wide range of intensity; and 4) that the mechanism underlying the discrimination of intensity be similar to that of man.

To decide whether the cat fulfils the first three requirements, a) threshold as a function of frequency and b) intensity discrimination as a function of intensity are considered in detail below.

The present state of our knowledge of intensity discrimination in man and cat does not enable any decision on the final requirement. However, both the formation of loudness (see p. 11) and intensity discrimination in man, appear to depend upon a frequency selective mechanism (the critical band). The DL for intensity may be understood in terms of the extra energy which must be added to a signal in order to increase the energy falling within a single critical band at any point on the frequency scale by a detectable amount (about 1 dB, see Zwicker (1975) for details). Thus, measurements of frequency selectivity in animals are reviewed since any animal not possessing such a frequency selective mechanism would be inappropriate as a model for human intensity encoding.

In the experiments reported in chapter five, the level of a tone was set, in the first instance, to give 4 dB more energy than a noise masker measured within a bandwidth equal to a human critical band. Thus from a purely technical point of view a consideration of critical band

in cats is required to demonstrate that such a procedure is not inappropriate.

1.3.1 Threshold of Hearing as a Function of Frequency: The Audiogram

The audiograms discussed below are all of the minimum audible field (MAF) type, that is to say, the animal was free to move in the sound field and the minimum levels of sound at the position of the animal's

head with the animal removed were taken as the threshold values. Audiograms have been determined for a wide variety of animals, including man, ape, monkey, bush-baby, tree shrew, cat, guinea pig, chinchilla, hedgehog, oppossum and goldfish (see reviews by Masterton et al., 1969; Jacob and Tavolga, 1967; Miller, 1970; Sokolovski, 1973).

Masterton et al. (1969) compared the audiograms of twenty-two different mammals and demonstrated that the human audiogram differed from that of other mammals in only one respect; man's high frequency limit is lower than that of any other mammal yet studied behaviourally. By comparison of the average high frequency limit of the mammals in their study with the albeit sparse data available on other vertebrate orders, they were able to conclude that high frequency hearing (above 32 kHz) is a uniquely mammalian characteristic. The large difference in high frequency hearing between mammals and non-mammals is due to the evolution of the middle ear ossicles in the former which well match the impedance of the air to that of the cochlear fluids at high frequencies (Johnstone and Sellick, 1972).

The variation of the upper frequency limit of hearing among mammals was very highly correlated with the maximum difference in the time of arrival of sound waves at the two ears; mammals which have available to them only small binaural time disparities (whether due to close set ears, or in the case of cetaceans, a marine environment) have extensive high frequency hearing. Since binaural time disparities and binaural intensity differences are known to be alternative cues used by animals for localizing a sound source, the correlation noted above appears to reflect the usefulness of these two cues for different mammals. High frequencies are attenuated more rapidly over distance and are more effectively shadowed by the head producing interaural intensity differences, than are low frequencies.

Thus while mammals with large heads can use binaural time disparities, mammals which have available to them only small time disparities between the two ears, are able to localize sounds accurately by using intensity differences between the two ears, which are more pronounced for high frequencies.

The puzzling feature of such comparisons is that since extensive high frequency hearing is clearly a primitive mammalian character, this ability must have disappeared in the course of the evolution of apes and man. Masterton et al. (1969) provide one possible explanation; once the ears became sufficiently far apart to provide accurate sound localization without resorting to high frequency spectral differences, sensitivity to such high frequencies became passively vestigial and was therefore gradually lost.

The audiograms of man and cat are compared directly in Fig. 8. Three main differences are evident:

1. The high frequency hearing of cats begins to decline at 20 kHz and has an upper limit of about 60 kHz. Mans' high frequency hearing declines at 10 kHz to an upper limit of approximately 20 kHz.

2. The most sensitive region for cats (i.e. the frequency region of lowest threshold) is about 7 - 10 kHz, whereas mans' most sensitive region is about 3 - 4 kHz.

3. Man and cat are equally sensitive only to frequencies of 500 Hz and below. Above this frequency the audiograms diverge progressively. The cat's maximum sensitivity (at approximately 10 kHz) is 20 dB below that of man (at approximately 3 kHz).

1.32 Intensity Discrimination: The Difference Limen

One of the earliest determinations of the DL in any animal is that of Dworkin (1935). In this study cats were trained to discriminate

Figure 8

Minimum audible fields of the cat (filled circles from Miller, Watson and Covell, 1963) and man (unfilled triangles from Sivian and White, 1933).

Figure 9

Sensitivity of the monkey to increments in the intensity of a wideband noise stimulus as a function of stimulus level.

d' is the signal detection detectability index (see Green and Swets, 1966).

(From Clopton, personal communication.)

Figure 8

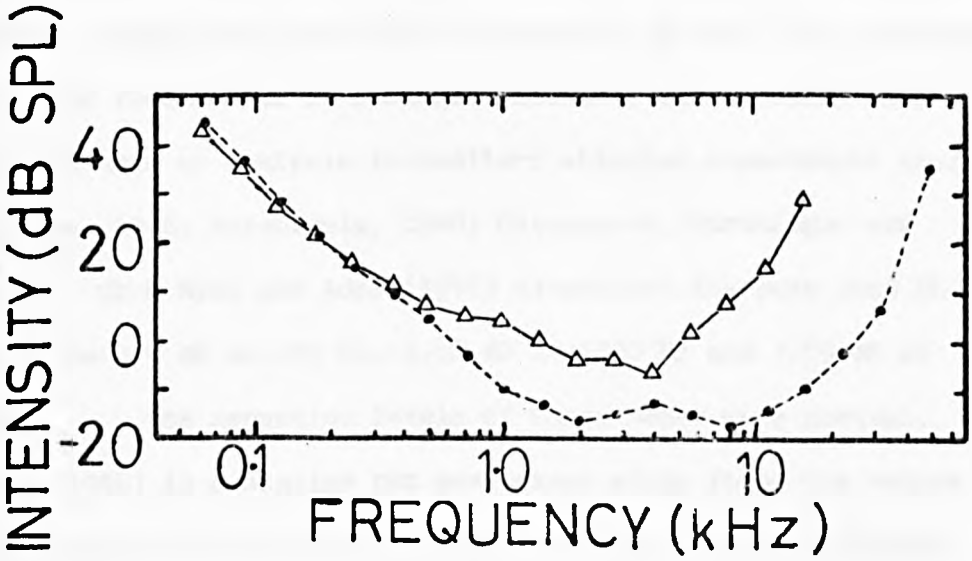
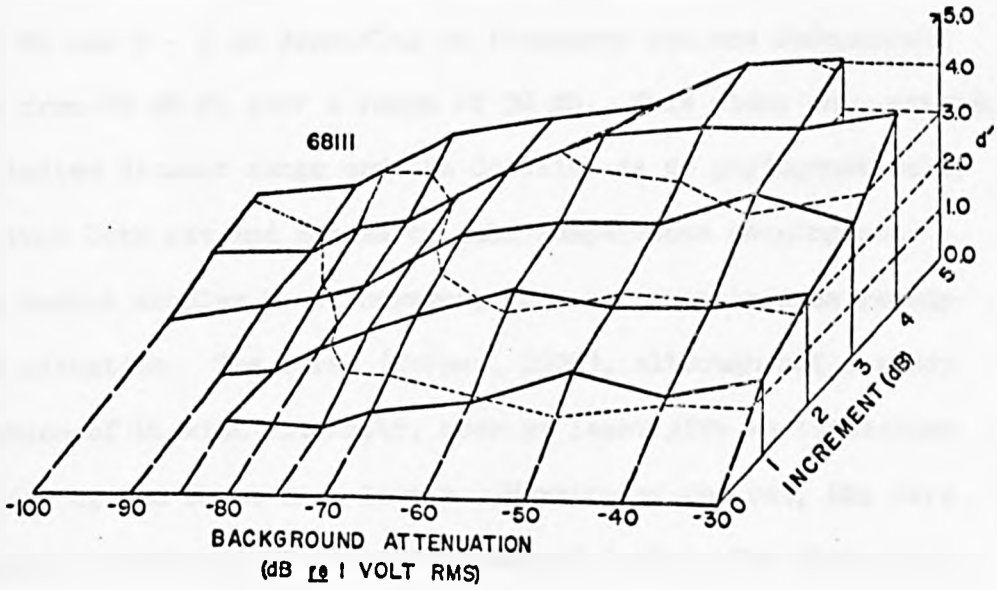


Figure 9



between tones which differed only in intensity and DLs of 4 dB at frequencies of 2600 Hz and 1500 Hz were determined at 50 dB above human threshold.

Several authors have reported measurements of the DL for intensity for particular frequencies at a single intensity level, which have commonly been used as controls in auditory ablation experiments (e.g. Raab and Ades, 1946; Rozenzweig, 1946; Osterreich, Strominger and Neff, 1971). Thus Raab and Ades (1946) determined the pure tone DL for cats to be 2.9 dB at 125 Hz, 1.82 dB at 1000 Hz and 3.89 dB at 8000 Hz. The sensation levels of these tones were unequal. Rozenzweig (1946) in a similar but more exact study found the values (mean of 3 cats) to be 2.0 dB at 125 Hz 40 dB SL, 2.4 dB at 1000 Hz 60 dB SL and 5.00 dB at 8000 Hz 60 dB SL. The data of Raab and Ades are clearly very comparable with those of Rozenzweig.

The important measure for the present purposes is the variation of DL with intensity (see Section 1.2.5 for human data) and until recently the only study which attempted this determination was on Goldfish. Jacobs and Tavolga (1967) were able to determine that the Goldfish DL was 3 - 6 dB depending on frequency and was independent of level from 20 dB SL over a range of 30 dB. This study only extended over a limited dynamic range and the Goldfish is so phylogenetically distant from both cat and man as to make comparisons meaningless.

Two recent studies have, however, gone some way towards remedying this situation. The first (Terman, 1970), although not a study of variation of DL with intensity, does at least give an indication of the size of the DL at high levels. Working on the rat, DLs were determined at levels of 70 and 100 dB SPL at 4 kHz. The DL at both levels was found to be about 4 dB. Thus at least in the rat no deterioration in intensity discrimination occurs with increase in intensity from 70-100 dB SPL.

The second (Clopton, 1972) is the most complete study of variation of DL with intensity for an animal which this author is aware of. The DL for white noise for m.nkeys was determined over an intensity range of 70 dB and Weber's Law was found to hold over most of this range. The value of the DL which is large near threshold (Fig. 9) falls to a value of approximately 1.5 dB as the stimulus level is increased to 30 dB above threshold and remains at about this value over the rest of the range tested. Particularly, there is no deterioration in the animal's discrimination performance at higher levels.

There is, however, a discrepancy between the data reported by Clopton and other behavioural measurements on the same animal reported in the literature. From the audiogram of Macaca Mulatta, the most sensitive frequency is around 12 kHz (Behar et al., 1965). At this frequency the width of the human critical band is about 2.5 kHz. The total energy of a noise increases with its bandwidth, therefore making the assumption of a similar critical band for monkeys, the energy within a critical band at 12 kHz is equal to the spectral density plus 34 dB (the increase in energy for a bandwidth increase of 2.5 kHz). The spectral density of the noise in this experiment was 45 dB SPL at '0' dB attenuation and therefore -55 dB SPL at -100 dB attenuation. That -100 dB is near threshold is evident from Figure 9. Therefore the energy of the noise within the critical band at noise threshold would be -55 plus 34 or -21 dB SPL. The tone threshold should therefore be -21 dB SPL. Again from the audiogram, we find that the level of the 12 kHz tone at threshold is about 3 dB. There is therefore a considerable discrepancy in the reported and expected threshold levels in these behavioural experiments. Taking lower frequencies this discrepancy becomes progressively larger due to the narrowing critical bands.

According to Clopton (personal communication), the discrepancy between his data and that of Behar et al., is probably due to the choice of the value of d' representing threshold. Behar et al. used a classical psychophysical method of adjustment to obtain threshold, which according to Jeffress (1964) should correspond to a d' of 1.5 - 2.0. Taking a d' of 2.0 from data supplied by Clopton, we get a 'threshold' in the region of -85 dB instead of -100 dB; this would still give a discrepancy of 9 dB from the data of Behar et al. The study of Behar et al. was, however, very conservative. The authors took the threshold to be the highest intensity available to the animal. It is conceivable that although the higher intensity was present at the position of the animal's head, that the animal was responding to the lower level signal also present. If such were the case it might account for the discrepancy between the threshold data of Clopton and that of Behar et al.

For the present purposes however, this does not affect the usefulness of the intensity DL data reported by Clopton. In monkeys the variation of the intensity DL for white noise with intensity has the same form as that determined for humans by Miller (1947) (cf. Figs. 6 and 11). The DL falls to a low value of about 1.5 dB and remains at this low value over a wide range, showing no deterioration at high levels.

Summarizing, therefore, many authors have reported DL measures for animals (goldfish - Jacobs and Tavolga, 1967; rat - Terman, 1970; monkey - Clopton, 1972; cat - Dworkin, 1935; Raab and Ades, 1946; Rosenzweig, 1946; Saunders, 1969; Osterreich et al., 1971)It is clear from these data that the discrimination ability varies considerably across species. The DL for intensity at moderate intensity levels decreases from primitive animals to man, ranging from 3 - 6 dB in goldfish to 0.5 dB in man.

However, whatever the absolute value of the DL at medium intensity levels it is maintained in both cases studied up to the highest levels tested. It is therefore reasonable to assume that the cat also shows no deterioration of its intensity discrimination ability over a wide dynamic range.

1.3.3 Frequency Selectivity: The Critical Band

'The critical band is that bandwidth at which subjective responses rather abruptly change' (Scharf, 1970) and is assumed to reflect a filtering process taking place within the auditory system. A wide variety of experimental paradigms have been employed to obtain estimates of the critical bandwidth (for details of those paradigms see Scharf, 1970). Thus, for example, the loudness of a band of noise is independent of its bandwidth up to the critical band and the loudness of a tone complex is independent of the frequency separation of its components up to the critical bandwidth (see Section 1.2.3). In these and other experiments the critical bandwidth is measured directly by manipulation of the frequency region over which signal energy is distributed.

In fact the term 'critical band' was first coined by Fletcher (1940) to refer to the critical bandwidth measured indirectly by masking a tone by a wideband noise. Such measures are now referred to as 'critical ratios' to distinguish them from directly measured critical bands.

Critical ratio experiments may be considered as an intensity DL experiment for signals within the critical band centred on the test tone frequency. If one assumes, as Fletcher did, that at masked threshold the energy of the tone and noise within the critical band are equal (i.e. S/N ratio is 0 dB) and that therefore the minimum

Figure 10

Dependence of the critical bandwidth on frequency.

Critical bandwidth as a function of the frequency at the centre of the band. After Scharf (1970) with the addition of the data of Pickles (1975) for the cat.

Figure 11

Dependence of the critical ratio on frequency.

The critical ratio measured in four species as a function of the frequency of the masked tone. The critical ratio is the difference between the spectrum level of the wide-band masking noise and the level of the just masked tone. After Scharf (1970) with the addition of the data of Pickles (1975).

Figure 10

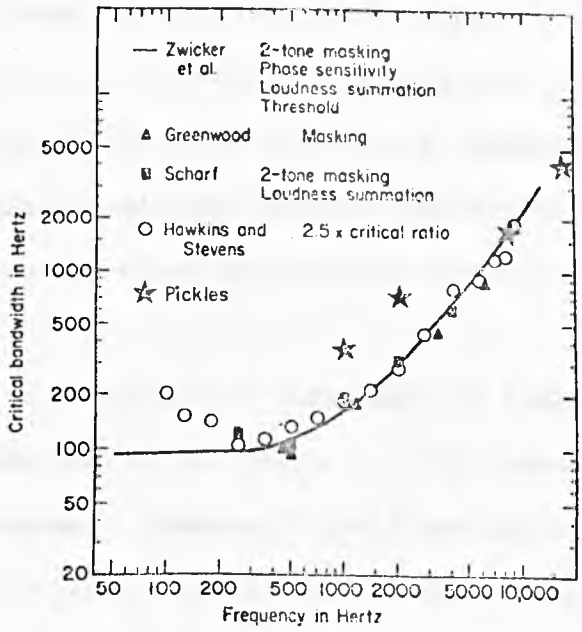
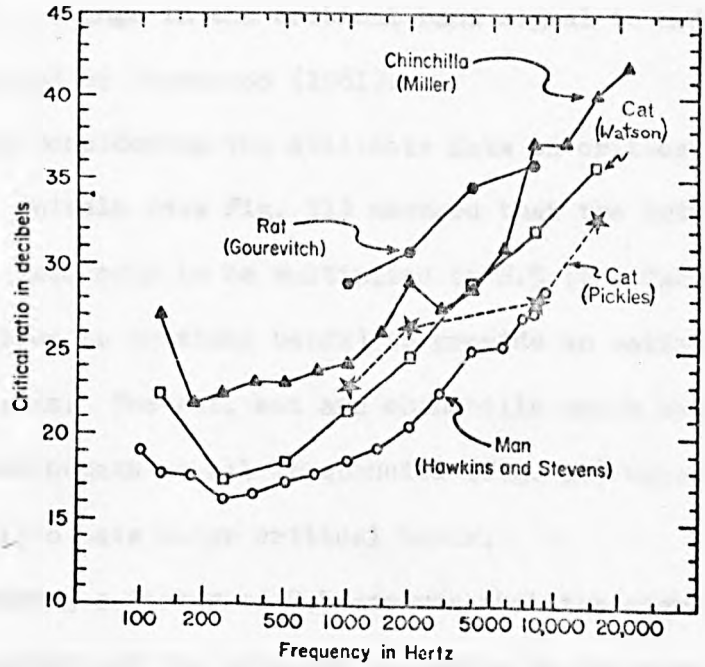


Figure 11



detectable change in energy within a single critical band is 3 dB, the critical ratio can be used to directly give a measure of the critical band. However, it is clear that such an assumption is incorrect, since critical bandwidths derived from critical ratio experiments give values 2.5 times smaller than directly measured critical bands.

This difference in absolute size disappears if instead of 0 dB S/N ratio at masked threshold a S/N ratio of -4 dB (corresponding to a factor of 2.5) is assumed. Greenwood (1961) and Zwicker (1958) have in fact measured critical band S/N ratios which vary from -3 to -8 dB. The minimum detectable energy change within a single critical band assuming a -4 dB S/N ratio then becomes 1.5 dB, which is consistent with directly measured values of Zwicker (1956) and Pick (personal communication).

Fig. 10 shows a summary of critical band estimations for man. The unfilled circles represent the critical ratio data of Hawkins and Stevens (1950) multiplied by 2.5. There is deviation at low frequency which may reflect a change in the critical band signal to noise ratio, as has been suggested by Greenwood (1961).

Scharf (1970) considering the available data on critical ratio determinations in animals (see Fig. 11) assumed that the critical ratio so obtained need only to be multiplied by 2.5 (the factor relating human critical ratios to critical bands) to provide an estimate of animal critical bands. The rat, cat and chinchilla which have critical ratios greater than humans at all frequencies (Fig. 11) were therefore presumed by Scharf to have wider critical bands.

However, assuming a factor of 2.5 assumes that the signal to noise ratio for animals at the critical bandwidth is the same as for humans. There is evidence which suggests that this is not in fact the case.

Bos and de Boer (1966) measured their own thresholds at five centre frequencies as a function of masking noise bandwidth. They observed that at narrow bandwidth the masking noise was so similar to the test tone that the detection task becomes effectively an intensity DL determination. They therefore suggested that in order to determine whether frequency resolution occurs it was necessary to compare the results of masking a test tone with narrow bands of noise, with the intensity DL for those same masking noises. The results of such comparisons indicated that the DL and masked threshold varied in a similar way as a function of bandwidth especially within the critical band. In the middle range of bandwidths a remarkable agreement was found between masking and discrimination thresholds. It appears that the amplitude fluctuations of the narrow bands of noise, which determine the maximum intensity discrimination, also determine the masked threshold for the tone. At wider bandwidths the frequency selectivity of the auditory system becomes apparent, resulting in a clear separation of masking and discrimination thresholds.

The masked threshold at about the critical bandwidth is therefore closely related to the difference limen for intensity of the noise. The cat has a DL for 1 kHz tones of 2 - 2.5 dB (see Section 1.3.2) which is several times greater than the human DL (see Section 1.2.5). One would therefore expect that the signal-to-noise ratio within a critical band at masked threshold would also be greater than the human value. One cannot therefore derive an estimate of cat critical bandwidth by multiplying critical ratio values by the human factor of 2.5, representing a signal-to-noise ratio of -4 dB. The assumption that the cat critical band is wider than the human critical band, based on critical ratio measures is apparently not justified. The critical bands of cat and human may possibly therefore be of the same order of magnitude. Consistent with this suggestion are the recent data of Evans, Rosenberg and

Wilson (1970) and Evans and Wilson (1973) who studied the effective bandwidth of cochlear fibres in the cat. Effective bandwidth is a physiological measure analogous to the critical band and the values obtained by these authors correspond very well with human critical band data over a wide frequency range. The authors concluded from this that the critical band property derives directly from the filtering properties of cochlear fibres and is therefore already determined at the cochlear level.

However, the only empirically determined critical bandwidths for the cat suggest that cat critical bands are indeed wider than human critical bands (Pickles, 1975). In the study of Pickles pure tones were masked by a noise of variable bandwidth but constant total power which was geometrically centred on the test tone. The critical bandwidth was estimated as that bandwidth of masking noise at which the tone masked threshold decreased (i.e. the point at which some of the noise energy falls outside of the critical band around the tone). The breakpoint values so obtained are plotted for comparison with human critical bands on Fig. 10. On the basis of this determination the cat critical bands are more than twice as wide as human critical bands at some frequencies.

Pickles (1976) examined the possibility that the discrepancy between his empirically determined critical bandwidths and the effective bandwidths of single cochlear fibres determined by Evans and his co-workers (1970, 1973) might be due to differences in the populations of cats used in the two studies. To eliminate this possibility he used the same cats to obtain both behavioural critical band estimates and critical band estimates from recordings from single cochlear fibres using the same stimuli and method. The estimates of critical bandwidth from single fibre recordings (which Pickles termed effective bandwidths)

from two cats were only 21% of the behavioural critical band estimates from the same animals.

There are, however, objections to Pickles's behavioural determinations of the cat critical band. A major criticism of the Pickles work lies in the choice of method for the determination of critical bandwidth. The paradigm chosen is essentially the same as that used by Bos and de Boer (1966) in human psychophysical experiments. These authors found that intensity fluctuations inherent in narrow bands of noise affect the detection of the tone. Taking this into account, Bos and de Boer used their data to derive estimates of critical bandwidth which were up to two or three times greater than other measures. Because of this, Bos and de Boer concluded that 'the accuracy with which these (critical band data) can be determined is so poor that one should consider masking experiments of this kind as totally unsuited to measure the critical bandwidth'. On the other hand, as Scharf (1970) pointed out, there is good agreement between human critical band measures determined using narrow band noise masking and other measures of the critical band.

Bos and de Boer (1966) also noted that the function relating discrimination threshold and bandwidth, for bands of noise narrower than the critical band, should have a slope of 1.5 dB/octave. Pickles, in estimating critical bandwidth, fitted his mean data with a function having zero slope for narrow bandwidths and 3 dB/octave for bandwidths wider than the critical band. By fitting Pickles's raw data from individual cats with a function with slopes of 1.5 dB/octave and 3 dB/octave it is possible in some instances to derive estimates of critical bandwidth closer to the effective bandwidth value of Evans et al. and to the single fibre critical bands of Pickles.

In conclusion, therefore, while the possibility remains that Pickles's data might be in error (by a factor of up to two according to Bos and de Boer (1966), taken at face value, they indicate that the behavioural critical bands of the cat are wider than both the effective bandwidths of single cochlear fibres and the 'critical bandwidth' of single cochlear fibres at the same frequency. If this is the case then the behavioural critical band is not determined directly by the filtering properties of single cochlear fibres. Since, however, the variation of the effective bandwidth of single cochlear fibres with frequency is very similar to the variation of the behavioural critical bands with frequency (Evans and Wilson, 1973), it seems reasonable to conclude that the behavioural critical band is derived from some combination of single cochlear fibre response areas.

1.3.4 Concluding Remarkes on Animal Behavioural Experiments

From the foregoing it can be seen that at least in terms of the audiogram, DL and critical band, human hearing differs from other animals' chiefly in the absolute size of the measured variable. Thus man has a narrower critical band, finer intensity discrimination but less extensive high frequency hearing. It seems reasonable to conclude that differences between human hearing and that of the higher mammals, at least, are only quantitative, not qualitative. In terms of the four requirements outlined in the introduction to this review, the cat would appear to be an appropriate animal model for the present study since

1) it is sensitive to a wide range of frequencies,

2) its absolute sensitivity is greater than that of man,

3) by inference from rat and monkey data, the cat is likely to maintain fine intensity discrimination over a wide range of intensity, and

4) other closely related measures, such as frequency selectivity, have been shown to be comparable in cat and man.

1.4 The Structure and Function of the Middle Ear

The ear may be conveniently divided into three parts: the external ear, the middle ear and the inner ear. The external ear consists of the pinna and the meatus which serve to conduct air-borne sounds to the tympanic membrane. Some alterations in the spectral composition of the incoming sounds take place in the passage through the external ear but they need not concern us here (for details see Wiener and Ross, 1946; Wiener, Pfeiffer and Backus, 1965).

The middle ear is an air filled cavity which opens via the eustachian tube into the nasopharynx. This tube which is opened momentarily during swallowing serves to equalise the static pressure in the middle ear with that in the environment. Within the middle ear cavity are three small bones (the malleus, incus and stapes) which are collectively known as the middle ear ossicles. The ossicles form a link between the tympanic membrane, to which is attached the malleus, and the oval window of the inner ear, to which is attached the foot of the stapes (see Fig. 12).

Sound impinging upon the tympanic membrane sets the three ossicles in motion thereby transferring the vibration to the inner ear. The ossicles are not essential for hearing, since in their absence sound impinging directly on the cochlea can be heard. The presence of the ossicular chain does, however, increase the sensitivity of the ear considerably. This increased sensitivity is clearly demonstrable clinically in cases where the ossicular chain is absent or damaged. Patients suffering from such conditions may experience hearing losses of 30 dB or more (Bekesy, 1936a).

The increased sensitivity is due to the action of the ossicles in matching the impedance of the air to that of the cochlear fluids (a suggestion first put forward by Helmholz (1877)). The impedance

Figure 12

Schematic diagram of the human middle ear (right side) seen from within.
(From Møller, 1972a.)

Figure 13

Threshold of the human middle ear reflex as a function of frequency.

The sensitivity of the acoustic reflex in man shown by the intensity required to produce 10 percent of the maximal obtainable impedance change (dashed lines). The solid line (▼) shows the threshold of audibility, and the curve is raised by 80 dB to facilitate comparison. Data from four subjects (X, ●, ■, ▲).

(From Møller, 1962.)

Figure 12

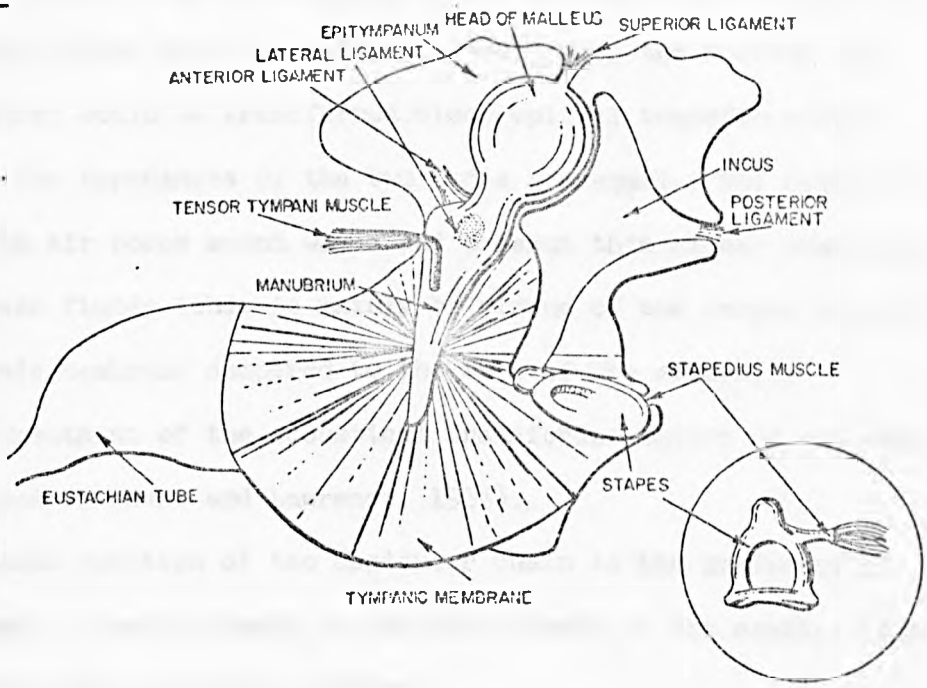
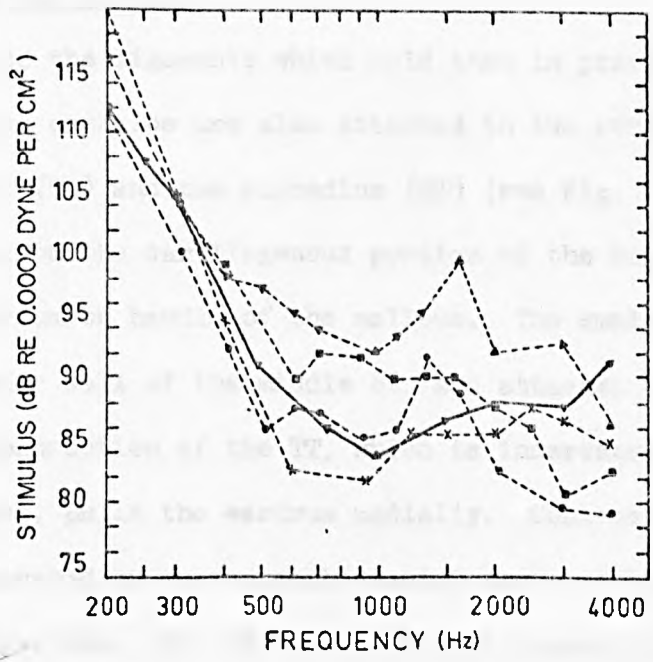


Figure 13



of the cochlear fluids is some 4000 times greater than that of air. If the sound waves were to impinge directly upon the cochlea very little energy would be transferred since optimal transfer occurs only when the impedances of the two media are equal. The ossicles transform the air borne sound waves and present this higher pressure to the cochlear fluids (this is mainly by virtue of the larger area of the tympanic membrane compared to the foot of the stapes; a detailed treatment of the acoustical transformer action of the ossicles may be found in Wever and Lawrence, 1954).

A second function of the ossicular chain is the preferential transference of sound energy to the oval window of the cochlea rather than to both oval and round windows.

Vibration amplitude of the middle ear ossicles increases linearly up to levels in excess of 130 dB SPL (Guinan and Peake, 1967).

1.4.1 The Middle Ear Muscles

In addition to the ligaments which hold them in position within the middle ear, the ossicles are also attached to two striate muscles, the tensor tympani (TT) and the stapedius (ST) (see Fig. 12).

The TT runs from the cartilagenous portion of the eustachian tube to the manubrium or handle of the malleus. The smaller ST lies within the posterior wall of the middle ear and attaches to the head of the stapes. Contraction of the TT, which is innervated by the fifth cranial nerve, pulls the eardrum medially. Contraction of the ST, which is innervated by the seventh cranial nerve, pulls the stapes in a posterior direction. The ST and the TT are diametrically opposed to each other, both pulling at right angles to the axis of their respective ossicles (Wever and Lawrence, 1954). The effect of such contractions is a stiffening of the ossicular chain and possibly

a decoupling of stapes and cochlea (Mundie, 1963) and thereby a modification of its transmission characteristics.

It is very well established that non-acoustic as well as acoustic stimuli activate the middle ear muscles. For the present purposes I shall concentrate on the reflex activation of the muscles by acoustic stimuli. Extensive reviews of both acoustic and non-acoustic activation of the middle ear muscles may be found in Kato (1913), Schaeffer and Giesswein (1926), Mangold (1926), Lüscher (1929), Kobrak (1930), Wever and Lawrence (1954), Jepson (1955), Wersäll (1958), Loeb (1964), Borg (1972) and Møller (1972a), those aspects of particular interest for the present study are dealt with in some detail below.

1.4.2 The Acoustic Middle Ear Reflex

The presence of the acoustic middle ear reflex has been recognised for almost a century (Henson, 1878). High intensity sounds (above about 80 dB SL) presented to one ear elicit contractions of the middle ear muscles in both ears (Pollak, 1886). Although in most animals both the ST and TT are reflex activated, in humans the TT only contracts as part of a startle reaction and the ST alone is reflex activated (Klockhoff, 1961; Djupesland, 1967).

The major reflex pathway consists of four neurones: i) the primary neurone from the cochlea to the ventral cochlear nucleus (VCN), ii) VCN to medial superior olivary nucleus (MSO), iii) interneurone from MSO to facial motor nucleus (for ST) or to trigeminal motor nucleus (for TT), iv) motorneurones. In addition a three neurone path for the ipsilateral ST reflex and parallel multisynaptic chains have been reported by other authors (Lorento de No, 1933 Borg, 1973).

1.4.3 Latency of the Middle Ear Reflex

A knowledge of the latency of the middle ear reflex is necessary, since if the latency were so long that intensity discriminations were completed before the muscles operated, then the reflex could have no effect on the way in which intensity of a signal is encoded.

Numerous authors have reported values for the latency of the activity of the middle ear muscles. The values obtained depend upon the animals, the sound levels used, the measurement methods and the criteria used to detect the muscle action. The results of a number of studies are summarised in Table 1. It can be seen from Table 1 that in all of the studies in which the effects of ST and TT were separable, the TT latency was found to be greater than for the ST. In man the TT does not appear to take part in the reflex and the ST is therefore responsible for the attenuation of low tones (Møller, 1965). In the cat Galambos and Rupert (1959) also found that the TT took little part in the reflex, which is contrary to the findings of Wever and Vernon (1955a). For the present purposes the latency from the sound onset to the first reduction in transmission of the sound is of most interest. In the cat this latency is consistently found to be about 10 ms from observations of the reduction of the cochlear microphonic by the action of the middle ear reflex (Hallpike, 1935; Galambos and Rupert, 1959).

1.4.4 The Threshold for Activation of the Middle Ear Reflex

The minimum intensity of a sound which activates the middle ear acoustic reflex is termed the reflex threshold. The human reflex threshold to contralateral stimulation as a function of frequency is shown in Fig. 13 together with the human absolute threshold curve (which has been elevated by 80 dB). The reflex threshold values

TABLE 1

BASIS FOR LATENCY MEASUREMENTS - INTERVAL BETWEEN:	LATENCY MS. ST	LATENCY MS. TT	SPECIES	METHOD	INVESTIGATOR
Start of sound and start of contraction		92 73	Dog	Direct observation	Henson, 1878
"	20	20	Rabbit & Cat	Optical recording of the muscle contractions	Kato, 1913
"	31-147 M = 73	74-143 M = 109	Rabbit	Isotonic myography	Kobrak, 1930
"	13	29	Rabbit	Isotonic myography	Tsukamoto, 1934
"	10-12		Rabbit	Isometric myography	Lorente de No, 1935
"	14	18	Rabbit	Isometric myography	Wersall, 1958
Start of sound and first action potential	9.8-11.4 M = 10.5		Man	Electronic recording	Perlman and Case, 1939
"		6-9	Cat	Electronic recording	Okamoto, Sato & Kirikae, 1954
First cochlear potentials and first action potential		12-13	Rabbit	Electronic recording	Bornschein and Krejci, 1952
"	6 ± 0.5	7 ± 0.7	Cat	Electronic recording	Eliasson and Gisselsson, 1955
LATENCY OF COMBINED ACTION OF TYMPANIC MUSCLES					
First cochlear potentials and first sign of decrease of these potentials	about 10		Cat	Electronic recording	Hallpike, 1935
"	10		Cat	Electronic recording	Galambos and Rupert, 1959
Start of sound stimulus and incipient movement of drum	7-10		Cat	Optical recording	Okamoto, Sato and Kirikae, 1954
Start of stimulus and incipient change of acoustic impedance	35-150		Man	Measurement of acoustic impedance	Metz, 1951
"	25-150		Man	Measurement of acoustic impedance	Møller, 1958

plotted in Fig. 13 are the intensities required to change the ear's acoustic impedance by 10% since impedance measurements near threshold are subject to wide variations (Møller, 1962).

From Fig. 13 it can be seen that the reflex threshold curves are almost parallel to the curve of absolute threshold. The human middle ear acoustic reflex is therefore activated by sounds which are in excess of about 80 dB above absolute threshold for frequencies from 200 - 4000 Hz (Møller, 1962; Jepson, 1951; Metz, 1952).

In the cat Wever and Vernon (1955a)determined the least sound intensity which produced a noticeable (1 - 2 μV) reduction in the magnitude of a 450 Hz cochlear microphonic. The reflex threshold followed closely the form of a curve joining values of intensity giving 50 μV of cochlear microphonic at various frequencies (100 - 10,000 Hz). Absolute threshold values can be obtained by extrapolation from the 50 μV cochlear microphonic curve. When this is done it is found that the reflex threshold curve in cat is parallel to the absolute threshold curve but elevated some 80 dB.

Thus it would appear that in man and cat at least, the middle ear reflex is activated at a constant level of approximately 80 dB above threshold.

1.4.5 Influence of Middle Ear Muscle Contraction on Sound Transmission

The activation of the acoustic reflex by a sound does not necessarily indicate that the transmission of that sound will be reduced. In fact in the rabbit at some frequencies (4000 - 8000 Hz), there is up to 20 dB difference between the intensity which activates the reflex, and the intensity at which attenuation of the activating sound takes place (Borg, 1972).

It can be seen in Fig. 14 that for the rabbit, the thresholds for

Figure 14

Thresholds for activation of the middle ear muscle reflex and for reflex attenuation of sound, as a function of frequency in the rabbit.

Threshold of the total reflex (St in conjunction with TT) is shown by the thin continuous line and it is identical to St threshold. Thresholf of TT is shown by the thin white line. Dark shaded area shows the region in which single pure tones are attenuated by the middle ear muscle contraction elicited by the pure tone itself.

(From Borg, 1972.)

Figure 15

Dependence of the amplitude of the cochlear microphonic potential on stimulus intensity, for a range of stimulus frequencies, with and without deactivation of the middle ear musculature with anaesthetic.

Data from 25 normally muscled ears (mean values). Ordinate divisions are 10 dB increments in sound intensity relative to human threshold.

(From Simmons, 1959.)

Figure 14

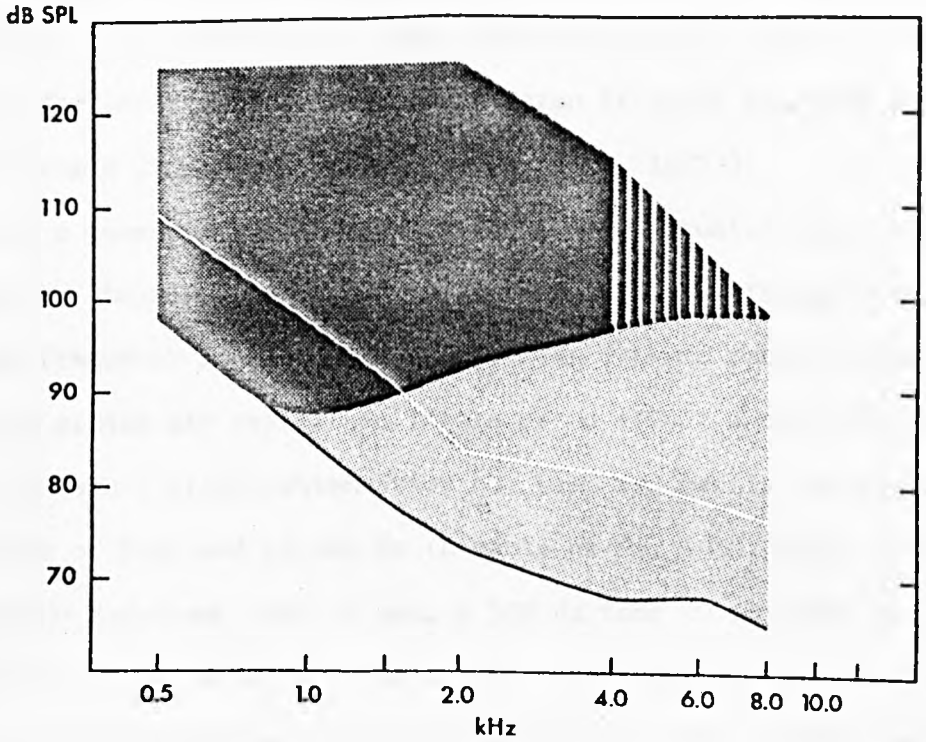
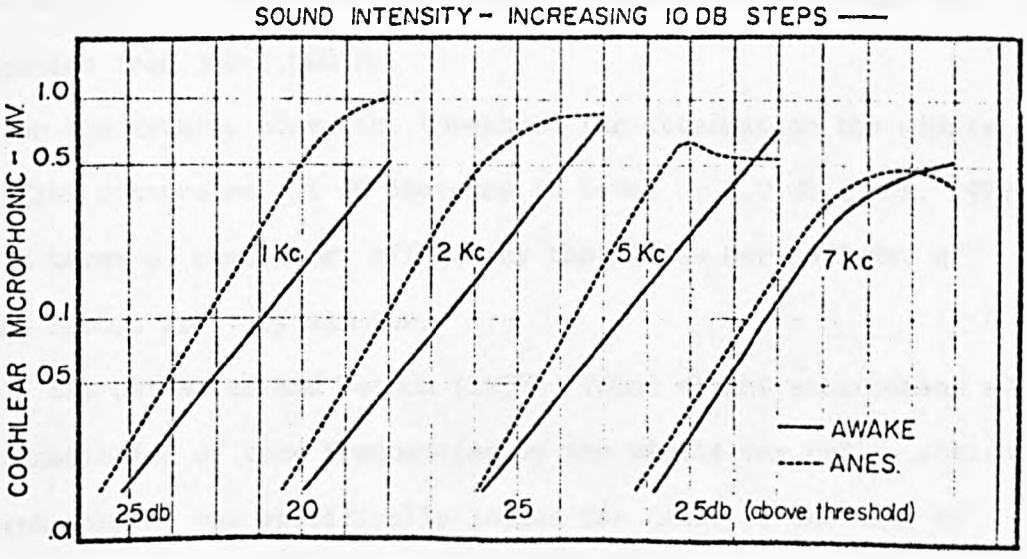


Figure 15



activation of the reflex (thin line) and attenuation of the sound (thick line) only coincide for low frequencies (up to 800 Hz). The threshold for influence on sound transmission is about the same in man and animals (90-100 dB SPL for tones (Borg, 1972)).

It is a common finding that for all animals studied the attenuation of sounds by the middle ear reflex is greater for low frequencies. The upper frequency limit of the attenuation depends upon the animal. In man the middle ear reflex has little or no effect above 2000 Hz, whereas in rabbit slight attenuation has been indirectly observed at frequencies of 8000 and 16,000 Hz (Lorente de No, 1935; Borg, 1972). Borg (1968)* inferred that in man, a 500 Hz tone 20 dB above reflex threshold was attenuated by 12-15 dB whereas a 1450 Hz tone 16 dB above reflex threshold was only attenuated by 0-6 dB. A 1 dB increase in the level of a 500 Hz tone at levels not exceeding 20 dB above reflex threshold is attenuated by 0.6-0.7 dB. At levels in excess of 20 dB above reflex threshold the reflex operates as an almost perfect regulator; a 1 dB increase in level is attenuated by about 1 dB. Almost perfect regulation at the highest intensities was found for frequencies from 300-2,000 Hz.

For the rabbit, above the threshold for attenuation the middle ear reflex attenuated a 1 dB increase in level by 0.7 dB (Borg, 1972). Thus in terms of regulatory efficiency the middle ear reflexes of man and rabbit are very similar.

In the cat Wever and Vernon (1955b) found slight enhancement of the transmission of some frequencies by the middle ear reflex action. Such enhancement was specifically looked for (also in the cat) by Galambos and Rupert (1959) who only found attenuation and no indications of any enhancement.

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* Borg (1968) investigated the role of the stapedius reflex in patients with unilateral Bells palsy (short duration paralysis of the VII nerve). The influence of the stapedius reflex on the stimulus tone was determined as the difference in intensity between paretic and recovered conditions producing identical charges in impedance in the contralateral ear.

1.4.6 Function of the Middle Ear Acoustic Reflex

The function of the middle ear muscles has been a subject of speculation for almost three centuries (see review by Wever and Lawrence, 1954). Not surprisingly, therefore, many possible functions have been proposed some of which have been shown to be untenable by experimentation, but many of which remain as possible suggestions. The following is a selection of some of these suggested functions, all of which have been previously reviewed in the literature indicated.

1. Protection of the inner ear from an intense sound delivered from an external source (Wever and Lawrence, 1954; Wersall, 1958; Loeb, 1964; Simmons, 1964; Borg, 1972; Suga and Jen, 1975).

2. Extension of the ear's dynamic range (Borg, 1972; Suga and Jen, 1975).

3. Attenuation of self stimulation (Suga and Jen, 1975).

4. Frequency selection as a result of changing the frequency characteristic of sound transmission across the ossicles (Wever and Lawrence, 1954; Suga and Jen, 1975).

5. Decrease of masking of high frequency sounds by low frequency sounds (Borg, 1972).

6. Stabilisation of the ossicular chain (Wever and Lawrence, 1954).

7. Alteration of the pressure of the labyrinthine fluid and by so doing altering the mechanical performance of the ear (Wever and Lawrence, 1954).

For the purposes of this dissertation, only two functions will be dealt with in detail (i.e. protection of the ear from overstimulation and extension of the ear's dynamic range). Both of these functions are a result of attenuation by the middle ear of incoming signals.

1.4.6.1 Extension of the dynamic range of the ear

Borg and Zakrisson (1973) showed that subjects with unilateral ST paralysis, suffered a significant decrease in their ability to discriminate nonsense syllables presented in the ear with ST paralysis above 100 dB SPL, compared to the ear with normal ST function. Below 100 dB SPL discrimination was equal on both sides and when the function of the ST had been regained, the discrimination above 100 dB SPL again became equal on both sides. These results were interpreted as indication that the middle ear reflex might reduce the generation of distortion products at high sound levels. The authors concluded that the ST reflex was extending the intensity range for speech discrimination by 15-20 dB, by acting to reduce high level distortion.

The same authors found a close correspondence between the threshold for the loss of discrimination in the ear with ST paralysis and the threshold for activation of the ST in the normal ear. Wever and Vernon (1955a) found a close correlation between the ST reflex threshold and the intensity at which the cochlear microphonic amplitude reached a maximum. Therefore the threshold for the loss of discrimination correlates with the intensity at which the cochlear microphonic is maximal. At levels of stimulation beyond those producing the maximum amplitude in the absence of ST reflex activity, the cochlear microphonic amplitude saturates. When the ST reflex is operative the range of intensity over which the cochlear microphonic amplitude increases linearly with intensity is extended. This is seen in the data of Simmons (1959) shown in Figure 15. In anaesthetised cats (i.e. ST reflex inactive) the cochlear microphonic amplitude increases linearly and then saturates as intensity is increased (dashed lines, Figure 15). However, in awake cats (ST reflex operational) the cochlear microphonic amplitude continues to increase as a function of intensity up to and beyond levels at which saturation takes place in the anaesthetised cat (solid lines, Figure 15). At 5 kHz this results in an increase of at least 20 dB to the range over which the amplitude of the cochlear

microphonic increases linearly with stimulus intensity (see Fig. 15). Thus it would appear that the middle ear reflex acts to extend the range of intensity over which the cochlear microphonic amplitude increases monotonically with intensity. Since Dallos (1973) has demonstrated that at levels at which the cochlear microphonic amplitude saturates, harmonics are generated in profusion, the action of the reflex reduces distortion at high levels.

Simmons's data are, however, somewhat at variance with the data of other investigators in that he finds effects of the middle ear muscles at moderate intensities not above a very high threshold level (see Fig. 15). The effect of the middle ear muscle activity is a linear compression of the intensity range. Thus for the 1000 Hz curves of Fig. 15, when the middle ear muscles are operative, an increase in intensity of 60 dB from 25 - 85 dB only produces the same increase in cochlear microphonic amplitude as a 45 dB increase in intensity when the muscles are inactive. In other studies such as that of Borg (1968) compression only takes place above threshold for reflex attenuation of sound. If compression does only occur above a high threshold value, then the sensitivity of the ear to small intensity changes should decrease above this threshold level. However, the DL for intensity remains constant up to levels of 100 dB SL (see Sections 1.2.5 and 1.3.3) which is some 20 dB above reflex threshold. If, therefore, the reflex is acting to compress the intensity range above the threshold for reflex attenuation of sound, then the CNS must compensate for the intensity reduction caused by the middle ear reflex.

There are at least two arguments against the proposition that the function of the middle ear reflex is to extend the ear's dynamic range. The first is that fine intensity discrimination of <u>high frequency</u> sounds is maintained over a wide range of intensity, despite the fact that the middle ear reflex has little effect on the transmission of

high frequency sounds. The second is that there is no indication that the growth of the loudness as a function of intensity for sounds too short to activate the reflex, is restricted above the threshold for reflex attenuation of sound (1000 Hz tones: Munson, 1947; Wright, 1965 - white noise: Stevens and Hall, 1966).

Thus it would appear that the middle ear reflex is neither a necessary or a sufficient mechanism to account for the wide dynamic range for intensity discrimination observed psychophysically.

1.4.62 Protection of the inner ear from fatigue or structural damage

Since the middle ear reflex does produce attenuation of intense sounds, it has been generally accepted that the middle ear reflex protects the inner ear from overstimulation by intense sounds (Wever and Lawrence, 1954; Wersall, 1958; Loeb, 1964; Simmons, 1964; Borg, 1972; Suga and Jen, 1975).

Fletcher and Riopelle (1960) measured the protective power of the reflex on humans; the temporary threshold shift (TTS) produced by a noise too short to activate the reflex was compared with TTS produced by the same noise when the reflex had been activated. TTS was found to be appreciably less in cases in which the middle ear reflex had been activated.

Hilding (1960) made similar comparisons on the cat by measuring the changes in cochlear microphonic. He compared the changes in cochlear microphonic produced by short impulses of sound (gun blasts) when alone or preceded by a reflex activating tone. Presenting the tone before a blast limited the resulting temporary and permanent reductions in the cochlear microphonic.

Thus the middle ear reflex certainly protects the inner ear from damage caused by intense sounds. There are, however, at least three possible limitations on the effectiveness of the middle ear reflex in protecting the inner ear.

The first is the latency between the onset of a sound and any reflex attenuation of that sound. The latency to the first signs of attenuation is probably of the order of 10 ms (see Section 1.4.3) and to maximum contraction of the middle ear muscles and hence by implication to maximum attenuation is considerably greater (91 ms for ST and 105 ms for TT (Wersäll, 1958)). Thus since practical impulses (e.g.

gunfire) can have rise times of from 0.1 - 75 ms (Doelling and Kryter, 1959) the protection afforded by the middle ear reflex against impulse noise is minimal.

The second limitation of the protective power of the reflex is that the response to continuous high level stimulation adapts. The adaptation begins immediately the contraction reaches its maximum value and in the rabbit reaches a steady-state of some 40 - 60% of maximum tension after 20 - 30 secs (Wersäll, 1958). The adaptation in the cat reaches a steady-state within $1\frac{3}{4}$ mins (Simmons, 1959). Nevertheless, Simmons (1960) showed that the muscles were capable of sustained protective action; traumatic sound (1000 Hz at 135 dB SPL) was presented to cats for two hours and the resulting changes in the cochlear microphonic were compared between awake cats (middle ear muscles operational) and anaesthetised cats (middle ear muscles inactivated). He concluded that: 'Reflex fatigue though it may still be a factor is neither rapid nor complete enough to nullify their (the muscles) effectiveness over a reasonably long period of time.' Thus adaptation to prolonged stimulation is not a serious limitation to the protective action of the acoustic reflex.

The final limitation is that the middle ear reflex offers little protection against intense high frequency sounds (especially above 7000 Hz, in the cat (Simmons, 1959)). Since it has been shown that noise damage to inner ear structures occurs at the most sensitive frequencies (4 kHz and above for the cat, see Miller, Watson and Covell, 1963), it is clear that in the cat the middle ear reflex offers little protection in the frequency region most susceptible to damage.

1.5 Functional Anatomy of the Peripheral Auditory System

The following is a brief description of the anatomy of the peripheral auditory system of the cat, which is the experimental animal used in the present study. The cat's peripheral auditory system differs only quantitatively not qualitatively from that of other mammals, including man.

1.5.1 Anatomy of the Inner Ear

The inner ear consists of the osseous labyrinth and the membranous labyrinth. The membranous labyrinth is made up of three parts: the vestibule, the semicircular canals and the cochlea. Only the cochlea need be considered in detail since it is within the cochlea that the transduction of sound energy into nervous activity takes place.

The cochlea is divided into two perilymph filled channels (the scala vestibuli and scala tympani) by means of an elastic partition. This partition consists of two membranes, Reissner's membrane and the basilar membrane. The space between these membranes forms a third cochlear channel, the scala media, which is filled with endolymph. Within the scala media, lying on the basilar membrane is the Organ of Corti which is the site of the auditory receptor cells and nerve endings (see Fig. 16).

1.5.2 Structure and Innervation of the Organ of Corti

The Organ of Corti consists of the tectorial membrane, the receptor cells (the hair cells) and their supporting cells (Fig. 16). In most mammals the hair cells are arranged in four rows; three rows of outer hair cells (OHCs) and one row of inner hair cells (IHCs).

The afferent nerve distribution is different for OHC and IHC. The basilar fibres (Fig. 17) are the only afferent fibres leading to

Figure 16

Cross section of the human cochlea. Upper, vertical section of the human cochlea showing Organ of Corti and adjacent structures. Lower, Organ of Corti and basilar membrane in greater magnification.

(From Rasmussen, 1943.)

Figure 16

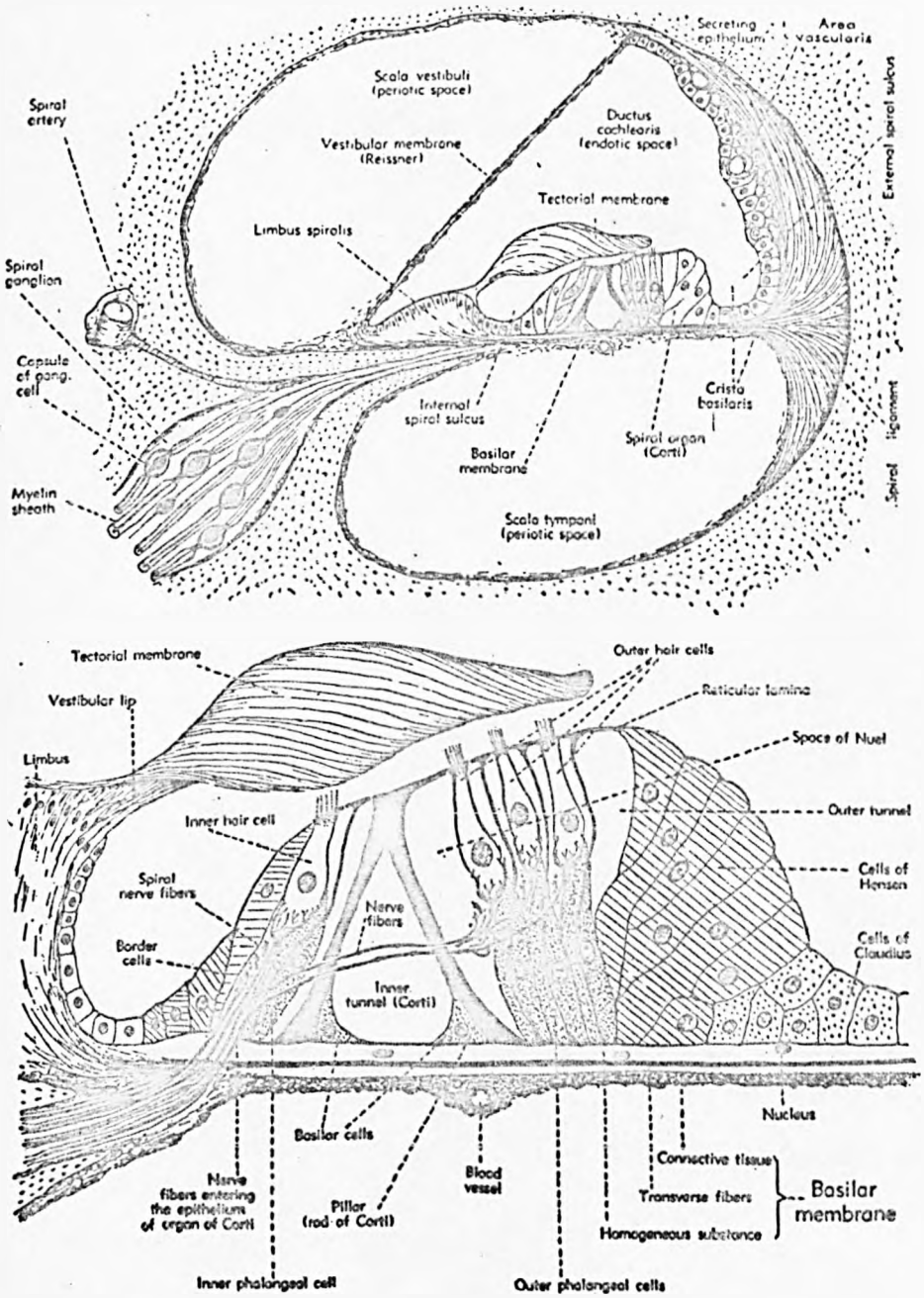
Secreting epithelium
Area vascularis
Scala vestibuli (periotic space)
Spiral artery
Ductus cochlearis (endotic space)
Vestibular membrane (Reissner)
Tectorial membrane
Limbus spiralis
Spiral ganglion
Capsule of gang. cell
Internal spiral sulcus
Cristo basilaris
Spiral organ (Corti)
Basilar membrane
Myelin sheath
Scala tympani (periotic space)
External spiral sulcus
Spiral ligament
Tectorial membrane
Outer hair cells
Vestibular lip
Reticular lamina
Space of Nuel
Limbus
Outer tunnel
Inner hair cell
Cells of Hensen
Spiral nerve fibers
Nerve fibers
Cells of Claudius
Border cells
Inner tunnel (Corti)
Nucleus
Basilar cells
Connective tissue
Blood vessel
Nerve fibers entering the epithelium of organ of Corti
Transverse fibers
Basilar membrane
Pillar (rod of Corti)
Homogeneous substance
Inner phalangeal cell
Outer phalangeal cells

Figure 17

Schematic representation of the innervation of the Organ of Corti.

(From Spoendlin, 1973.)

Figure 18

Schematic representation of the efferent synaptic connections in the Organ of Corti.

(From Spoendlin, 1973.)

Figure 17

All fibers in full black are efferent. Radial dendrites to the inner hair cells (D), inner spiral fibers (iS), tunnel spiral fibers (T), upper tunnel radial fibers (R), basilar fibers (B), outer spiral fibers (OS) and nerve endings at the base of the outer hair cells (N)

Figure 18

At the outer hair cells (OH) synaptic contacts are almost exclusively with sensory cells and at the inner hair cells (IH) only with the afferent dendrites (A). Efferent endings (E).

the OHCs. These basilar fibres are few in number, the whole cochlea containing only 2000 - 3000 (Spoendlin, 1969a) which represents only some 5% of the 50,000 neurones in the cochlear nerve.

Each IHC is innervated by about 20 afferent unbranched strictly radial neurones, the small endings of which form one synapse with the IHC (Spoendlin, 1973).

The afferents to the OHCs take a long spiral course (some 0.6 - 0.7 mm) as outer spiral fibres between the supporting cells, before sending their terminal collaterals to the hair cells (Fig. 17). In the last 200 μm of its course each of these fibres sends collaterals to about 10 OHCs, and each hair cell in the basal turn is provided with four afferent endings from different neurones (Spoendlin, 1969b).

The distribution of afferents is radial to IHCs and spiral to OHCs (Spoendlin, 1966). Some 95% of the afferent neurones of the cochlear nerve innervate the IHCs, the remainder innervating the OHCs. In contrast, the OHCs receive a greater proportion of the efferent innervation than do the IHCs.

The afferent cell bodies are located in the spiral ganglion. The axons of these cells make up the cochlear nerve, which is the only afferent pathway from the cochlea. The cochlear nerve consists of some 50,000 1 - 8 μm fibres, the majority of which have diameters from 2 - 6 μm (Gacek and Rasmussen, 1961; Hall and Rønning-Arnesen, 1974), which extend from the cochlea to the cochlear nucleus of the brain stem.

The efferent nerve supply to the Organ of Corti consists of some 500 fibres in the olivocochlear bundle which form the intraganglionic bundle and finally the inner spinal bundle and upper tunnel radial fibres (see Fig. 17). In the basal turn each OHC receives 6 - 8 axosomatic synapses from the upper tunnel radial fibres, a number

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which is gradually reduced toward the cochlear apex. In contrast, the inner spiral bundle fibres extend over a considerable (as yet undetermined) distance, forming axodendritic synapses on the afferent radial fibres from the IHCs (see Fig. 18 (Spoendlin, 1969a)).

1.5.3 The Course of the Primary Afferents

In order to provide a description of the course of the primary afferents in relation to the cochlear nucleus (CN) the gross anatomy of the latter will be considered first. For the present purpose the sub-division of the CN on the basis of the most conspicuous morphological features into three parts - the anteroventral (AVCN), posteroventral (PVCN) and dorsal (DCN) cochlear nucleus - will be used. These divisions are used merely for description, and a more detailed discussion of the cytoarchitecture of the CN is deferred to Section 1.5.4.

All afferent fibres from the cochlea terminate in the cochlear nucleus (Cajal, 1909; Lorente de No, 1933a, b; Powell and Cowan, 1962; Osen, 1970). The nerve fibres bifurcate near the point of entry into the cochlear nucleus forming the ascending branches which enter the AVCN and the descending branches which penetrate the PVCN and then continue into the DCN (Held, 1893; Cajal, 1909; Lorente de No, 1933a).

The ascending branches are gathered in small bundles which run rostrally and dorsally curving slightly in the lateral direction, at about 90° from the direction of the original cochlear fibre. The most dorsal ascending branches which emerge from the medial tip of the nerve root lie more caudally and medially than the more ventral ascending branches.

The descending branches continue in the direction of the original fibres, and in contrast to the ascending branches, are convergent and

become densely packed in their course between the cells of the PVCN. At the caudal extreme of the PVCN the descending branches curve laterally and rostrally at an angle of about 90°, entering the DCN where they continue in a direction approximately parallel to the ascending branches. The majority of the descending branches enter the DCN caudal to the root of the acoustic striae (see Section 1.5.5.), looping around the latter (Osen, 1970).

The most ventral fibres of the cochlear nerve root innervate the anterior AVCN and DCN, whereas the most dorsal cochlear nerve fibres innervate the posterior AVCN and DCN. As a consequence of this strictly ordered distribution of the cochlear nerve fibre branches, the primary afferents become arranged in the same tonotopical order in the DCN, PVCN and AVCN (Lorente de No, 1933a; Sando, 1965; Osen, 1970); this has also been found experimentally in single unit studies (e.g. Rose, Galambos and Hughes, 1959).

1.5.4 Anatomy and Cytoarchitecture of the Cochlear Nucleus

The CN has been the subject of extensive anatomical studies (e.g. Cajal, 1909; Fuse, 1913; Lorente de No, 1933a, b; Harrison and Warr, 1962; Harrison and Irving, 1965, 1966a, b; Osen, 1969a, b, 1970; Cohen et al., 1972; Kane, 1974; Brawer, Morest and Kane, 1974; Brawer and Morest, 1975). The CN forms the first relay centre in the ascending auditory pathway, each cochlear nerve fibre establishing contact with many cells (Lorente de No, 1933b). In addition, several tracts of descending fibres from higher auditory centres terminate in the CN (Held, 1893; Lorente de No, 1933b; Rasmussen, 1960, 1967). Subdivision of the complex has been made on cellular characteristics using Golgi (Lorente de No, 1933b; Brawer et al., 1974), protargol (Harrison and Irving, 1965, 1966a, b) and Nissl or Glees (Osen, 1969a;Brawer et al., 1974) staining techniques.

The classical study of Lorente de No (1933b) subdivided the cat CN into thirteen divisions; the DCN was dealt with in considerable detail, but no mention was made of the criteria used in the subdivision of the VCN. Both this and a later study by Harrison and Irving (1965, 1966a, b) did not deal with the entire cochlear nucleus complex. The study of Osen (1969a), however, subdivided the whole complex and provided a coherent description of the cytoarchitecture. This study was, however, limited by the use of cell body stains which do not reveal such neuronal features as dendrites and axons. A later study (Brawer et al., 1974) did not suffer from this limitation and therefore provided a more detailed scheme of subdivision.

Since, however, no attempt has been made in the present study to specifically relate responses to individual cell types it would be inappropriate to discuss these parcellation schemes in minute detail. The distribution of the nine cell types defined by Osen (1969a) are, however, briefly summarised in Fig. 19, in order to provide the background to some of the data discussed in later sections.

Briefly one can trace many features of the cytoarchitecture of the cochlear nucleus which are consistent in most of the studies in the literature. This is particularly true of the DCN, which is a complex structure, consisting of four layers; the ependymal, molecular, fusiform and polymorph layers (Fig. 19). The main differences between the studies of Osen (1969a) and Brawer et al. (1974) in this division of the cochlear nucleus, result from the more detailed Golgi based distinctions of the latter authors which divide up the cell types of Osen (the giant and small cells) into several types (radiate, horizontal and vertical giant cells, small stellate, small elongate and cartwheel cells).

Figure 19

Schematic representation of the distribution, within the cochlear nucleus, of nine cell types defined by Osen.

(From Osen, 1969a.)

Figure 19

large spherical cell · globular cell · octopus cell · pyramidal cell · giant cell
small spherical cell · multipolar cell · granular cell · small cell

Sagittal diagrams of the cat cochlear nuclei demonstrating the ventral nucleus isolated (in A) *and the ventral nucleus partly covered by the dorsal nucleus (in* B).

The distribution of the nine cell types (23) is indicated by different symbols (see key below). *B* demonstrates the course of the ascending (a. b.) and descending branches (d. b.) of the cochlear fibers and the fascicles of intrinsic fibers (i. f.) interconnecting the dorsal and ventral nuclei. In *B* merely the small cells and granular cells are shown in the ventral nucleus.

Abbreviations used in Fig

a. b.,	ascending cochlear branch
a. v. c. n.,	anteroventral cochlear nucleus
C,	caudal
cap,	peripheral cap of small cells
c. f.,	centrifugal fibers of Lorente de Nó
co. f.,	cochlear nerve fiber
co. rest.,	restiform body
co. trap.,	trapezoid body
coll.,	collaterals of primary fibers
c. r. d. c. n.,	central region of the dorsal cochlear nucleus
c. r. v. c. n.,	central region of the ventral cochlear nucleus
D,	dorsal
d.,	dendrite
d. b.,	descending cochlear branch
d. c. n.,	dorsal cochlear nucleus
ep.,	ependyma
floc.,	flocculus
gi.,	giant cell
gr.,	granular cell
gr. c. l.,	granular cell layer
h,	fibers mediating impulse to tigh tonal frequencies
i. f.,	intrinsic fibers
L,	lateral

The VCN is divisible into many areas on the basis of cell shape, size and packing density. These areas do not delimit distributions of particular cell types (except the central part of the PVCN which delimits the distribution of octopus cells), indeed the cell populations within these areas are in most cases heterogeneous. Since particular cell types occur in more than one area as defined by Brawer et al. (1974), and accepting that morphology of the cell and structure of the neuropil must play a crucial role at the synaptic level, one may question whether such parcellation schemes have a functional significance or whether it is the cell type irrespective of its location, which determines its response.

1.5.5 Projection of Cells of the Cochlear Nucleus on Higher Auditory Nucleii

Three afferent fibre tracts arise in the cochlear nucleus; the trapezoid body in the AVCN, the stria of Monakow (dorsal acoustic stria or DAS), in the DCN and the stria of Held (intermediate acoustic stria or IAS) in the PVCN. (Lorente de No, 1933b.) These are not, however, fibre tracts from single cell types in the cochlear nucleus to single higher auditory nucleii. The large and small spherical cells, globular and multipolar cells of Osen (1969a)project via the trapezoid body, each type ending in different higher nucleii. The large spherical cells project bilaterally onto the medial superior olive, whereas the small spherical cells project to the ipsilateral lateral superior olive (Osen, 1969b). The globular cells send their very thick axons across the midline to the contralateral medial trapezoid nucleus (Harrison and Irving, 1966b). The field of termination of the multipolar cells is not definitely settled, but fibres from regions of the PVCN in which such cells are found are reported to terminate bilaterally in certain periolivary nucleii (Warr, 1969).

The octopus cells project via the IAS (Lorente de No, 1933b; Harrison and Irving, 1966b; Osen, 1969b) and terminate bilaterally in the pre and peri-olivary nuclèii (Fernandez and Karapas, 1967; Warr, 1969).

The giant cells project via the DAS and the contralateral lateral lemniscus (Osen in Osen, 1970, unpublished observations), but their field of termination remains obscure. The fusiform cells also project via the DAS (Kane, 1974) onto the central nucleus of the contralateral inferior colliculus (Monakow, 1891; Fernandez and Karapas, 1967).

The small cells and granule cells do not project into areas outside the cochlear nucleus complex. The small cells usually have short axons which terminate within the complex, the majority apparently establishing contact with the fusiform cells (Kane, 1974), while others give rise to the system of association fibres interconnecting DCN and VCN (Lorente de No, 1933b; see Section 1.5.7). The granule cells have short plump axons which contact the somas and dendrites of the fusiform cells (Osen, 1970; Kane, 1974).

1.5.6 Efferent Connections to the Cochlear Nucleus

At least four major efferent pathways to the CN have been described (Lorente de No, 1933b; Rasmussen, 1960, 1967). The olivocochlear bundle (OCB) from the pre- and peri-olivary nucleii (Rasmussen, 1946; Rossi, 1968), passes through the vestibular root and gives off collaterals to the cochlear nucleus which terminate predominantly among the granular cells of the superficial layer of the AVCN (Rasmussen, 1967).

A second tract originating from the lateral superior olive passes through the vestibular root and converges along the medial margin of

the AVCN from whence the fibres disperse uniformly among the cells. This is the largest population of recurrent fibres which enter the cochlear nucleus (Rasmussen, 1967).

The two remaining major tracts innervate the DCN. The first described by Lorente de No (1933b), arrives at the cochlear nucleus via the caudal stream of the trapezoid body, passes between the descending trigeminal root and the AVCN or PVCN, and penetrates the DCN. The region of entry into the DCN was termed the nucleus centralis by Lorente de No (1933b) but is not differentiated by other authors. The source of this tract is reported by Rasmussen (1967) to be the Inferior Colliculus and the dorsal nucleus of the lateral lemniscus. The second tract to the DCN takes origin in the ventral nucleus of the contralateral lateral lemniscus and passes around the restiform body and enters the DCN via the dorsal acoustic stria (Rasmussen, 1960).

Rasmussen (1967) also reports centrifugal fibres from the homolateral superior olivary complex forming a minority of the endings in the PVCN.

The results of several studies have indicated that efferent synaptic terminations are found throughout the CN (Lorente de No, 1933b; Harrison and Irving, 1965; Lenn and Reese, 1966; Osen, 1970; Brawer and Morest, 1975; Kane, 1974). It would appear that apart from the globular cells (Osen, 1969a)which apparently receive predominantly primary input (Osen, 1970), most of the cell types of the cochlear nucleus receive centrifugal innervation. It is not possible at this time, however, to determine the exact source of the innervation to the different cell types.

1.5.7 Intrinsic Connections of the Cochlear Nucleus

In addition to the ascending and descending connections to the CN, there is also an intranuclear pathway which links the AVCN and DCN. This tract was first described by Lorente de No (1933b) and has since been confirmed by other workers (Harrison and Warr, 1962; Warr, 1969; Osen, personal communication). Within this pathway are fibres running in both directions between AVCN and DCN (Lorente de No, 1933b; Osen, personal communication to Evans). In addition, Osen suggests that an intranuclear pathway between DCN and PVCN might also exist.

1.6 Physiological Studies of the Cochlear Nucleus

The cochlear nucleus represents the first stage along the auditory pathway at which information carried by the discharge of single cochlear fibres can be recoded. It is perhaps not surprising therefore that the responses of single cells in the cochlear nucleus, even in response to a simple tone burst, are far more diverse and complex than the apparently homogeneous responses of the cochlear nerve (for a review of the available cochlear nerve literature to 1974 see Evans, 1975a).

1.6.1 Tonotopic Organisation

The first study of single unit responses in the auditory system was that of Galambos and Davis (1943). These authors intended initially to study single cochlear fibres and concluded subsequently that the recordings were in fact from cochlear nucleus cells (Galambos and Davis, 1948). In the following years other workers also obtained cochlear nucleus recordings (e.g., Tasaki and Davis, 1955) but it was not until over a decade after the original recordings that extensive qualitative and quantitative data were reported in the classical study of Rose, Galambos and Hughes (1959).

The Rose et al. study revealed a strict tonotopic organisation within each major subdivision of the cochlear nucleus (AVCN, PVCN, and DCN, see Section 1.5.3). Within each of these divisions the characteristic frequencies (CFs) of the neurones (i.e. the frequency to which the neurone is most sensitive) are arranged sequentially from high to low frequency, in the dorsal to ventral, posterior to anterior and medial to lateral directions. This ordering results from the precise branching and arrangement of the incoming cochlear fibres (see Section 1.5.3).

1.6.2 Classification of Unit Responses and the Location of Response Types Within the Cochlear Nucleus

These early studies found a wide variety of responses many of which were of an inhibitory nature (e.g. Galambos, 1944; Rose et al., 1959). No correlation was suggested, however, between the types of responses and their location other than the suggestion by Rose et al. that units having non-monotonic discharge versus intensity functions or build-up temporal patterns were located in the DCN.

The classification of single unit response types due to Kiang and Pfeiffer and their colleagues (Kiang,et al., 1965b; Pfeiffer, 1966) distinguishes responses which can at least be correlated with unit locations within the major subdivisions. These authors recognised five different types on the basis of interval histograms of spontaneous discharge and of post stimulus time histograms generated in response to short CF tone bursts 20 dB above threshold.

The five response types of the earlier paper (Kiang et al., 1965b) were reduced by Pfeiffer (1966) to four, two categories being combined into a single category termed 'primarylike' (see Table 2). The four different response types are illustrated in Fig. 20 and the interval histogram and location data summarised in Table 2. The first type is termed 'primarylike' due to its similarity to responses of primary fibres. Both 'primarylike' response types have inter-spike interval histograms of spontaneous discharges which have modes of less than 12 ms. The major difference between the two is that the decay of the inter-spike interval histogram is exponential for one response type (found in posterior AVCN and PVCN) and faster than exponential for the second (found only in AVCN). The latter also have a characteristic action potential waveform consisting of a positive deflection preceding the large negative spike. The envelope of the

Figure 20

Peri stimulus time histograms from four different cochlear nucleus units in response to CF tone bursts. The four responses are typical of the categories of response described by Kiang et al., 1965b and Pfeiffer, 1966. The first category 'primarylike', is represented by unit P77-10, the second 'chopper', by unit P27-9, the third 'pause', by unit P26-3 and the fourth 'on', by unit P115-3.

(From Pfeiffer, 1966.)

Table 2

Properties of interspike interval histograms of spontaneous activity and anatomical locations of units of the four categories described by Kiang et al., 1965b and Pfeiffer, 1966.

(From Pfeiffer, 1966.)

Figure 20

PST histograms of responses to tone-burst stimuli for four different units. The stimulus levels, relative to unit VDL, were: P77-10, 20 db; P27-9, 25 db; P23-6, 21 db and P115-3, 22 db. In each case, only the first 40 (of 100) msec of time after the presentation of each tone burst is shown. The titles of the individual histograms, in this and the remaining figures, specify the following: 1st row; cat and unit number, tone burst at characteristic frequency (TBCF), signal level in db re 200 v peak to peak into condenser earphone, repetition rate in bursts per second, and approximate duration in msec; 2nd row; type of histogram (PST), bin width, and number of discharges in sample of data computed. The last bin on all histograms is an "overflow" bin

Table 2

post stimulus time histograms of primarylike responses shows a maximum at onset which decays smoothly to a relatively steady discharge which is maintained for the duration of the tone burst.

The second response type the so-called 'chopper' consists of units whose post stimulus time histograms are characterised by distinct, regularly spaced peaks. Units with 'chopper-type' responses have been found in posterior AVCN, PVCN and DCN (see Table 2).

The third category of response pattern, the 'pauser' consists of units whose post stimulus time histograms are characterised by a pronounced dip following an initial peak. This type of response was only observed in the DCN. Generally, the response pattern for any unit did not differ substantially at higher levels from the pattern that prevailed at 25 dB above threshold. In contrast, definite changes in the response patterns for tone bursts of long duration do occur for some units. For example, 'pauser' units often showed the build-up type of response (as described by Rose et al., 1959) to long tone bursts.

The final category, the 'on' response, consists of those units whose PSTHs are characterised by an initial peak or peaks with little activity thereafter. 'On' responders were found in the IN (interstitial nucleus of Lorente de No (1933a,b) see Section 1.5.4, which approximately corresponds to the cochlear nerve root), the PVCN and on rare occasions in posterior AVCN and in DCN.

Recently Kiang et al. (1973) have been able to firmly associate the 'on' responses with the octopus cells of the PVCN and the 'pauser' or 'build up' responses with the fusiform layer of the DCN. For the most part, however, response types cannot be related exclusively to specific regions within the CN but can be related to the major subdivisions (DCN, AVCN and PVCN) and in a few cases to particular cell types.

Rose et al. (1959) suggested that the lack of precise correlation of response types to location within the cochlear nucleus might have been due to two factors: a) their analytical approach, which was the visual inspection of discharge patterns to manually chosen pure tone and click stimuli, and b) elimination of some significant differences between units by the deep anaesthesia employed in their study.

In a series of experiments complementary to that of Kiang et al., Evans and Nelson (1973a)explored the suggestions of Rose et al. by using systematic analyses and comparing responses under various anaesthetics with responses from unanaesthetised preparations. Using the degree to which inhibitory effects were produced by single tones and the relative extent of the band of inhibitory frequencies as criteria, they classified their data into five response categories:-

1. Sustained excitation only, over a restricted range of frequencies;
2. Excitation as in 1. but followed by inhibition of the spontaneous rate with the termination of the stimulus ('off inhibition');
3. Excitation as in 2. with inhibitory frequency bands extending above and/or below the excitatory band ('side band inhibition');
4. Predominantly inhibitory response, inhibition of spontaneous discharge took place over a relatively wide band of frequencies relative to the excitatory bandwidth and where both excitatory and inhibitory bands were found within 10 dB of threshold;
5. Wholly inhibitory response area.

The distribution of these response types was found to be a function of both location and anaesthetic. Type 1 was found most frequently in VCN, whereas Type 2 was found in all parts of the complex. Type 3 was most commonly found in the DCN and Types 4 and 5 were found almost exclusively in the unanaesthetised or chloralose anaesthetised DCN.

There were no significant differences between the AVCN and the PVCN in any of the anaesthetic states but the DCN differed from the VCN in two major respects.

Under all conditions the proportions of Types 3, 4 and 5 were substantially greater in DCN than VCN and Types 4 and 5 were almost never found in VCN whether or not anaesthetics were used.

The second difference was that while anaesthetic had no significant effects on responses of the VCN, profound differences were found between unanaesthetised and anaesthetised DCN preparations. Type 5 was almost never found in DCN under pentobarbitone or halothane anaesthesia but was the predominant response in DCN of unanaesthetised animals which either had intact auditory pathways or were decerebrate, followed by Types 4, 3 and 2 in that order. The effects of anaesthesia, while negligible in the VCN, seriously attenuated the inhibitory responses of the DCN tending to obliterate differences between VCN and DCN.

The study of Evans and Nelson (1973a) agrees very well with the results of Kiang and Pfeiffer and colleagues (Kiang et al., 1965b; Pfeiffer, 1966). Units which had purely excitatory responses and simple time courses, that is 'primarylike' units, were found to predominate in the VCN in both studies. From the PSTHs of units of Types 3 and 4 (of Evans and Nelson) in response to CF tones 20 dB above threshold, it is evident that these types correspond to the 'build up' or 'pauser' classifications of Pfeiffer (1966). Such responses were only found in DCN in both of these studies.

Recently the classification scheme illustrated in Fig. 21, which combines many of the features of both the Evans and Nelson and the Kiang et al. classifications has been used by Gisbergen (1974) and Gisbergen et al. (1975a, b, c). These authors initially divided the

Figure 21

The classification scheme of Gisbergen (1974), which depends upon excitatory and inhibitory responses, spontaneous activity and temporal discharge patterns.

The number of units contained in each category is indicated above every box. Absence of a number indicates that such units were not found. The number of units dropped at a branch point (because classification was not possible (N.C.) or because the set of data was inadequate (N.I.)), are indicated.

(From Gisbergen, 1974.)

Table 3

Distribution of the units in the various categories described by Gisbergen, 1974 (see Fig. 21).

(From Gisbergen, 1974.)

Figure 21

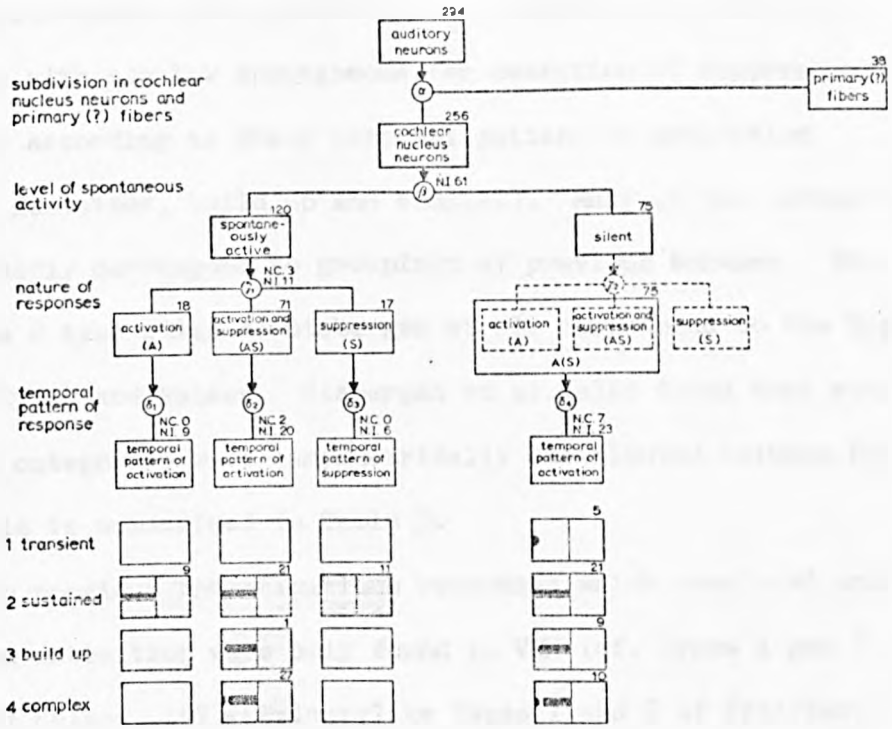


Table 3

Percentage of DCN neurons (granular layer units included) in each of the various categories (see text). For a given unit category percentages above 50 indicate predominant occurrence in the DCN, whereas percentages below 50 indicate predominant occurrence in the VCN.

	A	AS	S	A(S)	total
transient	-	-	-	18	18
sustained	0	24	100	11	28
build up	-	100	-	100	100
complex	-	90	-	20	69
not classified	-	100	-	63	72
not investigated	26	55	100	52	54
total	11	59	100	40	50

units according to the amount of inhibition shown (A = Activation only, AS = Activation and Suppression, S = Suppression only, A(s) = Activation with too low spontaneous for detection of suppression), and secondly according to their temporal pattern of activation (transient, sustained, build up and complex). Many of the categories obtained clearly correspond to groupings of previous schemes. For example, the S type units of Gisbergen et al. correspond to the Type 5 units of Evans and Nelson. Gisbergen et al. also found that many of the unit categories were assymmetrically distributed between DCN and VCN; this is summarised in Table 3.

As with previous investigations responses which consisted only of sustained activation were only found in VCN (cf. Types 1 and 2 of Evans and Nelson, 1973a; Primarylike Types 1 and 2 of Pfeiffer, 1966). S units (suppression only) were found only in the DCN (cf. Type 5 of Evans and Nelson, 1973a). AS and A(s) units (activation and suppression) were found in both DCN and VCN (cf. build up and pauser units of Pfeiffer, 1966; Types 3 and 4 of Evans and Nelson, 1973a). The distribution of the build up temporal pattern was found to be similar to that of the pyramidal cells (Osen, 1969a) a finding consistent with that of Kiang et al. (1973).

It is clear that the three classification schemes described which use temporal discharge pattern, amount of inhibition and a combination of both as criteria, all produce categories which are consistent with each other and which can be associated with particular subdivisions of the cochlear nucleus and in a few instances with particular cell types. There is, however, a considerable discrepancy between the distribution of some response types as found by different investigators. This will be more fully discussed in the following section.

1.6.3 Response of Single Units as a Function of Frequency

The major difference between the response of cells in the cochlear nucleus and of single cochlear fibres, is the presence in certain cochlear nucleus cells of frequency regions in which the activity of the cell is inhibited by single tones. Cells with entirely inhibitory response areas have been found occasionally in the unanaesthetised cat VCN (Moushegian et al., 1962; Evans and Nelson, 1973a)and in the DCN of cat (Gerstein et al., 1968; Evans and Nelson, 1973a). More commonly found are inhibitory regions contiguous with the excitatory response regions; the so-called 'inhibitory side-bands' (Galambos, 1944; Katsuki et al., 1958; Moushegian et al., 1962; Greenwood and Maruyama, 1965; Gerstein et al., 1968; Evans and Nelson, 1973a; Gisbergen et al., 1975a). Inhibitory responses are generally associated with cells located in the DCN; Gisbergen et al. (1975a)reported 96% of DCN cells in the barbiturate anaesthetised cat and 60% of the VCN cells showed inhibitory responses. Evans and Nelson (1973a) reported only 50% of DCN cells showing inhibitory effects in the barbiturate anaesthetised cat, rising to 92% in the unanaesthetised preparation. In the VCN, however, Evans and Nelson only found 10% of cells showing inhibitory responses irrespective of the anaesthetic state. Gisbergen et al., suggested that the differences in the proportions between their study and that of Evans and Nelson may have been due to two factors: 1) the finer frequency resolution used in their study might have facilitated detection of narrower inhibitory bands, and 2) off-inhibition was studied using 1 sec tone bursts and would therefore have been stronger and more easily detectable than in the Evans and Nelson study.

The Evans and Nelson study used 54 frequency steps of 0.74 kHz for units of CF 10 kHz and over, whereas Gisbergen et al. used 80

frequency steps of 1/40 octave, which for a unit of CF 12 kHz would be 0.225 kHz steps. Thus Gisbergen et al. would have detected side bands up to three times narrower than the Evans and Nelson study. The majority of Evans and Nelson Type 3 and 4 units had build-up or complex temporal discharge patterns and were located in the DCN. Gisbergen et al. also found that AS and A(s) neurones with build-up or complex temporal discharge patterns were located in the DCN. Thus the larger proportion of VCN neurones showing inhibition found by Gisbergen et al. must have had predominantly sustained temporal discharge patterns. If Evans and Nelson had not failed to detect very narrow side bands of such neurones they would have classified them as Types 1 or 2.

Assuming that the different proportions of VCN neurones showing inhibition is simply due to the higher resolution technique detecting narrower inhibitory areas, it suggests that the inhibitory side bands in VCN are narrower than in DCN.

Young and Brownell (1976) found differences in the unanaesthetised cat DCN in the proportions of response types 4 and 5 from the proportions reported by Evans and Nelson. Here again some of the discrepancy is attributed by the authors to differing techniques enabling identification of weak effects which might have been missed by the techniques of Evans and Nelson.

The frequency resolution of the method used by Young and Brownell was 0.1 or 0.2 octaves which for a unit with CF of 12 kHz would be of the same order as the resolution of the Evans and Nelson study, and could not therefore be a source of differences. One possible explanation of the differences in the proportions of Types 4 and 5 is that Young and Brownell used ether anaesthesia during the decerebration surgery. This anaesthetic is extremely long acting and unless recording was delayed by many hours the animal would still be

in a state of partial anaesthesia and Type 5 responses would only be found infrequently.

All of the studies of units showing inhibitory responses lead to the conclusion that the functional organisation of the DCN is more complex than the VCN and inhibitory phenomena are less widespread and less dramatic in the VCN than the DCN.

Greenwood and Maruyama (1965) undertook a detailed study of the variations in temporal patterns of discharge, with variation of stimulus parameters inside and outside the excitatory response areas. They were able to show that there was a continuous transition between frequency regions in which there occurred silent periods of no discharge, preceding a response or intervening between onset spikes and later firing, and frequency regions in which spontaneous discharge could be inhibited by single tones (inhibitory side-bands). Many stimuli exerted on a single unit both net excitatory and net inhibitory effects which succeed each other. Similar findings have been reported by Nelson and Erulkar (1963), Evans and Nelson (1973a), Gisbergen (1974) and Gisbergen et al. (1975a).

Several authors have considered the possibility that the extent of the excitatory response areas of single neurones might vary with their location within the CN and that units with inhibitory side-bands might have narrower response areas as a consequence. Some of these studies comparing the response areas of neurones from different CN sub-divisions with each other and with cochlear fibre response areas are reviewed and discussed with respect to the findings of the present study in Appendix C. At this stage it is sufficient to note that the presence of inhibitory side bands does not result in response areas consistently narrower than those of units only showing excitation. Furthermore, the extent of the excitatory response area is not

exclusively related to the location of the neurone.

1.6.4 Response of Cochlear Nucleus Cells as a Function of Intensity

Units in the VCN generally have monotonic rate functions similar to those of single cochlear nerve fibres, rising from spontaneous rate to saturation rate over 30 dB or so (Galambos and Davis, 1943; Rose et al., 1959; Greenwood and Maruyama, 1965; Møller, 1969).

However, in some cells located in the DCN, frequencies which are excitatory at levels near threshold become inhibitory at higher levels. The rate functions of such cells are therefore non-monotonic (Rose et al., 1959; Greenwood and Maruyama, 1965; Goldberg and Greenwood, 1966; Greenwood and Goldberg, 1970). Since the non-monotonic units in the study of Greenwood and Maruyama (1965) were not spontaneously active, they were unable to demonstrate whether the regions in which activity was reduced as stimulus intensity was increased were continuous with the regions in which spontaneous activity could be inhibited by single tones. Their data are, however, consistent with such a suggestion.

Further discussion of the way in which the discharge of single units in the cochlear nerve and nucleus varies as a function of intensity, is deferred to Chapter Three.

1.6.5 Function of the Centrifugal and Intranuclear Connections of the Cochlear Nucleus

It is apparent from Sections 1.5.2 and 1.5.6 that the cochlea and cochlear nucleus receive abundant efferent innervation. In general, the action of these descending pathways has been studied by stimulation of either the fibres in passage or the nuclei of origin. Despite considerable agreement between studies of the descending

pathways, their function remains obscure. The following is a brief survey of the major findings of studies of the descending pathways (for more detail, the interested reader is referred to the comprehensive reviews of Whitfield (1967), Klinke and Galley (1974), Demesdt (1975) and Evans (1975a: pp. 72 - 77).

Briefly, the effects of OCB stimulation on the cochlea are, a reduction of the CAP amplitude, an increase in the CM amplitude (Galambos, 1956; Fex, 1959) and inhibition of spontaneous and tone evoked activity of single cochlear fibres (Fex, 1962; Weiderhold, 1970; Weiderhold and Kiang, 1970). The inhibition of cochlear fibre discharge takes 40 - 110 ms to develop and seems to resemble a reduction in the level of acoustic stimuli. Thus the discharge rate versus intensity function is shifted to higher levels by amounts of 1 - 25 dB (Weiderhold, 1970).

The effects of stimulation of the crossed OCB on the CN have been investigated by Starr and Wernick (1968). These authors found both excitatory and inhibitory effects on spontaneous and tone evoked activity; inhibitory effects were encountered most often. The effects on the spontaneous activity persisted after sectioning of the cochlear nerve and were not therefore an indirect result of the OCB action on the cochlea. It is, however, unclear to what degree the inhibition of tone evoked activity reflected the inhibition of cochlear fibres.

The largest descending tract to the CN has been studied by Comis and Whitfield (1968). These authors found that stimulating the medial portion of the lateral superior olivary nucleus with direct-current, increased the spontaneous and tone evoked activity of single cells in the ipsilateral AVCN, in some cases reducing the threshold by up to 15 dB. Stimulation of the lateral portion of the lateral superior olivary nucleus evoked inhibition in cells of the DCN and in some cells of the VCN (Comis, 1970).

Comis and Whitfield (1968) also studied the effects of stimulating the dorsal and ventral nuclei of the contralateral lateral lemniscus. Stimulation of the ventral nucleus evoked inhibition of spontaneous and tone evoked activity in the DCN, whereas stimulation of the dorsal nucleus evoked both inhibition in the DCN and excitation in the VCN.

Presentation of acoustic stimuli to the contralateral ear also evokes inhibition in the CN (Pfalz, 1962; Klinke, et al., 1969; Mast, 1970b). This effect is mediated not by the crossed OCB but by pathways in the trapezoid body (Grubel et al., 1964). The inhibition evoked was frequency dependent; frequencies at either side of the CF were most effective in inhibiting the response to an ipsilateral CF tone (Klinke et al., 1969).

In summary, the descending pathways to the CN produce both excitatory and inhibitory influences on single CN cells. In the main, excitation is found in the VCN and inhibition in the DCN.

It would appear that, to a first approximation, the distribution of the inhibitory responses elicited by activation of the descending pathways, is similar to that of the inhibition observed in response to acoustic stimulation (see Sections 1.6.2, 1.6.3 and 1.6.4 above). Thus one may question whether the inhibition observed in response to acoustic stimulation is mediated by the descending pathways. Certainly, in the anaesthetised animal, the descending pathways do not mediate this inhibition since anaesthesia eliminates efferent activity (e.g. see Klinke et al., 1969). There remains, however, the possibility that the descending pathways may contribute to the tone evoked inhibition observed in the CN of unanaesthetised animals. Evans and Nelson (1973b) rejected this suggestion on two counts. 1. The latency of the inhibition observed in the CN to acoustic stimulation is short compared with that of the experimental activation of the descending pathways.

2. The inhibitory responses found in animals in which the descending pathways are severed are not significantly different from those of animals in which the descending pathways are intact.

These same authors showed that the latencies of excitation in the DCN were greater than for excitation in the VCN and the latencies for inhibition in the DCN were greater than for excitation in the VCN. Evans and Nelson were also able to demonstrate short latency inhibition in the DCN as a result of activation of the intranuclear pathway between VCN and DCN (see Section 1.5.7). They therefore suggested that 'the most likely interpretation of these data therefore is that the DCN receives its predominant, inhibitory (and possibly excitatory) input from the AVCN via the intranuclear pathway'. This suggestion is consistent with other physiological and anatomical data (see Evans and Nelson (1973b) for details).

Reviews of physiological studies of other aspects of cochlear nucleus activity will be found in the appropriate chapters.

1.7 Current Explanations of Intensity Coding

This discussion is an examination of the arguments for and against current models of intensity encoding in the peripheral auditory system. It has been included at this point for two main reasons: i) these models suggest ways in which sensitivity to small intensity differences may be maintained over a wide dynamic range; and ii) the psychophysical experiments designed to test the predictions of the models have led to the hypotheses which the present experiments have sought to test. The following paragraph is a brief recapitulation of the problem of encoding intensity differences which has already been mentioned in the preface to this chapter.

Galambos and Davis (1943) found the dynamic range of most 'auditory fibres' to be of the order of 30 dB. Although it was later found that these 'auditory fibres' were in fact cochlear nucleus cells, similar restricted ranges (30-50 dB) have also been found in cochlear nerve fibres (Kiang et al., 1965a). When these single nerve fibre dynamic ranges are compared with the range over which the auditory system can discriminate small intensity differences (up to at least 100 dB above threshold, see Sections 1.2.5 and 1.3.3) a considerable discrepancy is evident. At low stimulus levels a single cochlear fibre can certainly signal a difference in the stimulus intensity by a difference in its discharge rate, but above the stimulus level at which the fibre's discharge saturates, small level changes do not evoke changes in the discharge rate. A single cochlear fibre therefore appears incapable of signalling intensity differences in terms of differences in its mean rate of discharge over a range of intensity sufficiently wide to account for the psychophysical discrimination data.

Sachs and Abbas (1974) have, however, reported data which indicate that complete saturation of the discharge rate does not occur in all cochlear fibres. In some cochlear fibres a decrease in the slope of the rate function takes place at 20-50 dB above threshold and the discharge rate continues to rise albeit slowly as intensity is further increased. In the cochlear fibre

data of Evans (Section 3.3.4) all fibres, even those showing such a slope change, were saturated by 60 dB above threshold. At present, therefore, it is unclear whether the cochlear fibres having wide dynamic ranges (of the order of 80 dB) obtained by Sachs and Abbas (1974) are present in sufficient numbers to account for the psychophysical discrimination data. The data of Sachs and Abbas are considered in detail in Sections 3.1.2 and 4.4.6 but for the following discussion it is assumed that complete saturation of the discharge of the majority of cochlear fibres occurs at levels of 20-50 dB above threshold.

The two explanations considered below have been suggested as ways in which sensitivity to small intensity differences might be maintained over wide ranges of intensity, despite the restriction imposed by the limited single fibre dynamic ranges. Not surprisingly, considering that Galambos and Davis (1943) found a wide range of single unit thresholds, such a wide range has been incorporated in several formulations of the mechanism of loudness and intensity coding (e.g. Fletcher, 1953; Flanagan, 1965; Zwislocki, 1965). Thus, Fletcher (1953) assumed a range of single unit thresholds in excess of 90 dB, but only a limited single unit dynamic range. He suggested that the loudness of a 1 kHz tone could be signalled by the total discharge rate of a 'patch of nerves', which varied from 1-90,000 spikes persecond as the intensity was changed from 5-120 dB. It is easy to see how such a system could result in maintenance of differential sensitivity to intensity over a wide range of intensity, since over the whole range some elements would only be excited just above threshold. Such elements could therefore signal small intensity differences by large differences in their discharge rate. The ranges of single unit thresholds are discussed in detail in Section 3.1.1. It is sufficient at this stage to note that although wide ranges of minimum thresholds at any frequency have indeed been reported (Galambos and Davis, 1943; Katsuki et al., 1962; Kiang et al., 1965a; Mast, 1970a) it has been shown that these wide ranges were due to pooling of data from different animals and/or inadequate calibration of the sound equipment. The range of thresholds at any frequency found in a single ear is only of the order of 20 dB (first shown by Kiang, 1968).

Several authors have suggested that the information content of an auditory signal is conveyed by the totality of responses in the entire array of fibres in the cochlear nerve (e.g. Stevens and Davis, 1938, p. 406; Galambos and Davis, 1943; Fletcher, 1953, p. 112).

One such model is that due to Allanson and Whitfield (1955), who inferred the pattern of responses within the complete array of cochlear nerve fibres from the available responses of single cochlear nerve fibres. They used the data of Galambos and Davis (1943) which, although in fact from second order neurones, embodied responses which were later also found in the cochlear nerve. From these data Allanson and Whitfield constructed idealised iso-intensity response contours for a single fibre as shown in Fig. 22A. Assuming that the shape of such response contours was the same for all fibres they were able to construct the pattern of activity in the complete array of cochlear fibres as shown in Fig. 22B. This spatial pattern of activity within the cochlear nerve, defines both the frequency and the intensity of a signal; intensity is represented by the spread of the activity and frequency by the location of the region of active fibres within the total cochlear fibre array. At high stimulus levels the fibres most sensitive to the stimulus frequency become saturated and the pattern of active fibres becomes flat topped. At stimulus levels sufficient to form a central flat saturated region in the pattern of nerve activity, it is assumed that simple discriminations of frequency and intensity must be made on the basis of changes in the activity of fibres at the edges of the active region. Changes in intensity alter the spread of the pattern of activity and its edges therefore either converge or diverge. Changes in frequency alter the position of the active region and both edges therefore move in the same direction across the fibre array.

Figure 22

A - idealised iso-rate contours for a single cochlear fibre derived from Galambos and Davis (1943).

B - distribution of the mean discharge rates in the whole array of cochlear fibres assuming all fibres have iso-rate contours as in figure 1.

(From Allanson and Whitfield, 1955.)

Figure 23

Postulated temporal distributions of responses in the cochlear nerve to amplitude modulation, frequency modulation and simultaneous amplitude and frequency modulation.

(From Allanson and Newell, 1966.)

Figure 22

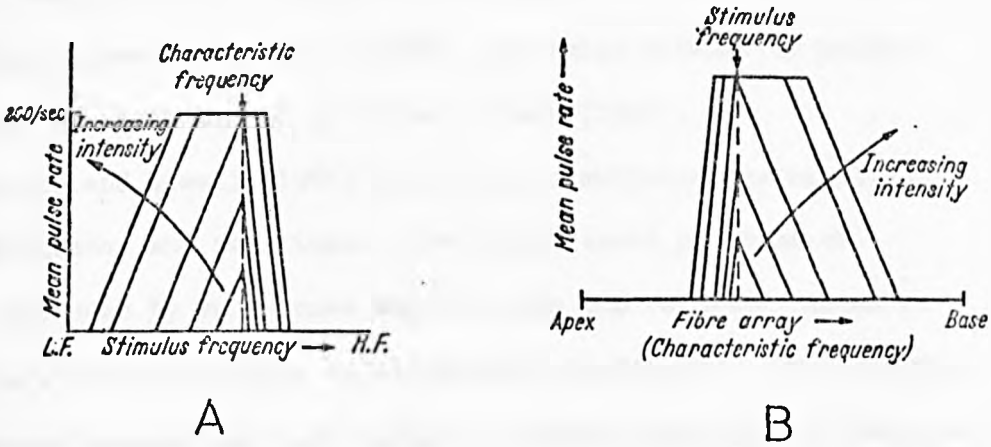
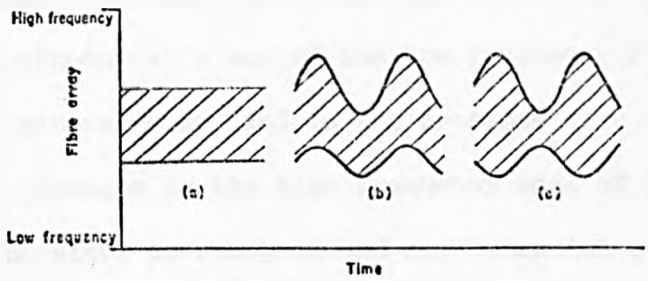
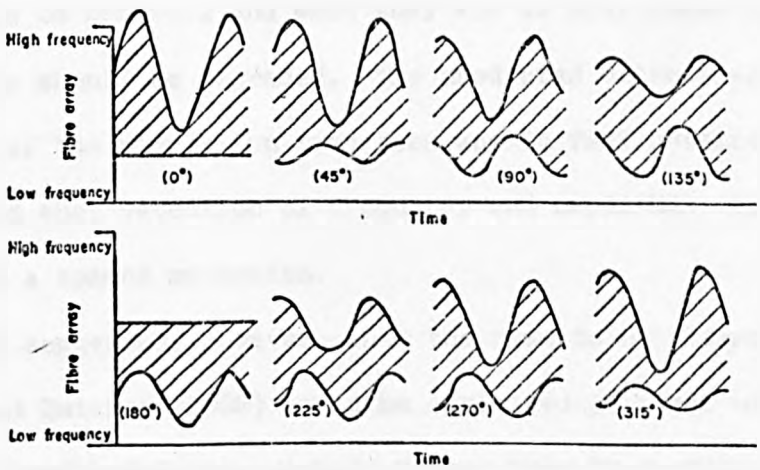


Figure 23



Postulated responses in auditory nerve to (a) a pure tone, (b) a frequency-modulated tone, and (c) an amplitude-modulated tone. Active regions in the nerve are indicated by shading.



Postulated responses in auditory nerve to a tone modulated simultaneously in frequency and amplitude.

The hypothesis that both the frequency and the intensity of a signal are encoded via a common mechanism has been tested for tonal stimuli by Allanson and Newell (1966), for noise stimuli by Zwicker (1962) and for tones masked by noise by Feth (1972).

Allanson and Newell (1966) used tones simultaneously modulated in both frequency and amplitude. The hypothetical patterns of activity produced by such tones depends upon the relative phases of the two modulation envelopes as illustrated in Fig. 23. The subjects were required to classify the signals as either amplitude or frequency modulated. The subjective responses to the mixed modulation signals was found to depend upon the phase angle between the modulation envelopes, therefore suggesting a common mechanism involved in the detection of frequency and amplitude fluctuations of the signal.

Zwicker (1962) sinusoidally varied the low frequency cut off and amplitude of an octave noise band in the presence of a high pass masking noise. Changes in the high frequency edge of the pattern of activity would therefore be obscured and any sensation of modulation would be due to temporal variations in the lower cut off frequency of the noise. When the amplitude fluctuations are in phase with the lower cut off frequency excursions, the sensation of modulation should be enhanced and when they are in anti-phase the modulation sensation should be degraded. The predicted enhancement and degradation of the modulation sensation was in fact obtained and Zwicker concluded that detection of frequency and amplitude fluctuations involved a common mechanism.

Feth (1972) suggested, however, that the results of Allanson and Newell (1966) and Zwicker (1962) could be explained in terms of the spectra of the mixed modulation signals rather than by variations in the patterns of activity generated by such signals within the auditory

system. He therefore compared the detectability of small intensity changes of a signal in the presence of a masking noise which obscured one edge of the hypothetical pattern of activity produced by the signal. Under such conditions, small frequency changes should augment or degrade the detectability of the intensity increment. No such alterations in the discriminability of the intensity increment were observed, unless the frequency change was large enough to be discriminated on its own. Feth concluded that his results could not be explained in terms of the simple model in which both intensity and frequency are represented in the pattern of activity in the cochlear nerve.

Recently the hypothesis that intensity is encoded via the spread of activity in the cochlear nerve has been tested by experiments on the discrimination of small intensity increments for signals in the presence of a bandstop masking noise. At high intensity levels such a masking noise should cause saturation of fibres at both edges of the region of activity produced by the signal in the cochlear nerve. Thus at high intensity levels at which (because of single fibre saturation) intensity discrimination is assumed to be dependent on changes in the activity at the edges of the region of active fibres, the discrimination of intensity should be considerably degraded by the presence of the bandstop masking noise.

The data of Viemeister (1972) and Moore and Raab (1974) indicated that for pulsed sinusoids in the presence of bandstop noise, no such degradation in intensity discrimination at high intensities is observed. However, as Viemeister pointed out in a later paper (Viemeister, 1974), for sinusoidal signals the stopband might not have been narrow enough to eliminate recruitment via spread of excitation within the stopband and the response of primary fibres

is also considerably different to sinusoids, clicks and noise (e.g. phase locking to sinusoids). Viemeister concluded that inferences about the effective limit produced by the bandstop noise on the frequency region over which intensity information is available, should be regarded as tenuous. He therefore studied the intensity discrimination of broad-band and band limited noises which do not suffer from such considerations. If the discrimination of intensity changes of broad band noise at high levels depends upon changes in the activity of fibres at high and low frequency regions, then introduction of a bandstop noise masker should produce an increase in the Weber fraction ($\Delta I/I$) which should be directly related to the level of the masking noise. No such large increase in the Weber fraction is observed for either broad-band or band limited signals in the presence of bandstop noise masker. Weber's law holds over at least an 80 dB range under these masking conditions (Viemeister, 1974).

Unlike the study of Viemeister in which both signal and masker were simultaneously gated, Moore and Raab (1975) studied discrimination of wideband and band limited noise bursts in the presence of a continuous bandstop noise background. Their results were similar to Viemeister's in that although the Weber fractions did increase with increasing level the effects were quite small. The absolute size of the Weber fraction depended upon the width of the masker stopband. For a masker which was 10 dB above the test noise the Weber fraction only increased by 0.9 dB for one subject and 2.3 dB for the other, over a 50 dB intensity range. Viemeister (1974) and Moore and Raab (1975) tested the possibility that subjects were able to make use of frequency components outside of the notch. To do this they filtered the wideband test noise to match the notch in the masker. Such filtering of the test noise had no significant effect on the Weber

fraction obtained and it was therefore concluded that the subjects were using information only from the frequency components of the test noise which were located within the notch in the masker.

The data of Moore (1975) is somewhat at variance with other discrimination data, in that it indicates that when subjects are deprived of information from the edges of the region of activity generated by a 1/3 octave band of noise, their discrimination deteriorates markedly, for some centre frequencies, as intensity is increased. Moore found that intensity discrimination of 1/3 octave noise bands when presented alone was essentially independent of the sensation level for all centre frequencies. When, however, these 1/3 octave noise bands were presented in a 2 octave masking noise, the discrimination performance was only independent of level for centre frequencies up to 4 kHz. At centre frequencies higher than 4 kHz the discrimination performance became progressively worse as the sensation level was increased. The DL for a noise of centre frequency of 6 kHz increased from about 2 dB to 7 dB over a range of 60 dB.

Recently, experiments similar to those of Moore (1975) have been conducted by Pick (personal communication). Intensity DLs were determined for one octave and 1/3 octave noise bands in the presence of a bandstop masking noise with appropriate stopbands. Pick found no significant differences in the shape of the DL versus intensity function for frequencies above and below 4 kHz. Specifically, the DLs for both one and 1/3 octave noise bands centred at 8 kHz in a bandstop noise also centred at 8 kHz, were independent of sensation level up to 90 dB SL (approximately 100 dB SPL). Weber's Law was shown to hold even for these high frequency bands of noise over a range of about 80 dB. It is not at all obvious why the data of Moore and those of Pick on the intensity discrimination of noise bands should be so markedly different.

From the foregoing it can be seen that predictions from simple fibre array models, in which intensity is represented by the spread of activity and frequency by the location of the active region within the total array, are not borne out by the results of bandstop noise masking experiments or the results of the high and low pass noise masking experiments of Feth (1972). It therefore seems reasonable to conclude as did Viemeister (1974) that

> 'the observers need not listen outside of a fixed frequency region, a spatial region presumably served by a fixed number of fibres, in order to detect small intensive changes over a large range of intensities. The implication is that a spread of activity along the cochlear partition is not necessary for the auditory system to maintain its wide dynamic range.'

1.8 The Present Study

It should be emphasised at this point that the experiments reported in this dissertation have been directed at the specific question of how information concerning intensity differences is carried by single neurones over a wide dynamic range. No attempt has been made to investigate the way in which intensity *per se* is represented in the auditory periphery.

The results of the different types of experiment employed in the present study are reported in separate chapters (3, 4, 5). Since these experiments deal with separate facets of the problem each of these chapters is written as a more or less separate investigation with an introduction and a detailed discussion of the results.

Finally, these data are brought together and discussed in chapter six with reference to the encoding of intensity, intensity differences, and of information relevant to frequency selectivity.

The experiments reported in chapter three investigated the suggestion that the limited dynamic range of single cochlear fibres may be reconciled with the psychophysical dynamic range, if the fibre thresholds are distributed over a wide range of intensity. More specifically, it has been suggested by several authors that the OHCs are some 30-40 dB more sensitive than the IHCs, and that a second high threshold population of fibres must exist in the cochlear nerve in addition to that already reported. (These arguments are largely refutable and the experiments upon which they are based are reviewed in Section 3.1.1.) If such a high threshold population of cochlear fibres does exist, it has been systematically overlooked, which, in fact, is not an unlikely eventuality since only two laboratories have published extensive data

(Kiang et al., 1965a, Kiang, 1968; Evans, 1972) and both use the same approach to the cochlear nerve.

All cochlear fibres terminate in the cochlear nucleus, which is readily accessible and tonotopically organized. Thus the probability of missing a minority population of neurones in the cochlear nucleus is considerably lower than the probability of missing a population of cochlear fibres. Single unit minimum thresholds were therefore measured in the cochlear nucleus and no indications were detected of a population of neurones with thresholds higher than those of cochlear fibres.

Also reported in chapter three are the results of a study of single neurone dynamic ranges at both the cochlear nerve and cochlear

nucleus levels. It was confirmed that cochlear nerve fibres become saturated within 20 - 60 dB of threshold. The dynamic ranges of monotonic cochlear nucleus cells extended over a similar range, but a few cells (of the 'sloping saturation' type, see Section 3.1.2) had dynamic ranges of up to 80 dB. A second population of cochlear nucleus cells, which had non-monotonic rate versus intensity functions, had dynamic ranges of up to 100 dB. It was suggested that such wide ranges reflected the spread of activity into lateral inhibitory areas at high intensities.

The dynamic range data reported in Chapter Three and in the literature, represent the range over which the mean discharge rate, measured over the whole duration of a stimulus, varies with intensity. The discharge of single cochlear fibres is not, however, stable over the duration of a stimulus of constant intensity, but declines with time after its onset. This reduction in the discharge rate with time is termed 'adaptation' and is discussed in some detail in Chapter Four. It has been suggested that adaptation is the result of a reduction in the gain of the system. If this were the case, then the response to small intensity increments should differ when they occur before or after adaptation. Smith and Zwislocki (1971) studied the adaptation of monotonic cochlear nucleus cells and its effect on the responses to small intensity increments. However, since the analyses of Smith and Zwislocki were only performed over a 10 dB range of intensity, their conclusions as to the behaviour of neurones in response to stimuli at intensities beyond those causing saturation of the discharge rate could not be derived from their data. Thus the experiments reported in Chapter Four were instigated in order specifically to test the conclusions of Smith and Zwislocki (1971) by performing a similar analysis over a much wider intensity range.

The conclusions of Smith and Zwislocki were, in the main, substantiated in that:

1. The responses to intensity increments were not affected by the adaptation process.

2. In some units the firing rate in response to a 200 ms tone burst, measured at 180 ms after its onset, saturated at a higher intensity level than the onset firing rate.

3. In some units, saturation of the firing rate measured at 180 ms after the stimulus onset did not limit the response to an intensity increment occurring at 180 ms after the stimulus onset.

It was concluded, however, that any extension to the dynamic range (as usually defined) due to the wider dynamic range of the firing rate measured at 180 ms after the onset, or in response to an increment at 180 ms, was still insufficient to account for the wide dynamic range for intensity discrimination shown psychophysically.

It is, nevertheless, evident that under conditions of bandpass noise masking, information concerning intensity differences is transmitted by neurones innervating a particular basilar membrane location, over an extremely wide intensity range. This, the experiments reported in Chapter Five were designed to examine directly. The responses of single neurones, to signals analogous to those used in the psychophysical masking experiments, were measured, in order to determine whether responses to such complex stimuli can be predicted from responses to single tonal stimuli (as reported in Chapters Three and Four).

In preliminary experiments several DCN units were analysed which did indeed respond to the bandstop noise and tone combination in a manner not readily predictable from the responses to single tones.

DCN units were found which responded to tone level changes in the presence of the bandstop noise masker over ranges of intensity of up to 110 dB. In order to investigate the mechanism for this extension of the single neurone's dynamic range, a series of parametric studies were undertaken in which the signal to masker intensity ratio and notch bandwidth of the noise were systematically varied. The results of such analyses clearly demonstrate that the very wide dynamic range of such neurones is the result of lateral inhibition which occurs at the level of the cochlear nucleus. Similar analyses performed on single cochlear nerve fibres failed to reveal responses which could not be predicted from the responses to single tones.

It was concluded that some cochlear nucleus cells re-encode the intensity information which is present in the cochlear nerve in some form other than the mean discharge rate. Similar considerations were also shown to apply to the encoding of information relevant to frequency resolution at supra-saturation levels of intensity.

CHAPTER TWO: GENERAL METHODS

This chapter will be devoted to a description of those methods common to all of the experiments performed in this study. Detailed descriptions of the stimuli and the analyses used in the different classes of experiments are deferred to the appropriate chapters.

Extracellular recordings were made from single neurones in the cochlear nucleus of twenty cats by means of microelectrodes inserted under direct vision, after aspiration of the overlying cerebellum. Following the cochlear nucleus recordings in eight of these cats, Dr. E. F. Evans inserted microelectrodes into the cochlear nerve and recordings were made from single cochlear fibres. Essentially the approach to the cochlear nucleus used was that of Katsuki et al. (1958) and the surgical methods those of Evans (1972) and Evans and Nelson (1973a).

2.1 The Physiological Preparation

i) Anaesthetic

Cats of mean weight 2.75 kg (range 1.9 - 4.5 kg) were anaesthetised with pentobarbitone sodium (veterinary nembutal 30 mg/kg). The initial induction dose was administered intraperitoneally and if the animal was not unconscious after 10 - 15 minutes a further intraperitoneal dose of 0.25 ml nembutal was given (approx. 5 mg/kg pentobarbitone sodium).

The depth of anaesthesia was assessed every two hours, and the required depth was maintained by intravenous injection of supplementary doses of on average 0.2 ml of nembutal (approx. 4 mg/kg pentobarbitone sodium). A variety of criteria were used in judging the depth of anaesthesia. As the depth of anaesthesia decreases, the pedal reflex

becomes more vigorous, the pupil diameter increases, the end tidal carbon dioxide concentration increases, and the mean and pulse blood pressures increase.

ii) Cannula insertion and physiological control of the preparation

The animal's head, neck and tail were shaved and a rectal thermister was inserted and sutured into place. The animal's temperature was maintained at 36 - 38°C by a heating blanket (Electrophysiological Instruments Ltd.), thermostatically controlled by the rectal thermister.

A subcutaneous injection of atropine sulphate (60 μg; 0.1 ml of 600 μg/ml) was given routinely as soon as the animal became unconscious and before commencement of surgery. During later experiments, especially those intended to continue for several days, 300,000 units of procaine penicillin were intramuscularly and 300,000 units subcutaneously, administered.

Both brachial veins were cannulated (with PP60 polythene tubing), one being routinely used for infusion with 5% Dextrose in water solution (at 0.05 ml/min) and the other for administration of supplementary doses of nembutal.

The right carotid artery was cannulated (with PP100 polythene tubing) to enable continuous monitoring of the blood pressure by means of a pressure transducer (Bell and Howell Ltd.) and a pen recorder (Devices Ltd.). Sodium citrate was continuously infused (at 0.01 ml/min) via the arterial cannula to eliminate the risk of blocking by blood clotting.

If the mean blood pressure fell below 100 mm Hg, methoxamine hydrochloride (a peripheral vasoconstricter) was added to the venous infusion to raise the mean blood pressure to above 100 mm Hg (a 1 ml ampoule of 20 mg/ml methoxamine hydrochloride was added to 100 ml of 5% Dextrose and a dose of 0.2 ml was often sufficient). Occasionally

depression of the blood pressure was accompanied by bradycardia, suggesting vagal inhibition; in such cases the sympathetic stimulant methylamphetamine was administered intravenously to raise the mean blood pressure to above 100 mm Hg (a 1.5 ml ampoule containing 30 mg of methylamphetamine was added to 100 ml of saline and a dose of 0.2 ml was usually sufficient).*

The trachea was cannulated (with a 6, 7 or 8 mm diameter glass 'Y' cannula) to reduce the dead space and allow artificial respiration by means of a Palmer 'Ideal' respiration pump (model 16/24). End tidal carbon dioxide concentration was measured by a Beckman LB-1 infra-red gas analyser, sampling from the tracheal cannula at a continuous rate of 200 ml/min, and was monitored on the pen writer and maintained at 4 - 5% by artificial respiration with a 60:40 mixture of air: oxygen. (This mixture ensured complete oxygenation of the blood without the risk of oxygen toxicity which results from prolonged respiration of pure oxygen.)

iii) Exposure of the cochlear nucleus

A midline incision and lateral retraction of the skin allowed the temporalis muscle on the left side of the skull to be separated from the skull and removed completely. The external auditory meatus was then mobilised and divided leaving a few millimeters of the internal auditory meatus distal to the bony ring of attachment. The musculature of the neck were then separated from their attachments along the nuchal ridge and the posterior aspect of the bulla was cleared of its periosteum. The animal was then transferred to a conventional stereotactic instrument and secured initially by means of ear bars and a conventional head holder (securing the head to the stereotactic instrument by the hard palate and infraorbital ridges). A brass plate was then screwed to the animal's skull and clamped to the stereotactic instrument. When

* Some support of the blood pressure was required in twelve out of the twenty animals but on no occasion was the mean pressure allowed to fall enough to produce elevations in thresholds of single neurones. The thresholds measured before and after support of the blood pressure were unaltered.

this plate had been attached the ear bars could be adjusted without movement of the head.

The bulla was then carefully dried and a hole was drilled through the posterolateral aspect. A stainless steel wire, insulated with teflon except at the tip, was inserted through this hole, making contact with the bony rim of the round window. This wire was used for recording click evoked gross neural cochlear 'action potentials' (CAPs). The visual detection threshold of the CAP was used to assess the condition of the cochlea at the outset and were monitored periodically throughout the experiment to check for cochlear deterioration.

The round window electrode was sealed into the bulla (with dental wax), along with a 10 cm length of 0.5 mm inside diameter nylon tubing. Since the animal was anaesthetised it could not equalise the pressure in the middle ear cavity with the atmosphere; oxygen uptake from the middle ear would therefore cause decreases in the static pressure. Such static pressure changes alter the transmission characteristics of the middle ear (Bekesy, 1941). The tubing was therefore used to provide a means of static pressure equalisation, whilst retaining the normal closed bulla conditions for the auditory experiments.

A large craniotomy was performed over the posterior fossa on the left side, extending arteriorly to the tentorium, medially to within a few millimeters of the midline, posteriorly to a few millimeters below the nuchal ridge and laterally to the Lambdoid suture. The dura was then removed and the lobes of cerebellum overlying the cochlear nucleus were aspirated away. In later experiments a spatula was inserted at this point in the proceedings, to draw back the cerebellum thus reducing the amount of cerebellum which had to be removed to allow adequate exposure of the cochlear nucleus. The area around the cochlear nucleus was irrigated with warmed (37°C) physiological saline

until sufficient clotting had occurred to prevent the nucleus from being obscured by haemorrhage.

iv) Insertion of the microelectrode and stabilisation of the recording site

The microelectrode was introduced under direct vision into the cochlear nucleus. The angle of approach was usually 20 - 25° from the horizontal plane and 1 - 1.5 mm from the lateral margin of the cochlear nucleus. (In some experiments in which it was desired to study neurones in the DCN, a penetration angle of 60 - 65° to the horizontal was often used.)

When the electrode had been positioned satisfactorily, 2% clear agar in physiological saline at 38°C was injected into the cavity and allowed to set, in order to stabilise the recording site. In some animals the stability proved to be inadequate, units being lost after only a few minutes. When this occurred, two strategies were employed to improve stability: a) the animal was sutured through the interspinous ligament between two lower thoracic vertebrae and supported by means of a 'bridge' across the stereotactic instrument; b) bilateral pneumothoraces were produced. The combination of the agar and a) and b) above usually gave sufficient stability and many units were recorded for 1 - 1½ hours.

When the electrode was in place and calibrations of the sound system (see Section 2.3) had been completed, the complete stereotactic instrument which was mounted on castors was wheeled into a double walled sound attenuating enclosure (modified after Thornton, 1967).

The microelectrode was then advanced remotely by means of a hydraulic system, consisting of two 1 ml luer lock syringes connected by polythene tubing, the whole being filled with liquid paraffin. The microelectrode could be advanced or retracted by a micrometer

'pushing' or 'pulling' the syringe piston. The backlash of this system, mainly due to the long length of tubing required to reach into the soundproof box, was of the order of $\pm$ 9 μm.

v) Insertion of electrodes into the cochlear nerve

After the cochlear nucleus recordings had been completed on eight cats, Dr. E. F. Evans inserted microelectrodes into the cochlear nerve. The final cochlear nucleus electrode was snipped off using fine bone nibblers and left in situ. The spatula holding back the cerebellum was removed without disturbing the agar and reinserted between the agar and the temporal bone. Whilst aurally monitoring the click evoked CAP, the spatula was gradually moved into position beside the cochlear nucleus and retracted medially exposing the cochlear nerve. A cessation of the CAP indicated that the cochlear artery had been obstructed and in such cases the spatula was removed and relocated. Once the spatula had been successfully located, microelectrodes could be introduced into the cochlear nerve under direct vision.

2.1.1 Choice of the Anaesthetic

Several studies have revealed that barbiturate anaesthesia has profound effects on the responses of neurones in the cochlear nucleus (see Sections 1.6.2, 1.6.3). Clearly then, the most appropriate preparation from which to draw comparisons with psychophysical data is the unanaesthetised animal, data from which is not confused by the effect of the anaesthetic. In the present study, however, sodium pentobarbitone anaesthesia has been used throughout. This would appear to be unjustifiable considering the data reviewed in Sections 1.6.2 and 1.6.3.

However, the experiments reported in Chapter Four were an extension of an interesting study by Smith and Zwislocki (1971, 1975) and Smith

(1973), which were performed using sodium pentobarbitone anaesthesia. To facilitate comparison between these studies the same anaesthetic has been used. Furthermore, the experiments of Chapter Four were designed to test the hypothesis that the adaptation occurring in primarylike cochlear nucleus units might provide a mechanism by which single units encode intensity over a wide range (see Section 1.6.2 and Chapter Four). The electrodes were therefore aimed to traverse the AVCN where such responses predominate. The responses of units in the VCN, according to Evans and Nelson (1973a), are not significantly different in the anaesthetised preparation from the unanaesthetised preparation.

In the bandstop noise masking experiments reported in Chapter Five the DCN proved to be the area of primary interest. In this case it was desired to compare the responses obtained from the cochlear nucleus with responses from the cochlear nerve for which, apart from a limited study of Simmons and Linehan (1968), no data on the unanaesthetised preparation is available. However, the results of Simmons and Linehan suggest that the responses of at least one cochlear nerve fibre is unaffected by anaesthesia. Therefore, comparisons between unanaesthetised cochlear nucleus preparation and anaesthetised cochlear nerve preparations could still be valid.

The second major comparison drawn was between the single neurone dynamic range and the psychophysically determined dynamic range. Use of anaesthesia enabled study of the responses of single units to intensity changes which were uninfluenced by the action of either the efferent nervous system or contraction of the middle ear muscles. If the psychophysical dynamic range depends upon these systems, then the results should indicate only a narrow single unit dynamic range, which as will be seen (Chapter Five) was not the case at the level of

the DCN, but was the case at the cochlear nerve level.

These DCN responses were clearly a result of interaction of excitatory and inhibitory influences. Evans and Nelson (1973a) found that the major effect of barbiturate anaesthesia was to reduce the amount of inhibition observed in the DCN. Since the responses observed in the DCN were heavily dependent on inhibition it was considered unnecessary to alter the techniques used.

2.2 Conduct of Experiments

i) Isolation of units

50 ms bursts of wideband random noise were presented every 200 ms as search stimuli, usually at approximately 50 dB SPL.

ii) Routine measurements on a unit

When a unit was isolated, the frequency threshold ('tuning') curve (FTC) was determined as a matter of routine. For animals 207 - 343 the FTC determinations and subsequent analyses, during and after the experiment, were performed manually. In later experiments (395 - 570) FTC determinations and subsequent analyses were performed automatically by a PDP-8 computer (see Evans, 1975b; Evans and Wilson, 1975). Spontaneous discharge rate was determined by taking up to twelve readings of the number of spikes occurring in successive one second intervals, using a Venner event counter (Type TSA 6634/2). Having determined the unit's FTC and spontaneous rate, data for other analyses were collected until the unit was 'lost' or until satisfactory analyses had been completed.

iii) Penetration marking

When the electrode penetration was completed (i.e. the electrode had passed through the cochlear nucleus) or if the electrode became blocked or broken, the agar was aspirated away and another electrode penetration was initiated. In early experiments using dye-filled electrodes, the electrode penetration was marked with dye deposits and the electrode was withdrawn completely. In later experiments, owing to the lack of success of dye injection (see Appendix D) the electrode was snipped off, using fine bone nibblers, a few millimeters from its point of emergence from the cochlear nucleus, and its tip (some 8 - 9 mm) left in situ during fixation. This procedure gave a very clear indication of the course of the electrode track in the cochlear nucleus sections.

iv) Calibration of the sound system

At the beginning and at the end of the experiment calibrations of the sound system were obtained. The initial and final sound calibrations and/or any other calibrations obtained during the experiment, were then averaged to obtain a single calibration curve from which corrections for the sound system could be taken. The calibration procedure is described in detail in Section 2.3.

v) Location of the recording site

After completion of the final calibration the animal was deeply anaesthetised and 0.5 ml of 1000 i.v. Heparin was administered intravenously. The jugular veins of both sides were then severed and the animal was rapidly perfused under pressure with 200 - 250 ml (approx. 10% of bodyweight) 20% formal saline at 37°C via the carotid artery. The brain was left in situ for several hours (usually overnight) with the electrode in situ and then the cochlear nucleus was removed for sectioning.

50μm frozen serial sections of the cochlear nucleus were cut and conventionally stained with cresyl violet for nerve cells. The sections were examined for signs of the electrode tracks (e.g. round cell infiltration or tissue disruption). As no dye deposits were successfully recovered, measurements taken during the experiment were used, in conjunction with the histology to determine the location of units recorded from. The two most useful measurements in this respect were micrometer depth readings and the CF of the neurone. The cochlear nucleus is strictly tonotopically organised (see Section 1.6.1). Thus a jump in CF from low to high frequency at a depth of say 2 mm along a penetration beginning in DCN would indicate the passage of the electrode tip from DCN to VCN. Use of such criteria enabled the anatomical location of units to within the major subdivisions of the cochlear nucleus (DCN and VCN).

2.3 Stimulating System

Tone signals from a low distortion oscillator (Dymar type 741) or voltage controlled oscillator (Brookdeal type 471) were gated with 5 ms rise and fall times by a two quadrant multiplier (Evans and Pick, to be published). Alternatively, white or filtered noise or 10 μs electrical pulses for the generation of acoustic clicks could be selected (see Fig. 24). The 10 μs pulses were used to measure the visual detection threshold of the click evoked CAP recorded at the round window. This measure indicated the physiological state of the cochlea. For example, a CAP threshold of -95 dB indicates a cochlea in good condition and single unit thresholds were often lower than mean cat behavioural thresholds.* A CAP threshold of -50 dB was, however, associated with single unit thresholds which exceeded the mean behavioural thresholds by tens of decibels. Throughout the experiment the CAP threshold was periodically monitored for signs of cochlear deterioration.

The tone or tones could be mixed with any of the alternative signals producing such complex sounds as those used in the increment studies (Chapter Four) or in the bandstop noise masking studies (Chapter Five). The levels of the various signals were adjusted prior to Mixer A by means of either the manual or computer controlled attenuators (see Fig. 24). For signals more than 40 dB below maximum, the output of Mixer A was fed via the output attenuator (which could be either manually or computer controlled) to a condenser microphone driver. For signals less than 30 dB below maximum, the output of Mixer A was fed via the output attenuator, a non-linear network and a Radford 15 w power amplifier to the condenser microphone driver. The non-linear network was required at maximum signal levels to restrict the harmonic distortion of the condenser microphone cartridge to less

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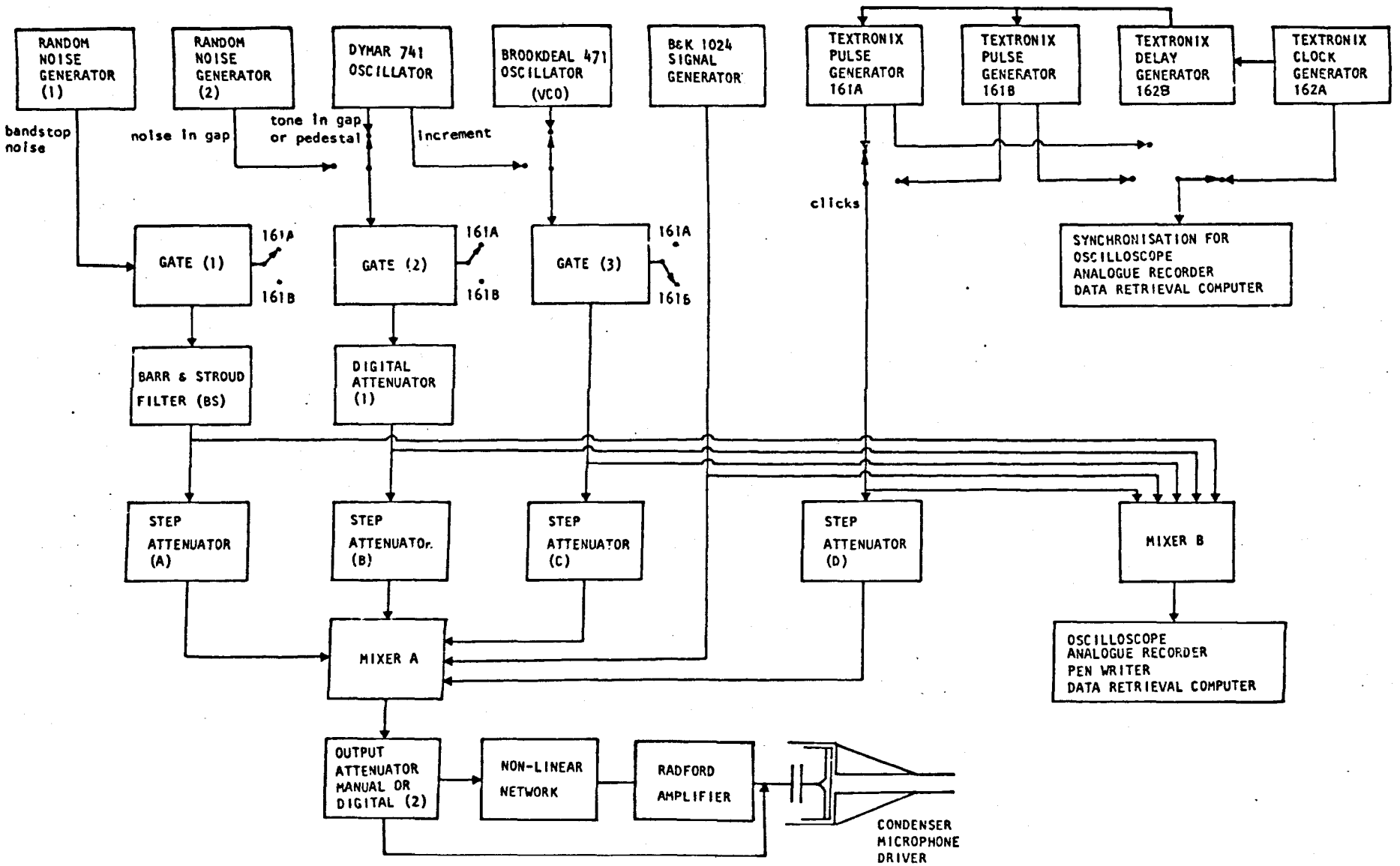
* The single unit thresholds were corrected to dB SPL at the tympanic membrane and compared with the minimum audible pressure (MAP) audiogram. The MAP audiogram was obtained from a mean minimum audible field audiogram with suitable correction for the pressure transformation due to the meatus (see Wiener, Pfeiffer and Backus, 1965).

Figure 24

Block diagram of the equipment for generating stimuli.

Figure 24


RANDOM NOISE GENERATOR (1)
RANDOM NOISE GENERATOR (2)
DYMAR 741 OSCILLATOR
BROOKDEAL 471 OSCILLATOR (VCO)
B&K 1024 SIGNAL GENERATOR
TEXTRONIX PULSE GENERATOR 161A
TEXTRONIX PULSE GENERATOR 161B
TEXTRONIX DELAY GENERATOR 162B
TEXTRONIX CLOCK GENERATOR 162A
bandstop noise
noise in gap
tone in gap or pedestal
increment
clicks
GATE (1)
GATE (2)
GATE (3)
161A
161B
SYNCHRONISATION FOR OSCILLOSCOPE ANALOGUE RECORDER DATA RETRIEVAL COMPUTER
BARR & STROUD FILTER (BS)
DIGITAL ATTENUATOR (1)
STEP ATTENUATOR (A)
STEP ATTENUATOr. (B)
STEP ATTENUATOR (C)
STEP ATTENUATOR (D)
MIXER B
MIXER A
OSCILLOSCOPE ANALOGUE RECORDER PEN WRITER DATA RETRIEVAL COMPUTER
OUTPUT ATTENUATOR MANUAL OR DIGITAL (2)
NON-LINEAR NETWORK
RADFORD AMPLIFIER
CONDENSER MICROPHONE DRIVER

than -45 dB for each component relative to the signal. The condenser microphone driver consisted of a Bruel and Kjaer 4134 ½" condenser microphone cartridge fitted with a 4 mm inside diameter probe cone and a 4 mm inside diameter probe tube. Polyurethane foam was used to critically damp the probe cone assembly to produce as flat a frequency response curve as possible.

This condenser microphone driver was fitted into an earmould (Fig. 25) tapered to fit snugly into the internal auditory meatus, which replaced the ear piece of the standard stereotactic instrument offset ear bars.

The sound pressure level at the tympanic membrane (in SPL ie. dB re 2×10^{-5} N/m^2) was determined by a critically damped Bruel and Kjaer 4134 ½" condenser microphone via a calibrated 1 mm diameter probe tube inserted through a hole in the earmould into the earmould cavity. The output of this microphone was high pass filtered to compensate for the reduced sensitivity at frequencies above 1 kHz due to the damping. With the condenser microphone driver removed it was possible to inspect the tympanic membrane without removing the earmould, the tip of the probe tube could therefore be approximated to the tympanic membrane under direct vision.

The condenser microphone driver system produced a signal level of about 100 dB SPL for an input voltage of 24 v R.M.S. (70 v peak to peak) over a frequency range of 1 - 40 kHz, and had a smooth response with deviations of less than 5 dB.

2.31 Calibration of the Sound System

i) Probe microphone calibration

In order to calibrate the probe tube microphone assembly a flat sound field was required. This was achieved by means of a Bruel and

Figure 25

Scale diagram of the tapered earmould, probe tube microphone and condenser driver used for delivering and monitoring acoustic stimuli.

Figure 26

Block diagram of the equipment used for calibration of the probe tube microphone and high pass filter.

Figure 25

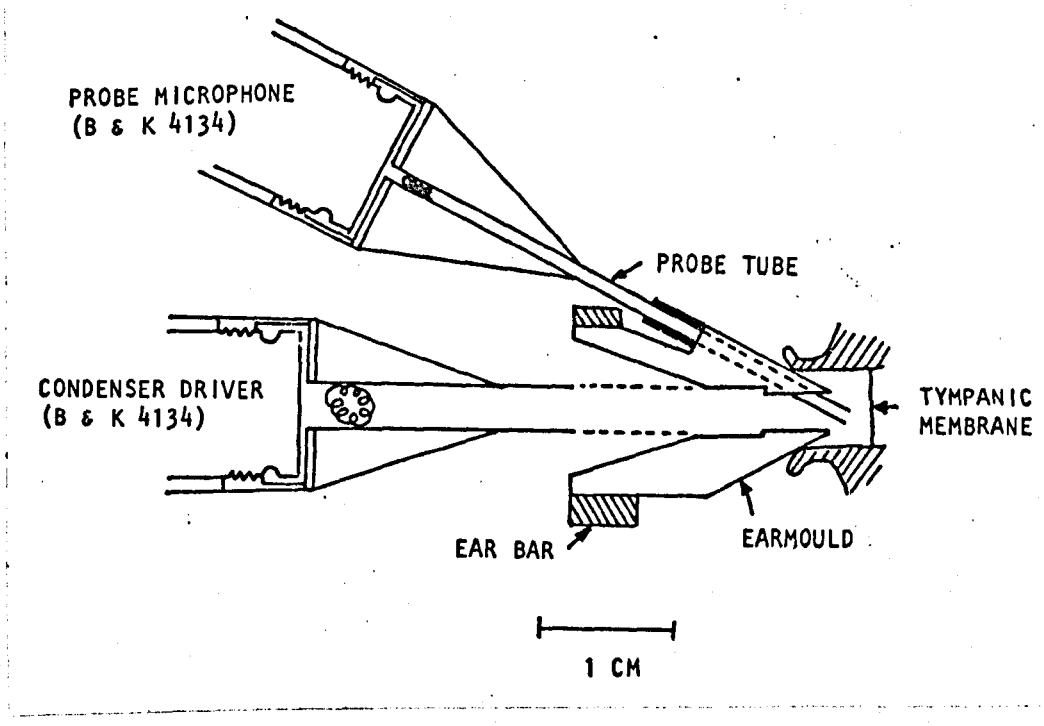
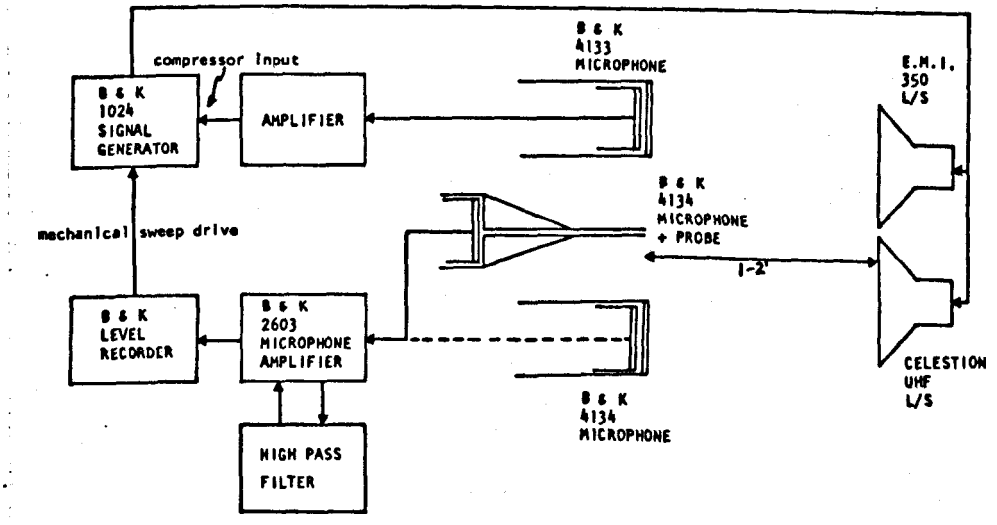


Figure 26



Kjaer 4133 ½" condenser microphone, the output of which was fed via an amplifier into the compressor circuit of a Bruel and Kjaer 1024 signal generator, which was fitted with a frequency doubler. The Bruel and Kjaer 1024 signal generator was used to drive an EMI series 350 loudspeaker bass unit and a Celestion UHF unit (see Fig. 26). To establish a reference level the sound field was then measured by the 4134 microphone (without its probe assembly or filtering), amplified by a Bruel and Kjaer 2603 microphone amplifier, and a permanent record made by a Bruel and Kjaer 2305 level recorder locked to the frequency sweep, as the frequency was automatically swept from 40 - 40,000 Hz. This process was then repeated with the probe assembly in place and with high pass filtering to compensate for the fall off in the probe microphone response due to the damping. The attenuation relative to the reference level, due to the probe assembly and high pass filtering could be measured, thus enabling the correction due to the probe assembly and filter and the non-flat frequency response of the 4134 microphone to be determined.

ii) Sound system calibration

Tone signals from the Bruel and Kjaer 1024 signal generator were introduced into Mixer A and the signal levels equated to the levels of the tones from the Dymar 741 and Brookdeal 471 oscillators (see Fig. 24). The output attenuator was then set to 10 dB below maximum output and the frequency swept automatically from 40 - 40,000 Hz. The probe microphone, in conjunction with the compensating high pass filter (see above), was used to sample the sound field at the tympanic membrane; its output was amplified by the Bruel and Kjaer 2603 microphone amplifier and a permanent record was made by the Bruel and Kjaer 2305 level recorder locked to the frequency sweep.

The intensity, in decibels sound pressure level, at the tympanic membrane represented by any attenuation can then be computed from the measured sound level by correcting for the non-

flat frequency response of the 4134 probe tube microphone, the attenuation due to the probe assembly and high pass filter and the microphone 'K' factor.

2.4 Data Collection

2.4.1 Microelectrodes

For the first ten experiments electrodes filled with Pontamine Sky Blue were used to enable the recording sites to be marked with blue dye deposits (Hellon, 1971). Since, however, the dye marking technique was unsuccessful (see Appendix D) for the remaining ten experiments 4M sodium chloride electrodes were used; these electrodes were easier to produce, less prone to blockage and gave better S/N ratios. Both types of electrode were prepared in the same manner except that the dye electrodes were tested for dye ejection.

The electrodes were prepared on a modified Palmer (H.104) microelectrode puller. The tips were then broken under a microscope (x 420) by advancing the micropipettes against a glass rod until the tips measured 1 - 2 μm outside diameter. The micropipettes were then filled with either a 2% solution of Pontamine Sky Blue in 0.5M sodium acetate, or 4M sodium chloride by injection via a 49 s.w.g. x 2½" (G31) needle. Large particles such as undissolved dye were removed by injecting the solutions into the micropipette through a Millipore filter (HAW PO 1300) with pore size of approximately 0.45 μm. At this stage the saline electrodes were ready for use and were stored tip down in 4M sodium chloride. The dye electrodes, however, were then inserted into a transparent horizontal cell filled with saline and examined with a low power microscope (x 100) for signs of contamination. Any electrodes containing foreign material were discarded at this stage. A variable current source providing up to 20 μA was then connected across the electrode/saline circuit (tip negative) and the tip was observed to see if the dye was being ejected. If dye was ejected with application of only 5 - 20 μA of current,

the electrode was regarded as satisfactory and was stored tip submerged in the dye solution used for filling.

The electrodes were freshly prepared the day before each experiment. The impedances of the electrodes were determined by measuring the voltage produced across the electrode by a pulse of 1 ms duration from a constant current source. Dye filled electrodes of impedance 5 - 10 MΩ or sodium chloride filled electrodes of 1.5 - 2.5 MΩ in physiological saline were selected.

2.4.2 Recording Techniques

Microelectrode potentials relative to an indifferent electrode in the animal's mouth were amplified via a unity gain negative capacitance amplifier (ELSA - 4: Electronics for Life Sciences). The potentials were then amplified and filtered with gain of x 100 and bandwidth of 200 - 5000 Hz (Isleworth Electronics Preamplifier). These signals were monitored visually and aurally and were recorded on one channel of an analogue magnetic tape recorder (Ampex SP300) at tape speeds of $7\frac{1}{2}$ i.p.s., or in later experiments $3\frac{3}{4}$ i.p.s.

Potentials from the round window electrode relative to the mouth electrode were amplified (Textronix 122 preamplifier bandwidth 80 - 1000 Hz) and monitored periodically on the oscilloscope as a means of checking the physiological condition of the cochlea. The synchronising pulse from one of the pulse generators (161A or B, 162A or B, see Fig. 24) was recorded on another channel of the analogue magnetic tape recorder to enable synchronisation on replaying. Also recorded on this channel was the voice commentary to allow correct identification of the recordings. The unattenuated outputs of the signal generators were fed via a separate mixer (Mixer B, Fig. 24) for monitoring purposes to the oscilloscope and to one channel of the analogue magnetic tape recorder.

A low impedance calibrator (Bioelectric Instruments Inc., Type CA5) was included in the 'ground' circuit to the animal so that calibration of the amplitude of the neural responses could be made during the course of the experiments.

The impedance of the microelectrode could also be measured during the course of an experiment. This facility was especially useful when using dye filled electrodes which were very susceptible to blockage.

2.5 Analyses

For all analyses involving counting, averaging or post stimulus time histogram generation spike signals from the microelectrode, or from the analogue tape replay in the off-line analyses, were separated from electrode noise by a Schmitt trigger discriminator, the threshold of which was continuously monitored by brightness modulation of the monitor oscilloscope.

Response areas were routinely determined for all units. Three determination methods have been used.

2.5.1 Manual Frequency Threshold Curves

The conventional manual FTC plotting method of Galambos and Davis (1943) has been employed. Briefly, 50 msec tone bursts with 5 ms rise fall time at a repetition rate of 5/sec were presented. The neurone's CF was determined and then the extent of the excitatory area measured by increasing the intensity in steps and at each level, decreasing the frequency towards the CF or increasing the frequency towards the CF until a response was detected by audio visual criteria. One major disadvantage with manual FTC plotting is that no quantatative information is provided on the presence or absence of inhibitory side bands or on the suprathreshold responses to the tone. This method was the slowest used, taking up to 10 mins for units with high spontaneous rates.

2.5.2 Automatic - Random Frequency/Intensity Plots

A PDP-8 computer was used to control the digital attenuator (Digital Attenuator 2, Fig. 24) and the frequency of the voltage controlled oscillator (Brookdeal type 471, Fig. 24) producing a series of 50 ms tone bursts with a repetition rate of 5/sec, the

frequency and intensity of which were independently and randomly varied (Evans, 1974, 1975b). A frequency intensity area of three octaves by 60 dB was covered in 1024 presentations i.e. 64 frequencies and 16 intensity steps of 4 dB. The number of spikes ellicited by a single presentation of any combination of one of the 64 frequencies with one of the 16 intensities was counted and recorded on a digital magnetic tape unit on the computer.

The number of spikes ellicited by a stimulus was also indicated on an oscilloscope in the experimental room, slaved to the computer display. The display took the form of a three octave by 60 dB frequency/intensity area, within which the response of the unit to a particular frequency intensity combination was represented by a vertical line at the appropriate position. The length of the line was proportional to the number of spikes counted during the presentation of that stimulus. The data recorded on digital magnetic tape was plotted off-line in the same form as this on-line display (see Figs. 65, 67).

The major advantage which is afforded by this form of response area determination is the wealth of quantatative data concerning supra-threshold responses to the tone, and in units with sufficient spontaneous rate, the extent and strength of the inhibitory response areas are readily seen (see Figs. 65, 67).

2.5.3 Automatic Frequency Threshold Curve Tracing

Thresholds as a function of frequency were determined using an automatic computer controlled paradigm (Evans and Wilson, 1975) analogous to that of Kiang, Moxon and Levine (1970).

Briefly, the PDP-8 computer was used to vary the frequency and intensity of a 40 ms tone burst (from the voltage controlled oscillator, Brookdeal type 471, Fig. 24) which had a 5 ms rise/fall time and was

presented every 130 ms. The intensity was varied in 1 dB steps over a maximum of 110 dB as the frequency was swept in 256 steps over a 3 octave range, first downward and then upward. The maximum intensity and centre frequency were selected by the experimenter according to the CF and minimum threshold of the unit under study. The threshold criterion was two extra spikes during the tone stimulus compared with an identical period immediately following the tone burst. The FTC was drawn out as it was being determined by computer control of an X-Y plotter.

The major advantage of this method is the rapidity with which a detailed FTC can be determined. The FTCs obtained are suitable for such measurements as the 3 and 10 dB bandwidths of the excitatory area and the high and low frequency slopes of the FTC. No information is available from these FTC determinations about the presence or absence of inhibitory sidebands or suprathreshold responses to the tone.

In practice in the two experiments in which this method was employed (cats 450 and 570), method 2 above was also used whenever possible, since in both cases data on the strength and extent of the inhibitory side bands was required in addition to a detailed excitatory response area.

CHAPTER THREE: THRESHOLDS AND DYNAMIC RANGES OF SINGLE PERIPHERAL AUDITORY NEURONES

3.1 Introduction

3.1.1 Thresholds of Single Auditory Neurones

The first single unit study of the peripheral auditory system suggested that the distribution of the minimum thresholds of FTCs of common CF was extensive. In a single animal the minimum thresholds at a single frequency varied by as much as 50 dB and in pooled data by 80 dB (Galambos and Davis, 1943). Subsequent studies appeared to confirm that such a range of thresholds existed and indicated that the extent of the range was of the order of 60 dB (e.g. Kiang et al., 1965a; Mast, 1970a). One study, that of Katsuki, Suga and Kann (1962), did not find a continuous distribution of minimum thresholds but found a bimodal distribution.

Kiang (1968) was the first to show that the variation in the thresholds reported in earlier studies, was mainly due to the pooling of data from different animals. The bimodal distribution reported by Katsuki et al. (1962) was attributed by Kiang (1968) to inadequacies in their stimulating system. Considering only data from a single ear and calibrating his sound system at the tympanic membrane, Kiang found the distribution of thresholds at any frequency to be no more than 20 - 30 dB. The most sensitive neurones of this distribution approached the behavioural audiogram (Fig. 27). This finding has since been confirmed by other authors (e.g. Evans, 1972).

There is, however, a considerable body of circumstantial evidence which appears to suggest that a second high threshold population of neurones might exist in the cochlear nerve. In the Organ of Corti

there are two populations of receptor cells; the inner (IHC) and outer (OHC) hair cells (for details see Section 1.5.2). It is the afferent neurones from these two populations of receptor cells which make up the cochlear nerve. Surprisingly, however, no indication of two populations of cochlear nerve fibres has been found; the responses of cochlear nerve fibres are remarkably homogeneous (Kiang et al., 1965a; Evans, 1972, 1975a). Several independent studies have nevertheless concluded that the fibres innervating the OHCs should have lower minimum thresholds than those innervating the IHCs. Davis et al. (1958) determined the amplitude of the whole nerve action potential (CAP) as a function of click intensity. In the normal animal, as the click intensity was increased, the CAP amplitude rose steadily from threshold until the intensity reached about 80 dB SPL. Beyond this level the CAP amplitude rose more rapidly with increase in intensity. The low level portion of the amplitude function (i.e. below 80 dB SPL) was not found in animals in which the OHCs were absent due to streptomycin poisoning. The authors concluded that the low level part of the function was due to activity in a population of neurones innervating the OHCs, whereas the high level part was due to neurones with higher thresholds innervating the IHCs. Subsequent investigations have also found CAP amplitude versus intensity functions like those reported by Davis et al. and have arrived at similar conclusions as to the origin of the two parts (Dallos and Wang, 1974; Eggermont and Odental, 1974; Naunton and Zerlin, 1976).

More recently Evans (1975b) and Özdamar and Dallos (1976) have proposed alternative explanations for the form of the CAP versus stimulus intensity function. Both schemes are essentially identical and are not based upon two populations of cochlear fibres with different thresholds, but rather upon the proportion of active fibres in a single

Figure 27

Minimum pure tone thresholds of single cochlear fibres from a single cat versus their CF, compared with a curve indicating the average behavioural threshold (interrupted line). Thresholds in dB SPL at the tympanic membrane. Open bulla. (Behavioural thresholds from the free-field measurements of Neff and Hind, 1955, and corrected for the outer ear response and to open bulla conditions using the data of Wiener et al., 1965, and Guinan and Peake, 1967, respectively).

(From Evans, 1975a, after Kiang, 1968.)

Figure 28

Rate versus level functions for two cochlear fibres for frequencies at, above and below characteristic frequency. Abscissa and ordinate show the relative intensity of sound and the number of impulses per second, respectively. Figures on the diagram represent frequencies of sound in kHz.

(From Nomoto et al., 1964.)

Figure 27

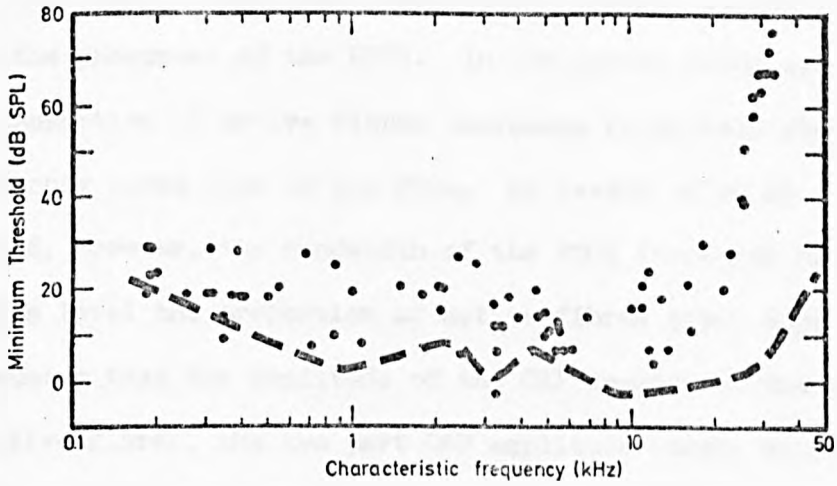
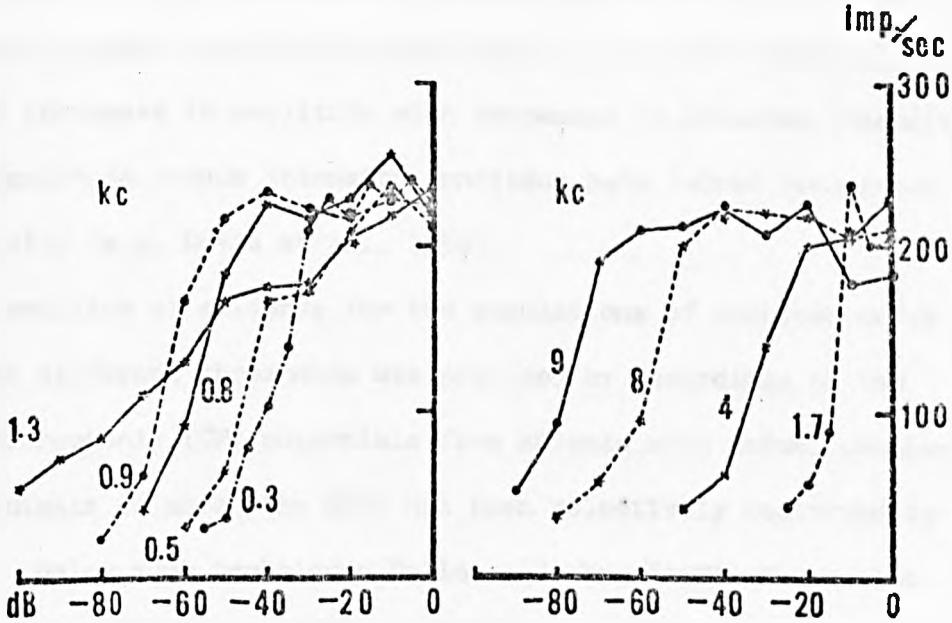


Figure 28



threshold population of cochlear fibres. The schemes may be summarised as follows. The rate at which the proportion of active fibres grows depends upon the sharpness of the FTCs. In the normal cochlea, at low levels, the proportion of active fibres increases relatively slowly due to the sharply tuned tips of the FTCs. At levels of 60 dB above threshold, however, the bandwidth of the FTCs increases markedly. Thus above this level the proportion of active fibres grows more rapidly. Assuming that the amplitude of the CAP depends on the proportion of active fibres, the two part CAP amplitude versus stimulus intensity function is therefore explainable in terms of a single threshold population of cochlear fibres. Similar considerations can be applied to the CAP amplitude versus intensity functions from kanamycin poisoned cochleas. Kanamycin poisoning results in the loss of the sharply tuned low threshold tips of cochlear fibre FTCs (Kiang, Moxon and Levine, 1970; Evans and Harrison, 1975). Thus in kanamycin poisoned cochleas only fibres with high threshold broadly tuned FTCs remain. The CAP amplitude versus stimulus intensity function from such cochleas would therefore be expected to be of high threshold and show rapid increases in amplitude with increases in stimulus intensity. Such CAP amplitude versus intensity functions have indeed been found experimentally (e.g. Davis et al., 1958).

A second line of evidence for two populations of cochlear nerve fibres with different thresholds was provided by recordings of the cochlear microphonic (CM) potentials from animals with normal cochleas and from animals in which the OHCs had been selectively destroyed by kanamycin. Using such techniques Dallos and Wang (1974) found that the CM from the IHCs was produced at a higher intensity than the CM of the OHCs. They concluded that the sensitivity of the IHCs was between 30 and 40 dB lower than that of the OHCs.

Several studies have suggested that the OHCs are more susceptible to damage by acoustic stimuli than are the IHCs (Beagley, 1965; Engstrom, Ades and Andersson, 1966). It should be noted, however, that greater susceptibility to damage does not necessarily indicate greater sensitivity.

Hair cell damage results from exposure to very high sound levels. Lower levels of sound do not produce hair cell damage but do produce swelling of the hair cell nuclei (Neuberg and Wustenfeldt, 1955). Nuclear swelling is observed in OHCs at lower sound levels than are required to produce swelling in IHCs. This swelling may be a reflection of the greater susceptibility of the OHCs to damage, or, since no permanent damage results, might indicate normal activity in the hair cells. One possible interpretation of these data is therefore that the OHCs are more sensitive than the IHCs.

On the basis of the studies of CM, noise susceptibility, hair cell swelling and CAP (although as discussed above the CAP data is open to alternative interpretations), it has been suggested that the cochlear nerve should contain two populations of nerve fibres; a high threshold population deriving from the IHCs and a low threshold population from the OHCs.

The data of Spoendlin (1973), however, suggest that the majority, if not all, of the fibres recorded in the cochlear nerve are afferent fibres from the IHCs. Since the most sensitive fibres have thresholds which fall on or near the cat's behavioural audiogram (Kiang, 1968; Fig. 27), it would seem unlikely that a second population of lower threshold fibres corresponding to the innervation of the apparently more sensitive OHCs should exist. To provide a mechanism to account for the wide psycho-physically determined dynamic range, the second population of cochlear nerve fibres would need to be of higher threshold which is not in agreement with the suggestion that the OHCs are more sensitive.

The available data from recordings of single fibre responses in the cochlear nerve demonstrate the existence of a single low threshold population of cochlear nerve fibres. If a second high threshold population does exist it has been systematically overlooked. This is not in fact unreasonable since only two laboratories have published nerve data extensive enough for this kind of population study (Kiang et al., 1965a; Kiang, 1968; Evans, 1972), and the surgical techniques and microelectrodes used in these laboratories are essentially identical. More importantly, these investigators used the same approach to the cochlear nerve. Thus if a minority population of fibres existed and was located in a discrete bundle within the nerve it is quite possible that it might have been systematically overlooked, as a result of always sampling the same part of the nerve.

All cochlear nerve fibres terminate within the cochlear nucleus complex (see Sections 1.5.3 and 1.5.4) and the complex is strictly tonotopically organised (see Section 1.6.1) and readily accessible for single cell recording. Thus a second high threshold population of neurones is much less likely to be overlooked at the level of the CN. Furthermore, if a minority of cochlear fibres were of smaller diameter than the remainder, the probability of recording from such fibres would be reduced. Since, however, the electrodes used in the present study of cochlear nucleus cells occasionally recorded from fibres of passage, we can be reasonably sure that they were capable of recording from the smallest cochlear nucleus cells. Thus any sampling bias due to the small diameters of cochlear fibres should not be a factor at the cochlear nucleus. The distribution of single unit thresholds in both cochlear nerve and cochlear nucleus has therefore been studied in order to determine if there is any evidence of a high threshold population of neurones at these levels.

3.1.2 Dynamic Ranges of Single Units

A number of authors have measured discharge rates of peripheral auditory neurones as a function of sound level for tones (Galambos and Davis, 1943; Nomoto et al., 1964; Wiederhold, 1970; Rose et al., 1971; Ruggero, 1973; Evans, 1974; 1975b;Sachs and Abbas, 1974). Although most of these authors were concerned primarily with issues other than dynamic range, their data nevertheless contains many features of interest to the present study.

Galambos and Davis (1943) reported that for most auditory fibres the maximum discharge rate was attained at sound intensities about 30 dB above minimum threshold. The auditory fibres referred to were in fact cochlear nucleus cells but similar dynamic ranges (20 - 50 dB) have been found for primary fibres by Kiang et al. (1965a).

The study of Nomoto et al. (1964), however, reveals a fibre (Fig. 28) which has a dynamic range in response to 180 msec CF (1.3 kHz) tone bursts of more than 100 dB with no indication of saturation effects. Of 78 neurones in this study, 8 were 'not "saturated" i.e. did not reach a plateau level no matter how strong the stimulus at least up to 80 dB at the animal's ear'. The exact meaning of this statement can only be inferred but since the free field sound system used had a maximum output of 80 dB SPL one presumes that these 8 units were not saturated even by the maximum sound pressure levels available to the authors. However, this paper follows on from that of Katsuki, Suga and Kanno (1962), in which two populations of fibres, with regard to threshold, were reported. If as Kiang (1968) concluded the 'high threshold' population were low frequency tuning curve tails of high CF fibres, then some of these 8 might well be high threshold tuning curve tails which would only be driven a few tens of decibels above threshold by maximum output of the sound system used, and

therefore were not saturated. However, whatever considerations apply to the other 8 fibres, the fibre illustrated (Fig. 28) clearly has low threshold and a very wide dynamic range. At about 30 dB above threshold, the slope of the rate-level function of the fibre shown in Fig. 28 decreases slightly. In this respect the CF rate-level function of this fibre resembles other cochlear fibre rate-level functions published by several independent authors (Wiederhold, 1970; Rose et al., 1971; Ruggero, 1973; Evans, 1974; Sachs and Abbas, 1974).

Sachs and Abbas (1974) obtained fine resolution (2 dB intensity interval) rate versus level functions from single cochlear fibres in cat in response to frequencies at CF and above and below CF. Their major findings may be summarised as follows:-

1. In response to CF tones, the rate level functions of some units increase to saturation over a range of 20 dB and then become flat. Other rate functions show a considerable slope change about 20 - 30 dB above threshold, but the rate continues to increase gradually over a range of 30 - 40 dB. There appears to be a continuum of behaviour between flat and sloping saturations; rate level functions which show sloping saturations over a considerable range of levels become flat at high enough sound levels.

2. For those units with the same CF in the same cat the rate level functions of which show a slope change at 20 - 30 dB above threshold, the slope of the rate level function at high intensities tends to be greater for units with high threshold than for lower threshold units (Fig. 29).

3. For frequencies above CF, slope of the rate-level functions decreases with increasing frequency.

4. Slopes of rate-level functions for frequencies below CF are either approximately equal to the slope at CF or increase to some maximum value as frequency decreases.

Sloping saturations (1. above) have also been found by a number of other authors (Nomoto et al., 1964; Wiederhold, 1970; Rose et al., 1971; Ruggero, 1973; Evans, 1974) but Sachs and Abbas's findings of a correlation between the slope of the sloping saturation and the fibre threshold has not been previously reported. Findings 3. and 4. above have also been previously reported in the literature (Nomoto, 1964; Wiederhold, 1970; Evans, 1974; Geisler, et al., 1974).

Sachs and Abbas proposed a model (Fig. 30A) to account for the relation of slope of saturation to threshold, and the dependency of the rate-level function slope for a single fibre on frequency. The model consists of a mechanical stage (the middle and inner ears which convert pressure at the tympanic membrane to basilar membrane displacement) followed by a saturating non-linearity (the mechanical to neural transducer which converts basilar membrane displacement to driven discharge rate). The model is based upon assumptions which in the light of present data are untenable. The first and foremost of these is the use of Rhode's (1971) data from squirrel monkey for the relationship of basilar membrane displacement to pressure at the tympanic membrane (Fig. 30B). These data are at variance with other basilar membrane measures in that they indicate a non-linear relation of displacement to pressure for frequencies at and above the most sensitive frequency at the point of measurement. It is upon this non-linearity that the model of Sachs and Abbas depends. Non-linear relations of basilar membrane displacement to pressure at the tympanic membrane have not been found in cat and guinea pig; this relation is linear in both of these animals (Johnstone and Boyle, 1967; Evans and Wilson, 1975; Wilson and Johnstone, 1975). Since the data of Sachs and Abbas is from cat cochlear nerve this would appear to invalidate the model.

Figure 29

Rate versus level function for five cochlear fibres showing the range of behaviours from flat to sloping saturations.

(From Sachs and Abbas, 1974.)

Figure 30

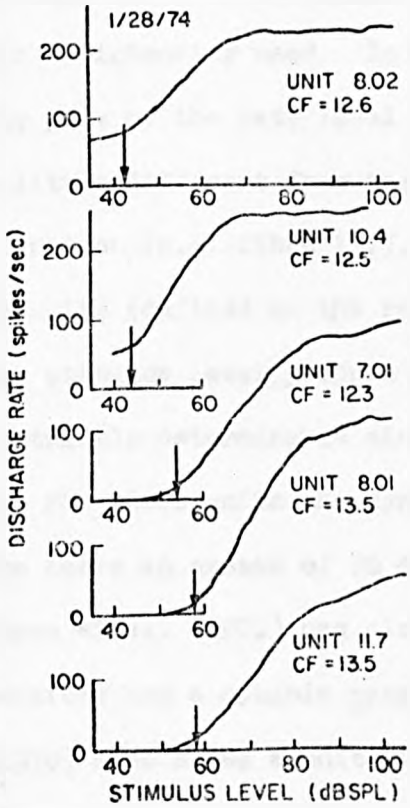
A. Block diagram of a model relating pressure at the tympanic membrane to cochlear fibre discharge rate.

B. The relationship of pressure and the basilar membrane displacement.

C. Two rate versus level functions derived from the model.

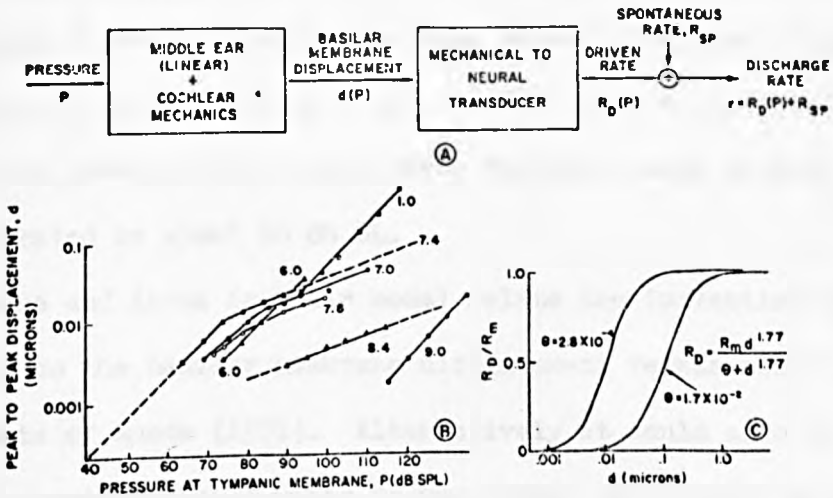
(From Sachs and Abbas, 1974.)

Figure 29



Rate-versus-level functions (at CF) for five fibers from the same cat (1/28/74). The fibers have CFs in the range 12.3–13.5 kHz. They are arranged vertically in order of increasing threshold. The arrows indicate thresholds.

Figure 30



(a) Block diagram of model relating sound pressure P at the eardrum to discharge rate in auditory-nerve fibers $r(P)$. $r(P)$ is assumed to be the sum of a stimulus-driven rate $R_D(P)$ and a spontaneous rate R_{SP}. The relationship between pressure and displacement d of the basilar membrane is given by the curves in (b), which are redrawn from Rhode (1971). The dashed lines represent our extrapolations of Rhode's data. The driven discharge rate R_D is related to displacement by a "transducer" function, two examples of which are shown in (c). In (c), R_D has been normalized by R_m, the saturation rate of the transducer. The two examples would correspond to two fibers with different thresholds θ.

Eleven of the fibres figured in Sachs and Abbas (1974) which have sloping saturations do not finally flatten out even at the highest levels of intensity used. In some cases the slope of the high intensity part of the rate level function (i.e. above about 30 dB above threshold)is little different from that of the rapidly rising part of the rate function (e.g. fibre 11.7, Fig. 29). Thus the dynamic range of such units (defined as the range of intensity over which changes in the stimulus level produce changes in the mean discharge rate) is not strictly determinable since the upper limit has not been reached. For these units the dynamic range is in excess of 50 dB and in some cases in excess of 70 dB. One sloping saturation unit depicted in Rose et al. (1971) has also not reached complete saturation and therefore has a dynamic range in excess of 60 dB. Wiederhold (1970) also shows a unit with a dynamic range of 60 - 70 dB. However, Evans (these data are described in Section 3.3.4) has found that in a sample of 57 cochlear fibres, 29 of which had rate versus level functions showing sloping saturations, the dynamic ranges varied from 20 - 60 dB with a mean of 41.5 dB. It would appear, therefore, that although fibres with wide dynamic ranges have been found in the cochlear nerve (see above), they are relatively uncommon (at least in Evans's data). The majority of cochlear fibres, even those showing rate versus level functions with sloping saturations, are saturated by about 60 dB SL.

Sachs and Abbas in their model relate the inflection in the rate function to the basilar membrane displacement versus sound pressure level data of Rhode (1971). Alternatively it could also be modelled by two processes contributing to the output of a single cochlear fibre (as suggested by Evans, personal communication), one process having low threshold, rapid rise and saturation 20 - 50 dB above

threshold and the other with high threshold and more gentle rise. Thus the total output would have low threshold, fast rise and then a change in slope where one process saturates and the other takes over. Evans and Wilson (1973) in considering the 'second filter' intimated that one possible mechanism might be an interaction of inner and outer hair cells (for a review of evidence for interaction between hair cells, see Evans, 1975a). Clearly, if the two hair cell populations have different output functions and both contribute to a single fibre's activity, some such two stage relation of output to level might be expected. The differing slopes of saturation might then reflect degrees of interaction of differing cochlear innervation.

An alternative explanation of the sloping saturation based on the findings of the experiments in Chapter Four is given in Section 4.4.7.

A study of single neurone dynamic ranges at both cochlear nerve and nucleus levels has been undertaken, which, in combination with the study of single neurone minimum thresholds has enabled an assessment of the range of intensity over which peripheral auditory neurones are able to encode intensity changes by changes in their mean discharge rate.

3.2 Methods

FTCs of single cochlear fibres and cochlear nucleus units were routinely determined using one of three methods (see Section 2.8 for details). Briefly, the three methods used were as follows:-

1. The conventional manual plotting method of Galambos and Davis (1943) in which the frequency and intensity of a tone burst are adjusted by the experimenter and the threshold for excitation of the neurone is determined at a range of frequencies by audio-visual criteria.

2. Tone bursts were presented in random sequence of frequency and intensity, controlled by a computer which concurrently counted the number of spikes evoked during each tone presentation. The counts were then displayed as the length of the line at the appropriate frequency - intensity locus in a graph of intensity versus frequency (60 dB x 3 octaves). E.g. Figs. 65 and 67.

3. Thresholds as a function of frequency were determined by an automatic computer controlled paradigm analogous to that used by Kiang, Moxon and Levine (1970).

The minimum threshold (i.e. at the CF) is taken as the 'threshold' of the unit for comparison purposes. The determination of this threshold is subject to error in both manual and automatic methods. The elimination of such errors is discussed in the results section.

Rate versus level functions in response to CF tones were obtained from both the increment and bandstop noise masking experiments (Chapters Four and Five). The rate versus level functions obtained in manual determinations were often considerably variable; because of this purely visual estimation of the dynamic range was not considered to be sufficiently consistent from unit to unit. The following procedure was therefore adopted. A smoothed sigmoid curve was drawn

through the raw discharge rate versus level data and this was used in determining the extent of the dynamic range. The dynamic range in dB was defined as the intensity difference between the level at which the discharge increased above spontaneous rate and the level at which the slope of the rate versus level function fell to 10 spikes/10 dB. This somewhat arbitrary choice of criterion for the upper extreme represented a discharge of 87.5 - 99% (mean 96.5%) of the maximum discharge rate of 13 units for which this was checked. Occasionally, for units with very low saturation discharge rates an alternative criterion of 5 spikes/10 dB was employed.

The rate versus level functions obtained by use of the computer to randomise the sequence of levels were extremely repeatable including fine detail. Thus no smoothing of the data was performed and the criteria described above were applied directly to the raw data.

Included in the dynamic range data are units in which the first 20 ms of a 200 ms CF tone burst was averaged to construct the rate function as well as units in which the spike rate was averaged over 500 ms. One might expect differences in the dynamic ranges measured at onset and over 500 ms (see Chapter Four) and therefore these data have been analysed separately.

3.3 Results

3.3.1 Pooled Cochlear Nucleus Threshold Data

Figure 31 shows the pooled threshold data from seventeen cats. No attempt has been made to select animals with comparable CAP thresholds. The CAP thresholds of these animals to 10μs clicks varied over a range of 44 dB with a standard deviation of 10.3 dB. This contrasts markedly with the nerve data reported by Kiang et al. (1965a), which consisted of data from twelve cats selected for CAP thresholds at the round window within 5 dB of one another. Due to this lack of selection of the data in Figure 31 one would expect that the range of thresholds at any frequency would be much greater than in the data of Kiang et al. (1965a). This is not in fact the case. Examination of Figure 31 reveals a range which at many frequencies is limited to 40 dB and does not exceed 60 dB at any frequency. These data therefore show the same or less scatter than comparable data reported in the literature (Kiang et al., 1965a; Mast, 1970a; Evans, 1972).

Kiang et al. suggested (1965a) that the wide variation in single unit minimum thresholds could not be explained by the pooling of data from different cats since results from individual animals showed almost as great a spread. They further suggested that variations in the resonant frequencies of the acoustic system from cat to cat might contribute to the spread above 10 kHz.

However, in the data presented in Figure 31 the thresholds have been corrected to dB SPL at the tympanic membrane and scatter of the points above 10 kHz is scarcely greater than at lower frequencies. In a later paper Kiang (1968) indicated that the wide scatter in earlier threshold data was probably due to two factors: i) the

Figure 31

Minimum pure tone thresholds of cochlear nucleus cells from seventeen cats versus their CF, compared with a curve indicating the average behavioural threshold (solid and broken line). Thresholds in dB SPL at the tympanic membrane. (The mean free-field behavioural thresholds of several studies were corrected for the outer ear response using the data of Wiener et al., 1965.)

Figure 32

Minimum pure tone thresholds of cochlear fibres (filled circles) and cochlear nucleus cells (open circles) from a single cat versus their CF. Thresholds in dB SPL at the tympanic membrane.

Figure 31

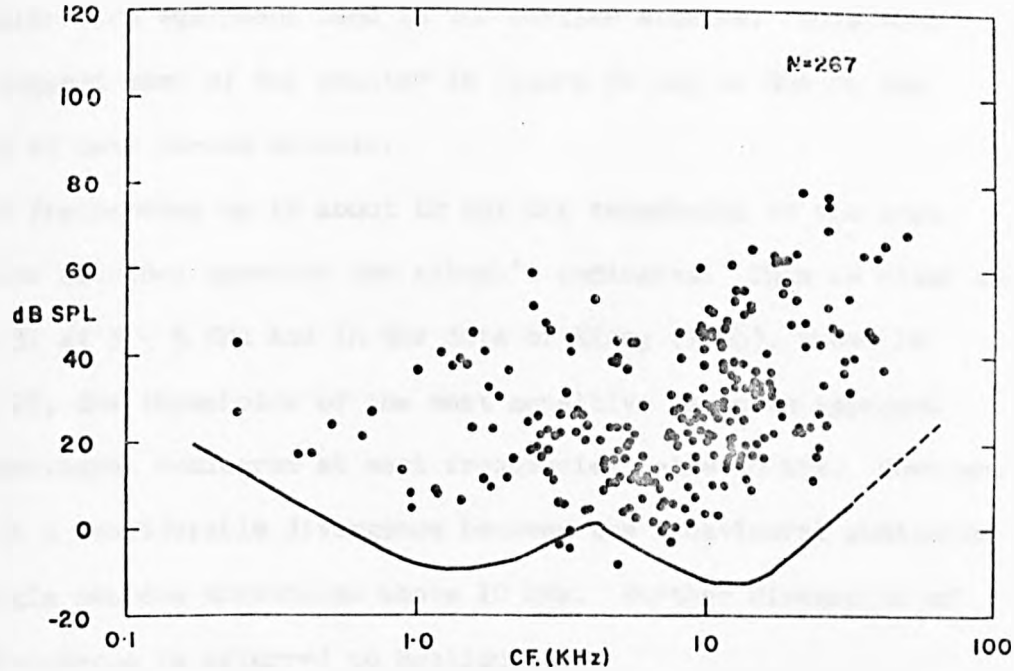
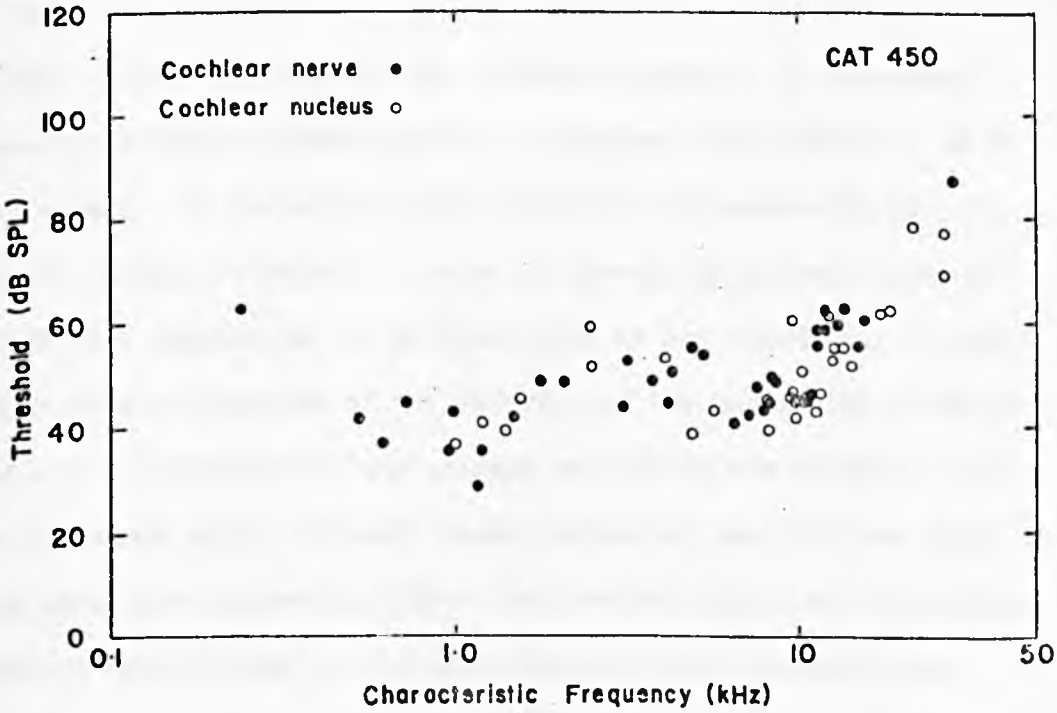


Figure 32



pooling of data across animals and ii) the inadequate sound producing and calibrating equipment used in the earlier studies. This then would suggest most of the scatter in Figure 31 may be due to the pooling of data across animals.

At frequencies up to about 10 kHz the thresholds of the most sensitive neurones approach the animal's audiogram. This is clear in Figure 31 at 3 - 5 kHz and in the data of Kiang (1968), shown in Figure 27, the thresholds of the most sensitive neurones approach the behavioural audiogram at most frequencies below 10 kHz. However, there is a considerable divergence between the behavioural audiogram and single neurone thresholds above 10 kHz. Further discussion of this divergence is deferred to Section 3.4.

3.3.2 Threshold Data from Individual Animals

When the data from individual animals are considered, the scatter of the thresholds at any frequency is considerably reduced. This was first shown by Kiang (1968) who reported threshold ranges of only 20 - 30 dB at any frequency (Fig. 27) in cochlear nerve fibres.

This is also the case in the cochlear nucleus. In seventeen animals the range of thresholds at any frequency is limited to 30 dB in any animal. In ten animals the range does not exceed 20 dB. In the seven animals in which the range of thresholds at any frequency is 30 dB this represents the maximum range at any frequency, it does not mean that the scatter of the majority of the thresholds in these animals is greater than in the animals exhibiting the narrower range. The wider range is due, in many cases, to one or possibly two units having thresholds unusually higher than the rest and therefore giving a wider threshold range at a single frequency not throughout the frequency range. Closer examination of the tuning curves of these

'odd' units does not reveal any unusual features which might explain the deviation from the rest of the threshold data. In one case the spontaneous rate was very high (approximately 125 spikes/sec) which as will be seen in Section 3.3.3 might have resulted in an erroneous threshold estimation. Conversely, in three units whose thresholds deviated from those of the majority the spontaneous rate was very low, two of these were silent and driven activity of these two units consisted only of a few spikes. In such units errors in estimating the threshold, due to the spontaneous discharge are minimal.

That the wide scatter of the thresholds in pooled data of Fig. 31 is due to threshold differences between animals is illustrated in Fig. 33. The lines in Fig. 33 join the thresholds of the most sensitive neurones at each frequency, for individual animals. It can be seen from this figure that although the threshold range in a single animal is quite limited (see above) the interanimal differences may be as much as 50 dB.

Despite the units which have thresholds differing from the rest of the population, the range of thresholds at any frequency in cochlear nucleus is clearly comparable with ranges of thresholds at any frequency reported for cochlear fibres by Kiang et al., 1965a, and Evans 1972. This point is made more convincingly by Figure 32.

The data shown in Figure 32 are our own threshold data from the cochlear nerve and cochlear nucleus obtained from a single ear, during a single experiment using, a single method of FTC determination (the cochlear nerve data were obtained by Dr. E. F. Evans). Deterioration of the physiological state of the cochlea causes increases in single cochlear fibre thresholds (Evans, 1972). Thus since the cochlear fibre threshold determinations followed those in the cochlear nucleus, the CAP threshold was monitored throughout to ensure that the

physiological condition of the cochlear remained unchanged (the CAP threshold varied by only a few dB in the course of the experiment and no trend with time was evident). The relationship of the CAP threshold to single neurone thresholds may be seen in Fig. 33 in which the CAP threshold (in dB attenuation) for each cat is shown at the end of the line joining the most sensitive thresholds of that animal. The lowest CAP thresholds are associated with the lowest neuronal thresholds. The majority of the data points in Figure 32 represent the threshold at CF of an FTC obtained by an automatic computer controlled paradigm analogous to that of Kiang, Moxon and Levine, 1970. (See Section 2.8.3 for details.) The manually determined threshold was sometimes used to eliminate errors caused by high spontaneous rates (see Section 3.3.3).

Thus the data of Figure 32 enable us to make direct comparisons of both the range and absolute values of the thresholds of neurones in the cochlear nerve and cochlear nucleus which are not confused by interanimal differences.

From Figure 32 it can be seen that the range of thresholds in cochlear nerve and cochlear nucleus are obviously very comparable both extending over the same 20 dB at any frequency.

Comparison of Figures 31 and 32 reveals that the thresholds of cat 450 (Figure 32) are on average higher than the rest of the cat population sample. This animal had a very wet and injected middle ear, suggestive of past middle ear infection. Furthermore, since the FTCs of this animal, although of high threshold, were nevertheless sharply tuned and not, therefore, of the high threshold, broadly tuned type found in animals with cochlear pathology (Evans, 1972); the relatively high thresholds probably resulted from transmission loss through the middle ear. It is clear from Figure 33 (in which the solid line joins the minimum thresholds of cat 450 at each

frequency) that this animal was not totally anomalous but represented the extreme of the range of interanimal sensitivity differences. Despite these higher thresholds the threshold range at any frequency remains unaltered. As one might expect, changes in cochlear nerve thresholds appear to affect changes in cochlear nucleus thresholds by the same amount and direction.

3.3.3 Error in Threshold Determinations Introduced by High Spontaneous Rates

Kiang et al. (1965a) noted that thresholds determined manually by audio-visual criteria (i.e. by listening to the spikes via a loudspeaker and observing the spikes on an oscilloscope to detect bursting of the discharge in response to repeated tone bursts), were often 5 - 20 dB higher than thresholds for the same fibres determined more objectively using PST histogram data. The magnitude of the error depends on the level of spontaneous discharges. The experimenters' task when determining the threshold of a silent unit or fibre is a simple detection of presence or absence of discharge. In fibres with high spontaneous rates this becomes a difference limen type of task detecting small changes in the discharge rate. High spontaneous discharge rates also affect the minimum threshold obtained from the computer controlled FTC determinations. In the automatic FTC tracing method (see Section 2.8.3 for details) with high spontaneous rates and limited sampling time the criteria for deciding if the cell is responding must be increased in order to obtain a reliable threshold measure. Choosing higher comparison criteria produces an iso-rate contour rather than a threshold curve; thus the 'threshold' as estimated from such a determination is somewhat higher than true threshold. In

Figure 33

Minimum tone thresholds of fourteen cats versus their CF. Each line joins the minimum tone threshold at each frequency for a single animal. Thresholds in dB SPL at the tympanic membrane. The parameters on the curves are the visual detection thresholds of the CAP in dB of attenuation.

Figure 34

The number of decibels by which the threshold determined by audiovisual criteria exceeded that determined from rate versus level functions versus the spontaneous discharge rate for thirty-one cochlear nucleus cells. The best fit regression line through the data is shown by the solid line. The dashed lines indicate one standard deviation either side of the regression line.

Figure 33

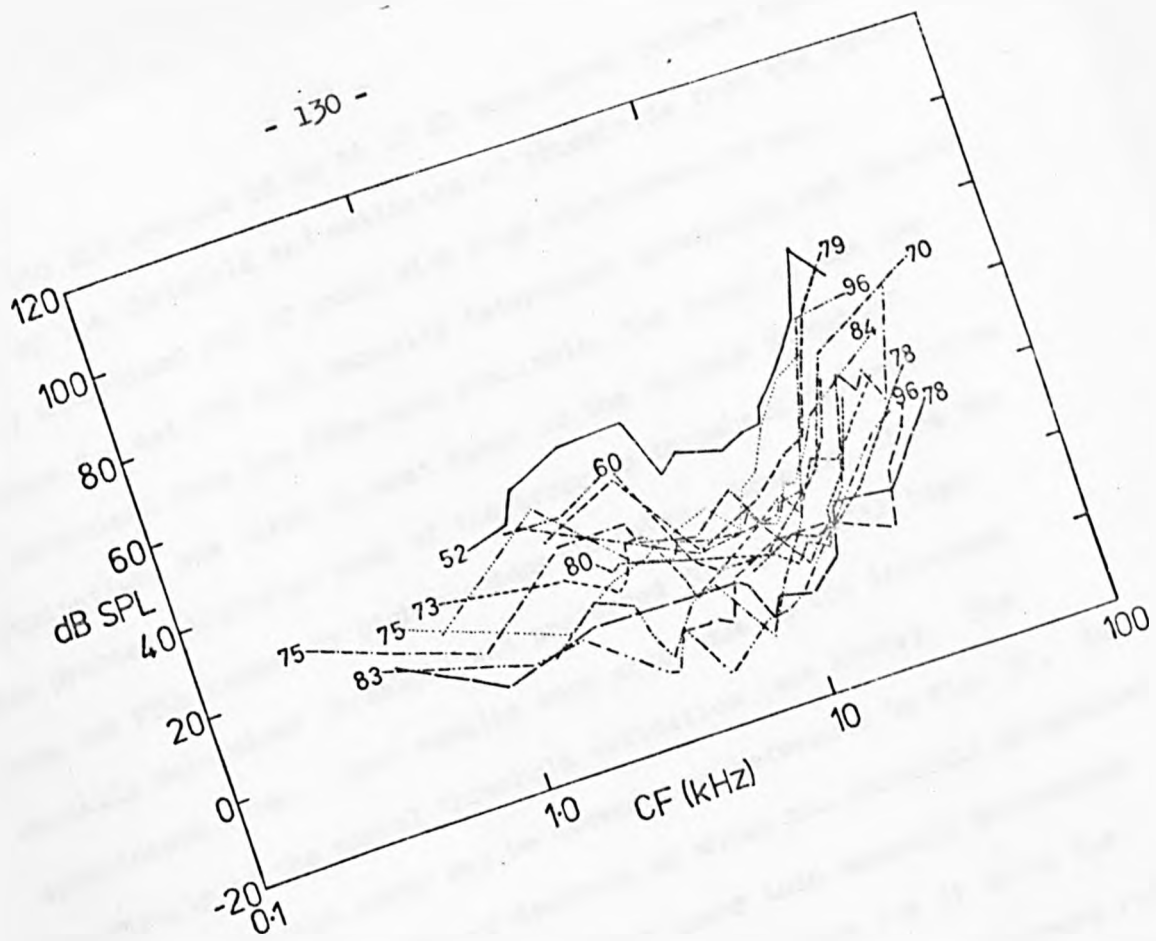
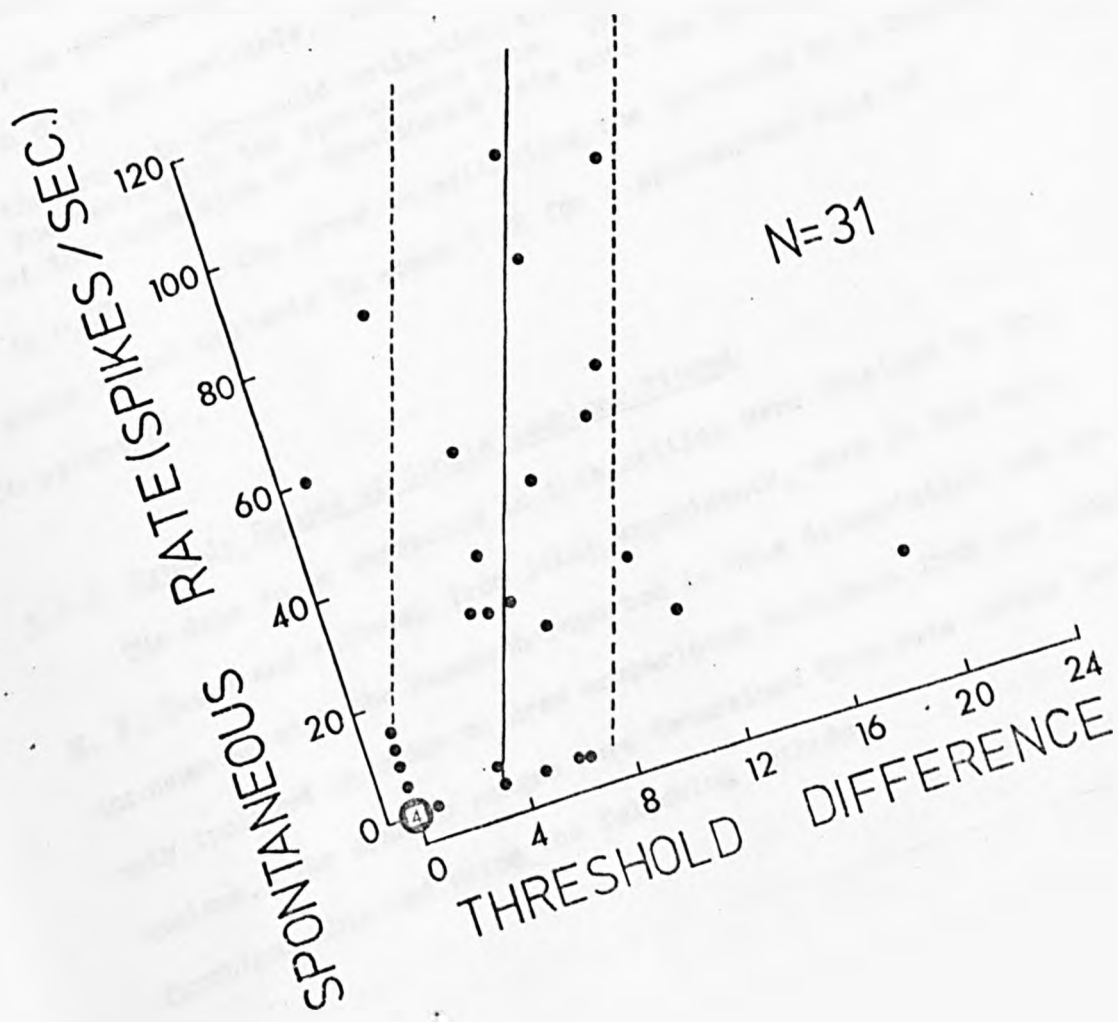


Figure 34



experiment 450 differences of up to 10 dB were noted between manual estimates of the threshold and estimates of thresholds from the automatically determined FTC of units with high spontaneous rates.

Since for cat 450 both manually determined thresholds and thresholds determined from the FTCs were available, the lower of the two determinations was taken in most cases as the minimum threshold. This process eliminates some of the error in threshold determination from the FTCs caused by high spontaneous rates. However, since the manually determined threshold was preferred for units with high spontaneous rates, there remains some error due to the increased difficulty of the manual threshold estimation (see above). The magnitude of this error may be assessed by reference to Fig. 34. In this figure, the number of decibels by which the threshold determined from rate versus level functions is lower than manually determined thresholds, is plotted against spontaneous rate for 31 units for which such data was available. Although there is not a strong relationship between the error in threshold estimation and spontaneous rate, the error clearly increases with the spontaneous rate. The slope of the regression of spontaneous rate onto the threshold difference is 0.07. Thus the error in estimating the threshold of a neurone by audio visual criteria is about 7 dB for a spontaneous rate of 100 spikes/sec.

3.3.4 Dynamic Ranges of Single Cochlear Fibres

The data to be described in this section were obtained by Dr. E. F. Evans and although from joint experiments, were in the main, unconnected with the research reported in this dissertation and are only included in order to draw comparisons with data from the cochlear nucleus. The dynamic ranges were determined from rate versus level functions obtained using the following methods.

1. The method described in detail in Section 2.5.2 was used to determine the response area of the fibre. Briefly, a computer was used to independently vary the frequency and intensity of a series of 50 ms tone bursts and to count the number of spikes evoked by each stimulus presentation. These spike counts were displayed at the appropriate position in a frequency versus intensity plot, as a bar, the length of which was proportional to the number of spikes. Thus the rate versus level function to CF tones could be obtained by plotting the number of spikes evoked by the CF tone at each intensity level. Some smoothing of the raw data was achieved by averaging the spike count at the CF with that obtained at the frequencies on either side of the CF.

2. A computer was used to pseudo randomly vary the intensity of a 500 ms CF tone burst over 13 levels (in 10 dB steps) and to count the discharge evoked during each stimulus presentation.*

For 57 fibres the mean dynamic range determined using method 1. above was 41.1 dB with a standard deviation of 9.7 dB and a range of 20 - 60 dB.

For 24 fibres the mean dynamic range determined using method 2. above was 35 dB with a range of 20 - 50 dB and a standard deviation of 9.1 dB.

Interestingly, the dynamic ranges determined for the onset 50 ms are significantly greater ($p > 0.05$) than those determined using 500 ms tones. This is the opposite of the findings in the cochlear nucleus (see Section 3.3.5.1). However, nearly all of the data using the longer tones were from a single animal and comparisons of pooled data using the shorter tones with a single animal's data may be misleading. This point is elaborated in Section 3.3.6.

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* The program for this analysis was written by the author and is shown in flow-chart form in Appendix B.

3.3.5 Dynamic Ranges of Individual Cochlear Nucleus Units

Cochlear nucleus units can be divided according to the dependence of their discharge rate upon intensity. Two categories are usually recognised, monotonic and non-monotonic units (Hilali and Whitfield, 1953; Rose et al., 1959; Greenwood and Maruyama, 1965). Non-monotonic units as the name suggests, have intensity rate functions in which increases in level of a stimulus can cause increases or decreases in discharge rate according to the overall level. This clearly leads to ambiguity in the interpretation of a particular firing rate since it may be evoked by very different stimulus levels. Non-monotonic units individually cannot therefore entirely specify the level of a stimulus in terms of mean discharge rate. These units are therefore dealt with separately in the following.

3.3.5.1 Monotonic cochlear nucleus units

Monotonic units in the cochlear nucleus, in general, display rate versus level functions which are sigmoid in shape resembling those of primary fibres. The same criteria as for the primary fibres (see Section 3.2) were therefore used for the determination of the dynamic range of cochlear nucleus units. The rate versus level function were obtained using two techniques:-

1. Twenty 200 ms CF tone bursts were presented at a level set by the experimenter and the discharge evoked during the first 20 ms of each burst was averaged. This process was repeated as the tone level was increased in 10 dB steps from levels below the threshold of the unit to levels at which the unit was saturated.
2. A computer was used to pseudo randomly vary the intensity of a 500 ms CF tone burst over 13 levels (in 10 dB steps) and to count the discharge evoked during each stimulus presentation. (See Appendix B.)

The mean onset dynamic range measured for 29 units, using method one above, was 39.1 dB with a standard deviation of 11.6

and a range of 21 - 70 dB.

The mean dynamic range, measured using method 2 above, for sixty one units was 45.9 dB with a standard deviation of 14.6 dB and a range of 20 - 80 dB. The difference between the means of these two samples though small is statistically significant ($p < 0.05$).

The response of primary fibres and primarylike cochlear nucleus units to CF tones, decays from an initially high discharge rate to a relatively steady discharge rate. The results of the experiments reported in Chapter Four indicated that in some CN units the range of intensity over which the steady-state discharge varied with stimulus level was wider than that over which the onset discharge varied with stimulus level. Since the discharge will have reached steady-state after 500 ms, the dynamic range measured with such tone durations should reflect the wider steady-state dynamic range. Thus the finding that dynamic ranges measured with 500 ms tones are significantly wider than those measured at stimulus onset is consistent with the findings of the experiments to be reported in Chapter Four.

3.3.5.2 Non-monotonic cochlear nucleus units

Whilst for units which have sigmoid rate functions dynamic range is quite easily definable it becomes more difficult for non-monotonic units. Examples of non-monotonic rate functions are shown in Fig. 35. As intensity is increased, the discharge rate initially increases from the level of spontaneous discharge and reaches a maximum rate of discharge. Further increases in intensity result in a reduction in the discharge rate. An increase in intensity results in either an increase or a decrease in the rate of discharges depending on the overall level. Thus if one defines the dynamic range of non-monotonic units to include the range over which increasing intensity is signalled by decreasing discharge rate, many of these units have very wide

Figure 35 A

Non-monotonic rate versus level functions for four cochlear nucleus cells determined by presentation of twenty CF tone bursts at each of an ascending series of intensities.

Figure 35 B

Non-monotonic rate versus level functions for four cochlear nucleus cells determined by using a computer to pseudo-randomly vary the level of a CF tone burst over thirteen levels separated by 10 dB intervals.

Figure 35 A

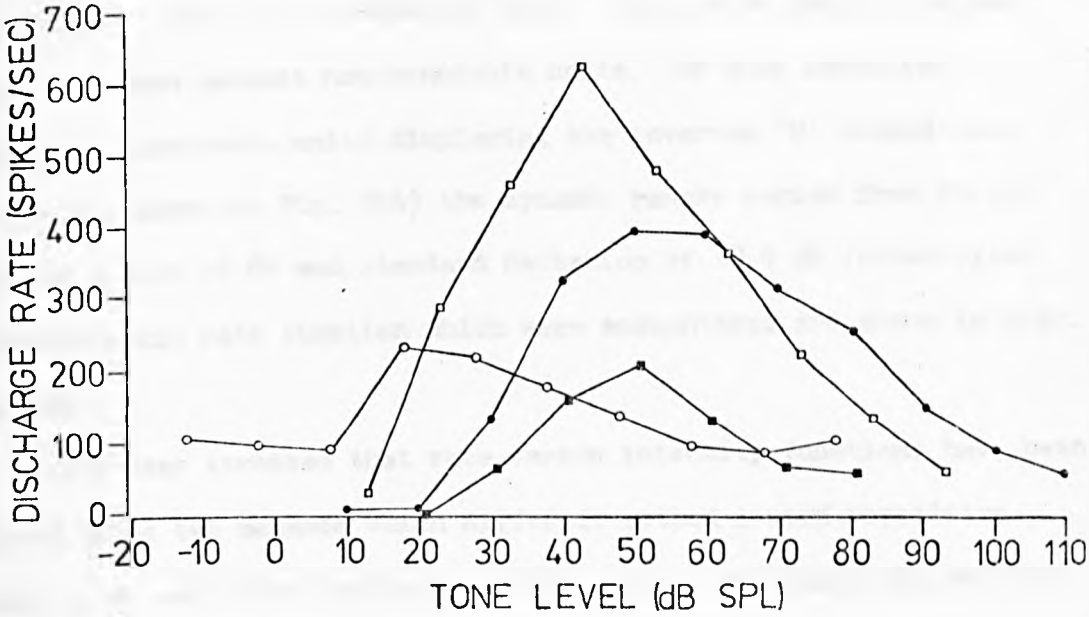
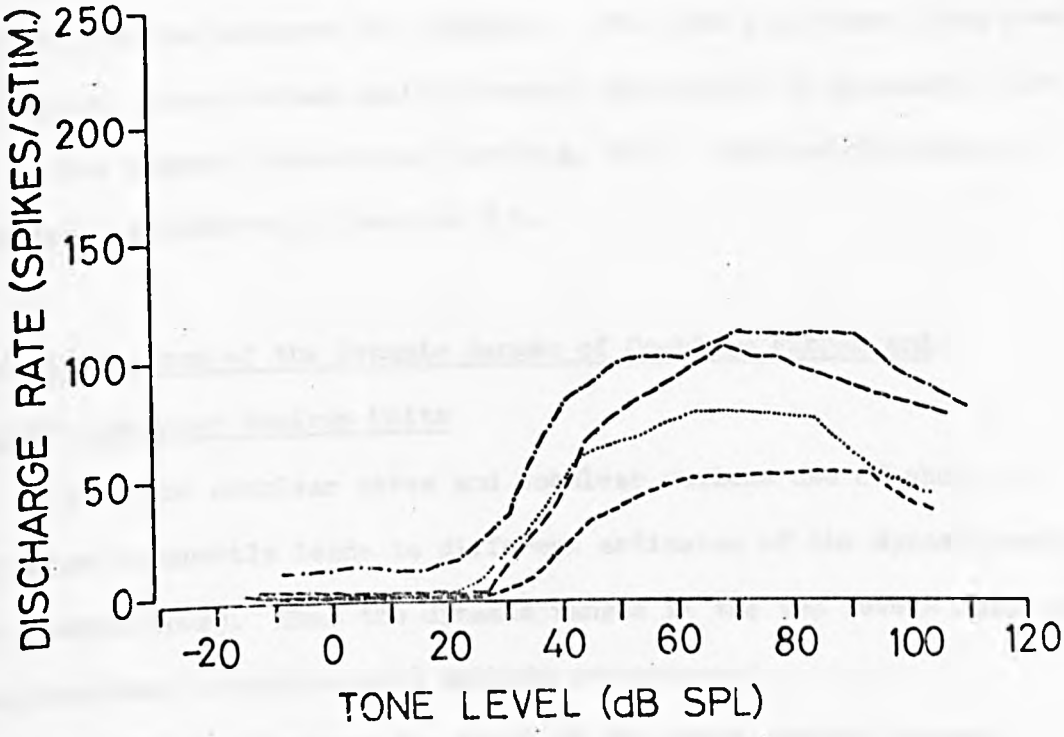


Figure 35B



dynamic ranges. Unit 231.15 (open squares, Fig. 35A) for example, has a dynamic range of the order of 80 dB. Such wide dynamic ranges are not uncommon amongst non-monotonic units. Of some seventeen strongly non-monotonic units displaying the inverted 'U' shaped rate function (as shown in Fig. 35A) the dynamic ranges varied from 40-100 dB having a mean of 65 and standard deviation of 18.4 dB (other types of non-monotonic rate function which were encountered are shown in Figs. 47 and 48).

It has been stressed that rate versus intensity functions have been obtained using two methods which differed: method 1 used repetitive stimuli in an ascending intensity series and the discharge was averaged over the onset 20ms, method 2 used a random intensity sequence and discharges were averaged over 500 ms. Strongly non-monotonic rate versus intensity functions were more often encountered using the former (method 1) than the latter (method 2). The non-monotonicity most frequently observed in the discharge of units in the automatic experiments consisted mainly of a reduction in discharge rate of up to 50% (and usually much less) only at the extremes of intensity. The rate functions often rose in a typical sigmoid shape and plateaued, decreasing in discharge rate only at the highest intensities (see Fig. 35B). Further discussion of these data is deferred to Section 3.4.

3.3.6 Comparison of the Dynamic Ranges of Cochlear Fibres and Monotonic Cochlear Nucleus Units

At both the cochlear nerve and cochlear nucleus use of short or long tones apparently leads to different estimates of the dynamic range (see Chapter four). Thus the dynamic ranges at the two levels obtained using the same (or equivalent) methods are compared.

The difference between the means of the onset dynamic ranges

obtained at the cochlear nerve and nucleus are not significant ($p < 0.05$).

The difference between the means of the dynamic ranges obtained in cochlear nerve and nucleus using 500 ms tones are significant ($p < 0.05$). However, as indicated earlier (in Section 3.3.4) nearly all of the cochlear nerve 500 ms data (19 units of 24) were obtained from the same animal and this therefore represents a comparison of a single animal's data with pooled data.

Thus the mean dynamic range of the cochlear nerve fibres obtained with 500 ms tones were compared with the mean dynamic range obtained from the same animal in the cochlear nucleus, using 500 ms tones and the difference was found to be not significant ($p < 0.05$).

Thus when appropriate comparisons are made, the data seem to indicate that there is no significant difference between the dynamic ranges of single cochlear fibres and those of monotonic cochlear nucleus units; however, such comparisons are based entirely on the mean and standard deviations of the samples. For the purposes of the present study the upper extreme is of interest.

The distribution of the dynamic ranges at the cochlear nerve and nucleus is shown by the histograms of Fig. 36 (the onset and 500 ms data have been pooled in this Figure). The modes of both the histograms are 40 - 44 dB. However, the dynamic ranges in the cochlear nucleus extend up to 80 dB whereas those at the cochlear nerve level only extend up to 60 dB. Of the seven cochlear nucleus units with dynamic ranges in excess of 60 dB, five showed sloping saturations (i.e. the slope of the rate versus level function decreases at about

Figure 36

A. Histogram of the number of monotonic cochlear nucleus cells having dynamic ranges in each 5 dB interval from 20-85 dB.

B. Histogram of the number of cochlear fibres having dynamic ranges in each 5 dB interval from 20-85 dB.

Figure 37

Dynamic ranges of monotonic cochlear nucleus cells from sixteen cats. The length of each line represents the dynamic range of a single cell plotted at the appropriate CF and threshold (in dB SPL at the tympanic membrane).

The thick solid and broken line represents the behavioural threshold. (The mean free-field behavioural thresholds of several studies were corrected for the outer ear response using the data of Wiener et al., 1965.)

Figure 36

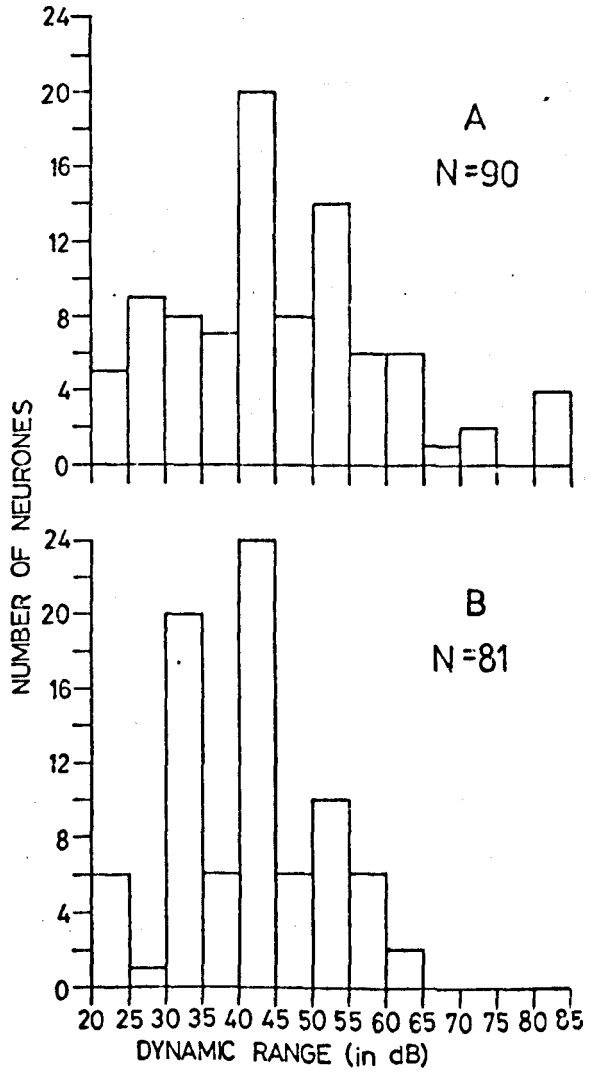
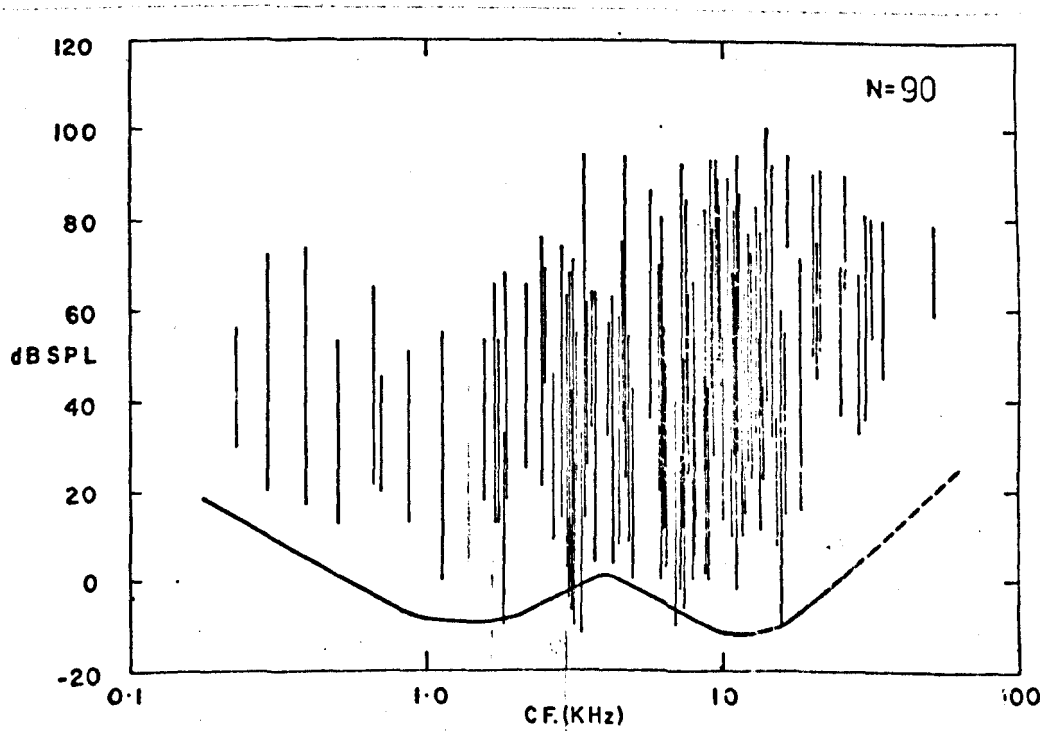


Figure 37



30 dB above threshold but continues to rise at a slower rate) which included all those with dynamic ranges of 80 dB and one of 76 dB.

50% of the cochlear nerve fibre sample had rate versus level functions which were of the sloping saturation type, but all were saturated at 60 dB above threshold. However, it is apparent from the literature reviewed in Section 3.1.2 that cochlear fibres have occasionally been encountered which showed rate versus level functions of the sloping saturation type and which as a consequence had dynamic ranges as wide as 80 dB. Thus although in the present cochlear nucleus data (obtained by the author) and cochlear nerve data (obtained by Dr. E. F. Evans) the widest dynamic range found in the cochlear nucleus is substantially wider than any found in the cochlear nerve, it would seem that given a large enough sample, wide ranges would also have been found in the cochlear nerve. (An alternative explanation of the lack of wide dynamic ranges in Evans' data is given in Section 4.4.7).

3.4 Discussion

3.4.1 Thresholds

The very wide range of single unit thresholds in pooled data shown in Figure 31 has been previously reported in both cochlear nerve and nucleus (Galambos and Davis, 1943; Kiang et al., 1965a; Mast, 1970a). The ranges of thresholds in the pooled data at any frequency from the present study, considering the wide range of individual animal sensitivities (as indicated by the CAP threshold), are narrower than those of Kiang et al. and Mast, being only of the order of 40 - 60 dB.

The finding of a very restricted range of thresholds of only 20-30 dB when data from a single ear are considered has been supported by the data of Dr. E. F. Evans for single cochlear nerve fibres. It has also been shown that a similar restricted range of thresholds is present in the cochlear nucleus.

The fact that absolutely no indication has been found of any high threshold population of single units in the cochlear nucleus suggests two possible conclusions. The first is that the high threshold population is still being systematically overlooked. If the electrodes used were able to sample all cells in the nucleus and a population were still overlooked these units must have zero spontaneous rate and have thresholds greater than approximately 60 dB SPL (since the search stimuli were routinely at about this level). This suggestion seems unlikely in the light of the fact that high neural thresholds have not been found by this or any other author (at least, not in the same animal as low threshold cells), using several different types of electrodes and despite being specifically looked for. * Secondly, therefore, on the basis of presently available data one must conclude that a single population of low threshold units is

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* Recently a wide range of thresholds in a single animal has been reported by Kiang et al. (1976) and Liberman (1977). These data are discussed in Section 6.1.

present in both cochlear nerve and cochlear nucleus.

At low frequencies it has been reported that phase locking has been observed at intensities below that required to raise the discharge rate above spontaneous rate (Hind, 1972, p. 51). Thus the behavioural threshold may not be determined at these frequencies by thresholds for increased firing in primary neurones. Thus the discrepancy between the mean behavioural audiogram and single unit thresholds at low frequencies, in Figure 31, may result from the determination of the threshold for increased firing rather than the threshold for phase locking which may be useable by the animal. However, in the cochlear fibre data of Kiang (1968) no discrepancy is evident at low frequencies and therefore the deviation of neural thresholds from the audiogram in Figure 31 may just be due to the relatively small sample of low frequency neurones encountered in the present study. The choice of the threshold criteria in physiological experiments is also a source of some discrepancy. The animal has available the simultaneous firing rate change in many units in order to detect the presence of a signal. The experimenter looking at only a single neurone may be using criteria for threshold far above that required by the animal for detection. However, the large divergence (up to 20 dB) between the thresholds of single units and the audiogram above 10 kHz is unlikely in my opinion to be completely explainable on these grounds. The behavioural measures at these frequencies are difficult since in the anechoic conditions used the animal's head position may have large effects on the audibility of the signals. Mean pressure transformation curves were used to correct the minimum audible fields to minimum audible pressures (at the tympanic membrane). It is evident from Wiener et al. (1965) that peaks and dips of the order of ± 10 dB occur in the pressure transformation curves at frequencies above 8 kHz. Assuming that the

animal maximises the available signal by moving head and meatus, it may be able to utilise such pressure transformation peaks. Thus the threshold in terms of sound pressure at the tympanic membrane would be higher than indicated by correction of the minimum audible field using the mean pressure transformation curve. Any error introduced by such factors would lower the behavioural threshold measure which would move it away from the single unit data. Thus at least some of the discrepancy may be explainable in such terms.

The audiogram in Figure 31 is the mean of several cat audiogram determinations, some of which extend up to 50 kHz. The correction curves to convert the minimum audible field to minimum audible pressure do not extend to these frequencies and this region is therefore plotted as a broken line. However, it is apparent from the MAF audiograms that the threshold at 50 kHz is still quite low, being of the order of 35 dB SPL (Neff and Hind, 1955; Miller, Watson and Covell, 1963). Very few units have been encountered at such frequencies and none at all at such low intensities. Even allowing for the possible errors discussed above, it is difficult to suggest how the cat hears these frequencies at such low intensities. This discrepancy may again be due to pooling of data across animals, since whilst we might expect that in one animal its audiogram should be a reflection of its lowest single unit thresholds, the relation of any animal's unit thresholds to a mean audiogram will be much less close due to the influence of animals with better or worse hearing. This is particularly exemplified by the data of Figure 32, cat 450, which had high single unit thresholds and must therefore have had high behavioural thresholds. The single unit thresholds of this animal bear no relation at all to the average audiogram shown in Figure 31. However, in a sample of nineteen cats, one would expect that the

single unit thresholds of some cats would approach the average audiogram at these frequencies.

The cat population used in the present experiments had a high incidence of middle ear infection. Deviations of individual animal thresholds from the mean behavioural audiogram might therefore reflect differing cat populations (the cats in this study having relatively worse than average hearing). This suggestion is, however, not consistent with the fact that the discrepancy is also present in the data of Kiang (1968).

3.4.2 Dynamic Range

The findings of Dr. E. F. Evans and of studies reported in the literature are that nearly all cochlear fibres are saturated within 20 - 60 dB of threshold.

However, a proportion of cochlear fibres do not completely saturate, but instead the slope of the rate function changes, producing a gradually sloping saturation. Fibres showing such sloping saturations may have very wide dynamic ranges if the sloping saturation portion is included (see Section 3.1.2), although the data of Evans indicate that the majority of fibres even with sloping saturations are saturated at levels 60 dB above threshold.

If discriminability of a change in signal level depends on the total change in the firing rate of all the active nerve fibres then a change of strategy would have to occur at higher levels. At low levels an intensity change of the order of a DL would cause quite large changes in discharge in a few fibres whereas at high levels the same intensity change would cause a small change in discharge in many fibres (assuming that fibres with sloping saturations are present in the nerve in sufficient numbers). This is because for a single fibre the first 40 dB or so of intensity could be signalled by a change in discharge rate of 200-300 spikes/sec, whereas the remaining

40 - 50 dB or more is only signalled by less than 100 spikes/sec (this is an approximation derived from the fibres in Fig. 29). A change in intensity of the order of a DL would only cause a few spikes/sec difference in firing rate at these high levels, and since the saturation firing rate is statistically variable a comparison between several channels would be necessary in order to separate fluctuations which occur even in response to a constant stimulus from changes which reflect input changes.

If the response to a small change in signal level consists of large output changes of a few fibres at low levels and small output changes of many fibres at higher levels then these cues must be equally effective since otherwise one would expect some discontinuity in the intensity DL* function at levels at which the slope change occurs and no such discontinuity has been found (see Section 1.2.5). These considerations apply to the white noise DL, since in the case of a pure tone, fibres with CFs remote from the stimulus frequency will not be saturated. When increases in the signal level bring it into the response areas of these remote CF fibres, small changes in the signal level will again be signalled by large discharge rate changes since these fibres are still unsaturated. Nevertheless, even for tonal stimuli the animal would have to apply different discrimination strategies at high and low levels which might be expected to produce a discontinuous intensity DL function.

The dynamic ranges of single cochlear nucleus units measured in this study, with the exception of the units with sloping saturations, are nearly all less than 60 dB. Even units with sloping saturations were all saturated by 80 dB above threshold. In Evans's data all cochlear fibres, even those with sloping saturations were completely saturated at 60 dB above threshold. However, a few cochlear fibres

* A discontinuous DL function is admittedly only predicted if the animal uses only a few alternative cues. If many different cues are utilised at different stimulus intensities, a continuous smooth function would be not unexpected.

have been reported in the literature (see Section 3.1.2) which have sloping saturations and are only saturated by levels of up to 80 dB above threshold. There would therefore appear to be good agreement between the dynamic ranges of single cochlear fibres and those of monotonic cochlear nucleus units.

3.4.3 Non-monotonic Rate Functions

The very wide dynamic range of some cochlear nucleus non-monotonic units indicates that some aspect of the cochlear nerve discharge is changing over very wide ranges of intensity, and that such changes provide the input to these cochlear nucleus cells. Since no cochlear nerve fibre has shown changes in its mean discharge rate over ranges of up to 100 dB (the dynamic range of at least one non-monotonic unit, see Section 3.3.5.2) the input to such cells cannot be in terms of the mean discharge rate of a single cochlear nerve fibre. The decrease in discharge of non-monotonic cochlear nucleus units to high level stimulation has been shown to be intimately related to side band inhibition (Greenwood and Maruyama, 1965), and the wide dynamic range of such units appears to be due to progressive increases in lateral inhibition. The rise to maximum discharge is not unlike the rise in monotonic units and cochlear fibres and might, therefore, be a reflection of either a single primary fibre input or input from an ensemble of cochlear fibres of common CF. Beyond this level the response would saturate if only due to excitatory input at a single frequency. There is, however, progressive spread of activity at higher levels to fibres of higher and lower CF than the stimulus frequency. This spread would lead to inputs to the cochlear nucleus cells which are of an inhibitory nature (i.e. the inhibitory side bands). As the excitatory input saturates, the signal will only just be encroaching into the response areas of fibres of higher and lower CF which presumably give rise to the inhibitory input. These

fibres could therefore provide inhibitory input to the non-monotonic cochlear nucleus neurones which can increase with stimulus level over a wide range.

Allanson and Whitfield (1955) and Whitfield (1967) considered the excitatory and inhibitory interactions required to reproduce such features of cochlear nucleus cell response as non-monotonic rate versus level functions. This non-monotonicity was modelled by afferent inhibition (from the fibre producing the excitatory input) mediated via an internuncial neurone (this scheme is less dependent on threshold differences between excitatory and inhibitory inputs than direct afferent inhibition). It was further suggested that lateral inhibition might result from efferent inhibition via an internuncial neurone. Their scheme differs from that outlined above in that in the former both the non-monotonic rate versus level function and lateral inhibition are attributed to afferent inhibition from fibres other than that producing the excitatory input (again presumably mediated via an internuncial neurone to reduce the dependence of the response on the threshold difference between the excitatory and inhibitory inputs). Basically then, spread of activity across the frequency continuum could be decoded at the cochlear nucleus by these non-monotonic neurones.

As suggested in Section 3.3.5.2, fewer strongly non-monotonic units were found in experiments in which the stimulus levels were randomised and the discharge averaged over 500 ms, that in experiments in which many presentations of high level stimuli followed each other in order to obtain mean discharge rates over the onset 20ms. Thus two possible explanations for the difference are suggested: 1) the strong non-monotonicity reflects inhibition at the onset which is of short duration and is therefore swamped by the later response when the discharge is averaged over 500 ms, or 2) the discharge rate of cochlear fibres (see Kiang et al., 1965a, p. 73). In the automatic analyses, the random ordering eliminated the continuous high level presentation. The very strongly non-monotonic rate versus level functions of cochlear nucleus units exposed to

repeated high sound levels compared to the automatic experiments, may therefore have been due to a build up of inhibitory influences produced by continuous high level stimulation. An experiment to determine if this is the case would be to present both serially and randomly ordered stimuli to the same unit and directly observe any differences. This experiment has not been performed.

3.4.4 The Range over which Single Cochlear Nucleus Units can Encode Intensity Differences

Fig. 37 summarises the dynamic range data obtained in this study from monotonic cochlear nucleus units. The vertical lines in Fig. 37 represent the extent of the dynamic range of each individual neurone plotted at the appropriate CF and threshold (in dB SPL at the tympanic membrane). Although the data in Fig. 37 are pooled from 16 animals and therefore encompass a wide range of minimum thresholds, the majority of cells are nevertheless saturated at tone levels of about 80 dB SPL. Only 16 cells were still unsaturated at tone levels of 85 dB SPL and all were completely saturated at tone levels of 100 dB SPL. Of the 16 cells saturating above 85 dB SPL all but 4 had dynamic ranges of 60 dB or less and had thresholds which were high compared to the mean behavioural threshold (indicated by the thick solid and broken line in Fig. 37). The majority of these high threshold units were from cat 450 (see Section 3.3.2). The 4 remaining cells showed rate versus level functions of the sloping saturation type (see Section 3.1.2) and as a consequence had dynamic ranges in excess of 70 dB.

In conclusion, therefore, the range of minimum thresholds at any frequency in both the cochlear nerve and cochlear nucleus is limited to 20 - 30 dB. Furthermore, few if any cochlear fibres and monotonic cochlear nucleus cells are capable of encoding small intensity differences over ranges comparable with the psychophysically determined dynamic range (which extends at least up to 100 dB SL or approximately 110 dB SPL,

see Section 1.2.5). There are, however, units in the cochlear nucleus (which have non-monotonic rate functions) which are capable of responding to signal level differences over very wide ranges of intensity (up to 100 dB). It is suggested that this might be as a result of integration by these units of activity from primary fibres with a range of CFs.

3.5 Summary

1. In both the cochlear nerve and the cochlear nucleus the range of thresholds at any frequency is no more than 20 - 30 dB.

2. The majority of cochlear nerve fibres have dynamic ranges of 20 - 60 dB. A few cochlear fibres which have sloping saturation type rate versus level functions may have dynamic ranges of up to 80 dB (reported in the literature but not found in the present study by Evans).

3. The majority of monotonic cochlear nucleus units have dynamic ranges of 20 - 60 dB. A few units of the present study which had sloping saturation rate versus level functions had dynamic ranges of up to 80 dB.

4. Non-monotonic units in the cochlear nucleus have dynamic ranges from 40 - 100 dB.

5. It is concluded that few, if any, single cochlear fibres and monotonic units in the cochlear nucleus can code signal level differences over intensity ranges comparable with the psychophysically determined dynamic range for humans.

6. That some neurones in the cochlear nucleus do show discharge rate changes in response to stimulus changes over a wider intensity range than single cochlear fibres, suggests that intensity is encoded in some dimension of the discharge of the fibres of the cochlear nerve other than the mean discharge rate of a single cochlear fibre. It is quite possible in this case that it is the spread of activity in the cochlear fibre array which is the relevant factor in the encoding of tonal stimuli at the high intensity levels.

CHAPTER FOUR: ADAPTATION AND THE RESPONSES TO INCREMENTS IN INTENSITY

4.1 Introduction

The responses of peripheral sensory neurones to a constant intensity stimulus are maximal at the stimulus onset and decay to a relatively steady level. This process is known as adaptation (e.g. Adrian and Zotterman, 1926) and appears to be a universal property of cochlear nerve fibres (e.g. Nomoto et al., 1964; Kiang et al., 1965a) and occurs in many cochlear nucleus cells (e.g. Rose et al., 1959; Pfeiffer, 1966; Mast, 1970a). Several mechanisms have been proposed to account for adaptation, the most widely accepted of which suggests that adaptation is the result of decreases in sensitivity or of the system gain. 'Gain control' mechanisms have been proposed to account for adaptation in Limulus photoreceptors (by Fuortes and Hodgkin, 1964) and in cochlear nerve fibres (by Siebert and Gambardella, 1968; Schroeder and Hall, 1973; and Evans, 1974).

If the adaptation observed in cochlear fibres is the result of a gain control mechanism, adaptation might well serve to extend the limited dynamic range of cochlear fibres to stationary tonal stimuli. One means of testing such a suggestion would be to determine the response of a cochlear fibre to a stimulus after adaptation has occurred. This could be accomplished by presenting a relatively long stimulus and determining the response to a second stimulus presented at some time after the onset of the adapting stimulus. If the two stimuli are of equal frequency, this is equivalent to determining the response of the neurone to an increment in the intensity of the adapting stimulus. The responses of single neurones to intensity increments are also of considerable interest when making comparisons with psychophysical data, since several studies of intensity discrimination

have used a paradigm which consisted of incrementing the intensity of a longer duration stimulus (e.g. Pollack, 1951; Miller, 1947; Harris, 1963). The comparison drawn in Chapter 3 was between the psychophysically determined dynamic range for intensity discrimination and the dynamic range of single neurones to stationary tonal stimuli. Thus since some of these psychophysical data were obtained using increments, it is of interest to determine the responses of single neurones to intensity increments and whether such responses are predictable from a knowledge of the neurones' responses to stationary tonal stimuli. One study in which the responses to intensity increments were measured, was that of Smith and Zwislocki (1971). These authors addressed themselves to the question of whether the responses of a primarylike cochlear nucleus cell to a small increment in the intensity of a CF tone burst, depended upon the adaptation which had preceded the occurrence of the increment.

They used stimuli which consisted of a 250 ms CF tone burst (the 'pedestal') which could be incremented in intensity by the addition of a short tone burst (20 ms) of the same frequency and phase. They determined peristimulus time histograms (using 10 ms bin size) in response to the pedestal and also in response to a pedestal and an increment which occurred at various delays after the pedestal onset. Their findings may be summarised as follows: the increase in firing rate due to a <u>small</u> increment in the pedestal intensity was independent of the time delay from its onset after that of the pedestal. However, the increase in firing rate due to a <u>large</u> increment in the pedestal intensity, increased as a function of the time delay of its onset after that of the pedestal. For sufficiently large increments in the pedestal intensity, the firing rate measured at the onset of the increment became independent of the time delay of the increment from the pedestal onset and approximated to the onset saturation firing rate. It was suggested by Smith and Zwislocki that the size of the increase in the firing rate, due to an increment in

the pedestal intensity, remained independent of the delay of its onset after that of the pedestal unless the total intensity (the intensity of the pedestal and that of the increment together) was sufficient to cause saturation of the firing rate measured at the pedestal onset. When the overall intensity did cause saturation of the onset firing rate the increase in firing rate due to the increment became larger as the delay of the increment from the pedestal onset was increased.

From these data Smith and Zwislocki came to the following main conclusions which are subject to certain qualifications as discussed below:

1. Whatever process was responsible for the adaptation of the firing rate had no effect on the response of the neurone to intensity increments.
2. The firing rate measured at the pedestal onset saturates at one level while the firing rate measured 100 ms after the onset of the pedestal saturates at a lower level.*
3. The saturation of the firing rate measured 100 ms after the onset of the pedestal does <u>not</u> limit the size of the response to increments in intensity.

The first conclusion is indeed consistent with their data. The remaining two conclusions, however, which are of crucial importance to the question of how increments are encoded in the discharge of

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* Implicit in Smith and Zwislocki (1971) and indeed in their subsequent publications (Smith, 1973; Smith and Zwislocki, 1975) is the notion that the discharge of single cochlear fibres falls to a relatively steady rate after about 150 ms. In fact this is only true when suitable time intervals are used to average the discharge rate. The discharge rate is approximately proportional to the logarithm of the time after the stimulus onset; a single time constant cannot therefore be defined. Thus the firing rate after 150 ms is only 'steady state' (their terminology) within the context of a relatively short tone (e.g. 200 ms) and using small bin sizes (e.g. 10 ms) to construct PSTHs.

peripheral auditory neurones, could not be arrived at from the data presented in the paper, primarily because the data were collected only over a 10 dB range of intensity. The 'levels' referred to in conclusion 2 presumably refer to level of discharges rather than intensity level since in the figure which is used to illustrate this conclusion (reproduced in Fig. 38A) the firing rate measured 100 ms after the pedestal onset has not unequivocally saturated whilst the firing rate measured at the pedestal onset appears to be approaching saturation. This is shown more clearly if the data are replotted on the more usual linear firing rate versus the logarithm of the intensity axes shown in Fig. 38B. Since the firing rate measured 100 ms after the onset of the pedestal has not definitely reached saturation, it is not possible to determine whether saturation of this firing rate does in fact limit the increase in firing rate in response to an increment occurring 100 ms after the pedestal onset. Indeed, from the fact that the firing rate at the onset of large increments in the pedestal intensity, approximates to the onset saturation firing rate, irrespective of the time of the occurrence of the increment, it would appear that the size of the increase in firing rate to an increment seems to be limited by saturation of the onset firing rate.

This brief consideration of the data and conclusions of Smith and Zwislocki (1971) suggests that several important questions raised by the paper have not been satisfactorily answered as these authors only employed a limited range of intensities. It has not been shown whether the firing rate measured at a delay after the stimulus onset does saturate at a lower level than the onset firing rate (whether 'level' refers to either firing rate or intensity). Further, and more significantly, it has not been shown whether small increments in intensity, superimposed a few hundred milliseconds after the pedestal onset, will still

Figure 38A

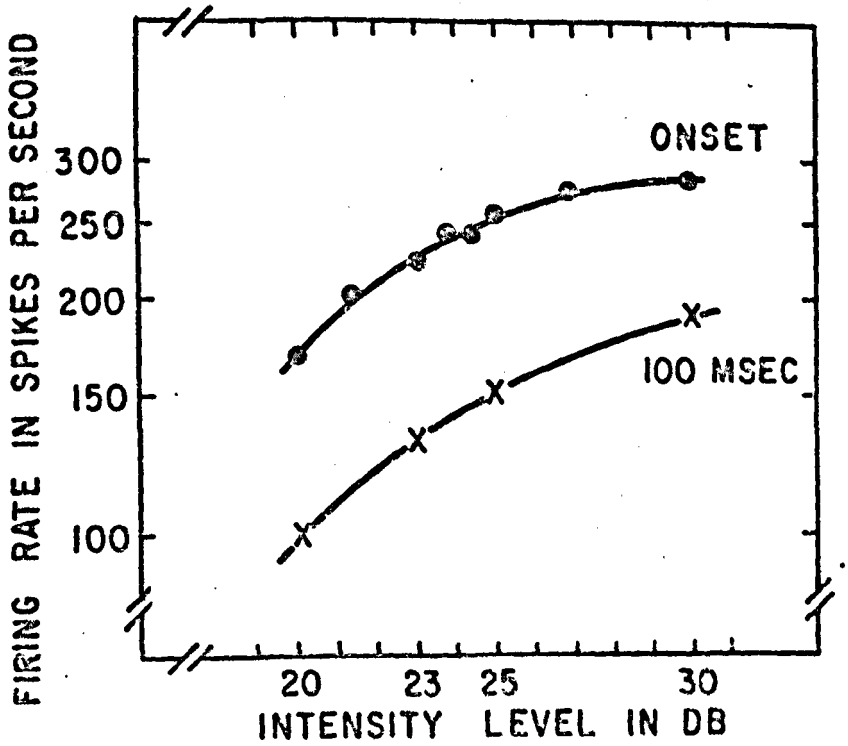
Rate versus intensity functions for the firing rate measured at the onset and after 100 ms in response to a CF pedestal.

(From Smith and Zwislocki, 1971.)

Figure 38B

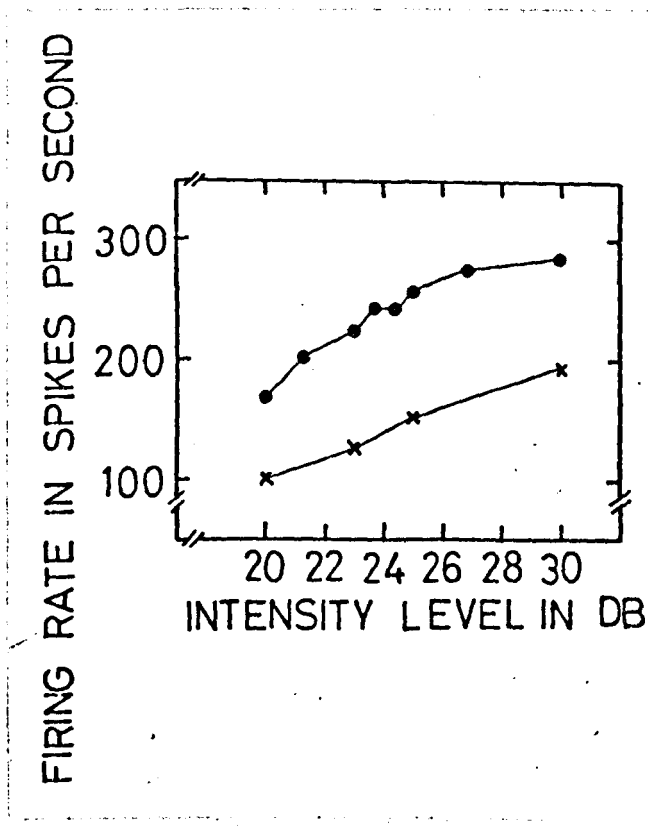
The same data as in Figure 38A but replotted on a linear firing rate scale. Symbols as in Figure 38A.

Figure 38A



Intensity functions produced by the pedestal alone at onset and at a time delay of 100 msec. Firing rates computed using 10-msec intervals. Unit C-11-5; CF—2.01 kHz.

Figure 38B



produce firing rate increases at intensity levels in excess of those at which the firing rate to the pedestal alone measured at this delay is fully saturated (as is suggested by the conclusions of Smith and Zwislocki).

Thus the present study was initiated, in which a similar paradigm to that of Smith and Zwislocki was used (for details of the exact method see Section 4.2), butthe analyses were performed over a wider range of intensities in order to directly test the conclusions of the earlier study of Smith and Zwislocki (1971).*

The results indicate that the firing rate measured 180 ms after the pedestal onset does indeed saturate at a lower discharge rate than the onset firing rate, but in many units this saturation occurs at a higher intensity level than for the onset firing rate. In the majority of neurones the responses to increments occurring 180 ms after the pedestal onset <u>were</u> limited by the saturation of the firing rate measured at this delay. However, for a minority of units in the present sample, responses to increments occurring at 180 ms after the pedestal onset were found at intensity levels beyond those at which the firing rate at this delay was saturated. These data are described in detail and discussed in relation to the more recent data of Smith (1973) and Smith and Zwislocki (1975) and to some psychophysical data on intensity discrimination and masking.

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* When this study was initiated only the data of Smith and Zwislocki (1971) were available. Subsequently Smith (1973) and Smith and Zwislocki (1975) have published more extensive data. In Smith (1973) some limited data were reported which were collected over a wide range of intensity and is in general consistent with the findings of the present study. These more recent data are discussed fully in Section 4.4.

4.2 Methods

An increment in the intensity of a 200 ms tone burst was produced by addition of a 20 ms tone burst of the same frequency and phase (the pedestal was produced by Dymar type 741 via Gate 2, Fig. 24 and the increment by Dymar type 741 via Gate 3, Fig. 24) either at the initial or final 20 ms (see Fig. 39). Both tone bursts had linear rise and fall of duration 5 ms. Increments of 3 and 6 dB were obtained by suitable attenuation of the 20 ms tone burst (using Step Attenuator C see Fig. 24). The frequency used was always equal to the CF of the unit under study.

Mean responses to twenty repetitions of the pedestal were compared with mean responses to twenty repetitions of the pedestal and increment. The two different stimuli were alternated at a rate of one presentation every 800 ms to reduce the effects of fluctuations in sensitivity, spontaneous rate or habituation effects.

This alternation was achieved by means of four Tektronix waveform generators, as illustrated in Fig. 40 (two Type 162 and two Type 161). The pulse output of the 162A triggered a second 162 generator and the sawtooth outputs of both were used to trigger two 161 square wave generators (see Fig. 40). Thus gating signals for the increment tone signal were produced only for every other pedestal gating signal (see Fig. 39).

The intensity of the tones was stepped in 10 dB intervals from below the threshold of the unit to intensities driving the unit at maximum (saturation) rate. The responses to twenty presentations of the pedestal and twenty of the tone on pedestal, forty in all were recorded on analogue magnetic tape for analysis after the experiment. Analysis during the experiment consisted of separately accumulating the spike counts during the initial and final 20 ms periods of a presentation.

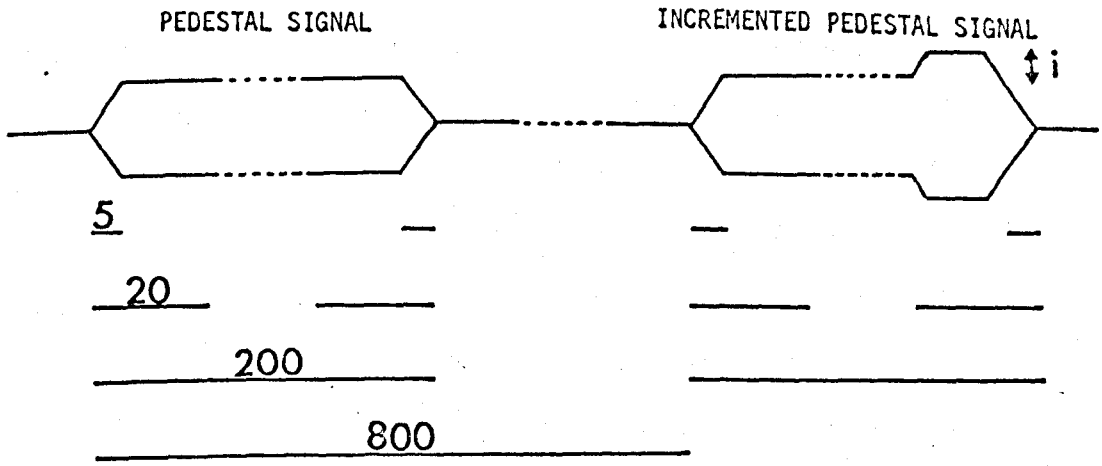
Figure 39

The stimulus paradigm used to compare the responses of single neurones to a non incremented and an incremented CF pedestal. The figures which indicate the rise/fall time, increment duration, the pedestal duration and the repetition period, respectively, are all in milliseconds. 'i' represents the intensity increment which was either 3 or 6 dB.

Figure 40

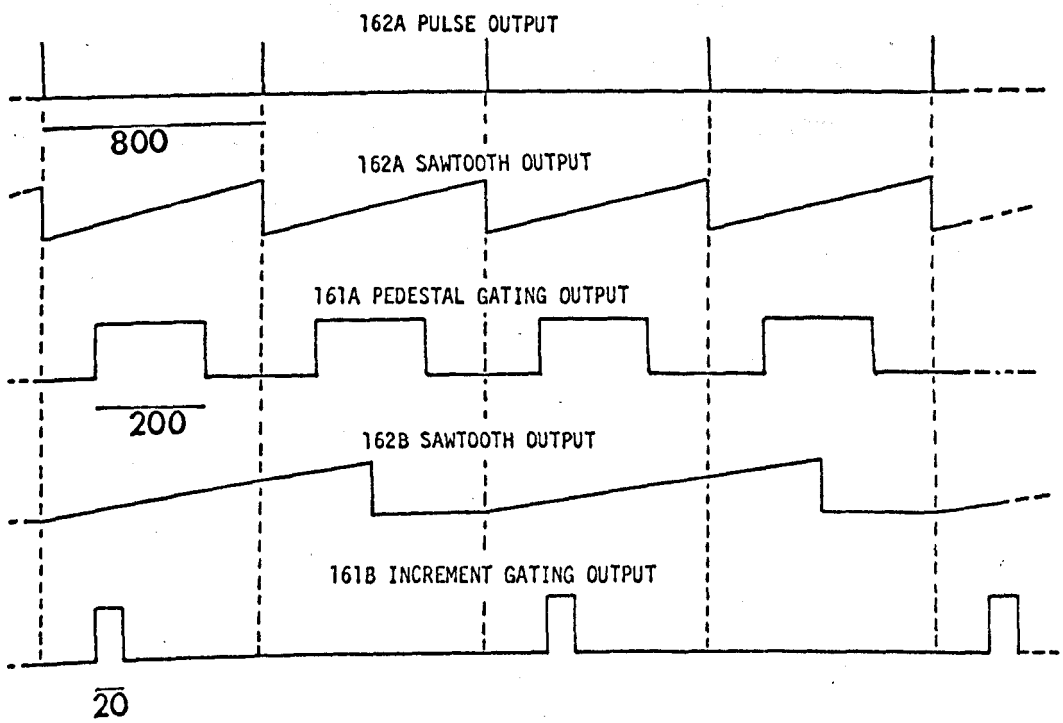
The outputs of the four Tektronix waveform generators which produced an increment to the intensity of alternate pedestals (see text for full details). The figures which indicate the repetition period, the pedestal duration and the increment duration, respectively, are all in milliseconds.

Figure 39



STIMULUS PARADIGM USED IN THE INCREMENTAL STUDIES

Figure 40



TEKTRONIX WAVEFORM GENERATOR OUTPUTS

This was done by event counters, two for the pedestal stimulus and two for the incremented pedestal stimulus, with a suitable gating network which switched the responses to the appropriate counters. (For block diagram see Appendix A.) Analysis after the experiment consisted of

1. Construction of PSTHs, these were generated by replaying the analogue magnetic tape record of the unit's responses to twenty repetitions of the pedestal and pedestal and increment stimuli. The responses to the two different stimuli were fed via the event counter gating network and into separate channels of a Nuclear Chicago Data Retrieval Computer which was triggered from voltage pulses from the Tektronix 162A recorded on another track of the analogue recorder. The PSTHs were therefore built up from the responses to alternate stimuli which were fed to different channels of the computer.

2. The raw single unit responses were replayed from the analogue recorder onto an oscilloscope and photographed using a Grass Instrument Co. Kymograph camera, model C4N, giving permanent records of the S/N ratio which were used to ensure that only a single neurone was discriminated.

4.3 Results

For the purposes of this study, units which had primary-like discharge characteristics (see Section 1.6.2) and therefore had the adaptation characteristics described by Smith and Zwislocki, were studied. The electrodes were aimed to traverse the AVCN in order to obtain as many primary-like units as possible. In the course of these experiments, however, several DCN units were also examined, some of which had non-monotonic discharge characteristics.

The accumulated spike counts obtained during the experiment (see Section 4.2) were converted to spikes/sec and plotted as discharge rate versus intensity (e.g. Fig. 43). The firing rates measured at the onset and after 180 ms of both the pedestal and pedestal + increment are plotted in each figure, thus enabling direct comparison.

The dynamic range for the firing rates measured at the onset and after 180 ms and for the increase in firing rate to an intensity increment were obtained using the criteria described in Section 3.2, from smoothed curves drawn by eye through the data.

4.3.1 Adaptation

The first point to emerge from the data was that (as in the cochlear fibre data of Kiang et al. (1965a)), with the exception of levels close to the unit's threshold, adaptation occurred in primary-like cochlear nucleus cells at all levels tested including those at which the discharge rate is saturated. This can be deduced from the fact that the firing rates measured at the pedestal onset (filled circles and continuous lines, Figs. 43 to 48) are consistently higher than firing rates measured at 180 ms after the onset (open triangles and dashed lines, Figs. 43 to 48). The amount of adaptation which occurs, however, varies from neurone to neurone as can be seen by

comparison of inset 1, Fig. 43 with inset 1, Fig. 44. The upper PSTH in each inset is the response to the incremented pedestal and the lower to the non-incremented pedestal. Thus if one compares the lower PSTHs it is evident that the amount of adaptation occurring in unit 236.08 (Fig. 43) is much less than in unit 236.17 (Fig. 44). This comparison is between responses to a single intensity level (which is in fact different for the two units) and while the amount of adaptation occurring in many units was independent of the pedestal intensity in other units the amount of adaptation varied as a function of the pedestal intensity. This is illustrated in Fig. 41, in which the firing rate at the pedestal onset is plotted against the firing rate after 180 ms. For units 236.08 and 236.09 (Fig. 41, a and b) the points all fall approximately on a single line indicating that the ratio of the onset firing rate to that measured at 180 ms is constant and hence the relative adaptation occurring is constant. Although intensity is not an explicit variable in these plots, it is implicit since the higher firing rates are evoked by the higher intensities. Thus for units 236.08 and 236.09 the adaptation occurring is constant as a function of intensity including those levels at which the onset firing rate is saturated.* For the remaining two units in Fig. 41 (236.17 and 292.09) the points deviate from a single line at onset firing rates of 400 and 250 spikes/sec respectively, indicating that the relative adaptation occurring decreases. It can be seen in Fig. 44 that an onset discharge rate of 400 spikes/sec for unit 236.17 is approaching the saturation of the onset firing rate. From this and other similar plots it can be concluded that for those units in which the amount of adaptation decreases with intensity, the decrease begins at the intensity at which the onset firing rate begins to saturate.

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* 400 sp/sec for 236.08 and 450 sp/sec for 236.09 from Figs. 43 and 45 respectively.

Of thirty-one units for which sufficient data was obtained to allow such analysis, sixteen showed constant adaptation at all intensity levels and the remaining fifteen showed a decrease at high discharge rates (and hence at high intensity levels).

The inference from these data is that, for some units, the firing rates measured at the pedestal onset and at 180 ms will have different dynamic ranges. The onset discharge rate adapts less at intensity levels beyond those at which it saturates and the firing rate at 180 ms therefore continues to increase with intensity and will therefore have a wider dynamic range. For those units which show constant adaptation with increasing intensity, the onset saturation rate will always adapt to the same rate at 180 ms and hence the dynamic ranges of the two firing rates will be equal.

This has been investigated directly by plotting the firing rates at onset and 180 ms against the pedestal intensity. These data are described in the following section.

4.3.2. Dynamic Ranges of the Firing Rates Measured at the Onset and After 180 ms in response to a Pedestal & duringan Intensity Increment

As was suggested in the introduction to this chapter, in addition to the question of whether the firing rates measured at the onset and after 180 ms of a pedestal saturate at the same firing rate or intensity level, the question of whether such saturation limits the response to small intensity increments has also been investigated. This has been accomplished by measuring the discharge rates in response to alternated incremented and non-incremented pedestals (see Section 4.2).

Two different increments have been used, 3 dB and 6 dB. There were no significant qualitative differences between the responses of

different units to the two increment sizes, although both sizes of increment were not used on a single unit so no direct comparison has been made. The values 3 and 6 dB were chosen to be small relative to the pedestal intensities and to allow direct comparison with previously reported data.

The firing rates measured at the onset and after 180 ms of the non-incremented pedestal and during an increment occurring either at the onset or after 180 ms have been plotted against the pedestal intensity. The incremental firing rate was defined by taking the difference between the responses to the incremented and non-incremented pedestals at the appropriate times after onset. Comparison of the dynamic ranges for the onset, 180 ms and incremental firing rates for each unit revealed four main types of response (labelled arbitrarily A, B, C and D).

Units in response types A, B and C all exhibit monotonic rate versus intensity functions and those of type D have non-monotonic rate versus intensity functions. Types A, B and C are illustrated diagrammatically in Fig. 42. Units of type A have dynamic ranges for all three firing rates which are equal. Type B units have dynamic ranges for the incremental and 180 ms firing rates which are equal and wider than for the onset firing rate. Type C units have equal dynamic ranges for the onset and 180 ms firing rate but the dynamic range for incremental firing rate is wider. Units of type D all have non-monotonic rate versus intensity functions but in other respects represent a mixture of response types. It was not possible to formulate generalisations with respect to the measured firing rates which applied to all of the units in category D and therefore several types of response are described in Section 4.3.2.4.

It should be pointed out, however, that the types of response labelled A, B and C are separable only in terms of differences in the dynamic ranges of the onset, 180 ms and incremental firing rates. In terms of their maximum dynamic range the three groups are not separable; the maximum dynamic ranges of units in groups A, B and C respectively were 70, 72 and 80.

Figure 41

Plots of the firing rate for 4 units 236.08, 236.09, 236.17 and 292.09, labelled accordingly, in response to 20 repetitions of a pedestal measured at the onset versus the firing rate measured 180 ms after the pedestal onset. Both firing rates were averaged over a 20 ms period. The dashed lines represent the level of spontaneous activity. The filled circles represent values obtained as the intensity was progressively increased and the open triangles values obtained as the intensity was progressively decreased.

Figure 42

Schematic representations of the three types of response A, B and C.

Figure 41

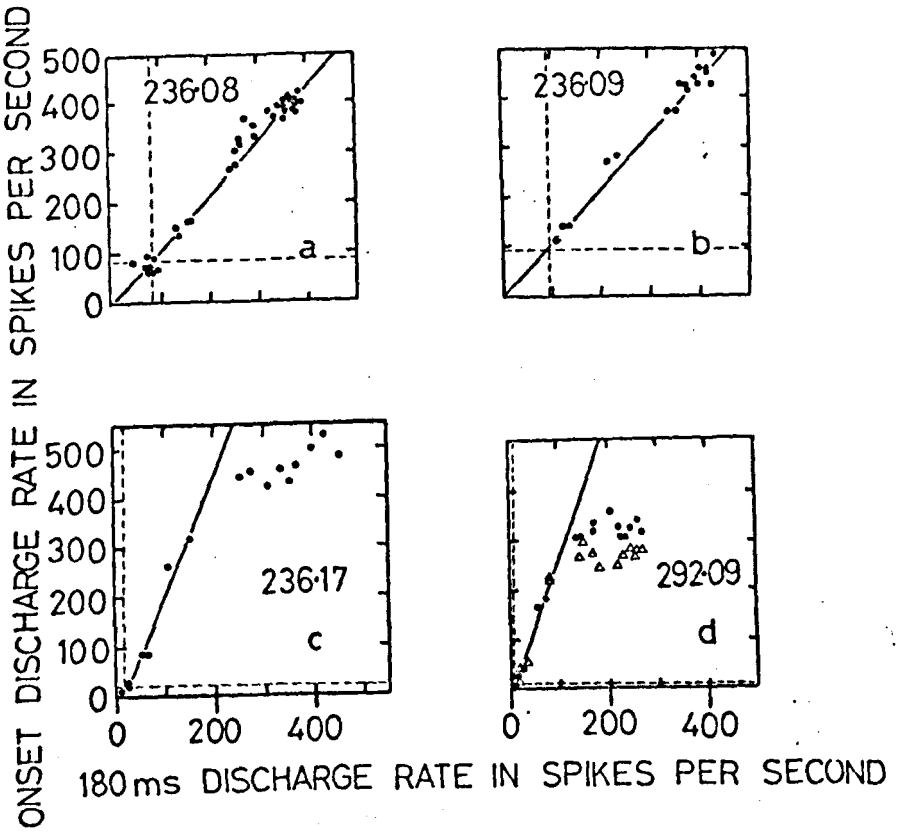
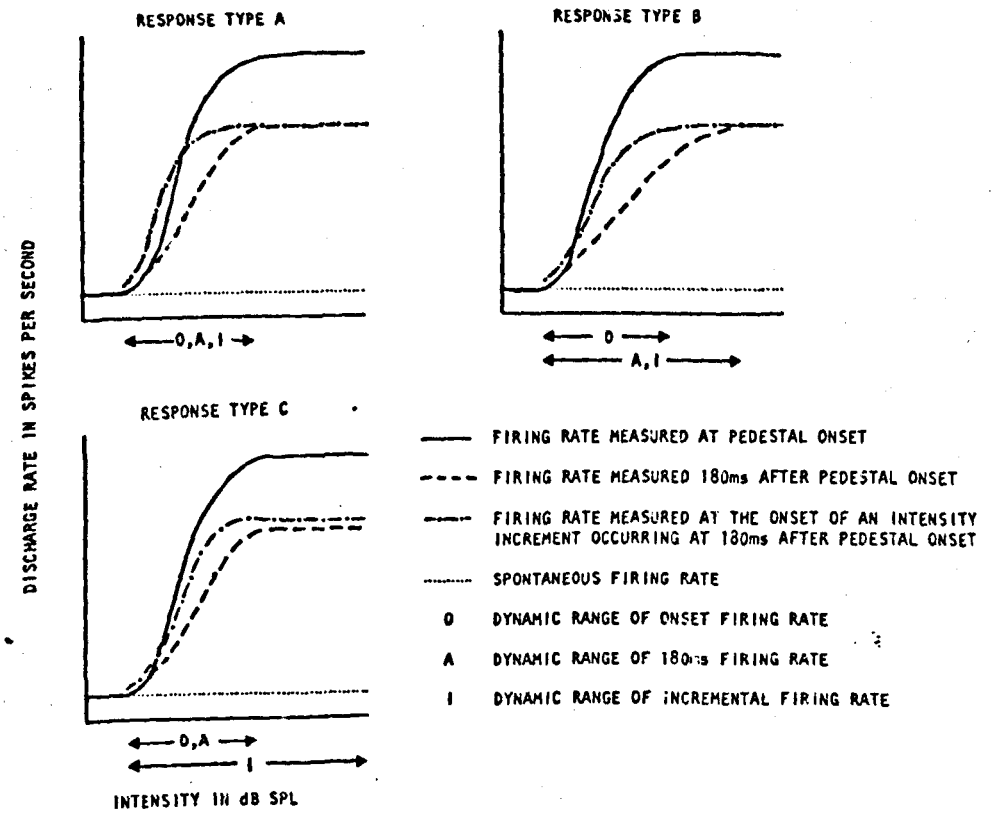


Figure 42



Sufficient data were obtained on thirty-two units to enable division into the differing response types. Of these thirty-two, twenty were located in the VCN, seven in the DCN and five in the region of small cells which separates the VCN and DCN.

4.3.2.1 Type A: Units in which the dynamic ranges of the firing rates in response to a pedestal measured at its onset and after 180 ms and during an intensity increment irrespective of its delay from pedestal onset were all equal (11 units)

A typical example of this type of response was shown by unit 236.08 which is illustrated in Fig. 43. Considering first Fig. 43A, the firing rate measured at the onset (filled circles and continuous lines) and at 180 ms (open triangles and dashed lines) in response to a pedestal show clear saturation above 40 dB SPL. The dynamic ranges for the firing rates measured at both the onset and after 180 ms are therefore 49 dB. The firing rate measured during a 6 dB increment which coincided with the pedestal onset (filled squares and dot-dash lines, in Fig. 43A), became equal to the onset response to a non-incremented pedestal at 40 dB SPL. The incremental firing rate (open squares) therefore falls to zero at the intensity level at which the onset response to the non-incremented pedestal saturates and therefore also has a dynamic range of 49 dB. Not surprisingly, there is reasonable agreement between the measured incremental firing rate (open squares) and the incremental response predicted by taking the firing rate from the onset firing rate versus intensity function at the intensity corresponding to the pedestal and increment (open circles).

In Fig. 43B the filled squares and dot-dash line indicates the firing rate measured during a 6 dB increment occurring 180 ms after the pedestal onset. This firing rate becomes equal to that of

Figure 43

Responses of a cochlear nucleus unit (CF 3.15 kHz) to an incremented and a non-incremented pedestal (increment size 6 dB). Figure 43A shows the responses to a non-incremented and an onset incremented pedestal. Figures 43B and C show the responses to a non-incremented pedestal and to a pedestal incremented at 180 ms after its onset. Figure 43B was obtained by progressively increasing the pedestal intensity and Figure 43C by progressively decreasing the pedestal intensity. Tha arrow against the ordinate indicates the level of spontaneous discharges.

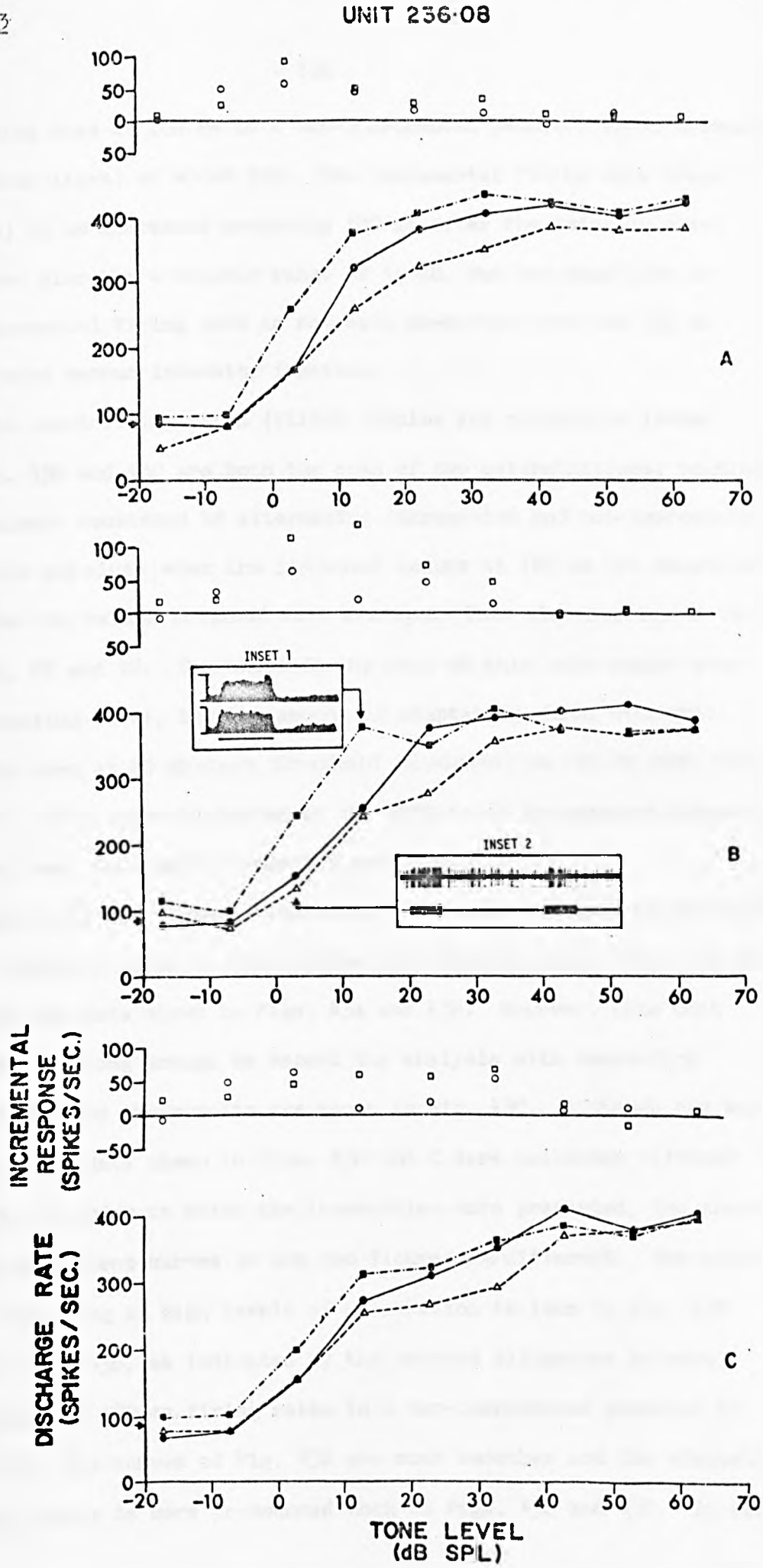
Inset 1 - PSTHs obtained by averaging 20 repetitions of both incremented (upper) and non-incremented (lower) pedestals of the intensity level indicated by the arrow. The bin-width is 5 ms and the vertical calibration is 40 spikes/bin.

Inset 2 - A sample of the raw data (upper trace) obtained at the intensity level indicated by the arrow to an incremented and non-incremented pedestal as indicated by the lower trace.

KEYS

A	1) ●——●	Firing rate measured over 20 ms beginning at pedestal onset.
	2) △- - -△	Firing rate measured over 20 ms beginning 180 ms after pedestal onset.
	3) ■-·-·■	Firing rate measured over the initial 20 ms of an increment in intensity presented at the onset of the pedestal.
	4) □ □	Increase in firing rate produced by the increment in the pedestal intensity (i.e. the difference between 1) and 3) above).
	5) ○ ○	Increase in firing rate produced by the increment in the pedestal intensity as predicted from 1) above.
B & C	1) ●——●	As in A above.
	2) △- - -△	As in A above.
	3) ■-·-·■	Firing rate measured over the initial 20 ms of an increment in intensity presented 180 ms after pedestal onset.
	4) □ □	Increase in firing rate produced by the increment in pedestal intensity (i.e. the difference between 2) and 3) above).
	5) ○ ○	Increase in firing rate produced by the increment in pedestal intensity as predicted from 2) above.

Figure 43


UNIT 236-08
A
B
C
INSET 1
INSET 2
INCREMENTAL RESPONSE (SPIKES/SEC.)
DISCHARGE RATE (SPIKES/SEC.)
TONE LEVEL (dB SPL)

the firing rate at 180 ms to a non-incremented pedestal (open triangles and dashed lines) at 40 dB SPL. The incremental firing rate (open squares) to an increment occurring 180 ms after the pedestal onset therefore also has a dynamic range of 49 dB, but the magnitude of the incremental firing rate is not well predicted from the 180 ms firing rate versus intensity function.

The onset firing rates (filled circles and continuous lines) of Figs. 43B and 43C are both the mean of two determinations; routinely the analysis consisted of alternating incremented and non-incremented pedestals and since when the increment occurs at 180 ms the onsets are equivalent the two values obtained were averaged. This also applies to Figs. 44B, 45, 46B, 47 and 48. The onset firing rate of this unit adapts even at saturation rates, but the amount of adaptation which this unit exhibits even at 20 dB above threshold is minimal as can be seen from inset 1 Fig. 43. (The upper histogram is the PSTH to an incremented pedestal and the lower to a non-incremented pedestal.)

Routinely the presentation of the pedestals was made sequentially in an ascending order of intensities (see Section 4.2). This was the case for the data shown in Figs. 43A and 43B. However, this unit was held for long enough to repeat the analysis with descending intensities and the results are shown in Fig. 43C. Although the way in which the data shown in Figs. 43B and C were collected differed only in the order in which the intensities were presented, the shapes of the equivalent curves in the two figures are different. The adaptation occurring at high levels of stimulation is less in Fig. 43C than in Fig. 43B, as indicated by the reduced difference between the onset and 180 ms firing rates to a non-incremented pedestal in Fig. 43C. The curves of Fig. 43A are much smoother and the adaptation at high levels is more pronounced than in Figs. 43B and 43C. In fact

there is a gradual progression from Fig. 43A through Fig. 43B to Fig. 43C; the adaptation becomes less pronounced and the curves less smooth. This reflects the order in which these data were collected since the data of Fig. 43A were collected first followed by that of Fig. 43B and then that of Fig. 43C. Thus it would appear that the differences between the three sets of rate versus level functions of Fig. 43 are due to the fatiguing effects of prior high level stimulation, not to such factors as the reversal of the presentation order.

For the eleven units showing this type of response the mean dynamic range (for onset, 180 ms and incremental firing rates) was 46.1 dB with a standard deviation of 14.5 dB and a range of 24 - 70 dB.

4.3.2.2 Type B: Units in which the dynamic ranges of the firing rates measured at 180 ms after the onset of a pedestal or during an intensity increment occurring at 180 ms from the pedestal onset were equal and were wider than that of the firing rate measured at the pedestal onset (6 units).

A typical example of this type of response is shown in Fig. 44, for unit 236.17. Fig. 44A shows the response of the unit to a CF tone pedestal and to a CF tone incremented by 6 dB at its onset. The onset firing rate (filled circles and continuous lines) to the non-incremented pedestal is saturated at 47 dB SPL and has a dynamic range of 30 dB. The firing rate measured during a 6 dB intensity increment which occurred at the start of a pedestal became equal to the onset firing rate to a non-incremented pedestal at 47 dB SPL and the incremental firing rate (open squares, Fig. 44A) also therefore had a dynamic range of 30 dB. The incremental firing rate to an onset incremented pedestal is again reasonably well predicted by the onset firing rate versus intensity function (open circles) to the non-incremented pedestal.

Figure 44

Responses of a cochlear nucleus unit (CF 0.39 kHz) to a non-incremented and an incremented pedestal (increment size 6 dB). Figure 44A shows the responses to a non-incremented and an onset-incremented pedestal. Figure 44 B shows the responses to a non-incremented pedestal and to a pedestal incremented at 180 ms after its onset. The arrow against the ordinate indicates the level of spontaneous discharges.

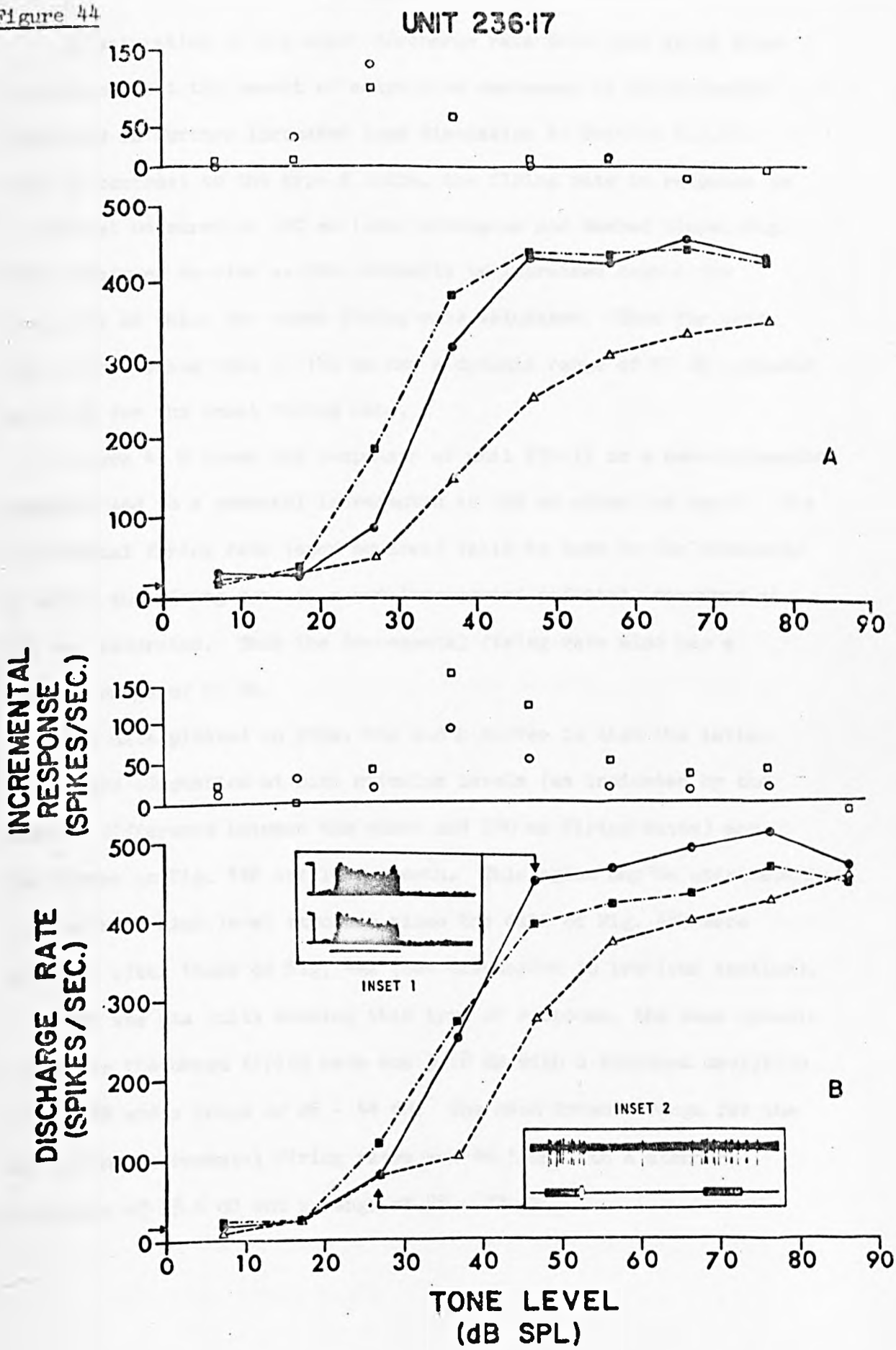
Inset 1 - PSTHs obtained by averaging 20 repetitions of both incremented (upper) and non-incremented (lower) pedestals at the intensity indicated by the arrow. The bin width is 5 ms and the vertical calibration 40 spikes/bin.

Inset 2 - A sample of the raw data (upper trace) obtained at the intensity level indicated by the arrow to an incremented and a non-incremented pedestal as indicated by the lower trace.

KEYS

A	1) ●——●	Firing rate measured over 20 ms beginning at pedestal onset.
	2) △- - △	Firing rate measured over 20 ms beginning 180 ms after pedestal onset.
	3) ■-·-■	Firing rate measured over the initial 20 ms of an increment in intensity presented at the onset of the pedestal.
	4) □ □	Increase in firing rate produced by the increment in the pedestal intensity (i.e. the difference between 1) and 3) above.
	5) O O	Increase in firing rate produced by the increment in the pedestal intensity as predicted from 1) above.
B	1) ●——●	As in A above.
	2) △- - △	As in A above.
	3) ■-·-■	Firing rate measured over the initial 20 ms of an increment in intensity presented 180 ms after pedestal onset.
	4) □ □	Increase in firing rate produced by the increment in pedestal intensity (i.e . the difference between 2) and 3) above).
	5) O O	Increase in firing rate produced by the increment in pedestal intensity as predicted from 2) above.

Figure 44


UNIT 236-17
INCREMENTAL RESPONSE (SPIKES/SEC.)
DISCHARGE RATE (SPIKES/SEC.)
A
B
INSET 1
INSET 2
TONE LEVEL (dB SPL)

At saturation of the onset discharge rate this unit still shows adaptation, but the amount of adaptation decreases as the stimulus intensity is further increased (see discussion in Section 4.3.1). Thus in contrast to the type A units, the firing rate in response to a pedestal measured at 180 ms (open triangles and dashed lines, Fig. 44A) continues to rise as the intensity is increased beyond the intensity at which the onset firing rate saturates. Thus for unit 236.17 the firing rate at 180 ms has a dynamic range of 57 dB compared to 30 dB for the onset firing rate.

Figure 44 B shows the responses of unit 236.17 to a non-incremented pedestal and to a pedestal incremented at 180 ms after its onset. The incremental firing rate (open squares) falls to zero at the intensity at which the firing rate to a non-incremented pedestal, measured at 180 ms, saturates. Thus the incremental firing rate also has a dynamic range of 57 dB.

The data plotted in Figs. 44A and B differ in that the latter shows less adaptation at high stimulus levels (as indicated by the reduced difference between the onset and 180 ms firing rates) and the curves in Fig. 44B are less smooth. This again may be attributable to the prior high level exposure since the data of Fig. 44B were obtained after those of Fig. 44A (see discussion in previous section).

For the six units showing this type of response, the mean dynamic range for the onset firing rate was 31.8 dB with a standard deviation of 7.0 dB and a range of 25 - 44 dB. The mean dynamic range for the 180 ms and incremental firing rates was 46.5 dB with a standard deviation of 15.6 dB and a range of 28 - 72 dB.

4.3.2.3 Type C: Units in which the dynamic ranges of the firing rates in response to a pedestal measured at its onset and after 180 ms were equal and were narrower than that of the firing rate measured during an intensity increment occurring at 180 ms after pedestal onset (4 units).

Unit 236.09 shown in Fig. 45 is an example of a type C response. In this unit the amount of adaptation occurring is independent of intensity up to and including intensities at which the onset firing rate saturates (as discussed in Section 4.3.1). Thus the firing rates measured at the onset (filled circles and continuous lines, Fig. 45) and at 180 ms (open triangles and dashed lines) in response to a pedestal, have the same dynamic range which in this case is 45 dB. In contrast to the response types A and B, however, the firing rate measured during a 6 dB increment occurring at 180 ms (filled squares and dot-dash lines, Fig. 45) remains consistently higher than the firing rate at 180 ms to a non-incremented pedestal. Thus the incremental firing rate (open squares, Fig. 45) for this unit has a dynamic range in excess of 80 dB.

The mean dynamic range for the onset and 180 ms firing rates for the four units in this category was 37.8 dB with a standard deviation of 8.1 dB and a range of 27 - 45 dB; this compares with a mean dynamic range for the incremented firing rate of 58 dB with a standard deviation of 16.1 dB and a range of 45 - 80 dB.

The dynamic range for the incremental firing rate of unit 236.09 is 77% greater than for the onset and 180 ms firing rates. For the remaining units of this type the increases were 25%, 74% and 39% (36 - 45, 27 - 47 and 43 - 60). Three of these units, including 236.09 were located in the VCN and the other in the DCN. One unit of this type has also been reported by Smith (1973).

Figure 45

Responses of a cochlear nucleus cell (CF 3.39 kHz) to a non-incremented pedestal and to a pedestal incremented by 6 dB at 180 ms after its onset. The arrow against the ordinate indicates the level of spontaneous discharges.

Inset 1 - PSTHs obtained by averaging 20 repetitions of both the incremented (upper) and non-incremented (lower) pedestals at the intensity indicated by the arrow. The bin width is 5 ms and the vertical calibration 40 spikes/bin.

Inset 2 - A sample of the raw data (upper trace) obtained at the intensity level indicated by the arrow to an incremented and a non-incremented pedestal as indicated by the lower trace.

KEY

1) ●——● Firing rate measured over 20 ms beginning at pedestal onset.

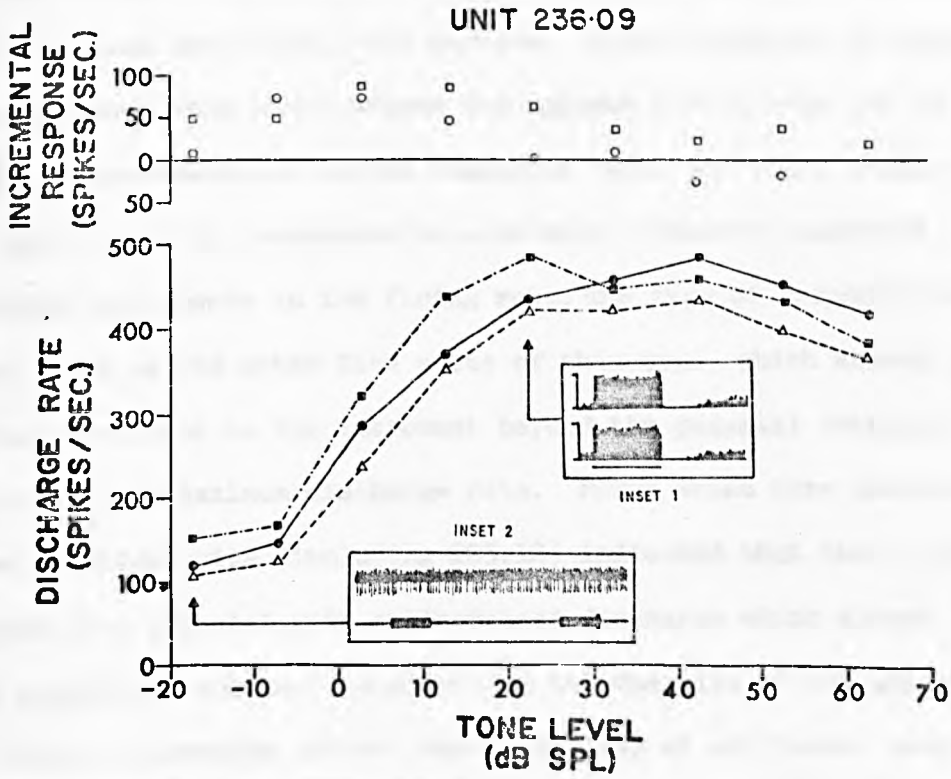
2) △- - -△ Firing rate measured over 20 ms beginning 180 ms after pedestal onset.

3) ■-·-·■ Firing rate measured over the initial 20 ms of an increment in intensity presented 180 ms after pedestal onset.

4) □ □ Increase in firing rate produced by the increment in pedestal intensity (i.e. the difference between 2) and 3) above).

5) O O Increase in firing rate produced by the increment in pedestal intensity as predicted from 2) above.

Figure 45


UNIT 236·09
INCREMENTAL RESPONSE (SPIKES/SEC.)
100
50
0
50
DISCHARGE RATE (SPIKES/SEC.)
500
400
300
200
100
0
INSET 1
INSET 2
-20
-10
0
10
20
30
40
50
60
70
TONE LEVEL (dB SPL)

4.3.2.4 Type D: Units with non-monotonic intensity rate functions (11 units)

The responses of these units are only alike in that none of them have monotonic rate functions. Six of these units showed a reduction at high levels of stimulus in both the discharge rates measured at onset and at 180 ms. An example of such a response is shown in Fig. 46 for unit 223.12. This unit is unusual in that 6 dB increments occurring at both the onset and at 180 ms produce increases in firing rate even beyond the firing rate maximum. Since increases in pedestal intensity beyond that which evokes the maximum firing rate (50 dB SPL, Fig. 46), cause decreases in the discharge rate, one would predict that small intensity increments to such high intensity pedestals would cause decrements in the firing rate. The type of response shown by unit 223.12 was not found in the other five units of this type, which showed no consistent response to the increment beyond the pedestal intensity which evoked the maximum discharge rate. PSTHs which were obtained for two of these units (including 223.12) indicated that these units responded to a pedestal with an increased discharge which showed little adaptation and was sustained for the duration of the pedestal. This temporal discharge pattern was maintained at all levels even those at which increases in stimulus level caused reduction in mean firing rate. Plots of discharge rates measured at the onset versus the discharge rate at 180 ms for these units indicated that the amount of adaptation was independent of level for four of the six units.

The remaining five units had complex temporal discharge patterns of the build-up or pauser type (Pfeiffer, 1966, described in Section 1.6.2). As a consequence the onset spike count at low stimulus levels was less than that measured at 180 ms. When the discharge measured at the onset of a pedestal is plotted against that measured at 180 ms

Figure 46

Responses of a cochlear nucleus unit (CF 2.5 kHz) to a non-incremented and an incremented pedestal (increment size 6 dB). Figure 46A shows the responses to a non-incremented and to an onset incremented pedestal. Figure 46B shows the responses to a non-incremented pedestal and to a pedestal incremented at 180 ms after its onset.

Inset 1 - PSTHS obtained by averaging 20 repetitions of both the incremented (upper) and non-incremented (lower) pedestals at the intensity indicated by the arrow. The bin width is 5 ms and the vertical calibration 40 spikes/bin.

Inset 2 - A sample of the raw data (upper trace) obtained at the intensity indicated by the arrow to an incremented and a non-incremented pedestal as indicated by the lower trace.

KEY

A

1) ●——● Firing rate measured over 20 ms beginning at pedestal onset.

2) △--△ Firing rate measured over 20 ms beginning 180 ms after pedestal onset.

3) ■-·-■ Firing rate measured over the initial 20 ms of an increment in intensity presented at the onset of the pedestal.

4) □ □ Increase in firing rate produced by the increment in the pedestal intensity (i.e. the difference between 1) and 3) above).

5) O O Increase in firing rate produced by the increment in the pedestal intensity as predicted from 1) above.

B

1) ●——● As in A above.

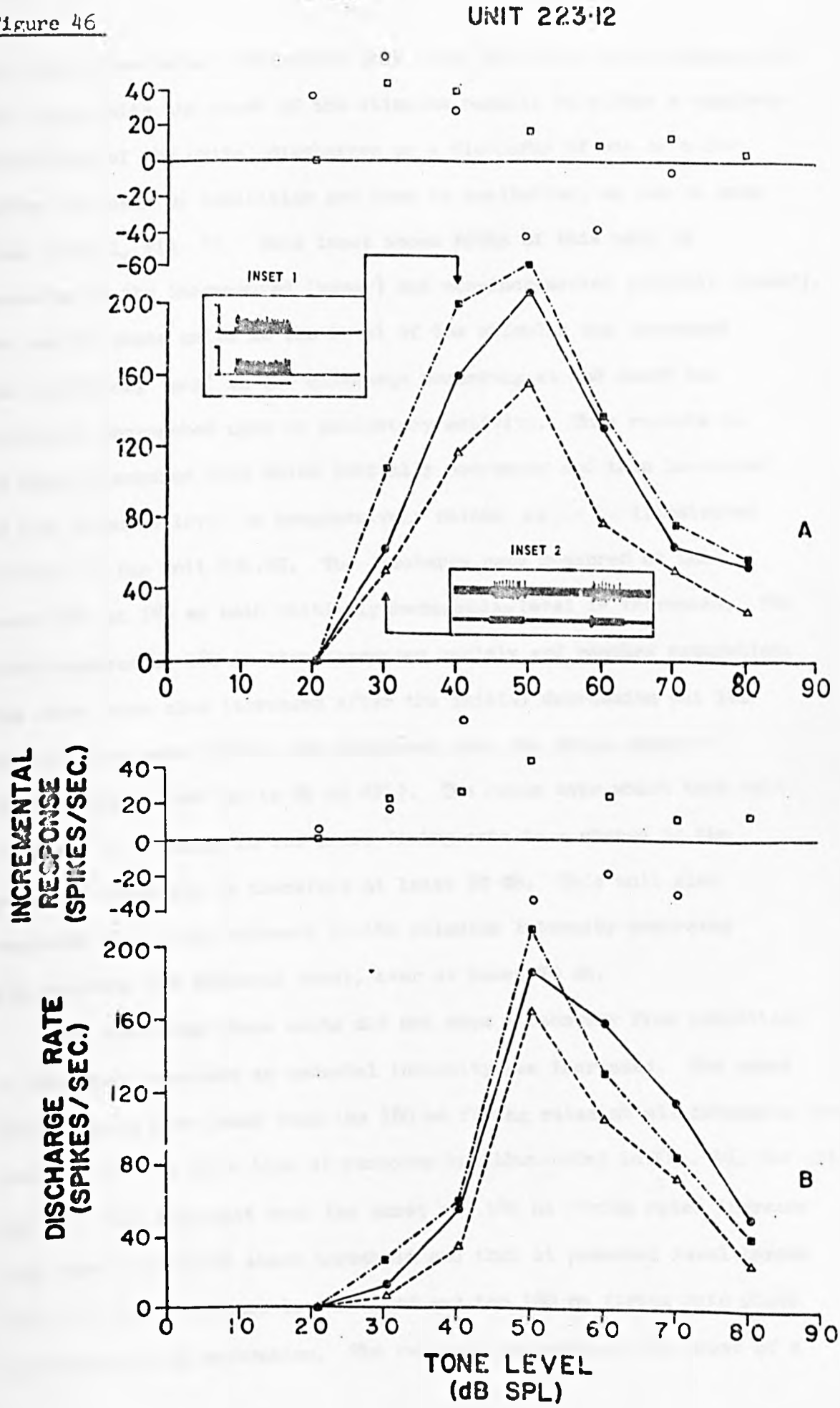
2) △--△ As in A above.

3) ■-·-·■ Firing rate measured over the initial 20 ms of an increment in intensity presented 180 ms after pedestal onset.

4) □ □ Increase in firing rate produced by the increment in pedestal intensity (i.e. the difference between 2) and 3) above).

5) O O Increase in firing rate produced by the increment in pedestal intensity as predicted from 2) above.

Figure 46


UNIT 223-12
INSET 1
INSET 2
A
B
INCREMENTAL RESPONSE (SPIKES/SEC.)
DISCHARGE RATE (SPIKES/SEC.)
TONE LEVEL (dB SPL)

for these five units, the points fall below the line of zero adaptation. For these units the onset of the stimulus results in either a complete inhibition of the units' discharges or a discharge of one or a few spikes followed by inhibition and then by excitation, as can be seen from inset 1, Fig. 47. This inset shows PSTHs of this unit in response to the incremented (upper) and non-incremented pedestal (lower). For two of these units as the level of the stimulus was increased the inhibitory 'gap' in the discharge occurring at the onset was gradually encroached upon by excitatory activity. This results in an onset discharge rate which initially decreases and then increases as the stimulus level is progressively raised as illustrated in Fig. 47 for unit 236.02. The discharge rate measured at the onset and at 180 ms both initially decreased as level is increased. The rate measured at 180 ms then increases rapidly and reaches saturation. The onset rate also increases after the initial depression but its rise is much more gradual and continues over the whole range of intensities tested (up to 80 dB SPL). The range over which this unit responds by a change in its onset firing rate to a change in the pedestal intensity is therefore at least 70 dB. This unit also responds to a 6 dB increment in the stimulus intensity occurring 180 ms after the pedestal onset, over at least 70 dB.

The ramaining three units did not show a recovery from inhibition of the onset response as pedestal intensity was increased. The onset firing rates were lower than the 180 ms firing rates at all intensity levels above 30 dB SPL. This type of response is illustrated in Fig. 48, for unit 292.03. For this unit both the onset and 180 ms firing rates increase over the first 10 dB above threshold and then at pedestal level beyond this the onset response is inhibited and the 180 ms firing rate rises monotonically to saturation. The response measured at the onset of a

Figure 47

Responses of a cochlear nucleus cell (CF 8.6 kHz) to a non-incremented pedestal and to a pedestal incremented by 6 dB at 180 ms after its onset.

Inset 1 - PSTHs obtained by averaging 20 repetitions of both the incremented (upper) and non-incremented (lower) pedestals at the intensity indicated by the arrow. The bin width is 5 ms and the vertical calibration is 40 spikes/bin.

Inset 2 - A sample of the raw data (upper trace) obtained at the intensity indicated by the arrow to an incremented and a non-incremented pedestal as indicated by the lower trace.

KEY

1) ●—● Firing rate measured over 20ms beginning at pedestal onset.
2) △- - -△ Firing rate measured over 20ms beginning 180 ms after pedestal onset.
3) ■-·-·■ Firing rate measured over the initial 20ms of an increment in intensity presented 180 ms after pedestal onset.
4) □ □ Increase in firing rate produced by the increment in pedestal intensity (i.e. the difference between 2) and 3) above).
5) o o Increase in firing rate produced by the increment in pedestal intensity as predicted from 2) above.

Figure 48

Responses of a cochlear nucleus unit (CF 10.3 kHz) to a non-incremented pedestal and to a pedestal incremented by 3 dB at 180 ms after its onset.

KEY

As in Figure 47.

Figure 47

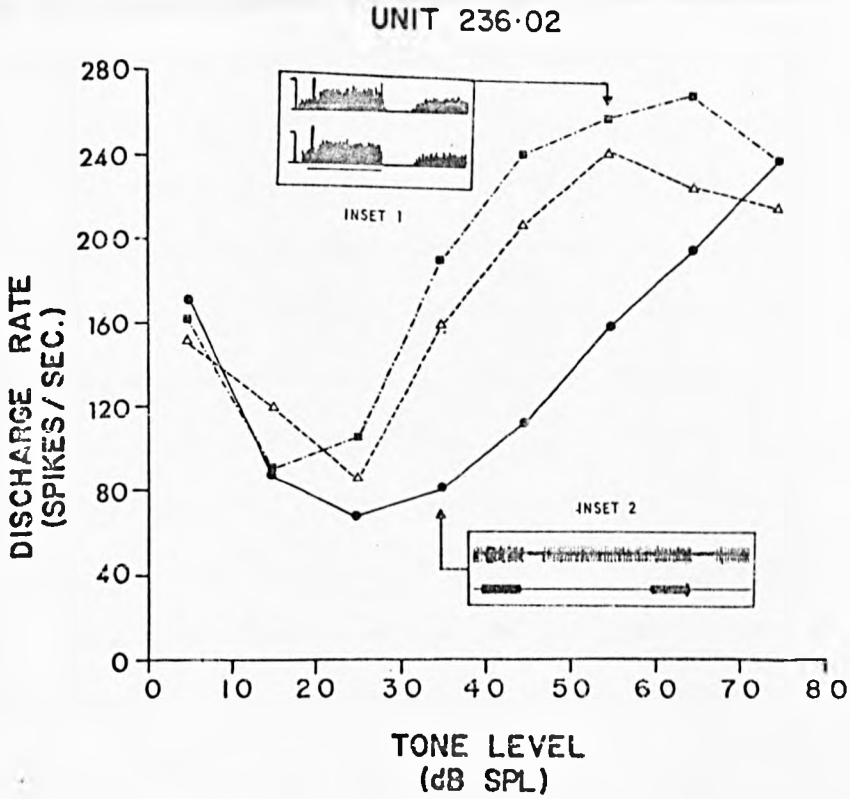
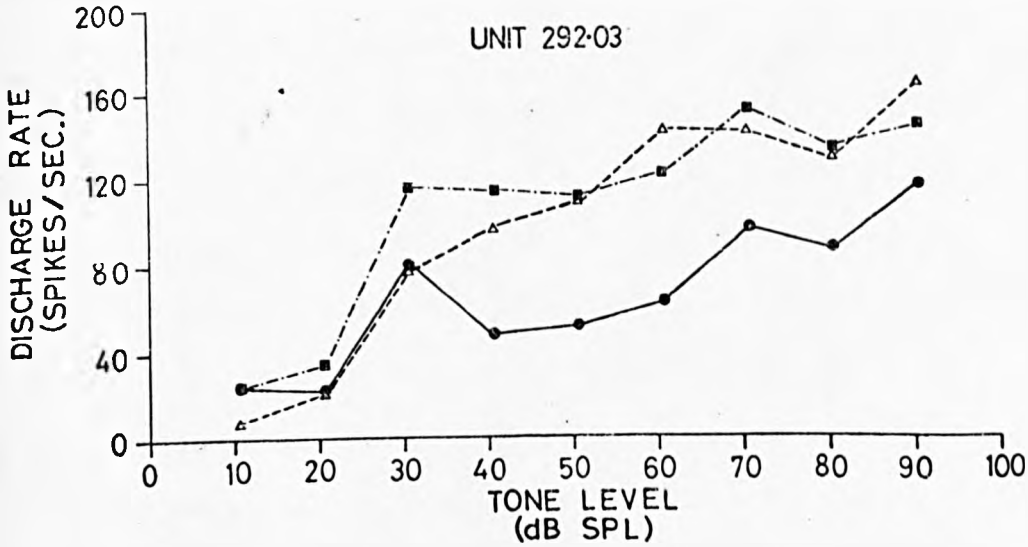


Figure 48



3 dB increment at 180 ms becomes equal to the 180 ms firing rate to the pedestal at intensity levels at which the latter saturates.

4.4 Discussion

As suggested in the introduction to this chapter, the data described in the foregoing were obtained in order to test the conclusions drawn by Smith and Zwislocki (1971). The first conclusion tested was whether the firing rate measured at some time after the pedestal onset saturated at a lower 'level' than the onset firing rate. It is clear from the present data that the firing rate of monotonic the cochlear nucleus cells, in response to a pedestal measured at 180 ms after its onset, does indeed saturate at a lower discharge rate than does the onset response. However, the intensity level at which the 180 ms firing rate saturates, is in some units, substantially higher than for saturation of the onset response. Thus, if the 'level' alluded to by Smith and Zwislocki referred to firing rate, the present data are consistent with their conclusion, whereas if the 'level' referred to is an intensity level the present data are inconsistent with their conclusion.

Smith and Zwislocki's second conclusion was that the saturation of the firing rate measured at 100 ms after the pedestal onset did not limit the neurones response to intensity increments. The responses of only a few neurones in the present study (those of response type C) were found to be in keeping with this conclusion. For the majority of units (those of response types A and B and some of type D) saturation of the firing rate measured at 180 ms did limit the response of the neurone to intensity increments occurring at this time delay.

Subsequent to the completion of the present study, Smith and Zwislocki published extensive data on the responses of cochlear nerve fibres to tone pedestals and to increments in intensity (Smith, 1973; Smith and Zwislocki, 1975). Although the present data are in good qualitative agreement with the more recent cochlear nerve data of Smith and Zwislocki (1975),

there are some quantitative differences which will be discussed in the appropriate sections below. From these more recent data Smith and Zwislocki developed a model which accounted for most of their data. This model is consistent with much of the present data but fails to account for some of the present findings and will therefore be described and its shortcomings demonstrated.

The only other directly comparable data of which this author is aware, is that of Hassan and Boerger (1974) who also measured the responses of cat cochlear nerve fibres to intensity increments. These authors found that the response to an intensity increment increased with the time at which it occurred after the pedestal onset. This is in agreement with some of the data of Smith and of the present study (see Section 4.4.2), but since the frequencies and levels of the pedestals and increments were not quoted, it is not possible to make useful quantitative comparisons with these data.

4.4.1 Adaptation

Although adaptation was observed in monotonic cochlear nucleus cells at nearly all pedestal intensities (see Section 4.3.1), the amount of adaptation* which occurred varied considerably from neurone to neurone. In some units the amount of adaptation which occurred was independent of the pedestal intensity whereas in others the amount of adaptation occurring decreased at high pedestal intensities. This variation of adaptation with pedestal intensity is considered in more detail later in this section.

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* i.e. the degree to which the onset firing rate was reduced after a specified time, in this case after 180 ms.

Smith (1973) reported values for the ratio of the onset firing rate to the firing rate measured at 150 ms (which is a measure of the relative adaptation) of from 1.9 to 3.2 for cochlear nerve fibres; this compares with values of 1.08 to 2.35 for the cochlear nucleus cells in the present study in which the adaptation occurring was independent of pedestal intensity. This comparison suggests that at least in one population of cochlear nucleus cells the adaptation which is observed is on average less pronounced than in cochlear nerve fibres. However, if those cochlear nucleus neurones are considered which show adaptation dependent on pedestal intensity (type B), values for the ratio of the onset firing rate to the 180 ms firing rate of up to 18.2 have been found at low pedestal intensities; such large values (18.2, 6.0 and 4.0) have only been found in three units, the remaining units had ratios between 1.29 and 2.73. Smith (1973) also notes a greater variability amongst units of the cochlear nucleus compared with the cochlear nerve as well as more pronounced adaptation in some units.

For cochlear nerve fibres, Smith (1973) reported that on average the amount of adaptation decreases at high pedestal intensities. Taking the median responses of ten cochlear fibres he found a decrease in the ratio of onset firing rate to the 150 ms firing rate from 2.54 to 2.22 as the pedestal level was raised from 6dB to 17dB above threshold. This decrease is considerably smaller than the decreases observed in some of the cochlear nucleus units in the present study. Unit 236.17 for example (see Fig. 41C and 44) has a ratio of onset firing rate to 180 ms firing rate of 2.1 up to an onset firing rate of 400 spikes/sec, which corresponds to a stimulation level of some 30 dB above threshold. This ratio falls to a value around 1.0 (representing no adaptation) as the pedestal level is increased to some 70 dB above threshold. However, in the present

data the largest decrease in the amount of adaptation to a pedestal took place above the intensity at which the onset firing rate saturated (see Section 4.3.1) and Smith's cochlear fibre data were, in the main, only collected up to levels of 30 dB above threshold. Thus the more pronounced decrease in adaptation as a function of pedestal intensity found in the present study compared to that of Smith may reflect the different intensity ranges over which the data were collected rather than genuine differences between cochlear nerve and cochlear nucleus.* Smith (1973) also found more pronounced decreases in adaptation with pedestal level in the cochlear nucleus compared with the cochlear nerve. It should be noted, however, that Smith's cochlear nucleus data were in some cases collected over a range of intensities comparable with the present study and will therefore be subject to the considerations outlined above.

4.4.2 Responses to Increments

The dependence of the response of cochlear nucleus cells to increments in intensity (either at onset or 180 ms after the onset of a pedestal) has been described in detail in Section 4.3.2. Smith (1973) also measured the responses to intensity increments as a function of the pedestal intensity of single units in the cochlear nucleus and of single cochlear nerve fibres. His data were, in the main, collected only over a limited range of pedestal intensities (30 dB or so). However, he determined the responses of a few cochlear fibres to intensity decrements, and of a few cochlear nucleus cells

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* This point is considered again in Section 4.4.6 in which it is suggested that decreases in the amount of adaptation occurring as a function of pedestal level may be as great in some cochlear nerve fibres as in some cochlear nucleus cells of the present study.

to intensity increments, over ranges of pedestal intensity comparable with the present study (up to 60 dB). When a sufficient range of pedestal intensities were employed the responses of cochlear nerve fibres to intensity increments or decrements fell to zero when the firing rate saturated (the fibres illustrated in Smith (1973) were all of response type A and had dynamic ranges for onset and 150 ms firing rates which were equal). Smith's data from the cochlear nucleus are limited but nevertheless he found one unit in which responses to increments at 150 ms could be detected beyond the intensity at which the firing rate at 150 ms was saturated (i.e. of response type C). Thus it would appear that as far as these data are comparable the present findings are in agreement with those of Smith (1973).

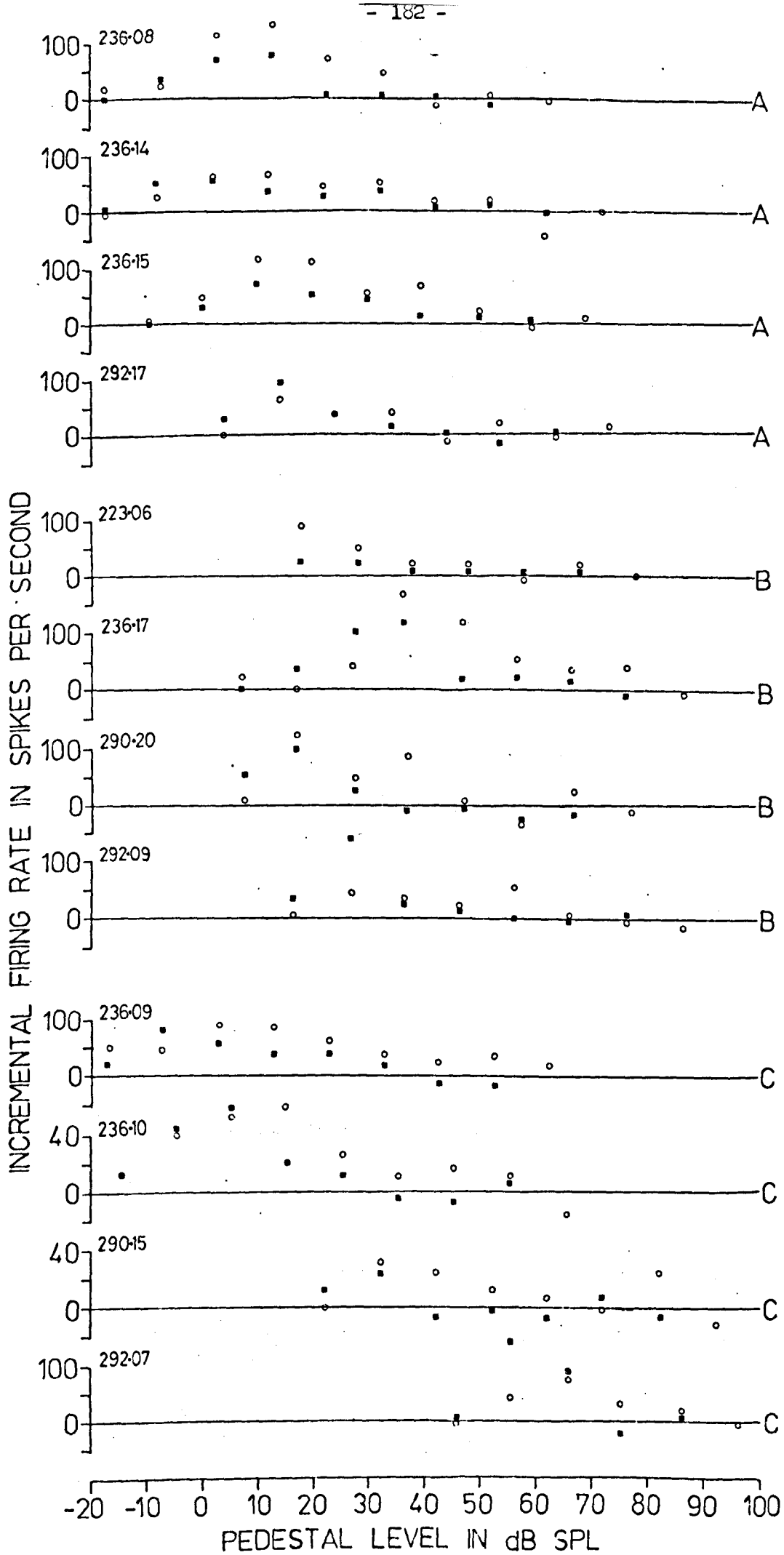
In addition to the effect of pedestal intensity on the responses to increments in pedestal intensity, Smith also determined the effect of varying the time of occurrence of the intensity increment. He found that the response to an intensity increment varied monotonically with its delay from the pedestal onset. Thus in later experiments he only compared the responses to increments applied at the onset and at 180 ms after the onset of a pedestal. His findings are therefore directly comparable with those of the present study and may be summarised as follows:- When intensity increments or decrements are added to tone pedestals of moderate intensity level (i.e. from about 10 dB above threshold up to the level at which saturation effects begin), the resulting changes in firing rate are nearly independent of the time delay of the increment from the pedestal onset. However, when either the incremental or pedestal intensity are sufficiently high, the changes in the firing rate in response to an increment increase as a function of its delay from pedestal onset.

These features are also evident in the present data, some of which are illustrated in Fig. 49. In this figure the incremental

Figure 49

Incremental firing rates plotted against pedestal level for twelve cochlear nucleus units. The incremental firing rate is the difference between the responses to the incremented and non-incremented pedestals at the appropriate time after onset. The open circles are the measured incremental firing rates in response to an increment in the pedestal intensity occurring at 180 ms after its onset. The filled squares are the response to an increment in the pedestal intensity occurring at its onset as predicted from the onset firing rate versus intensity function. The letters A, B and C indicate the type of response shown by the unit (see text).

Figure 49


236·08
236·14
236·15
292·17
223·06
236·17
290·20
292·09
236·09
236·10
290·15
292·07
100
0
40
A
B
C
INCREMENTAL FIRING RATE IN SPIKES PER · SECOND
-20 -10 0 10 20 30 40 50 60 70 80 90 100
PEDESTAL LEVEL IN dB SPL

firing rate in response to an increment which occurs at 180 ms after the pedestal onset (open circles) is compared with the corresponding incremental response predicted from the onset rate versus intensity function* (filled squares) as a function of the pedestal intensity level. The responses to increments of twelve units are illustrated in Fig. 49; all four units of response type C are shown (lower plots labelled C) and eight others, chosen arbitrarily from units of response types A and B (labelled accordingly in Fig. 49).

In all twelve units, above a level of about 20 dB above threshold and below the level at which saturation of the onset firing rate occurs, the increment occurring at 180 ms produces a greater change in firing rate than that predicted in response to an increment at the pedestal onset. Thus above 20 dB above threshold the response to an increment increases as a function of its delay from pedestal onset which is in agreement with the findings of Smith (except that he found incremental responses which increased with delay at levels above 8 dB above threshold). Below 20 dB above threshold a range of behaviours can be seen. In some units (e.g. 236.08, 236.10, 236.14 and 290.15) the intensity increment produces almost equal changes in the units' firing rates when at onset or at 180 ms. Thus in these 4 units, for pedestal intensities below 20 dB above threshold, the response to an increment was approximately independent of its delay from the pedestal onset. This finding is also consistent with the findings of Smith. In other units (e.g. 236.17, 292.09, 292.07 and 292.17) the intensity increment produces a smaller firing rate change when presented at 180 ms than when presented at the pedestal onset (i.e. the response

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* Although increments were also presented at the onset, the considerable variability between consecutive analyses on a single unit (see Section 4.3.2.1 and Fig. 43) was considered too great for making direct quantitative comparisons of the two incremental responses. Further, since responses to increments at the onset could be predicted from the onset firing rate versus intensity function, this method was used for obtaining onset incremental responses for quantitative comparison.

to the increment decreases when delayed after the pedestal onset). Smith (1973) and Smith and Zwislocki (1971) also found, in certain cases discussed below, decreases in the response to an intensity increment as a function of its delay from the onset of a low intensity pedestal. Smith attributed the very slight decreases he observed to the effect of a noisy threshold (see Smith, 1973, p. 143). Smith and Zwislocki (1971) found only one example of a decreasing incremental response and therefore considered this to be an atypical response and excluded it from further analyses.

At high pedestal levels, the wider dynamic range of the 180 ms firing rate compared to the onset firing rate for units of response type B, will result in an incremental response which is larger when the increment is delayed from the pedestal onset. In the extreme, at pedestal levels at which the onset firing rate is saturated no change in firing rate will occur in response to an intensity increment at the onset. An increment occurring at 180 ms will, however, still produce a firing rate change since the firing rate at 180 ms is not saturated. Since these considerations only apply to units of response type B and not those of types A and C and further, since increases in incremental response are observed in some units at levels well below the level at which the onset saturated (e.g. 236.08, in which the incremental response increases with time delay even at 20 dB above threshold) they do not provide a sufficient explanation of why the incremental response increases with delay for medium to high pedestal levels. (This point is discussed further in Section 4.4.3 below in relation to the model of Smith (1973).)

4.4.3 A Model of Short Term Adaptation and its Relation to the Present Data

In this section as the heading suggests, the model which Smith (1973) developed to account for his findings in cochlear nerve

fibres and single cochlear nucleus cells is briefly described and the degree to which the present data are consistent with the model is examined.

The model illustrated in Fig. 50 was developed to account for the responses of cochlear fibres to changes in the intensity of a pedestal and consists of three stages in cascade: i) an input saturating non-linearity; ii) a linear decay stage, and; iii) an output saturating non-linearity.

Smith considered two possible mechanisms for the decay stage. 1. A multiplicative automatic gain control process, and 2. a linear additive process. From his findings that responses to increments in pedestal intensity did not adapt as did the response to the pedestal* he concluded that the decay stage was linear rather than multiplicative.

The decay stage plus the input saturation accounts for most of the features which Smith observed; the input saturation determines the onset, 180 ms and incremental firing rate versus intensity characteristics and the decay stage produces the constant adaptation as a function of pedestal level observed in many units (i.e. the ratio of the onset firing rate to the 180 ms firing rate was constant as a function of pedestal level). The output non-linearity was included to account for the decrease in the amount of adaptation which is observed at high pedestal levels in some units. Thus when the output of the decay stage exceeds a certain value it saturates and since the output is greater at the onset of a pedestal than at 180 ms, the onset saturates at levels at which the 180 ms firing continues to increase. At high pedestal levels the ratio of onset firing rate to

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* i.e. the responses to increments were either constant or increased as a function of the delay from the pedestal onset whereas the firing rate to the pedestal decreased as a function of time.

the 180 ms firing rate therefore decreases. Smith examined high resolution PSTHs to determine whether the onset firing rate showed any signs of limiting. Since he could detect no limiting of the onset response he concluded that the output saturation was not a 'hard' saturation but had a gradual cut-off.

The data from some cochlear nucleus cells in the present study, however, are not consistent with an output saturation with a gradual cut-off. From the model, the input saturation determines the maximum dynamic range of any part of the discharge, thus the 180 ms firing rate (which is unaffected by the output saturation) represents the input saturation characteristic. The difference between the 180 ms and the onset firing rates then reflects the additional effect of the output saturation. Thus for unit 236.17, illustrated in Fig. 44A, the saturation of the onset firing rate (filled circles) at a lower pedestal level than the 180 ms firing rate (open triangles) is modelled by the output saturation. The flat top of the onset firing rate versus intensity function suggests that the output saturation has a sharp cut-off. This is not, however, consistent with the high resolution PSTH analyses of Smith which showed no indication of limiting of the onset response and from which he inferred that the output saturation had a gradual cut-off.

The major shortcoming of the model with respect to the present data is its inability to account for the behaviour of units of response type C. Smith was well aware of this difficulty and in fact uses a unit of response type C as an illustration of one of the effects which are not accounted for by his model. Since the input saturation is responsible for the onset, 180 ms and incremental firing rates versus intensity functions, no incremental responses should occur beyond intensities at which the input exceeds the input saturation level and the model is therefore unable to account for responses of

Figure 50

A model of short-term adaptation (occurring over less than one second). The linear decay stage is preceded by a saturating 'input' non-linearity and followed by a saturating 'output' non-linearity. The output function, g, is assumed to be linear except for a saturation at high outputs. (From Smith and Zwislocki, 1975.)

Figure 51

Responses of unit 152.1 from Møller (1974b) to amplitude modulated tones.

A. Ratio of the discharge rate modulation depth to the stimulus modulation depth (Gain in dB), plotted against sound intensity. The parameters are the modulation rates in Hertz.

B. Rate versus intensity function for the same unit determined using 50 ms tones at 10/sec.

Threshold for this unit was about 25 dB SPL.
Modulation depth was 30%.
Frequency of the tones was equal to the CF (12.8 kHz).

Figure 50

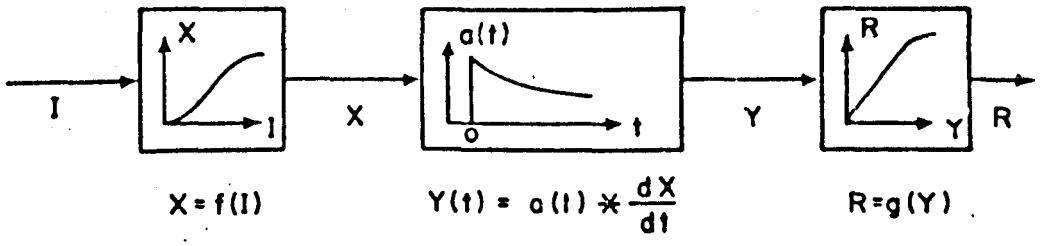
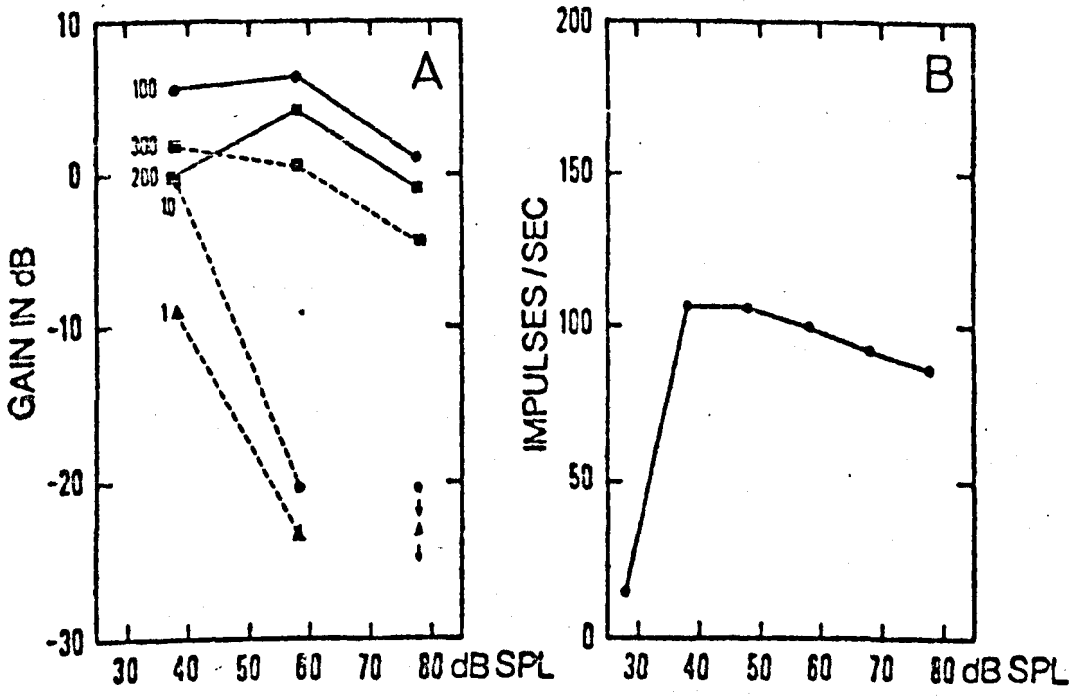


Figure 51



type C. It should be pointed out, however, that the model was developed mainly from considerations of the responses of cochlear fibres and no responses to increments beyond the intensity at which the firing rate to the pedestal saturates have been found in cochlear fibres. This does not exclude the possibility that type C responses occur in cochlear fibres, since only Smith's data on incremental responses of cochlear fibres is available and these, in the main, were collected at levels below saturation of the discharge rate. If it can be shown that no type C responses are ever found in the cochlear nerve then such a response must be the result of re-encoding of the activity in single cochlear fibres at the cochlear nucleus.

Smith invokes the operation of the output saturation to account for the increasing responses to an intensity increment as a function of its delay after the pedestal onset. Such an explanation can, however, only account for an incremental response which increases with delay at high stimulus levels*. Below the level at which the output saturation takes effect an incremental response which increases with delay is a departure from Smith's model, which only predicts incremental responses which are independent of the delay from the pedestal onset. Smith concluded that the increased incremental response at 180 ms compared to the onset response for low level stimuli was due in some way to the adaptation process and he termed this effect 'enhancement'. This effect has also been seen in the present data (see Section 4.4.2).

4.4.4 Non-monotonic Units

Group D contains units which maintain sensitivity to signal

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* See Section 4.4.2 for a similar discussion which is based on differing dynamic ranges for the onset and 180 ms firing rates which according to the model are due to the output saturation.

level changes over very wide ranges of stimulus intensity (see Section 3.3.6.2). It is surprising, therefore, that the majority of these units (8 out of 11) did not show consistent responses to small intensity increments over a similar wide range. The dynamic range of the majority of the group D neurones to intensity increments was no greater than that of monotonic neurones.

4.4.5 Additional Evidence for the Maintenance in some Cochlear Nucleus Cells of Sensitivity to Small Intensity Changes at Levels Beyond those at which the Discharge Rate to Stationary Stimuli is Saturated

Møller (1971, 1972b, 1973, 1974a, b) measured the modulation of the mean discharge rate of cochlear nucleus cells in response to amplitude modulated CF tones. He found that the depth of modulation of the discharge rate depended upon the rate of modulation of the stimulus, such that the discharge modulation depth was maximal at rates of 100 - 300 Hz, at which it exceeded the stimulus modulation depth by factors of 2 - 15 dB. For rates of modulation producing maximal discharge modulation, he found that the depth was independent of the average stimulus intensity up to and beyond intensities at which the discharge rate to unmodulated tones saturated. This is illustrated in Fig. 51A, from Møller (1974b) in which the ratio of the discharge rate modulation depth to the signal modulation depth (the gain in dB) is plotted against the average intensity level. For modulation rates of 100, 200 and 300 Hz (solid circles and continuous lines, solid squares and continuous lines and solid squares and

broken lines, respectively) the gain was approximately independent of the stimulus intensity. Fig. 51B illustrates the rate versus intensity function for the same unit to unmodulated CF tones. It is clear by comparison of Figs. 51A and 51B that even at intensities 40 dB above that at which the discharge to unmodulated stimuli saturates, a signal modulation of 30% produces a discharge rate modulation of the order of 30% (0 dB gain in Fig. 51A). Furthermore, the fidelity with which the modulation waveform is reproduced by the discharge modulation is similar at intensities above and below those at which the discharge to unmodulated stimuli saturates (Møller, 1974b).

Møller (1976, 1977) failed to find a similar maintenance of sensitivity to small intensity changes (amplitude modulation) in cochlear nerve fibres, over ranges of intensity in excess of the dynamic range of the fibres to unmodulated stimuli (the range of sensitivity to intensity changes was of the order of 30 dB). He therefore suggested that the wider range over which the discharge rate of cochlear nucleus cells is modulated by amplitude modulated stimuli, reflects the input to such cells from cochlear fibres of different CFs. Thus as intensity is increased and activity spreads to fibres of higher and lower CFs the cochlear nucleus cells still receive input from unsaturated cochlear fibres (Møller, 1976). If such were the case and the fibre inputs to the cells were excitatory, then the cochlear nucleus cells should have a wide dynamic range even to stationary stimuli and should have excitatory response areas much broader than a single cochlear fibre. It is evident from the data discussed in Appendix C that the excitatory bandwidths of cochlear nucleus cells are in the main no different from those of cochlear fibres and the dynamic ranges of monotonic cochlear nucleus cells are not significantly different from those of cochlear fibres (see Chapter Three). Thus a purely excitatory input to cochlear nucleus cells from fibres of very different CFs seems untenable.

In Section 3.4.3 it was suggested that the spread of activity, as intensity is increased, to fibres producing inhibitory inputs to cochlear nucleus cells (inhibitory sidebands), might provide an explanation of the non-monotonic rate versus intensity functions. From examination of Møller's data it can be seen that none of the published PSTHs are primary-like and at least two of the cells had non-monotonic rate versus intensity functions (one in 1972b and one in 1974b). Furthermore, Møller (1974b) states that 'the frequency modulation of the discharge frequency in units with a diminishing discharge rate (non-monotonic units) is reversed in phase compared with units in which the discharge rate increases with sound intensity'. Thus it would appear that at least part of Møller's data may be the result, not of an excitatory input to the cochlear nucleus cells, but rather, of modulation of the lateral inhibitory input to such cells which is activated by spread of activity with increasing intensity.

4.4.6 Psychophysical Implications of Adaptation

Although adaptation reduces the rate of discharge over time, the response to an intensity incremental may either remain constant or increase with time delay. Thus an intensity increment will produce a larger relative increase in discharge rate when delayed from the onset of a pedestal. Smith and Zwislocki (1971, 1975) and Smith (1973) made similar assumptions to those of Zwislocki (1972), specifically that 'signal-to-noise' ratio in the neural domain determines signal detectability, and that the 'noise' is the firing rate produced by the pedestal, the 'signal' being the incremental response. From this they argued that an increment in intensity should be more detectable when delayed from signal onset, or put another way, that to maintain signal detectability at a constant level, the intensity increment required would be less when the increment occurs

after a delay from pedestal onset. Similar effects termed the 'overshoot' effect have been found psychophysically (Scholl, 1962; Elliott, 1965; Zwicker, 1965 ; Green, 1969). Smith and Zwislocki (1971) suggested that the psychophysical masking overshoot may be related to the increase in neural signal-to-noise ratio which results from a constant or increasing incremental response. They obtained a value of 5 dB for the reduction in increment level to maintain constant neural signal-to-noise ratio (i.e. detectability). This compares very well with data of Elliott (1965) and Green (1969), for the difference in masking at stimulus onset and after a delay. There are, however, several important objections to such a correspondence between the physiology and the psychophysics. The major objection arises from the paper of Zwicker and Fastl (1972) in which they put forward a series of conditions necessary for observance of the overshoot phenomenon. The first of these is that the overshoot is largest if the critical band spectra of signal and masker are <u>different</u> and virtually non-existent when they are identical, which is clearly not the case in the incremental experiments of Smith and Zwislocki. Zwicker and Fastl (1972) also suggest that the data of Green and part of Elliott's data are not concerned with true masking overshoot but are due to energy splatter caused by abrupt gating of the signals and it is these experiments which produce the 5 dB masking difference. The second point is that overshoot is observed in backward masking which is unlikely to take place as peripherally as the cochlear nucleus and cochlear nerve (Watanabe and Simada, 1971). Finally the calculation of Smith and Zwislocki (1971) has only been performed for a single unit; furthermore, for signals of equal frequency and phase the value of increment level difference based on their figures should be 9 dB not 5 dB* Thus it

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* Thanks are due to Drs. Wilson and Pick for advice on this calculation.

is not possible as yet to directly relate physiological measures of incremental sensitivity to measures obtained psychophysically.

Moore and Raab (1975) considered the possibility that discrimination of short (10 ms) and longer (250 ms)signals might differ significantly, indicating the relative importance of the transient (onset) and steady state portions of the neural firing pattern. Using a two interval forced choice procedure they presented subjects with noise bursts differing only in intensity. The increase in the Weber fraction at high levels was not greater for the shorter duration noise burst and the form of the Weber function was similar for the two durations. Even for the 10 ms stimulus the DL was essentially independent of level from 31-91 dB SPL. Thus small changes in intensity must be signalled in the onset firing rate at least over the limited dynamic range used in the study of Moore and Raab.

4.4.7 Comparison of the Psychophysically Determined Dynamic Range with the Intensity Range over which Single Units can Encode Intensity Differences

The purpose of this section is to reassess, in the light of the data reported in this chapter, whether single neurones can encode intensity differences over an intensity range comparable with the psychophysically determined dynamic range for intensity discrimination.

In Chapter Three, units were described which had extremely wide dynamic ranges as a result of gradual increases in the firing rate with intensity beyond 'saturation'. (The so-called sloping saturation effect.) The data reported in this chapter enable an alternative explanation of this type of behaviour, in terms of the contribution of the firing rates measured at the onset and after a delay from the onset, to the discharge rate averaged over the whole duration of a tone burst (of up to 500 ms). For units of types A and

C averaging the discharge over the duration of the stimulus will produce estimates of the neurone's dynamic range equal to that obtained by measuring either the onset or 180 ms firing rate. However, for units of response type B, the 180 ms firing rate has a wider dynamic range than the onset firing rate. Thus averaging the firing rate over the whole 200 ms burst would produce a rapid increase in firing rate with intensity up to the level at which the onset firing rate saturates. Beyond this level, the increases in the 180 ms firing rate will result in the firing rate averaged over the whole burst continuing to increase but at a slower rate. Thus the firing rate averaged over the whole burst will show a sloping saturation.

This explanation has been tested empirically by averaging the firing rate of a type B unit over the whole pedestal duration and plotting this firing rate obtained against the pedestal intensity. (To do this the analogue magnetic tape recordings of the raw data of unit 236.17 shown in Fig. 44A were replayed via the gated counters using a 200 ms duration gate. See Section 4.2. for details.) The results of this analysis are shown in Fig. 52(filled triangles) along with a replot of the onset and 180 ms firing rates shown in Fig. 44A (filled circles and open triangles respectively). The rate versus intensity function for the firing rate averaged over the whole 200 ms is of the type described by Sachs and Abbas (1974) for cochlear fibres as having a sloping saturation. Thus the sloping saturation is seen to be a result of changes in the firing rate taking place at some delay from the stimulus onset. This is in accordance with some recent observations of Pickles (1977; personal communication), who measured the threshold of single cochlear fibres to a tone masked by an intense noise. When the continuous masking noise caused saturation of the fibre's discharge rate, no tone threshold was determinable until a certain time from the noise onset.

Figure 52

Discharge rate versus intensity functions for a single cochlear nucleus unit.

Figure 53

Dynamic ranges of the firing rates of cochlear nucleus units measured at onset and after 180 ms and in response to an intensity increment at 180 ms. Only neurones for which all three values were measured are included in this figure. The onset dynamic ranges of these units were included in the pooled data plotted in Fig. 37. The vertical lines represent the dynamic range of each single unit plotted at the appropriate threshold and CF. Lines with no sumbols other than filled triangles (see below) indicate units in which all three firing rates had equal dynamic ranges. The filled triangles indicate the threshold as determined by audio-visual criteria where this was different from that determined from the discharge rate versus intensity function. The open circles indicate the dynamic range of the onset firing rate, the small filled circles the dynamic range of the firing rate measured at 180 ms and the open squares the dynamic range of the response to an intensity increment. The heavy line along the lower extremes of the dynamic ranges represents the mean cat behavioural thresholds (see Section 1.3.1).

Figure 52

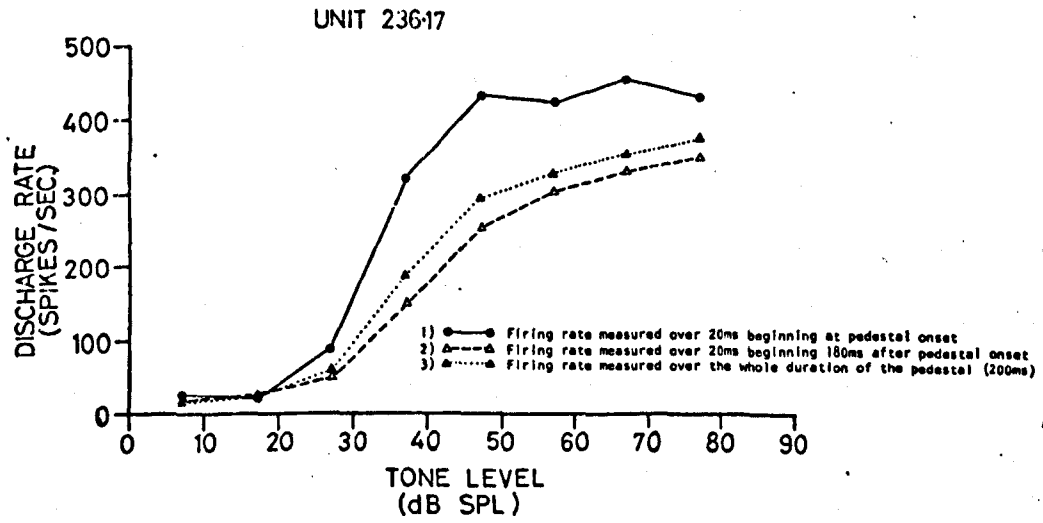
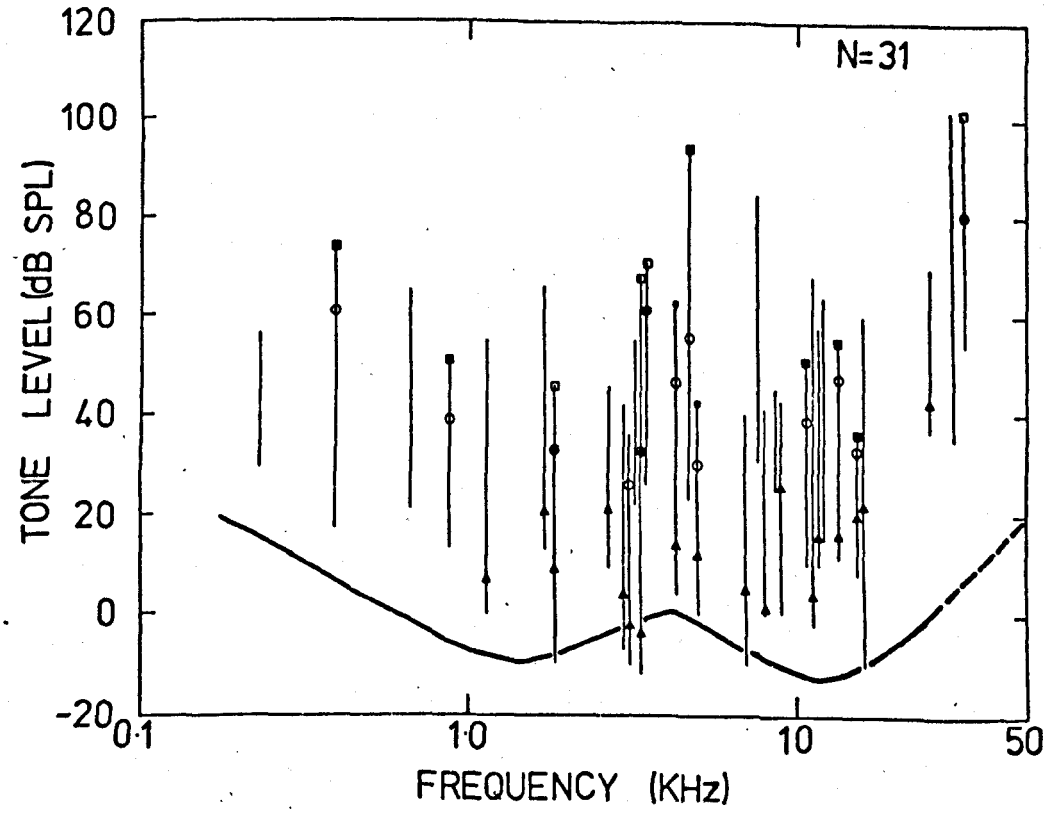


Figure 53



when a definite threshold to the tone was obtained (it should be noted, however, that the delay before a tone threshold was obtained was of the order of seconds and therefore may not be strictly comparable to the present effects which occur over less than one second).

The explanation of the sloping saturation given above also enables the reconciliation of some other findings in the literature. The size of the incremental response increases monotonically with the delay of the increment from stimulus onset (Smith, 1973). Thus it seems reasonable to assume that the dynamic range for the firing rate measured at various times after stimulus onset also increases monotonically with the delay. Thus the finding of Sachs and Abbas (1974) of sloping saturations which in some cochlear fibres extended up to 80 dB SL in response to 400ms tones would be consistent with the findings of Evans (personal communication) that in response to 40 ms tones the fibres with sloping saturations were all saturated at 60 dB SL. The significant difference found in Chapter Three between the dynamic ranges of the firing rates measured over the onset 20 ms or over the whole of a 500 ms tone is also consistent with this explanation.

Such an explanation of the sloping saturation would suggest that in order to obtain the rate versus level functions described by Sachs and Abbas (1974) which are shown in Fig. 29, the degree to which the adaptation decreases with increasing intensity must be as large in some cochlear fibres as it is in some of the cochlear nucleus units of the present study (see earlier discussion in Section 4.4.1).

In Chapter Three it was concluded that few if any cochlear fibres were capable of encoding intensity differences over ranges comparable with the psychophysically demonstrated dynamic range. Those fibres with wide dynamic ranges (e.g. from Sachs and Abbas, 1974) had rate versus intensity functions of the sloping saturation type.

If intensity discrimination at high intensities depends upon these

cochlear fibres with sloping saturations and the explanation of such responses given above is correct then one might expect for short duration signals (e.g. 20 ms) discrimination would deteriorate at levels of about 40 dB SL at which the onset firing rate becomes saturated. However the findings of Moore and Raab (1975) (over a 50 dB range) and of Campbell and Lasky (1967) (over an 83 dB range) using 10 and 20 ms tones respectively indicate that the discrimination of short tones improves with intensity up to and beyond 40 dB SL in the same way as it does for longer tones. The onset 20 ms of the cochlear fibre discharge therefore appears to convey all the information necessary for subjects to discriminate small differences in intensity at least up to 80 dB above threshold (from Campbell and Lasky, 1967).

It is unfortunate that these experiments were not conducted over a wider intensity range since, in our physiological data, the distribution of thresholds and dynamic ranges even for relatively short stimuli could span 80 dB. Nevertheless, at 80 dB above threshold nearly all fibres in our sample were saturated and a deterioration in discrimination would be predicted which is not found psychophysically.

In view of this limitation of the psychophysical data a contribution to the discrimination of intense long duration stimuli by the wider dynamic range of the later firing, although unlikely, cannot be entirely excluded. It is therefore appropriate in the following to examine the possible magnitude of this contribution.

The dynamic ranges over which units of response types A and B responded to intensity increments were equal to the dynamic range of the firing rate measured at 180 ms. Inclusion of the sloping saturation in the determinations of the dynamic range of the units illustrated in Figure 37 therefore also defines the dynamic range of such units to intensity increments. However, this is not true for units of response type C in which the dynamic range to intensity increments could not be predicted from the responses to pedestals. Thus in Figure 53 the data reported in this chapter are summarised taking into account the differing dynamic ranges of the onset, 180 ms and incremental firing rates. The length of the vertical lines in Figure 53 represents the dynamic range of a single neurone at the appropriate frequency and the filled triangles represent the thresholds as determined by audio-visual criteria if this was different from the thresholds as determined from the rate versus level functions. (See section 3.3 for discussion of this difference.) Vertical lines with

no symbols apart from the filled triangles represent units of response type A in which the onset, 180 ms and incremental firing rates all had equal dynamic ranges. The open circles represent the dynamic range for the onset, the small filled circles the dynamic range for the 180 ms firing rate and the open squares the dynamic range of the unit to intensity increments. The solid line across the lower extremes of the vertical lines represents the mean behavioural thresholds for the cat (see Section 1.3.1). All but a few neurones are saturated and no longer show responses to small intensity increments at levels of 80 dB SPL. The few units which do respond to intensity changes above this level had high minimum thresholds whether due to very high CFs (which normally have high thresholds, see Section 3.3.1) or due to the thresholds of the particular cat from which they were obtained being higher than average (such animal to animal threshold variation is discussed in Section 3.4). The maximum range over which primary-like cochlear nucleus units signal changes in stimulus level, even taking no account of the differences in unit thresholds is only of the order of 80 dB. This value still falls short of the intensity over which fine intensity discrimination is preserved as determined psychophysically.

In conclusion, while the utilisation of the wider dynamic ranges obtained in response to longer duration stimuli could provide an extension of the dynamic range over which primary-like cochlear nucleus neurones can code intensity changes, this extension is not very great and does not bring the single unit ranges into agreement with the range determined psychophysically.

In order to test the specific conclusions of Smith and Zwislocki (1971) we have concentrated on primary-like units in the cochlear nucleus

which presumably reflect directly the primary input. The non-monotonic units which we have analysed, in general (although the data are too limited for firm conclusions), seem to have wider dynamic ranges. Since no such wide range is present in the firing rate of the primary input, these cells must be decoding the intensity information which either derives from many primary fibres or is encoded in a single primary fibre in terms other than the mean discharge rate. Possible mechanisms for such a decoding will be discussed in the next chapter in which such cells are studied in greater detail.

Summary

1. With the exception of levels near threshold, adaptation takes place in monotonic cochlear nucleus cells at all intensity levels, including those causing saturation of the discharge rate.

2. The relative amount of adaptation occurring in monotonic units in the CN either remains constant with increasing stimulus level or decreases.

3. The firing rates measured at the onset and at 180 ms after the onset of a stimulus, saturate at different discharge rates.

4. The dynamic range for the firing rates measured at the onset and after 180 ms after the onset of a stimulus and in response to an intensity increment are not equal for all units. For some units the response to an intensity increment could not be predicted on the basis of their responses to stationary tonal stimuli. Differences in the dynamic range for the firing rates measured at onset and after 180 ms provide a possible explanation for the 'sloping saturation' type of rate versus intensity function.

5. Extensions to the intensity coding capability of single neurones due to the wider dynamic ranges of the firing rates

measured at 180 ms after the stimulus onset and in response to an intensity increment at 180 ms are insufficient to account for the psychophysically determined dynamic range.

6. Some non-monotonic cochlear nucleus cells do respond over ranges of intensity sufficient to account for the psychophysical dynamic range. The wide dynamic range of such cells suggests that inter alia they decode the intensity information which is present in the primary fibre input in some form other than large changes in the mean discharge rate of fibres of CF equal to that of the cells, such as by integrating input from fibres of higher and lower CF.

CHAPTER FIVE: RESPONSES OF UNITS IN COCHLEAR NERVE AND COCHLEAR NUCLEUS TO SIGNALS IN THE PRESENCE OF BANDSTOP NOISE

5.1 Introduction

In Section 1.7 some recent explanations of intensity coding were discussed; the concepts underlying these explanations involved spread of activity to unsaturated cochlear fibres at intensities for which fibres with CF at the signal frequency were saturated. The simplest explanation concerned spread of activity to unsaturated fibres within a limited frequency band around the signal frequency by virtue of a range of single fibre sensitivities. This was shown to be untenable by physiological measurements of single fibre thresholds (see Chapter Three).

A second notion was that intensity was encoded via a spread of activity to fibres of higher and lower CFs. In particular, Allanson and Whitfield (1955) and Siebert (1965) stressed the importance, for discrimination tasks, of responses of fibres in the cochlear nerve at the edges of the region of activity. These models have been tested psychophysically using a relatively intense masker which consisted of simultaneous high and low pass (bandstop) noise. This masker should drive into saturation the fibres at the high and low frequency edges of the region of activity due to the signal alone (upon which discrimination is deemed to depend). Thus at high intensities, under conditions of bandstop noise masking, a deterioration in the DL is predicted as fibres at the edges of the active region become important for discrimination. That no such deterioration is observed at high intensities suggests that a spread of activity across the frequency continuum is not a necessary condition for the maintenance of the very wide dynamic range for intensity discrimination.

Under conditions of bandstop noise masking, subjects are apparently able to utilize intensity information which is signalled over a very wide range of intensity by the fibres of CF equal (or near) to the signal frequency. (Viemeister, 1974; Moore and Raab, 1975.)

Thus, in the experiments reported in Chapters Three and Four, the dynamic range of cochlear fibres and single cochlear nucleus cells to stationary CF tones (presented alone) was measured, and possible extensions to this range which result from the adaptation process were assessed. Some monotonic cochlear nucleus cells had dynamic ranges of as much as 80 dB, as a result of a 'sloping saturation' (see Chapter Three). Even this range of 80 dB which is wider than the usually accepted values is still insufficient to account for the psychophysically determined dynamic range (see Chapters Three and Four for discussion).

Given the implicit assumption that measurements from cat neurones can be applied to human psychophysical data, a knowledge of the responses of cochlear fibres and cochlear nucleus cells to CF tonal stimuli presented alone, does not, therefore, provide an explanation of the way in which sensitivity to intensity changes is maintained when the spread of excitation is limited, as for example, in conditions of bandstop noise masking. We have, therefore, looked directly at the responses of single cochlear fibres and cochlear nucleus cells, under stimulus conditions analogous to those used in the psychophysical bandstop noise masking experiments. We examined the discharge of neurones in response to a signal at their CF for any aspect which changed systematically with the level of the signal over a wide intensity range. The initial study was performed at the level of the cochlear nucleus, since the author was already familiar with the necessary techniques.

The results of this study showed that under conditions of bandstop

noise masking, there were indeed cells in the cochlear nucleus which responded to signal level changes by discharge rate changes, over a dynamic range comparable with that measured psychophysically. Thus in later experiments, after completion of the cochlear nucleus recordings, Dr. E. F. Evans inserted an electrode into the cochlear nerve and measurements of the responses of cochlear fibres to the signal in the presence of the bandstop noise masker were obtained both by Evans and Palmer. It was found that cochlear fibres did not respond to signal level changes in the presence of bandstop noise over ranges wider than their dynamic range to the signal alone.

5.2 Methods

In the psychophysical experiments discussed above, a variety of levels of signal were presented at each bandstop noise masker level, and the DL was determined from the psychometric function obtained. The direct physiological analogy to these experiments would be to measure complete rate versus intensity functions for the signal at each level of the masking noise. However, since the time available for analysis on any one unit was limited, a somewhat more restricted procedure was adopted in which the discharge of the neurone was measured as the signal level was varied over 20 dB (in 10 dB steps) about the level of the masker which was itself presented at a variety of levels 20 dB apart.

Two methods have been used to set the levels of masker and signal, a manual method and an automatic computer controlled method. The many factors common to both methods will be described first.

500 ms bursts of signal (either a CF tone from the Dymar 741 oscillator or white noise from noise generator 2, Fig. 24) were presented simultaneously with a 500 ms burst of bandstop noise masker at a repetition rate of one presentation every 1.3 s. The bandstop filtering of the masker was achieved by use of a Barr and Stroud EF2 filter giving slopes of 36 dB/octave from the selected cut off frequencies. The relative levels of signal and masker could be separately adjusted by step attenuators (step attenuators A and B, Fig. 24).

In the psychophysical investigations of discrimination of signals in the presence of bandstop masking noise, a variety of stop bandwidths and signal to masker intensity ratios have been employed. Thus the choice of a particular stop bandwidth and signal to masker intensity ratio for the present experiments was somewhat arbitrary and indeed

in later experiments the effect of varying these parameters was deliberately explored. Also, since Viemeister (1974) was able to demonstrate) that the discrimination of white noise signals was not degraded by the presence of bandstop noise masking, white noise 'signals' have been used as well as CF tones.

The initial stop bandwidth and signal to masker intensity ratio were chosen to be analogous to the psychophysical experimental paradigm used in our own laboratories.(Pick, unpublished experiments.)

The bandwidth of the stop band of the masker was set at a value equal to three times the human critical bandwidth at the CF of the unit. The stop band was geometrically centred at the unit's CF (F1 to F2, Fig. 54). This width of stop band was chosen by Pick to be wider than the critical bandwidth of the human ear, even allowing for possible increases in this bandwidth as a function of level.

Pick measured the DL for discrimination of increments and decrements in the intensity of a band of frequencies within a wide band noise. Thus the signal to masker intensity ratio was 0 dB. The level of the tone in the present experiments was adjusted to give 4 dB greater energy than the noise within the pass band of the bandstop noise masker measured in a bandwidth equal to a single human critical bandwidth centred at the CF of the unit under study. Units were found in the present study which responded monotonically to signal level changes in the presence of bandstop masking noise over wide intensity ranges. These effects were observed over a range of signal to masker intensity ratios. Since 4 dB was near the centre of this range it proved post hoc to be an almost optimal setting. One problem in setting the signal to masker intensity ratio was drift in the output of the Grayson Stadler noise generator. The noise level was set up at the beginning of experiments and was found to have

drifted by up to 3 dB by the end of some experiments. This drift was extremely slow and the signal to masker intensity ratio would have remained approximately constant throughout the analysis of any single unit. There is, thus, some uncertainty as to the exact signal to masker intensity ratio used in the analysis of some units.

The stimulus parameters have been set using values of human critical bandwidths (from Scharf, 1970). There is good quantitative agreement between these critical bandwidth values and cat cochlear fibre effective bandwidths (Evans and Wilson, 1973). There are, however, some recent behavioural data in cat which appear to suggest that the critical band may be several times wider than the cochlear fibre of effective bandwidth (see Section 1.3.3; Pickles, 1974, 1975, 1976). It is quite clear however, from study of the effect of changing the signal to masker intensity ratio and stop bandwidth that the initial values chosen for these parameters (+4 dB and 3 critical bands) were nearly optimal.

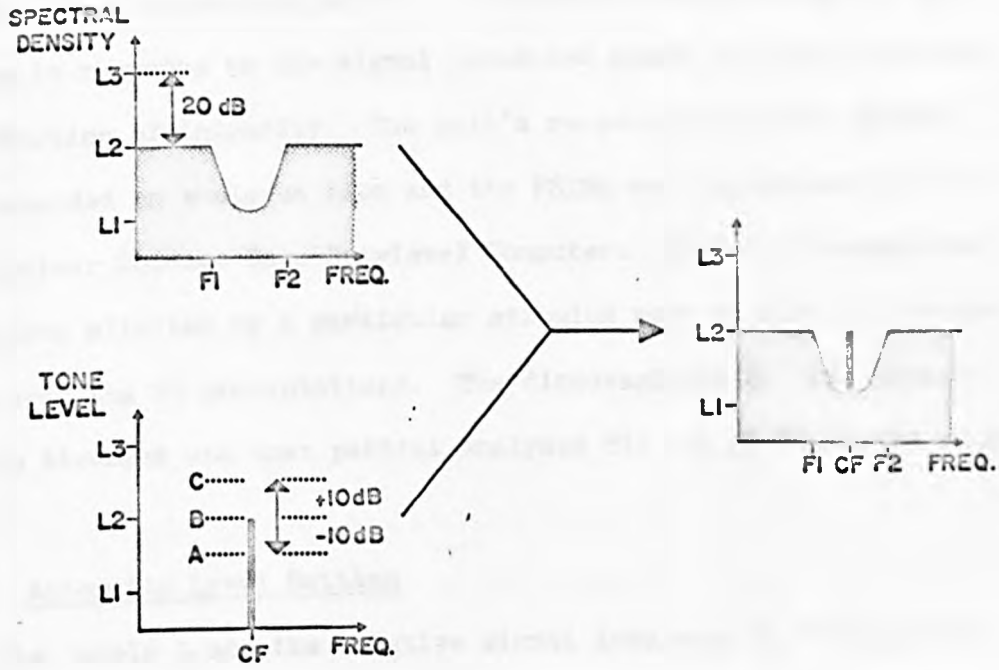
Briefly, the analysis consisted of measuring the discharge of a neurone in response to a signal presented at three levels relative to the bandstop masking noise over a range of masking noise levels. The bandstop noise masker was presented at a variety of levels L1 to L6 separated by 20 dB intervals (see Fig. 54). At each of these levels L, the signal was presented at three levels (A, B, C in Fig. 54) separated by 10 dB; +14 dB, +4 dB and -6 dB relative to the masker level (within a bandwidth equal to a human critical bandwidth at the frequency of the unit's CF, see above). Thus an overlapping series of signal intensities was presented (since L1 +14 dB equals L2 -6 dB).

The following two methods have been used to set the levels of signal and masker.

Figure 54

Stimulus paradigm used in the experiments to investigate the effect of bandstop noise masking. The masker is shown diagramatically in the upper left and the CF tone signal in the lower left. The masker was presented at a series of levels L_1 to L_6 (L1, L2 and L3 are shown) 20 dB apart. The signal was then presented at three levels A, B, C spanning 20 dB at each masker level. The tone at level B was 4 dB more intense than the noise within the passband of the masker, measured in a bandwidth equal to a single human critical bandwidth centred at the signal frequency (CF.).

Figure 54


SPECTRAL DENSITY
L3
20 dB
L2
L1
F1
F2
FREQ.
TONE LEVEL
L3
C
+10dB
L2
B
-10dB
A
L1
CF
FREQ.
L3
L2
L1
F1 CF F2
FREQ.

5.2.1 Manual Level Setting

The level L was set on the output attenuator (see Fig. 24) and the three levels of the signal (A, B, C, Fig. 54) were set on the step attenuator (Attenuator B, Fig. 24). After 20 presentations of each of the three relative signal levels at any masker level the masker level was increased by 20 dB and another series of 60 stimuli were presented. When time permitted, the discharge of the neurone in response to the signal + masker was also measured as the intensity was changed in descending order. In addition the discharge of the neurone in response to the signal presented alone, was also measured as a function of intensity. The unit's responses to these stimuli were recorded on analogue tape and the PSTHs were generated off-line on a Nuclear Chicago Data Retrieval Computer. During the experiment the spikes elicited by a particular stimulus were counted and accumulated over the 20 presentations. The disadvantages of this method are its slowness and that partial analyses did not yield useful data.

5.2.2 Automatic Level Setting

The levels L and the relative signal levels A, B, C (Fig. 54) were set using a PDP-8 computer to control two digital attenuators (Digital Attenuator 1, for the relative signal levels, Digital Attenuator 2 for the overall level, see Fig. 24) using a programme specially written for this analysis (see Appendix B, for the flow diagram). The filter cut off frequencies, tone signal frequency and the levels of signal and masker were set manually. Six levels of masker, giving a range of 120 dB were used, making a total of 18 different combinations of signal and masker for one complete analysis (3 signal levels at each masker level). Each 18 presentations contained each of these combinations in a random order. During the analysis

there was visual feedback to the experimenter consisting of a plot of spikes/stimulus versus signal level, on an oscilloscope slaved to the computer display. The display was continuously updated as presentation of each series of 18 stimuli was completed. The data were stored on digital magnetic tape and plotted after the experiment. This automatic setting method had many advantages over manual setting of the stimulus parameters. The foremost of these was its speed; a complete analysis only took 20 seconds and the continuous updating of the display enabled termination of the analysis when consistent averages were obtained (as determined by visual inspection), therefore limiting the analysis in most cases to only 3 or 4 presentations of each stimulus. Many different analyses could therefore be performed in a short period. This enabled parametric studies of effects of changing the stop bandwidth and the signal to masker intensity ratio. In addition, since the number of spikes elicited by each presentation of a particular stimulus was stored separately, standard deviations of the discharge elicited by the repetitions of a stimulus about the mean value could be calculated. These provide an indication of the significance of small differences in mean discharge rate and are shown in Figs. 56-59, 63-65, 69-73. The automatic method eliminated any order effects since stimuli were randomly ordered. The major disadvantage of this method was that since the stimuli were randomly ordered it was not possible to simply generate PSTHs from analogue taped records of the neuronal responses.

5.3 Results

The results from both the manual and automatic techniques were entirely consistent and provided complementary information. The data points of the rate versus intensity functions measured manually were obtained sequentially, whereas those of the automatically measured rate versus intensity functions were obtained in random sequence thus eliminating any effect of the ordering of the stimuli. In addition the automatic method provided some indication of the significance of the differences in mean discharge rate. Information on the temporal patterning of the discharge was obtained by generating PSTHs from the manually collected data. In experiments in which the computer was employed it was also used to obtain detailed measurements of the neurone's response area including any inhibitory regions present (see Section 2.5.2 for details of method).

5.3.1 Responses of Neurones in the Cochlear Nerve and Cochlear Nucleus to Signals in Bandstop Noise Masker using a 3 Critical BandwidthStopband and a Signal to Masker Intensity Ratio of +4 dB.

5.3.1.1 Classification of neurones

In response to the signal and bandstop noise stimulus two qualitatively different types of response were observed at the level of the cochlear nucleus and the neurones have been classified into two groupings accordingly. A single criterion served to separate the two response types: the range of masker levels over which the neurone responded to signal level increases by monotonic discharge rate increases.

Neurones of one type responded to signal level changes over the range investigated (20 dB) at each masker level by monotonic discharge rate changes for all levels of the masker at which the signal was supra-threshold.

Neurones of the second type only responded to changes in signal level by monotonic discharge rate changes for a few of the masker levels investigated at which the signal was suprathreshold. For neurones of this type, the range of intensities over which the neurone responded to signal level changes in bandstop noise was usually equal to the dynamic range of the neurone to the signal presented alone.

All but one of the cochlear fibres studied showed responses of the second type.

Although this separation of the cochlear nucleus neurones is based only on rate versus intensity functions to the signal in bandstop noise, the two groups of neurones also differed with respect to other features (e.g. inhibitory side bands), which suggests that the division may reflect some functional differences.

5.3.1.2 Response of cochlear nerve fibres to CF tones in the presence of bandstop noise (31 fibres)

Following several of the cochlear nucleus experiments, electrodes were inserted into the cochlear nerve of the same side by Dr. E. F. Evans and responses of nerve fibres were determined in the same animal under conditions identical to those used in the cochlear nucleus recordings by both Evans and Palmer. The responses of six cochlear fibres to CF tones in the presence of bandstop noise were measured using the manual technique by Palmer and in later experiments the responses of 25 cochlear fibres were measured by Evans using the automatic method.

Since the cochlear fibre FTC appears to represent the inverse of the frequency response function of a linear filter (Evans and Wilson, 1973), we should predict that the response to a tone and bandstop noise combination should be very similar to the response to the tone alone. The fibre should respond only to the stimulus energy falling within its FTC, which since the masking noise stopband is centred on

the FTC will not be much increased by the presence of bandstop noise.

For the majority of cochlear fibres studied these predictions were indeed borne out. Of the 31 fibres (CFs 1 - 28 kHz) studied, 19 showed responses to the CF tones in bandstop noise which were indistinguishable from those to CF tones presented alone. The remaining 12 showed some affects of the noise masker. Eleven of these 12 fibres showed responses similar to those illustrated in Figs. 55 and 56 for fibres 327.50 (data obtained manually) and 450.41 (data obtained automatically). The twelth fibre was somewhat anomalous and will be described separately.

In Fig. 55 the response to the CF tone presented alone is shown by the dashed line. This fibre responds to changes in tone level over a range of some 60 dB from 31 - 91 dB SPL, describing a typically sigmoid function. Each triplet of points joined by solid lines represents the responses to the three tone levels presented at each bandstop noise level (see Section 5.2). Below the fibre's threshold to the tone alone, no graded response is seen to different levels of bandstop noise or tone. Once the level of the tone exceeds the fibre's threshold, increases in tone level at each noise level cause increases in the discharge rate. At levels of tone which when presented alone cause saturation, the fibre does not respond to changes in tone level at a particular noise level. The discharge rate in response to a CF tone presented in bandstop noise thus rises from threshold to saturation over the same range of intensities as in response to the CF tone presented alone. This fibre, therefore, exhibits a monotonic increase in discharge in response to the signal in bandstop noise over a range of some 60 dB from 31 - 91 dB SPL.

It is apparent, however, that factors other than the energy within the FTC must be influencing the discharge rate. Over the

Figure 55

Rate versus intensity functions for cochlear fibre 327.50 (CF 2.55 kHz).

The dashed line is the response to a CF tone presented alone.

The dot-dashed line is the response to a wideband noise presented alone.

The three circles joined by continuous lines represent the responses to the three tone levels at each level of bandstop masking noise. The filled circles are data obtained as the intensity was progressively increased and the open circles are data obtained as the intensity was progressively decreased.

Figure 56

Rate versus intensity functions for cochlear fibre 450.41 (CF 0.73 kHz).

The dashed line is the response to the CF tone presented alone.

The groups of three filled circles joined by continuous lines are the responses to the three tone levels presented at each level of bandstop masking noise.

The top of the figure shows the standard deviation of the individual spike counts about the mean values plotted in the lower part of the figure.

Figure 55

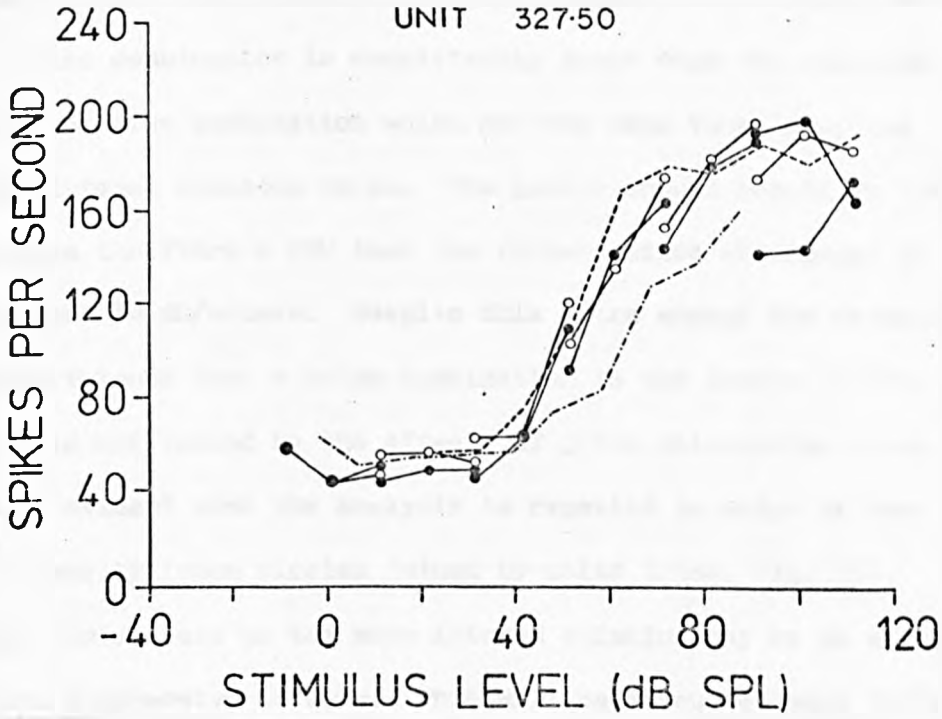
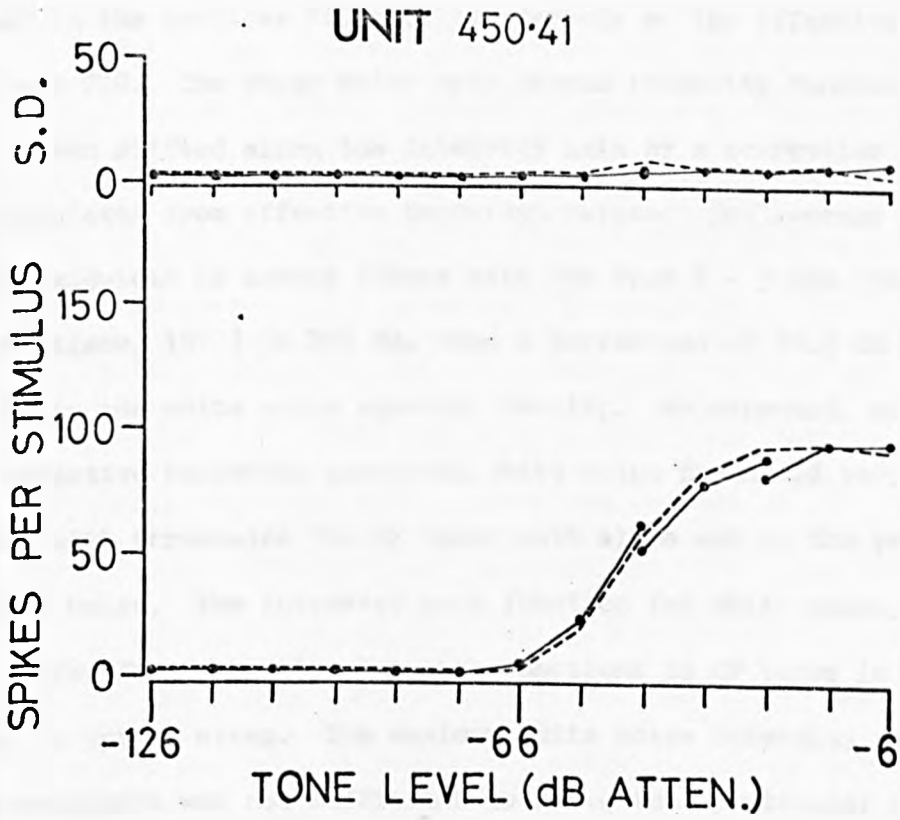


Figure 56



rising part of the rate versus intensity function, the response to a tone + noise combination is consistently lower than the response to the tone + noise combination which has the same tone level and 20 dB less intense bandstop noise. The latter should result in less energy within the fibre's FTC than the former, since the slopes of the filter are 36 dB/octave. Despite this extra energy the response to the more intense tone + noise combination is the lesser of the two. This is not caused by the effects of prior stimulation since it is still evident when the analysis is repeated in order of descending intensity (open circles joined by solid lines, Fig. 55). This lower firing rate to the more intense stimulus may be as a result of two-tone suppressive effects. This will be discussed more fully later.

The response of fibre 327.50 to white noise stimuli are shown by the dot-dash line in Fig. 55. For wideband noise signals the energy within the cochlear fibre filter depends on the effective bandwidth of the FTC. The white noise rate versus intensity function has therefore been shifted along the intensity axis by a correction factor calculated from effective bandwidth values. The average effective bandwidth of twenty fibres with CFs from 2 - 3 kHz (from Evans and Wilson, 1973) is 295 Hz, thus a correction of 24.7 dB has been added to the white noise spectral density. As expected, correction for the effective bandwidth makes the white noise threshold very comparable with thresholds for CF tones both alone and in the presence of bandstop noise. The intensity rate function for white noise, does however differ from the intensity rate functions to CF tones in that the slope is not as steep. The maximum white noise intensity available from our equipment was not sufficient to drive this particular unit into saturation.

Figure 56 provides additional evidence that the effects of the bandstop noise described for fibre 327.50 above are not due to effects of prior intense stimulation. The data of Fig. 56 were obtained using the automatic method in which the different combinations of masker and signal levels were presented in random order. The features described for 327.50 (Fig. 55) are readily seen in the responses of fibre 450.41 (Fig. 56). In particular the lower discharge in response to a tone in bandstop noise compared to the same tone level presented in a 20 dB less intense bandstop noise may be seen over the rising part of the rate versus intensity function. These features, although consistent from fibre to fibre, only reached a level of statistical significance ($P < 0.01$) for the two values at -26 dB for unit 450.41.

The remaining unit (570.83) which showed the most extreme effect of bandstop noise masking is illustrated in Fig. 57. This fibre, although having a dynamic range to the tone presented alone of only 40-50dB (Fig. 57B) shows a monotonic increase (albeit a small increase) to increases in signal level in the presence of the bandstop noise over some 80dB (Fig. 57A). For the triplets of responses to tones labelled a, b and c in Fig. 57A the differences in discharge between the responses to a tone at its least intense and most intense relative to each masker level are all significant at $p<0.05$. Furthermore the differences in discharge rate in response to the same tone levels at two different masker levels (i.e. between a and b, b and c) are both significant, one at $p<0.1$ and the other at $p<0.05$. However, it should be noted that the data points of Fig. 57A are mean values of only two readings and any statistical inferences are consequently to be regarded with caution. It is surprising, however, considering the homogeneity of responses usually assumed for the cochlear fibre population, that responses showing no trace of an effect of the bandstop noise masker, are found together with responses such as those in Fig. 57.

Figure 57

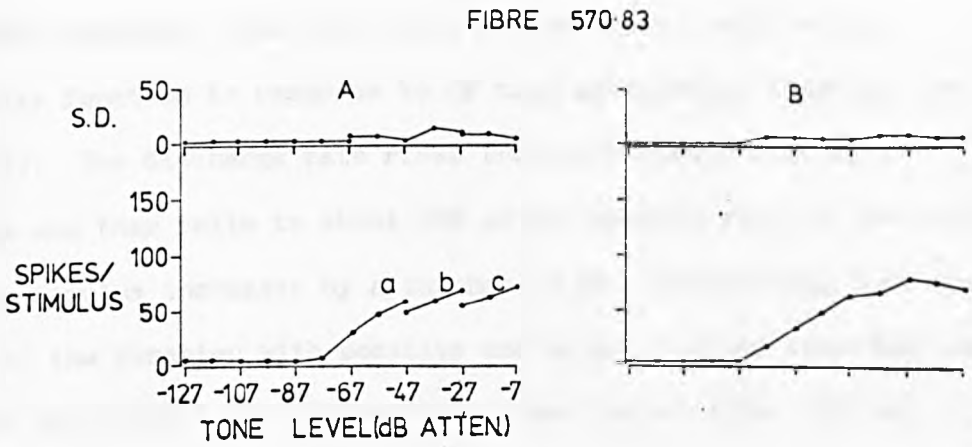
Rate versus intensity functions for cochlear fibre 570.83 (CF 5.9 kHz).

Figure 57A shows the responses of this fibre to a CF tone presented in bandstop noise masker. The three filled circles joined by continuous lines are the responses to the three tone levels at each level of bandstop noise masker.

Figure 57B shows the response of this fibre to the CF tone presented alone.

At the top of both Figs. 57A and 57B is shown the standard deviation of the individual spike couhts about the mean value plotted in the lower part of the figure. The letters a, b and c are used to designate the responses at three masker levels and are referred to in the text.

Figure 57


FIBRE 570·83
A
B
S.D.
50
0
150
100
50
0
SPIKES/
STIMULUS
a
b
c
-127 -107 -87 -67 -47 -27 -7
TONE LEVEL(dB ATTEN)

5.3.1.3 Category 1: Cochlear nucleus neurones responding monotonically to signal level increases only over a limited range of masker levels

This category consists of fifty-five cochlear nucleus neurones of CFs 0.5 - 50.5 kHz. Forty-one of these were analysed using the automatic method and 14 by the manual method, examples of both are given below. 31% of the neurones were located in the DCN, 65% in the VCN and 4% in the region of small cells between the DCN and VCN.

Figure 58 shows the responses of VCN unit 323.07, which was analysed manually. This unit has a non-monotonic rate versus intensity function in response to CF tone stimulation (dashed line, Fig. 58). The discharge rate rises from spontaneous rate to a maximum and then falls to about 50% of the maximum rate as the level of the stimulus increases by a further 30 dB. Considering both the parts of the function with positive and negative slope (see Sections 3.3.6.2 and 4.3.2.4 for discussion of this point) this unit has a dynamic range to CF tones of about 60 dB.

When the CF tone is presented in the presence of bandstop noise, the shape of the intensity rate function becomes more like the sigmoid shape of primary fibres. Changes in the tone level at a particular noise level only produce monotonic changes in the unit discharge rate over a range of about 30 dB; beyond 55 dB SPL changes in the level of the CF tone at any noise level do not produce significant discharge rate changes.

Fig. 59 shows the responses of DCN unit 570.17 which was analysed automatically. Fig. 59A shows the response to the CF tone (9.7 kHz) presented alone. The discharge rate rises monotonically from threshold (14 dB SPL) to saturation over 46 dB. When the tone is presented in

Figure 58A

Rate versus intensity functions for VCN unit 323.07 (CF 15.6 kHz).

The dashed line and open circles is the response to the CF tone alone.

The sets of three filled circles joined by continuous lines are the responses to the three tone levels presented at each level of bandstop noise masker. The arrow against the abscissa shows the average spontaneous rate measured during the analysis. The spontaneous rate of this unit when first encountered was 118 spikes/sec. The inset is a photograph of the response of this neurone to the tone alone at the intensity level indicated.

Figure 58B

PSTHs obtained by averaging the responses of unit 323.07 to 20 repetitions of tone alone and tone + bandstop noise stimuli. The numbers at the right of the histograms are the tone level in dB SPL for each analysis. The bin width is 10 ms.

Figure 58A

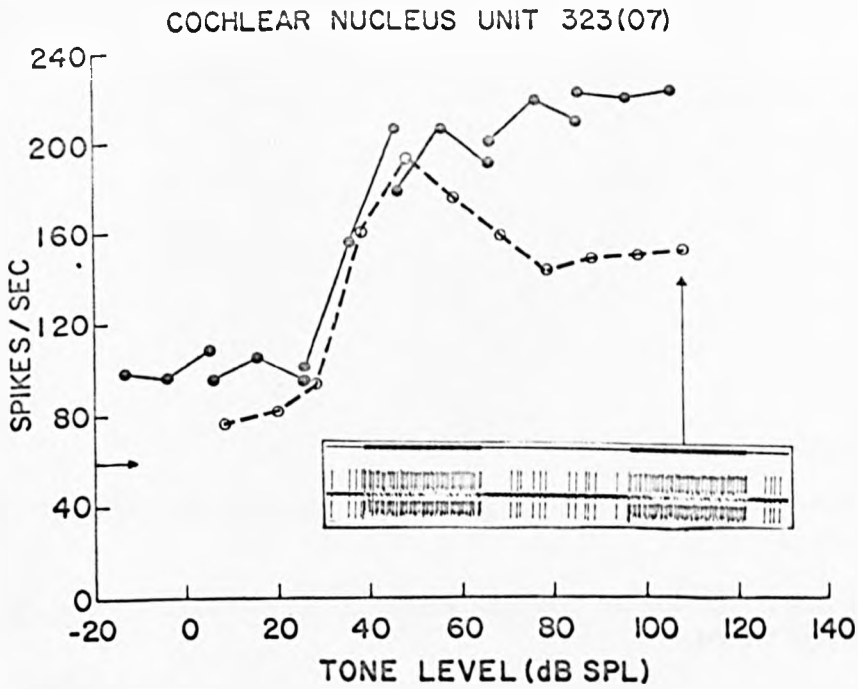


Figure 58B

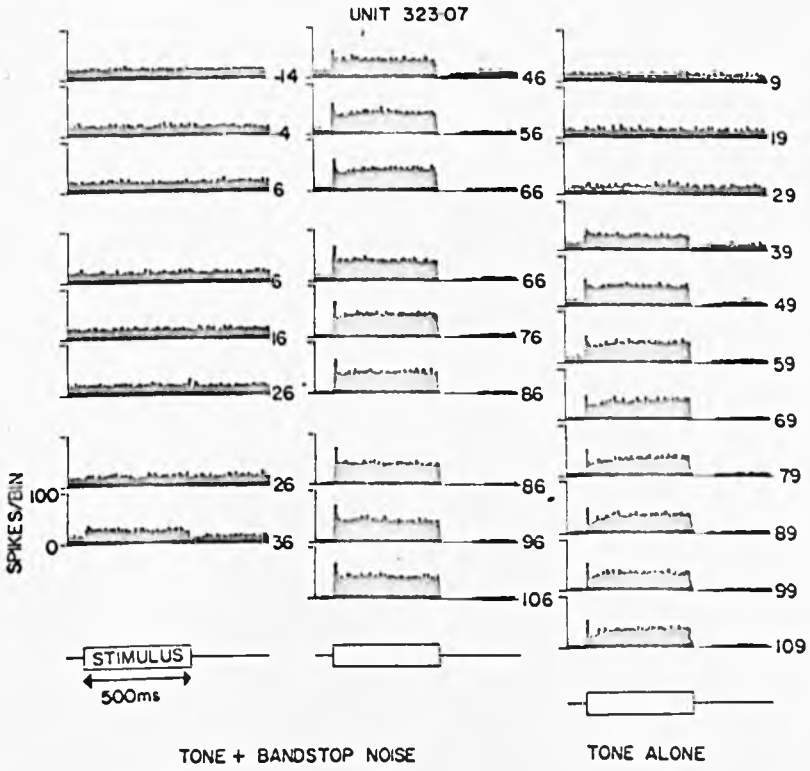


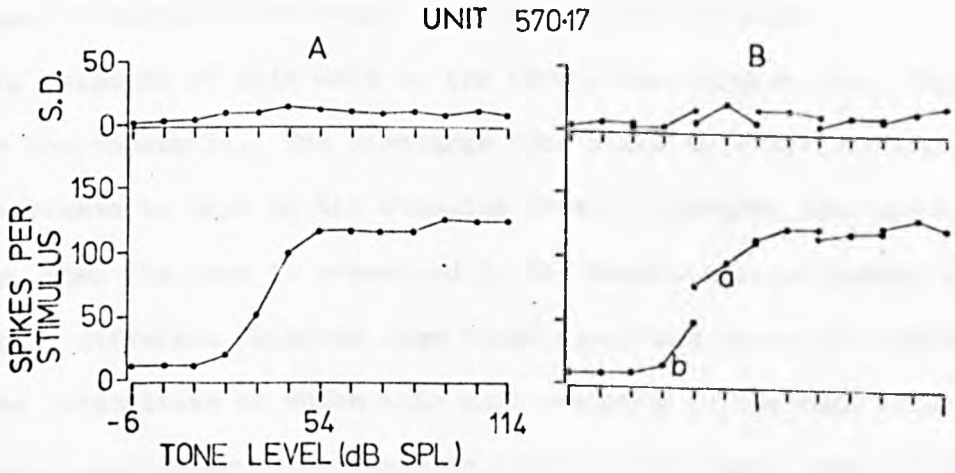
Figure 59

Rate versus intensity functions for DCN unit 570.17 (CF 9.55 kHz).

Figure 59A shows the responses of this unit to the CF tone presented alone.

Figure 59B shows the responses to the CF tone + bandstop noise masker. The sets of three filled circles joined by continuous lines in Fig. 59B are the responses to the three tone levels at each masker level. The standard deviation of the individual spike counts about the mean value is shown at the top of each figure. The letters a and b are used to indicate the responses at two masker levels which are referred to in the text.

Figure 59


UNIT 570·17
A
B
S.D.
50
0
150
100
50
0
SPIKES PER STIMULUS
a
b
-6
54
114
TONE LEVEL (dB SPL)

bandstop noise (Fig. 59B) this unit shows a monotonic change in discharge rate to tone level changes at only two masker levels (labelled a and b in Fig. 59B) and thus has a dynamic range under the conditions of bandstop noise masking of 40 dB. Above a tone level of 54 dB SPL the response of this unit saturates whether or not the bandstop masking noise is also present.

A variant of this type of response is shown in Fig.60A for DCN unit 333.03. This response is clearly very different from either of the two described above, and, as will become apparent is much more like the responses of units in the second category described below.

The response of this unit to the tone alone (broken line, Fig. 60A) is non-monotonic. The discharge rate rises to a maximum and then decreases to zero as the stimulus level is further increased. However, when the tone is presented in the bandstop noise masker a completely different response from those described above is observed. At those intensities at which this unit responds to the tone + bandstop noise combination, increases in tone level at each noise level cause monotonic increases in discharge rate. The same tone level produces markedly different discharge rates depending on the relative level of the bandstop noise. For example a tone level of 36 dB SPL produces a discharge of over 120 spikes/sec with the bandstop noise level of -14 dB relative to the tone (point labelled a in Fig. 60A; see Section 5.2); the same tone level produces no spikes when presented in a bandstop noise 6 dB more intense than the tone (point labelled b in Fig. 60A). When the bandstop noise level is increased beyond a certain limit the unit is inhibited completely, and changes in discharge rate in response to changes in the level of the tone are therefore prevented. This unit responds to tone level changes in bandstop noise only at two of the masker levels at which the tone is suprathreshold (i.e. the dynamic range of this unit to the tone in bandstop

Figure 60A

Rate versus intensity functions for DCN unit 333.03 (CF 2.39 kHz).

The dashed line is the response to the CF tone alone.

The sets of three circles joined by continuous lines show the responses to the three tone levels at each masker level. The filled circles indicate data obtained as the intensity was progressively increased and the open circles indicate data obtained as the intensity was progressively decreased. The inset shows a photograph of the response of this neurone to the tone + bandstop noise at the intensity indicated. The responses marked a and b are referred to in the text.

Figure 60B

PSTHs obtained by averaging the responses of unit 333.03 to 20 repetitions of the tone + bandstop noise stimulus. The numbers at the right of each histogram are the tone level in dB SPL for each analysis. The bin width is 10 ms.

Figure 60A

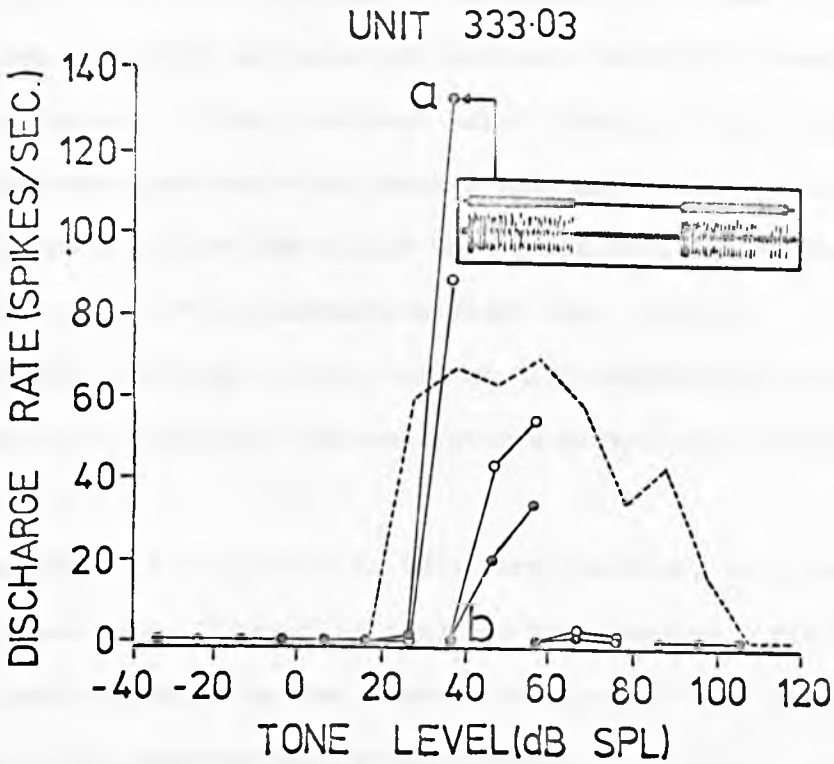
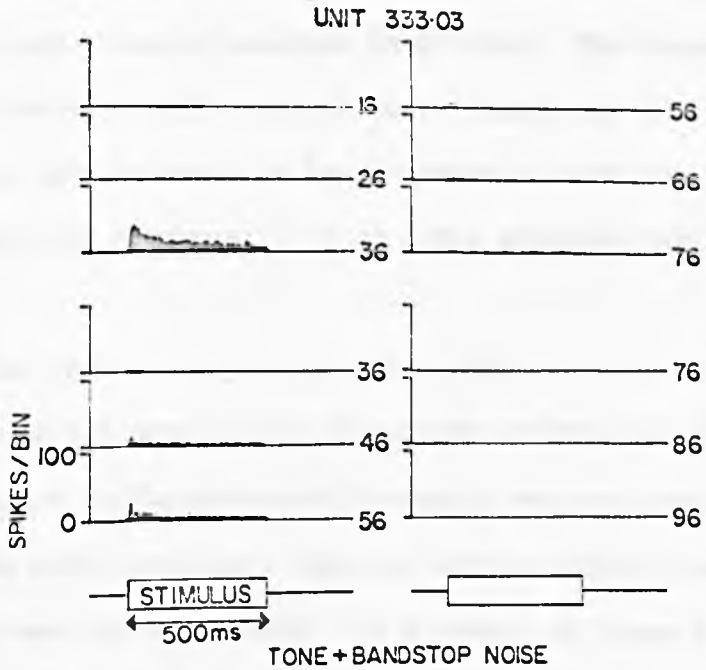


Figure 60B



noise is only 40 dB). This type of response in which the bandstop noise radically alters the response of the unit to the tone is common among the second category of units but complete inhibition does not occur in the latter. As will be shown later (Section 5.3.2) alteration of parameters such as signal:masker intensity ratio or stop bandwidth radically affect the single unit responses. It is possible that suitable choice of the parameters might have reduced the total inhibition shown in this unit at high intensities thus allowing monotonic discharge increases over a wider range of masker levels.

The responses of 4 neurones in this first category were also measured using a wideband noise 'signal' in bandstop noise masker. All four neurones showed responses to the wideband noise which were similar whether or not the bandstop masker was present.

Of the 55 neurones in this first category 25 did not have inhibitory sidebands and 18 had inhibitory side bands. The majority of the remaining 12 neurones had very low rates of spontaneous discharge which obviates detection of sideband inhibition. The range of intensity over which the 55 neurones showed monotonic discharge rate changes to tone level changes in the presence of bandstop noise varied from 20 - 70 dB with a mean of 37.5 dB and a standard deviation of 12.5 dB.

Eight units from one experiment have been excluded from this classification as the single unit thresholds of this animal were very high and therefore sufficient sound intensity was not available to stimulate these units with more than one or two masker levels at which the tone was suprathreshold. As a result of these high thresholds most of these units would have been artificially classified into the first category if included in the sample.

5.3.1.4 Category 2: Cochlear nucleus neurones which responded monotonically to signal level changes at all masker levels at which the signal was suprathreshold.

This category consists of 56 neurones with CFs of 0.7 - 29 kHz of which 77% were located in the DCN, 16% in the VCN and 7% in the small celled region between DCN and VCN. Forty-one of these neurones were analysed with the automatic method and 15 by the manual method (see Section 5.2); examples of data from both methods are given.

The responses of 2 neurones which were analysed manually are shown in Fig. 61 and 62 for units 323.06 and 323.10. Unit 323.06 is shown for a number of reasons: i. that it has a CF of 20.0 kHz (a point which will be considered in the discussion); ii. that it is the most striking example of this response type found in the preliminary experiments. Unit 323.10 is shown as the range of intensity over which changes in signal level, in the presence of the masking noise produce monotonic discharge rate changes is very wide.

Considering first the response of 323.06 to the tone presented on its own (dashed lines, Fig. 61A). The discharge rises to a maximum over 60 dB (from 39 - 99 dB SPL).

In response to the tone in bandstop noise, however, this unit shows a response which cannot be predicted from the response to the tone. At each level of bandstop noise, increases in the tone level cause monotonic increases in discharge rate (at tone levels above the unit's threshold). Increases in bandstop noise level at a particular tone level cause inhibition of the discharge to below the spontaneous discharge rate. Further increase of the tone level then again produces increases in the discharge rate (cf. unit 333.03 in the previous section). For this unit even changes in signal level from 98 - 118 dB SPL still evoke very large changes in the discharge rate. This

Figure 61A

Rate versus intensity functions for DCN unit 323.06 (CF 20.0 kHz). The open circles and dashed line is the response to the CF tone presented alone. The sets of three filled circles joined by continuous lines are the responses to the three tone levels at each masker level. The inset shows a photograph of the response of this neurone to the tone + bandstop noise stimulus at the level indicated. The arrow against the absissa indicates the spontaneous discharge rate of the neurone.

Figure 61B

PSTHs obtained by averaging the responses of unit 323.06 to 20 repetitions of the tone and tone + bandstop noise stimuli. The numbers at the right of each histogram indicate the tone level in dB SPL for each analysis. The bin width is 10 ms.

Figure 61A

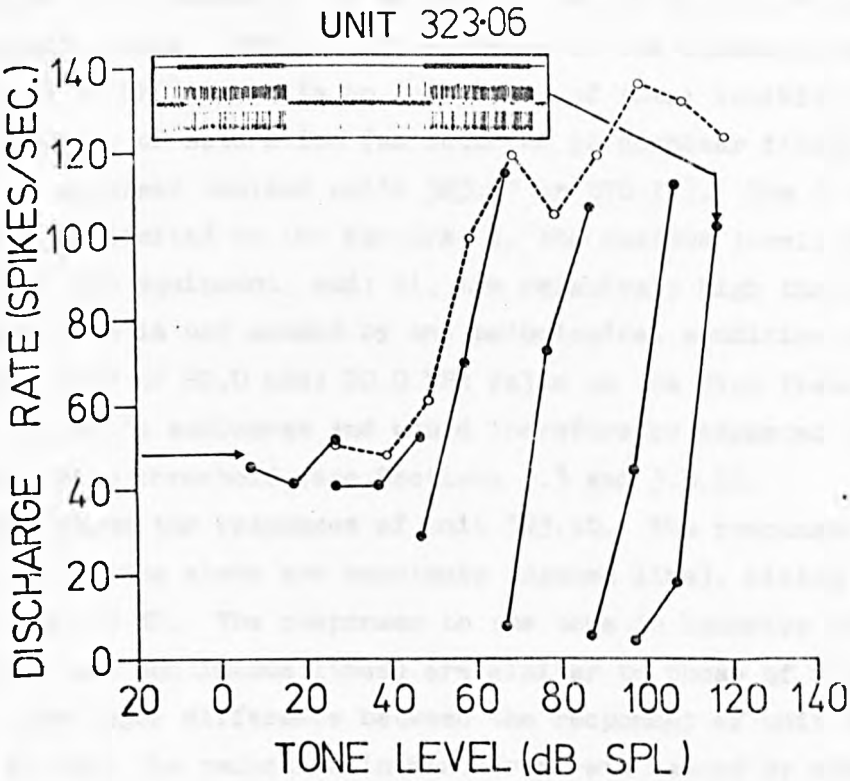
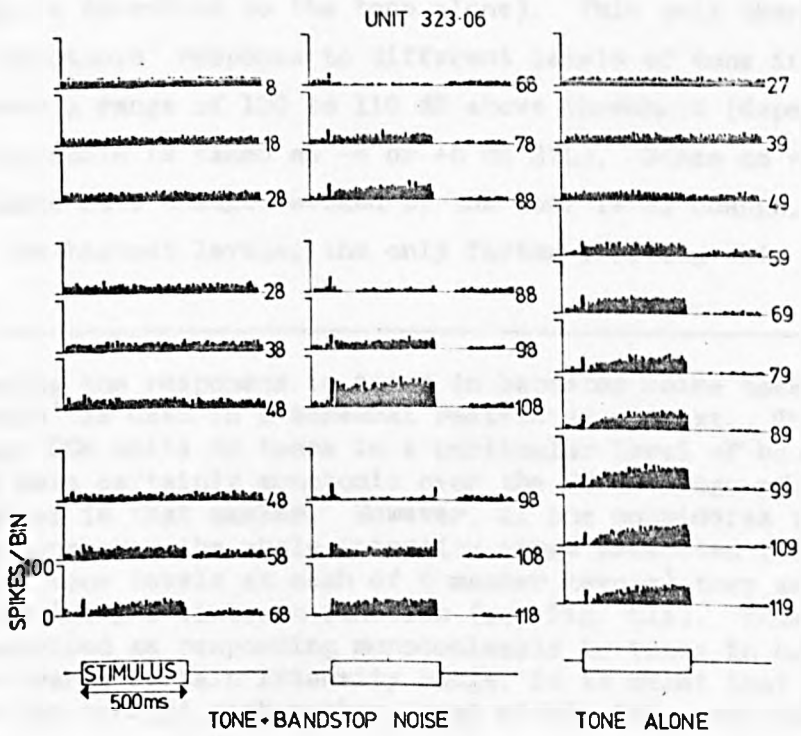


Figure 61B



unit, therefore, responds monotonically to tone level changes in bandstop noise from threshold, 38 dB SPL, up to 118 dB SPL or over an 80 dB dynamic range. Even at the extremes of the intensity ranges presented (118 dB SPL) there is no indication of total inhibition (as in unit 333.03) or of saturation (as occurred in cochlear fibres 327.50 and 450.41 or cochlear nucleus units 323.07 or 570.17). The 80 dB dynamic range is limited by two factors: i. the maximum levels of sound available from the equipment, and; ii. the relatively high threshold of this unit which is not caused by any pathological condition since this unit had a CF of 20.0 kHz; 20.0 kHz falls on the high frequency cut off of the cat's audiogram and would therefore be expected to be of relatively high threshold (see Sections 3.3 and 3.3.2).

Fig. 62A shows the responses of unit 323.10. The responses of this unit to the tone alone are monotonic (dashed line), rising to saturation over 60 dB. The responses to the tone in bandstop noise (solid circles and continuous lines) are similar to those of unit 323.06 (Fig. 61). The major difference between the responses of unit 323.10 and 323.06 is that the reduction in discharge rate caused by noise level increases does not bring the discharge down to spontaneous rate or below as is the case for unit 323.06. Over the whole range of intensities presented to this unit increases in tone level <u>at any bandstop noise level</u> cause 'monotonic'*increases in discharge rate (at tone levels above the unit's threshold to the tone alone). This unit therefore exhibits a 'monotonic' response to different levels of tone in bandstop noise over a range of 100 to 110 dB above threshold (depending on whether threshold is taken as -4 or +6 dB SPL). Since no reduction in the discharge rate change, evoked by the tone level change, is observed at the highest levels, the only factor limiting this range

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* In discussing the responses to tones in bandstop noise masker, the term 'monotonic' is used in a somewhat restricted context. The responses of many DCN units to tones in a particular level of bandstop noise masker were certainly monotonic over the 20 dB range of tone levels presented in that masker. However, if one consideres the response to the tone over the whole intensity range presented (i.e. a 20 dB range of tone levels at each of 6 masker levels) they are non-monotonic describing a sawtooth function (see Fig. 61A). Thus when a unit is described as responding monotonically to tones in bandstop noise masker over a certain intensity range, it is meant that the responses to the tone <u>at each masker level</u> within the range were monotonic.

Figure 62A

Rate versus intensity functions for DCN unit 323.10 (CF 8.7 kHz). The open circles and dashed line is the response to the CF tone presented alone. The sets of three filled circles joined by continuous lines are the responses to the three tone levels at each masker level. The inset shows a photograph of the response of this neurone to the tone + bandstop noise stimulus at the level indicated. The arrow against the absissa indicates the spontaneous discharge rate of the neurone.

Figure 62B

PSTHs obtained by averaging the responses of unit 323.10 to 20 repetitions of the tone and tone + bandstop noise stimuli. The numbers at the right of each histogram indicate the tone level in dB SPL for each analysis. The bin width is 10ms.

Figure 62A

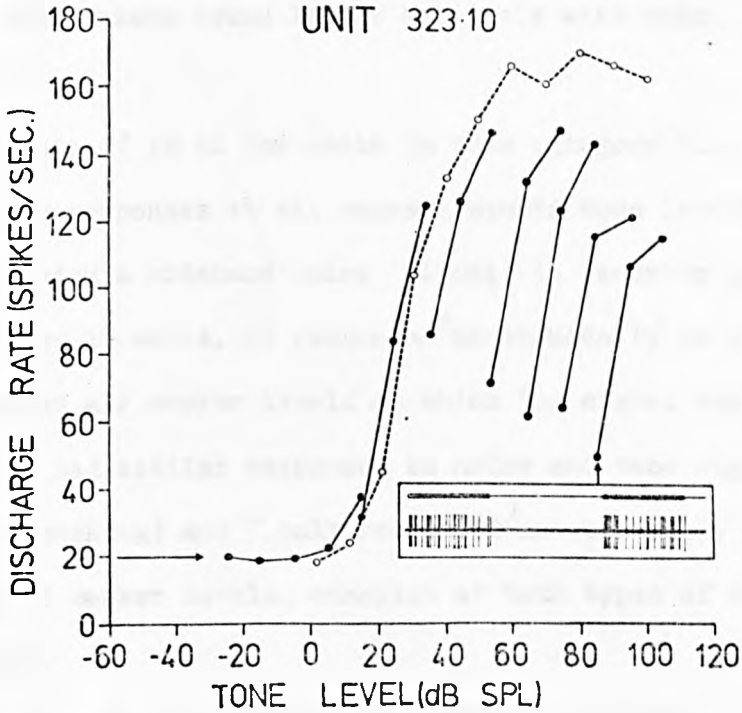
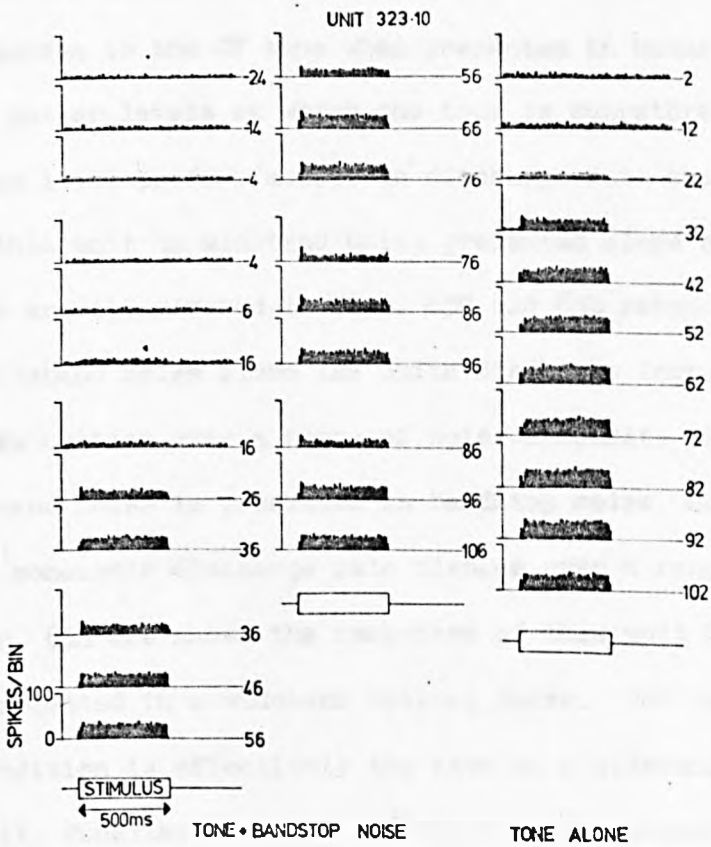


Figure 62B



to 110 dB is the maximum sound levels available with which to test this unit.

The responses of 19 of the units in this category (i.e. which showed monotonic responses at all suprathreshold tone levels) were also measured using a wideband noise 'signal' in bandstop noise masker. Of these 19 units, 12 responded 'monotonically' to the noise signal changes at all masker levels at which the signal was suprathreshold (i.e. had similar responses to noise and tone signals in bandstop noise masking) and 7 only responded 'monotonically' over a limited range of masker levels; examples of both types of response are given below.

The responses of unit 473.21 to a variety of stimuli are shown in Fig. 63. Fig. 63A shows the responses of this unit to the CF tone (14.9 kHz) presented alone. The discharge in response to the tone rises from threshold to saturation over 60 - 70 dB. Fig. 63B shows the responses to the CF tone when presented in bandstop masking noise; at all masker levels at which the tone is suprathreshold, changes in tone level produce 'monotonic' discharge rate changes. The responses of this unit to wideband noise presented alone or with bandstop noise are illustrated in Figs. 63C and 63D respectively. In response to wideband noise alone the units discharge increases from threshold to saturation over a range of noise intensity of 40 dB. When the wideband noise is presented in bandstop noise, however, the unit produces 'monotonic' discharge rate changes over a range of 80 dB. Finally in Fig. 63E are shown the responses of this unit to a wideband signal presented in a wideband masking noise. Not surprisingly, since this condition is effectively the same as a wideband noise rate versus intensity function (e.g. Fig. 63C), the unit exhibits only a relatively narrow dynamic range under these conditions. (The data shown in Fig. 63E are the only data which we have obtained of

Figure 63

Rate versus intensity functions for unit 473.21 (CF 14.9 kHz).

Figure 63A is the response to the CF tone signal presented alone.

Figure 63B is the response to the CF tone signal + bandstop noise masker.

Figure 63C is the response to a wideband noise signal presented alone.

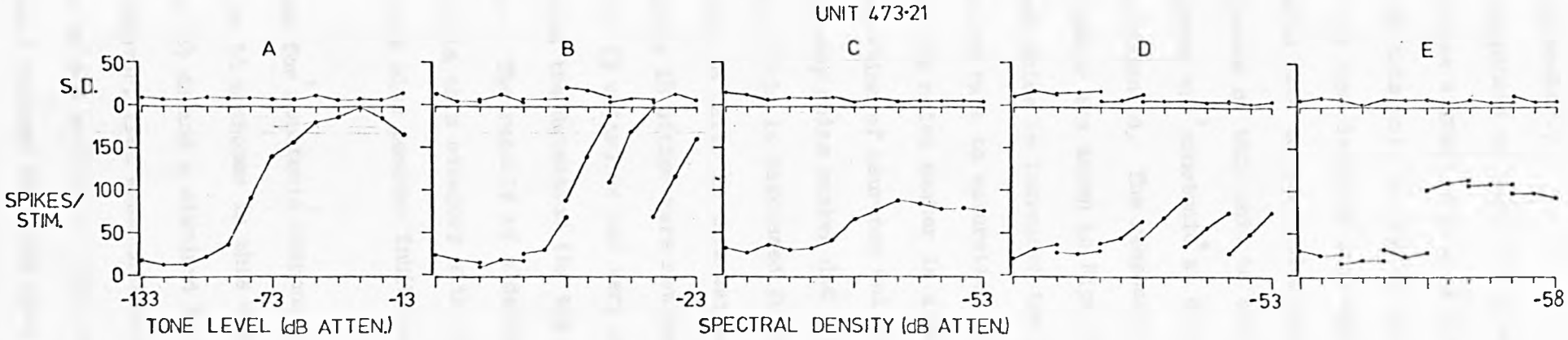
Figure 63D is the response to the wideband noise signal + bandstop noise masker.

Figure 63E is the response to the wideband noise signal + wideband noise masker.

In Figures 63B, D and E the sets of three solid circles joined by continuous lines are the responses to the three signal levels at each masker level.

The standard deviation of the individual spike counts about the mean value is shown in the top part of the figures.

Figure 63


UNIT 473-21
A
B
C
D
E
S.D.
50
0
150
100
50
0
SPIKES/
STIM.
-133
-73
-13
-23
-53
-53
-58
TONE LEVEL (dB ATTEN.)
SPECTRAL DENSITY (dB ATTEN.)

wideband noise signal and masker.)

Fig. 64 shows the responses of unit 570.03 which only responded to changes in wideband noise signals over a limited range of masker levels. The responses of this unit to the CF tone (3.5 kHz) are shown in Fig. 64A. As the tone level is increased the discharge rate increases from spontaneous rate to saturation rate over 60 - 70 dB. Fig. 64B shows the responses of this unit to the CF tone in bandstop noise masker; the responses are 'monotonic' at all masker levels at which the tone is suprathreshold. The responses to wideband noise alone and in bandstop masker are shown in Figs. 64C and 64D respectively. As the level of wideband noise is increased the discharge rate increases from spontaneous rate to saturation rate over only 40 dB whether or not the bandstop noise masker is also present.

A substantial proportion of neurones which responded 'monotonically' to tone signals in bandstop noise masker did not show similar responses to white noise signals. This is discussed further in Section 5.4.1.

Thirty-eight of the 56 units in this category had clear inhibitory sidebands. The remaining 18 either were not tested for the presence of side band inhibition (3 units) or had very low rates of spontaneous discharge which obviated the detection (by the methods used) of side bands, even if present. The results of widening the masker stop bandwidth for one unit in this category with low spontaneous discharge suggest that these units also possess inhibitory side bands (see Section 5.3.2.2).

The dynamic range for 'monotonic' responses to tone signals in bandstop noise for the 56 neurones in this category varied from 50 - 110 dB with a mean of 83 dB and a standard deviation of 12 dB. It should be evident, however, from examination of Figs. 61 - 64 that little deterioration in the ability of this group of neurones to respond to signal level changes occurred even at the highest levels

Figure 64

Rate versus intensity functions for DCN unit 570.03 (CF 3.47 kHz).

Figure 64A is the response to the CF tone signal presented alone.

Figure 64C is the response to the wideband noise signal presented alone.

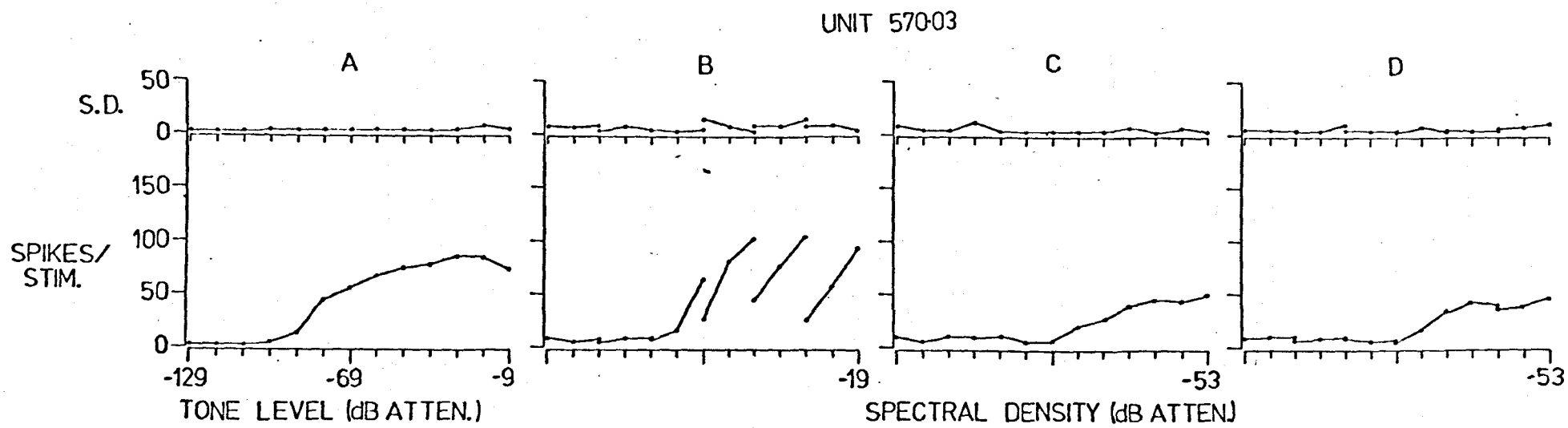
Figure 64B is the response to the CF tone signal + bandstop noise masker.

Figure 64D is the response to the wideband noise signal + bandstop noise masker.

In Figures 64B and D the sets of three filled circles joined by continuous lines are the responses to the three signal levels at each masker level.

The standard deviation of the individual spike counts about the mean value is shown in the top part of the figures.

Figure 64


UNIT 570·03
A
B
C
D
S.D.
50
0
150
100
50
0
SPIKES/
STIM.
-129
-69
-9
-19
-53
-53
TONE LEVEL (dB ATTEN.)
SPECTRAL DENSITY (dB ATTEN)

employed. Thus the above dynamic ranges only represent the maximum range of the units, as measurable with our equipment, not necessarily the maximum range over which the units could respond to signal level changes.

5.3.2 Parametric Studies of the Effects of Varying the Bandstop Noise Stop Bandwidth and the Signal to Masker Intensity Ratio

5.3.2.1 Preface

It is clear from the results described above, that at the cochlear nucleus, neurones are present which respond to signal level changes, in the presence of a bandstop masking noise, over a range of intensity comparable with the dynamic range for intensity discrimination determined psychophysically. The remaining experiments reported in this chapter sought to extend these observations with two separate objectives.

The first objective was to extend the generality of the data obtained using only a single stop bandwidth (3 critical bands) and signal to masker intensity ratio (+4 dB). In the psychophysical experiments of Viemeister, Moore and Pick (see Sections 1.7 and 5.1) a variety of stop bandwidths and signal to masker ratios were employed, and while the absolute size of the DL depended upon the width of the stop band, its constancy as a function of intensity was not critically dependent on either stop bandwidth or signal to masker intensity ratio. Thus in attempting to compare the present single unit data with the psychophysical data it is essential to determine whether the responses which we have measured are tolerant of changes in the stimulus parameters. The effects of independently varying the stop bandwidth and signal to masker intensity ratio have therefore been studied.

The second objective of the following experiments was to elucidate

the mechanism by which the cochlear nucleus cells are able to display signal level changes over a very wide range of intensity as discharge rate changes, apparently in the face of saturation of the majority of cochlear fibres. Examination of the similarities and differences between the responses of neurones in the two major categories described above provide some circumstantial evidence about the mechanism.

PSTHs of units 323.07, 333.03, 323.06 and 323.10 are shown in Figs. 58B, 60B, 61B and 62B respectively. In response to the CF tone alone, none of these neurones shows a primarylike temporal discharge pattern (i.e. a high onset discharge which decays smoothly to a relatively steady rate). Unit 323.07 (Fig. 58B) has a primarylike temporal pattern at 39 dB SPL and a suppression following the onset at higher intensities which makes the pattern a 'pauser' type (see Section 1.6.2). Unit 323.06 (Fig. 61B) also shows a 'pauser' type pattern and 323.10 (Fig. 62B) a 'build-up' pattern. When the tone is presented in bandstop noise masker the temporal pattern of 323.07 (Fig. 58B) becomes more primarylike as the suppression following the onset is reduced and eventually overcome by the action of the bandstop noise (the rate versus intensity function for this unit is also more sigmoid to the tone + masker than to the tone alone). For units 323.06 and 323.10 the bandstop noise has a tonic suppressive effect at its most intense relative to the tone and the pattern remains complex (by which we mean the pattern shows both excitatory and suppressive effects) for all combinations of masker and signal.

Of the units which only responded 'monotonically' to the tone at a few masker levels (category 1 above) PSTHs were obtained for 11 units of which 36% were primarylike and the remainder were complex. Of the units which responded monotonically at all masker levels (category 2 above) PSTHs were obtained for 15 units of which only 13% were primary-like and the remainder were complex.

Thus the majority of neurones which showed 'monotonic' responses to the signal in the presence of bandstop noise, over a wide intensity range had complex temporal discharge patterns and in addition several had non-monotonic rate versus intensity functions to the tone alone. These are both response properties which have been shown to be associated with the presence of strong inhibitory regions within the unit's response area (e.g. Greenwood and Maruyama, 1965). In fact <u>every</u> unit in category 2 for which the presence of inhibitory side bands was specifically tested, they were found to be present. Provided signals are present which increase over wide intensity ranges in both excitatory and inhibitory regions of the response area, it is easy to see how the action of the bandstop noise on these inhibitory areas could be 'biassing' the unit's discharge rate, thereby maintaining its sensitivity to small signal level changes. Further discussion of the nature of the input to these cochlear nucleus cells will be presented in Section 5.4.2.

The hypothesis that biassing of the unit's discharge caused by masking noise energy within the inhibitory sideband was tested directly by two methods. 1. By progressively increasing the stop bandwidth, and 2. by altering the signal to masker intensity ratio. Both of these methods alter the amount of masking noise energy which falls within the inhibitory side bands. Increasing the stop bandwidth progressively reduces the amount of masker energy in the side bands and we should expect a corresponding progressive reduction in the observed biassing effect. In the extreme when no noise energy falls in the side bands the observed response should be similar to the signal presented alone. Similarly in increasing the signal to masker intensity ratio, the masking noise energy in the inhibitory side bands for a particular signal level will be progressively reduced and one might expect a reduction in the observed biassing effect. These

predictions are indeed borne out as will be seen from the results described in the following sections.

5.3.2.2 Responses of cochlear nucleus units to signals in bandstop noise masker as a function of the stop bandwidth

The effect of varying the stop bandwidth of the masking noise was investigated for 12 units (with CFs between 1.73 and 29 kHz). The 12 units were of the second category, i.e. they responded 'monotonically' to signal level changes at all masker levels. For 11 of these units CF tone 'signal' was used and a white noise 'signal' for the remaining one. The responses to both of these signals were qualitatively similar. The responses to a wideband signal in wideband masker were measured for only one unit and no biassing was observed under these conditions (see Fig. 63).

All of the units studied, with a variety of stop bandwidths, responded in a similar manner and two typical responses are shown in Figs. 65 and 67. The top part of both figures shows the automatically determined frequency/intensity response areas (see Section 2.5.2 for details of method). Unit 403.03 (Fig. 65) has an excitatory area with CF of 6.6 kHz flanked on either side by inhibitory side bands (as indicated by the reduction of the spontaneous discharge). The length and position of the bars labelled B-G indicate the stop bandwidths and centre frequencies used.

The series of rate versus intensity functions in response to tones in the presence of the masker are presented in order of increasing stop bandwidth. 'A' represents the responses to the CF tone presented in wideband noise; the unit (403.03) responds 'monotonically' to the tone over some 90 dB. 'G' represents the responses to the CF tone presented alone (which may be thought of as the tone presented in a masker with an infinite stop bandwidth). This unit responds monotonically to the tone alone,

Figure 65

Variation of rate versus intensity functions with increasing masker stop bandwidth. The top part of this figure shows the response area of DCN unit 403.03 (CF 6.62 kHz). The length of the lines is proportional to the number of spikes elicited from the neurone by a single presentation of a 50 ms tone plotted at the appropriate frequency and intensity (see Section 2.5.2 for details of the method).

The lower part of the figure shows the rate versus intensity functions of this neurone in response to a tone presented either alone or in a masking noise. 'A' is the rate versus intensity function in response to the tone presented in wideband noise masker and 'G' the response to the tone presented alone. The width of the masker stopband (3 dB down points) used for the rate versus intensity functions 'B' to 'F' is indicated in relation to the neurone's response area by the lines labelled accordingly. In the rate versus intensity functions 'A' to 'F' the continuous lines join the responses to the three tones presented at each masker level. At the top of each rate versus intensity function is shown the standard deviation of the individual spike counts about the mean value. The dashed arrows and the numbers on the rate versus intensity function 'C' are referred to in the text.

Figure 65

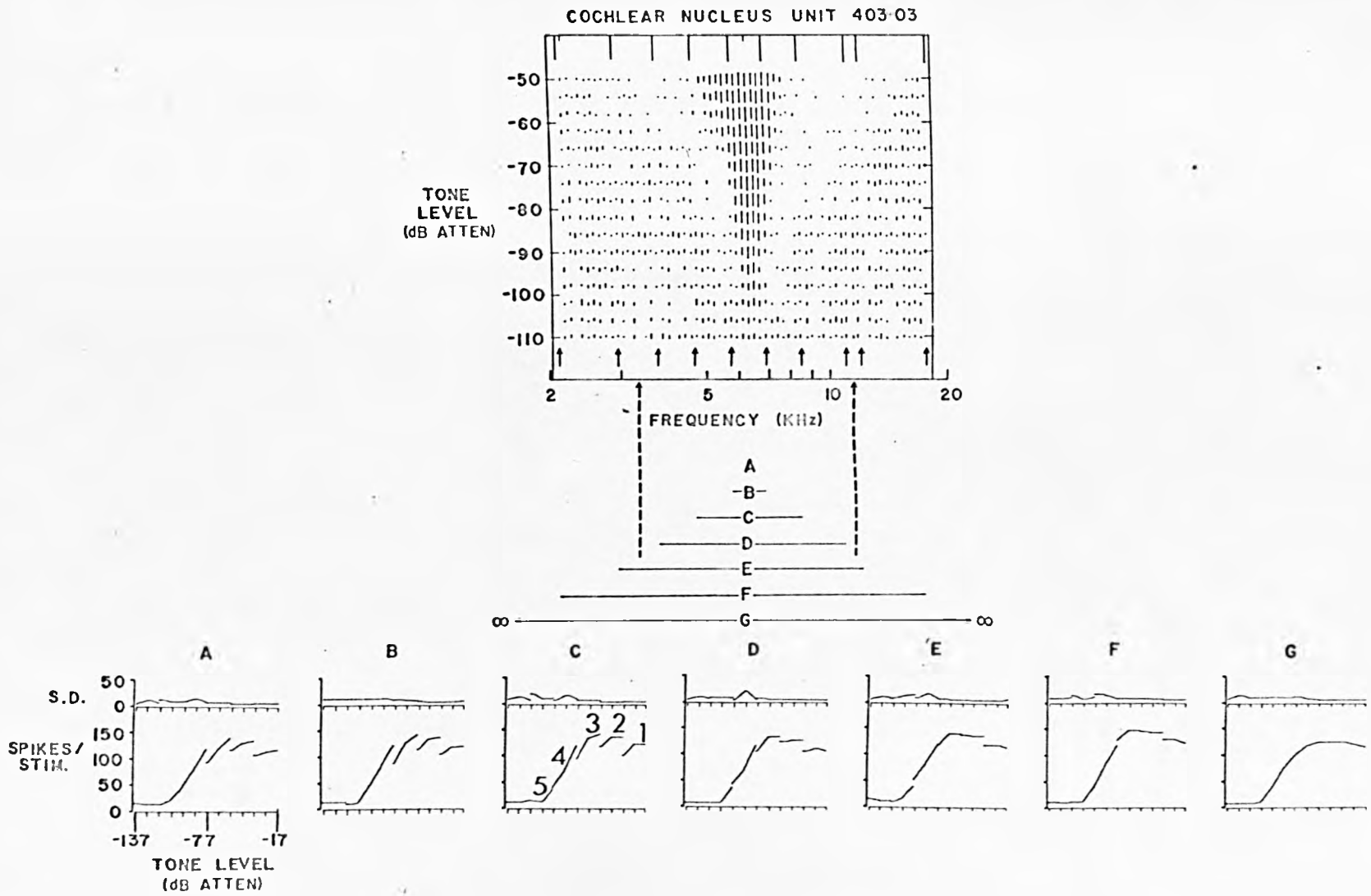

COCHLEAR NUCLEUS UNIT 403-03
TONE LEVEL (dB ATTEN)
-50
-60
-70
-80
-90
-100
-110
2
5
10
20
FREQUENCY (KHz)
A
B
C
D
E
F
G
∞
S.D.
SPIKES/ STIM.
50
0
150
100
50
0
-137
-77
-17
TONE LEVEL (dB ATTEN)
1
2
3
4
5

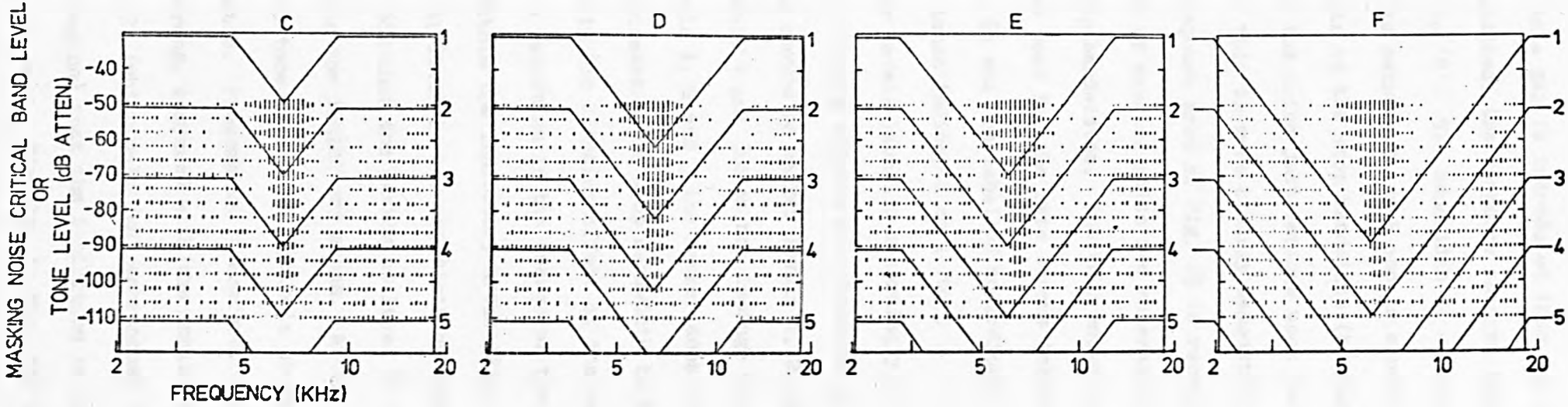
Figure 66

A schematic representation of the spectra of the bandstop masking noise with respect to the response area of unit 403.03. The four sets of masking noise spectra C, D, E and F are shown as continuous lines drawn on copies of the response area of unit 403.03 (see Section 2.5.2 for details). The spectra shown (C, D, E and F) correspond to the masking noises used to obtain the rate versus intensity functions C, D, E and F shown in Fig. 65. The five levels of masker labelled 1 to 5 correspond to the levels of masker at which the sets of responses labelled 1 - 5 in Fig. 65 were obtained.

The masker spectra are positioned on the abscissa at the tone intensity which is equal to the intensity of the noise in the masker passband measured within a bandwidth equal to a human critical band centred at the unit's CF.

Figure 66

UNIT 403·03



over about 40-50 dB. As a gap is introduced into the wideband noise and is prograssively widened, the response changes from one similar to 'A' to one similar to 'G'. The bandwidth at which most of this transformation occurs is between D and E and is shown by the dashed arrows in Fig. 65. This is the stop bandwidth (between D and E) at which the shoulders of the noise just impinge upon the inhibitory regions of the response area. This is more clearly demonstrated by Fig. 66.

In Fig. 66 the response area of Fig. 65 is reproduced and the spectra of five levels of masking noise are schematically indicated for four different stop bandwidths. The four masker spectra in Fig. 66 correspond to those used for the rate versus intensity functions C, D, E and F in Fig. 65 and are labelled accordingly. The responses to the sets of three tones indicated as 1 to 5 in Fig. 65C were obtained at the masker levels labelled accordingly in Fig. 66.

In Fig. 65C, no biassing effects are observed to masker levels 4 and 5, but biassing occurs to masker levels 1, 2 and 3. In Fig. 66C the masker at levels 4 and 5 does not impinge upon the inhibitory areas whereas at levels 1, 2 and 3 the masker does overlap the inhibitory areas. Increasing the stop bandwidth to that of Fig. 65D leads to a reduction in the biassing effect of the masker at levels 1, 2 and 3 and also a reduction in the energy of the masker at these levels which falls within the inhibitory areas (Fig. 66D). In Fig. 65E only the masker at level 1. has any biassing effect although it can be seen in Fig. 66E that the masker at level 2. as well as at level 1. impinges upon the inhibitory areas. At the stop bandwidth shown in Fig. 66E the tone is tens of decibels above the masker in the region of the notch. Presumably, therefore, the excitation due to the tone is so strong, compared with the inhibition produced by the masker at level 2. (which only just encroaches into the inhibitory areas in the notch region) that the inhibition is completely overcome and no biassing is observed. Finally, in Fig. 65F the biassing

produced by the masker at level 1. is further reduced as is the degree to which the masker overlaps the inhibitory areas in Fig. 66F.

In the case of unit 403.03, therefore, the effect of the masker seems to be, at least qualitatively, explainable in terms of the amount of masker energy falling within the inhibitory side bands which are evident even for single tone stimuli. This is, however, not the case for all of the units studied. Unit 473.09, for example, which is described in detail below, shows a number of features not present in the responses of unit 403.03. Fig. 67 shows the responses of unit 473.09. The response area of this unit has an excitatory region centred at 3 kHz (CF) flanked by a weak low frequency and a strong high frequency inhibitory area. The responses to the CF tone in bandstop noise masker again change from being similar to the tone presented alone ('F') to being similar to the tone in wideband noise ('A'). This change occurs between responses 'D' and 'E' which represents a stop bandwidth as indicated by the broken arrows. As in unit 403.03 we see that this corresponds to the stop bandwidth at which the shoulders of the masker noise just impinge on the inhibitory regions of the response area. The degree to which the masker overlaps the inhibitory side bands of this unit is better seen in Fig. 68.

Fig. 68 is again a representation of the masker spectra with respect to the response area, as in Fig. 66. Thus the three maskers shown, C, D and E, represent those used in measurements of the rate versus intensity functions C, D and E in Fig. 67. The responses to tones labelled 1, 2, 3 and 4 in Fig. 67 were obtained at the masker levels 1, 2, 3 and 4 in Fig. 68. Thus in Fig. 67E we see that only masker level 1. produces any biassing at all and this is very weak. In Fig. 68E it is clear that only masker level 1. impinges on the inhibitory side bands. The responses of unit 473.09 (Figs. 67, 68) thus appear similar to those of unit 403.03 (Figs. 65, 66). There

Figure 67

Variation of the rate versus intensity function with increasing masker stop bandwidth. The top part of this figure shows the response area of DCN unit 473.0((CF 2.88 kHz). The length of the lines is proportional to the number of spikes elicited from the neurone, by a single presentation of a 50 ms tone, plotted at the appropriate frequency and intensity (see Section 2.5.2 for details of the method).

The lower part of the figure shows the rate versus intensity functions of this neurone in response to the CF tone either presented alone (F) or presented in a masking noise (A to E). A is the rate versus intensity function to the tone presented in wideband masking noise. The width of the masker stop band (3 dB down points) used for the rate versus intensity functions B to E is indicated in relation to the response area by the lines labelled accordingly. In the rate versus intensity functions A to E the continuous lines join the responses to the three tones presented at each masker level. At the top of each rate versus intensity function is shown the standard deviation of the individual spike counts about the mean value. The dashed arrows and the numbers on the rate versus intensity function C are referred to in the text.

Figure 67

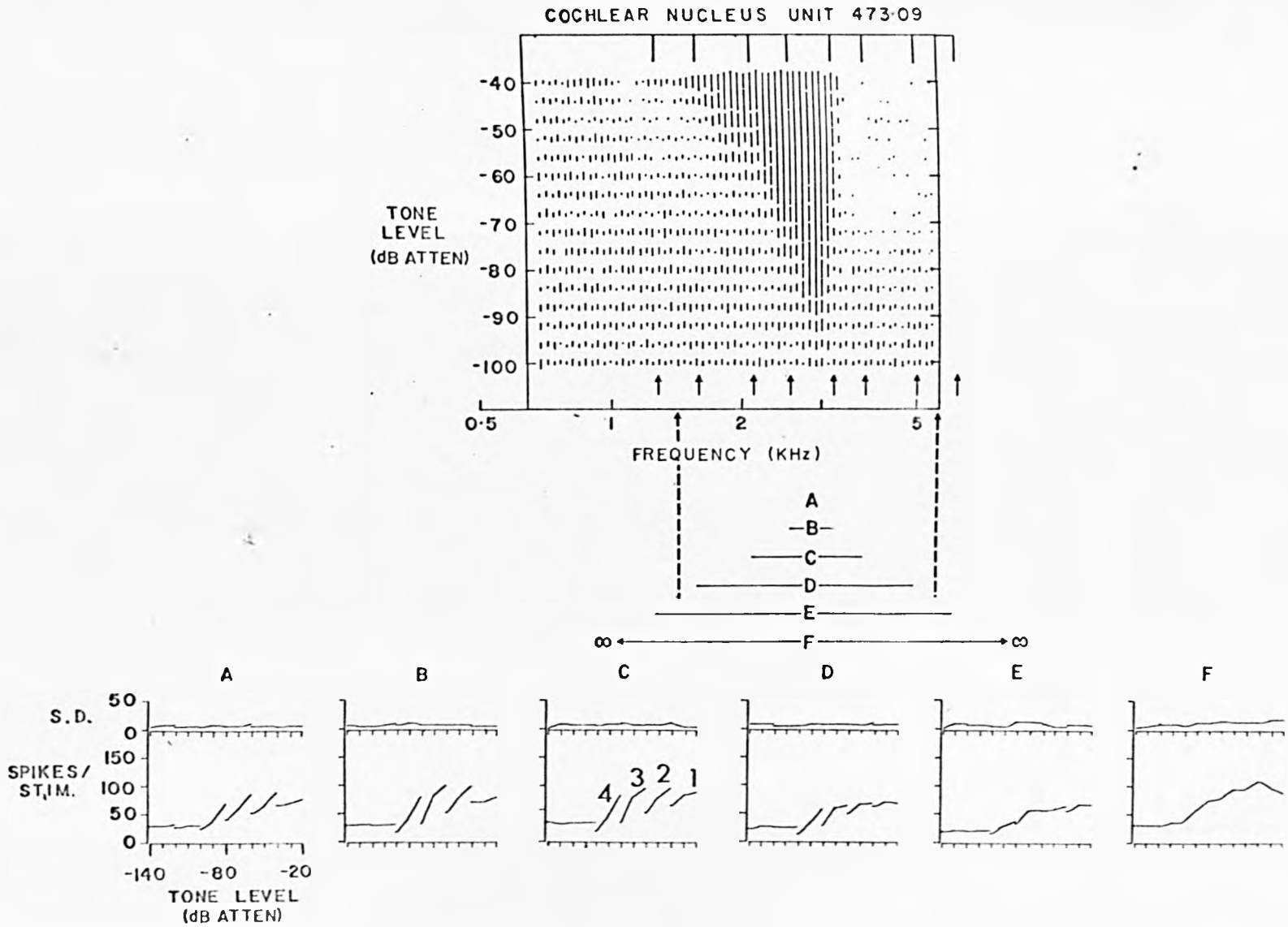
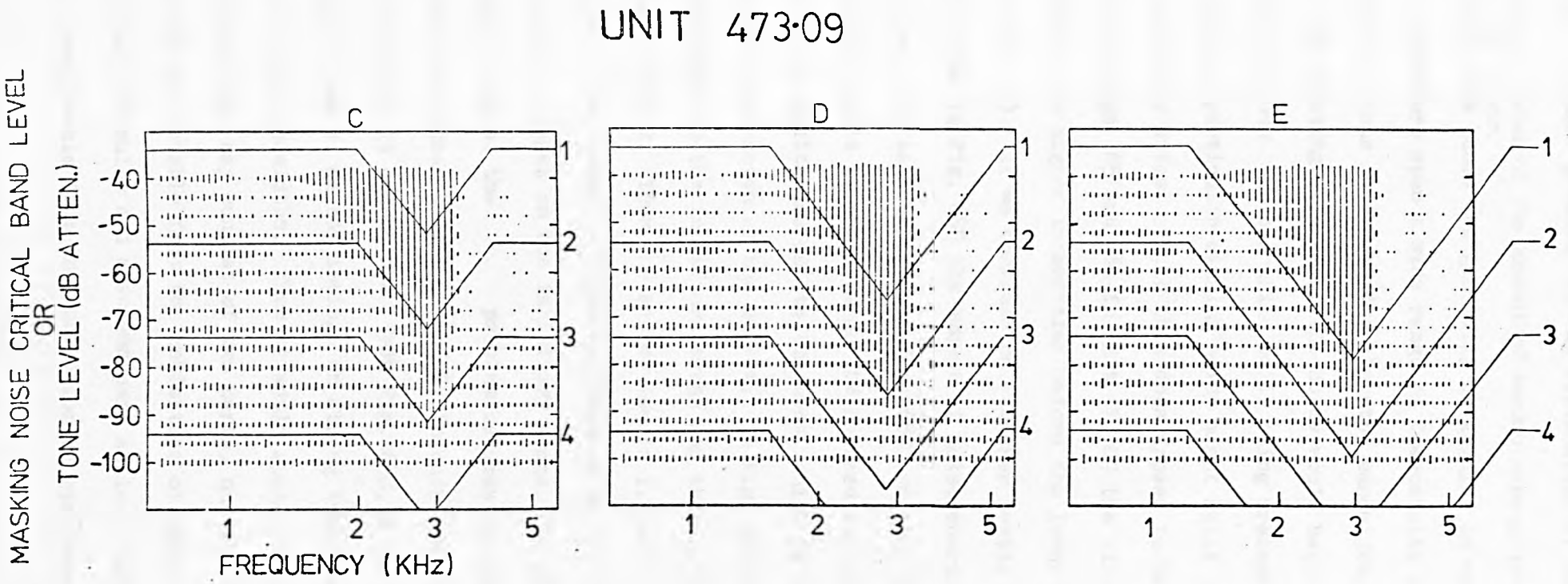

COCHLEAR NUCLEUS UNIT 473-09
TONE LEVEL (dB ATTEN)
-40
-50
-60
-70
-80
-90
-100
0·5
1
2
5
FREQUENCY (KHz)
A
B
C
D
E
F
∞
∞
S.D.
50
0
SPIKES/ STIM.
150
100
50
0
-140
-80
-20
TONE LEVEL (dB ATTEN)
4
3
2
1

Figure 68

A schematic representation of the spectra of the bandstop masking noise with respect to the response area of unit 473.09. The three sets of masking noise spectra C, D and E are shown as continuous lines drawn on copies of the response area of unit 473.09 (see Section 2.5.2 for details). The spectra shown (C, D and E) correspond to the masking noises used to obtain the rate versus intensity functions C, D and E shown in Fig. 67. The four levels of masker labelled 1 to 4 correspond to the levels of masker at which the sets of responses labelled 1 to 4 in Fig. 67 were obtained.

The positioning of the masker spectra on the abscissa is described in the legend of Figure 66.

Figure 68


UNIT 473·09
C
D
E
MASKING NOISE CRITICAL BAND LEVEL
OR
TONE LEVEL (dB ATTEN.)
-40
-50
-60
-70
-80
-90
-100
1
2
3
4
5
FREQUENCY (KHz)

is, however, a major problem in the explanation of the responses of unit 473.09 purely in terms of the amount of masker energy present in its inhibitory side bands.

Inhibitory side bands are generally triangular in shape (e.g. Fig. 65) and therefore span a wide range of frequencies at higher intensity levels. Thus in increasing the stop bandwidth, we might expect that the biassing effects of the noise would begin to diminish at low masker levels while still being present at higher levels, at which a particular masking noise might still impinge on the wider inhibitory areas. While this does appear to be the case for unit 403.03 (Figs. 65 and 66) in unit 473.09 the biassing effect seems to fail at the higher intensities before the lower (e.g. response D, Fig. 67). If we consider only masker levels 1. and 2. it is evident that in Fig. 68D the amount of noise energy within the inhibitory side bands is less than in Fig. 68C and thus the biassing effect of masker levels 1. and 2. might be reduced sufficiently to be overcome by the excitation due to the tone, which is some 30 dB more intense than the notch of the masker. In Fig. 68E only masker level 1. encroaches on the inhibitory areas and thus no biassing is seen to masker level 2. Thus the masker levels 1. and 2. behave as we would expect - the amount of biassing depends on the extent to which the masker impinges on the inhibitory areas. If we now consider masker levels 3. and 4. the problem becomes apparent :- biassing occurs to masker levels 3. and 4. in responses A, B, C and D in Fig. 67 and yet it can be seen from Fig. 68C, D and E that masker levels 3. and 4. do not impinge on strong inhibitory areas at any of these notch bandwidths. Thus it would appear that the responses observed in this unit may consist of two parts, one at high masker levels which is predictable from the inhibition of spontaneous rate by a single tonal stimulus and a second part at lower masker levels which is not predictable from the inhibition of spontaneous rate by

a single tone. There appears to exist a region within the response area of this unit in which inhibition occurs when a stimulus is simultaneously present at the CF. This region stretches from near threshold at the CF over a range of frequencies (at least as wide as the stopband in Fig. 68D), which is quite sharply delimited (since the biassing fails completely to masker levels 3. and 4. between the stop bandwidths indicated in Fig. 68D and E). Such an inhibitory area which is apparently only seen when more than one stimulus is presented simultaneously may reflect either two-tone suppression at the cochlear nerve or true two-tone inhibition (e.g. Galambos, 1944) at the cochlear nucleus. Since the expanse of the inhibitory area in the frequency domain is quite wide even at very low intensities it is unlikely that it reflects two-tone suppression at the cochlear nerve which is usually limited to a narrow band of frequencies at low intensities (see Evans, 1975afor review).

In summary, the biassing effects which we observe at the level of the cochlear nucleus appear to be a result of lateral inhibitory effects and as such disappear when a wide enough stop band is introduced into the wideband noise masker. Not all of the responses observed, however, are attributable to the inhibitory areas in which a single tone will inhibit spontaneous activity. The further investigation of the inhibitory effects of simultaneous presentation of more than a single tone are beyond the scope of this dissertation.

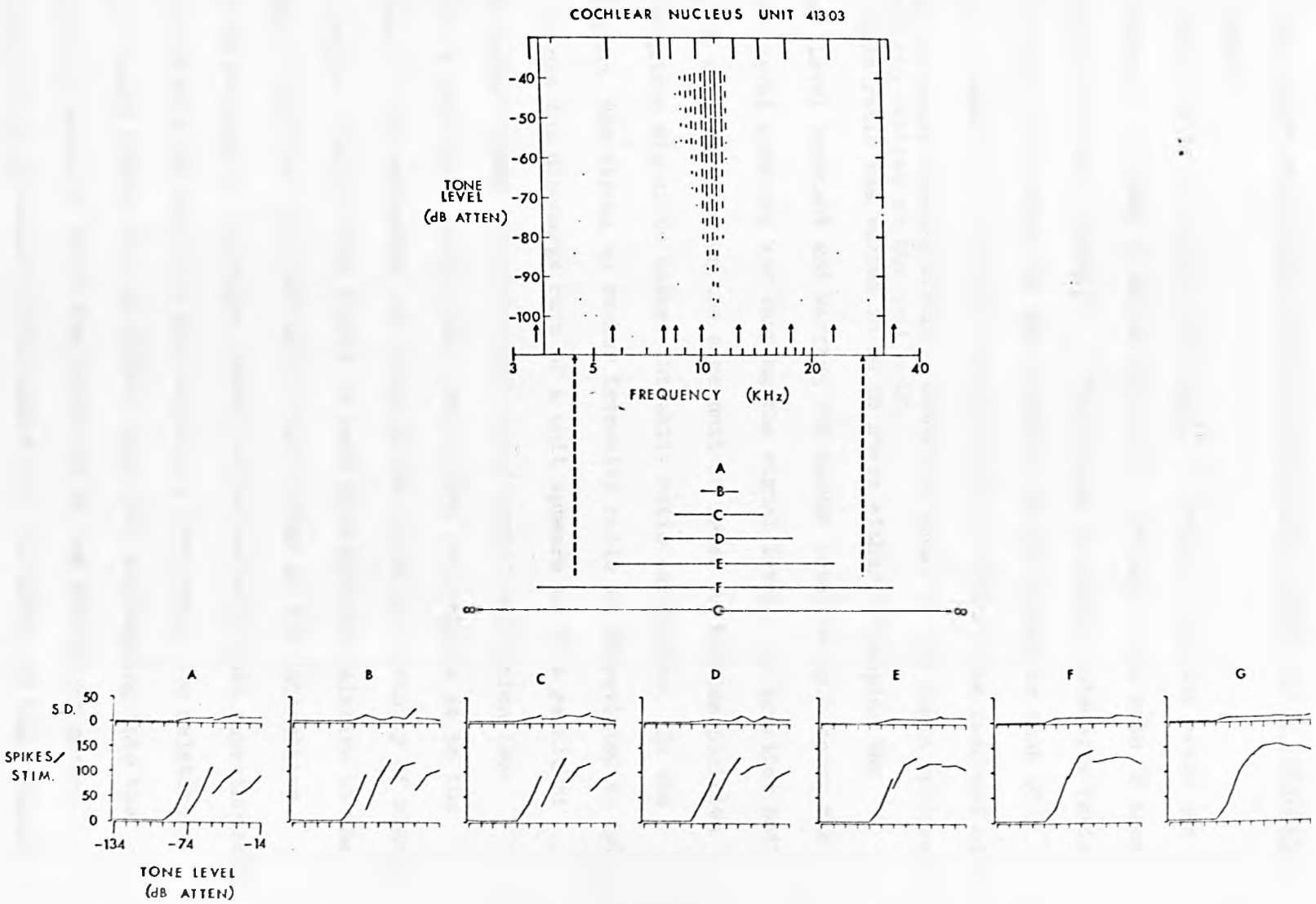
A final example of the effect of varying the stop bandwidth is given in Fig. 69 for unit 413.03 which has virtually zero spontaneous discharge rate. In this unit the change from responses like those of the tone in white noise to those like the tone presented alone takes place between responses 'E' and 'F', as shown by the broken arrows. The low spontaneous discharge rate of this unit obviated

Figure 69

Variation of the rate versus intensity functions with increasing masker stop bandwidth. The top part of this figure shows the response area of DCN unit 413.03(CF 11.0 kHz). The length of the lines is proportional to the number of spikes elicited from the neurone by a single presentation of a 50 ms tone plotted at the appropriate frequency and intensity (see Section 2.5.2 for details of the method).

The lower part of the figure shows the rate versus intensity functions of this neurone in response to the CF tone either presented alone (G) or presented in a masking noise (A to F). A is the rate versus intensity function to the tone presented in wideband masking noise. The width of the masker stop band (3 dB down points) used for the rate versus intensity functions B to F is indicated in relation to the response area by the lines labelled accordingly. In the rate versus intensity functions A to F the continuous lines join the responses to the three tones presented at each masker level. At the top of each rate versus intensity function is shown the standard deviation of the individual spike counts about the mean value. The dashed arrows are referred to in the text.

Figure 69


COCHLEAR NUCLEUS UNIT 41303
TONE LEVEL (dB ATTEN)
-40
-50
-60
-70
-80
-90
-100
3
5
10
20
40
FREQUENCY (KHz)
A
B
C
D
E
F
G
S.D.
50
0
SPIKES/ STIM.
150
100
50
0
-13.4
-7.4
-1.4
TONE LEVEL (dB ATTEN)

detection of any inhibitory areas present but it nevertheless behaves as if it had inhibitory side bands.

5.3.2.3 Responses of cochlear nucleus units to signals in bandstop noise masker as a function of signal: masker noise intensity ratio

The effects of varying the signal to masker intensity ratio has been studied for some 26 units (CFs 2.47 - 29 kHz) using both CF tone and wideband noise 'signals'. The signal to masker intensity ratio is defined as the ratio of the intensity of the signal to that of a wideband masker (of spectral density equal to that of the passband of the bandstop noise masker) within a bandwidth equal to the human critical bandwidth centred at the unit's CF.

This ratio was varied in 10 dB steps either by keeping the signal level constant and varying the masker level or by keeping the masker level constant and varying the signal level. In practice both methods were employed on the same unit in order to provide positive and negative signal to masker intensity ratio excursions. In the following, the signal to masker intensity ratio is abbreviated to S/M.

Since the discharge rate of a unit appears to be a result of both masker evoked inhibition and signal evoked excitation (see previous section), one can make qualitative predictions as to the effect, on the responses, of changing the relative intensity of signal and masker. As the tone signal is made more intense relative to the masker the biassing effect should fail first at low intensities. This is because at the signal levels which are only just suprathreshold the tone will be well into the excitatory area while the relatively less intense masker will be either only just encroaching into the inhibitory areas or below the threshold of the inhibitory areas. The inhibition produced by the masker will therefore be insufficient to overcome the excitation produced by the tone and no biassing will be observed. At higher signal levels, although the masker will be

well into the inhibitory areas, the tone will still be producing relatively more excitation than the masker inhibition and one would expect that any biassing taking place would be weaker and thus the slopes of the lines joining the three tone responses at each masker level would therefore be reduced. As the S/M is further increased a point will be reached at which no masker level will be suprathreshold and the only response observed will be excitation to the tone.

Decreasing the S/M ratio should initially produce proportionally more inhibition due to the masker and the slopes of the lines joining the three tone responses at each masker level should be increased. Further decreases in the S/M ratio should result in the response to the masker becoming much stronger than the response due to the tone and it will therefore dominate the observed response. The above predictions are well fulfilled by the examples shown in Fig. 70 (unit 473.09), Fig. 71 (unit 570.03) and Fig. 72 (unit 473.21). All of the units in category 2 studied with various S/M ratios showed responses similar to those of these units.

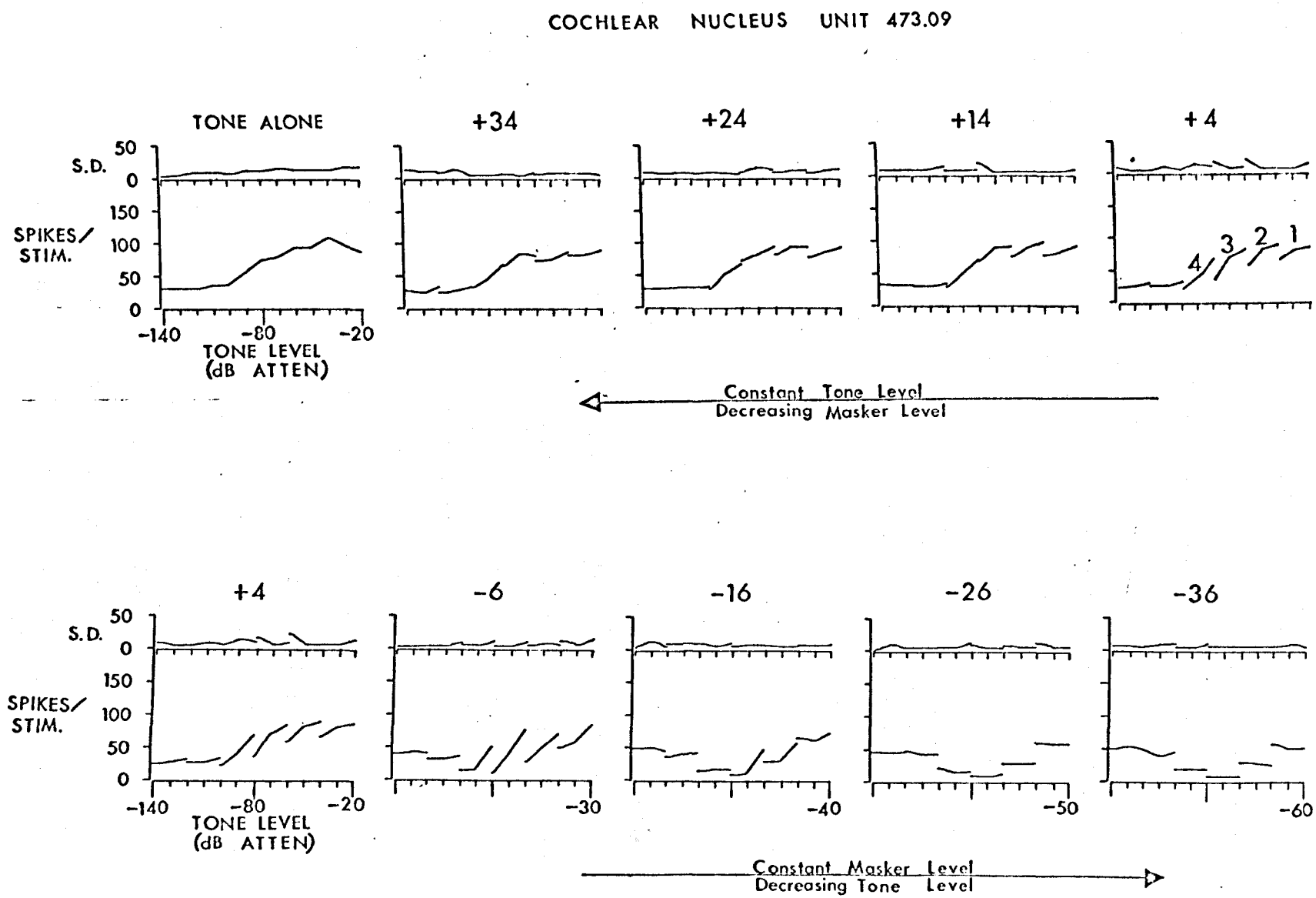
In Figs. 70 - 73 rate versus intensity functions for the CF tone (Figs. 70, 71, 73) and wideband noise (Fig. 72) are illustrated for a range of S/M ratios. The individual rate versus intensity functions have the same form as those described earlier in this chapter, in that the continuous lines join the responses to the three tones measured at each level of masker. Above each graph the S/M ratio is indicated and the graphs are arranged in order of descending S/M ratio.

Looking first at the responses of unit 473.09 (Fig. 70) we see that at a S/M of +4 dB (as indicated by the figure above the rate versus intensity functions) this unit responds monotonically to the tone over a range of 80 dB. When the S/M ratio is increased to

Figure 70

This figure shows rate versus intensity functions of unit 473.09 in response to either a tone signal alone or to a tone signal in bandstop noise masker (stop band 3 human critical bandwidths) at different signal to masker intensity ratios. The signal to masker intensity ratio is defined as the ratio of the energy of the signal to that of a white noise (of spectral density equal to that of the passband of the bandstop noise) within a human critical band at the unit's CF and is indicated in dB above each rate versus intensity function. At the top of each rate versus intensity function is shown the standard deviation of the individual spike counts about the mean value. In all rate versus intensity functions, except that to the tone alone, the continuous lines join the responses to the three tone levels at each masker level. The numbers on the +4 dB rate versus intensity function are referred to in the text.

Figure 70


COCHLEAR NUCLEUS UNIT 473.09
TONE ALONE
+34
+24
+14
+4
S.D.
SPIKES/ STIM.
50
0
150
100
50
0
-140
-80
-20
TONE LEVEL (dB ATTEN)
4
3
2
1
Constant Tone Level
Decreasing Masker Level
+4
-6
-16
-26
-36
-30
-40
-50
-60
Constant Masker Level
Decreasing Tone Level

+14 dB the biassing effect of the masker disappears at masker levels labelled 3 and 4. The responses to the three tones at masker levels 3 and 4 show clear biassing effects at S/M of +4 dB, but little or none at all at S/M ratio of +14 dB. The slopes of the lines joining the three responses to the tones at the two highest masker levels (1 and 2) are also reduced. At +24 dB this reduction in slope is more pronounced and by a S/M of +34 dB the response looks very like that to the CF tone presented alone.

As the S/M ratio is decreased the first effect (at S/M of -6 dB) is an increase in the slopes of the lines joining the three responses to the tone at masker levels 2, 3 and 4, due presumably to more pronounced inhibitory effects of the masker, which at low levels reduces the discharge rate to below the spontaneous discharge rate. Further decrease to a S/M ratio of -16 dB results in the masker inhibition becoming dominant, the tone only producing increases in the discharge rate at its most intense level relative to each masker level. Finally at a S/M ratio of -26 dB changes in the tone level at each masker level do not produce discharge rate changes and the only observed response is apparently that to the bandstop noise masker which inhibits the discharge to below spontaneous rate at low intensity levels and causes weak excitation at the higher intensity levels. This is despite the fact that the threshold of this unit to the CF tone is -100 dB, which means that the tone will be exciting the unit at 50 dB above its threshold at its highest level of the -26 dB S/M rate versus level function.

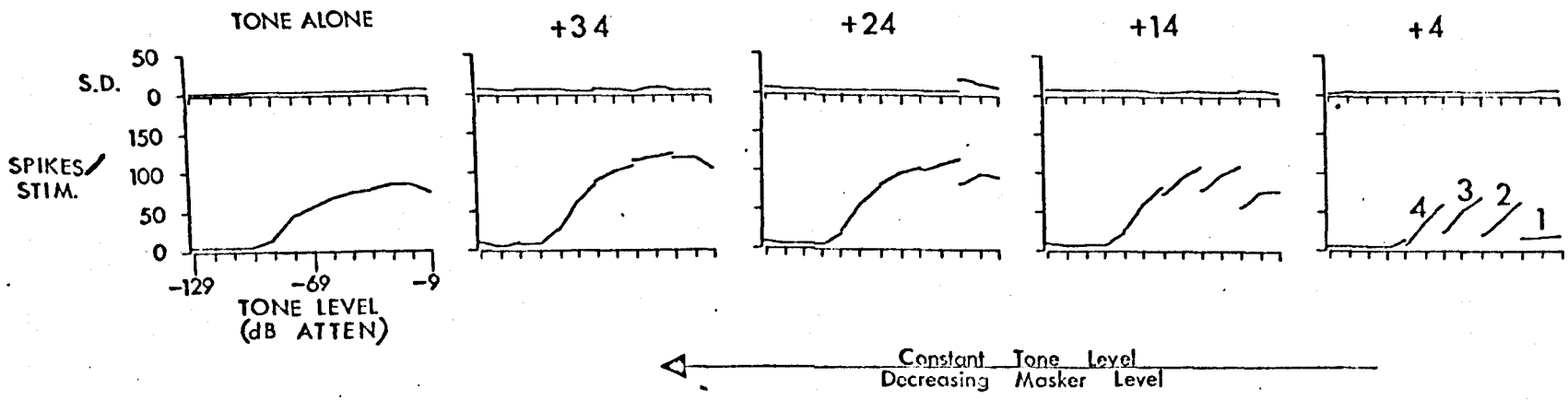
Fig. 71 shows the results from unit 570.03 plotted in a similar manner; the same features are recognisable for this unit. At +4 dB S/M ratio this unit responds 'monotonically' to the tone over a range of some 80 dB (see +4 dB lower row; it is not clear why the tone

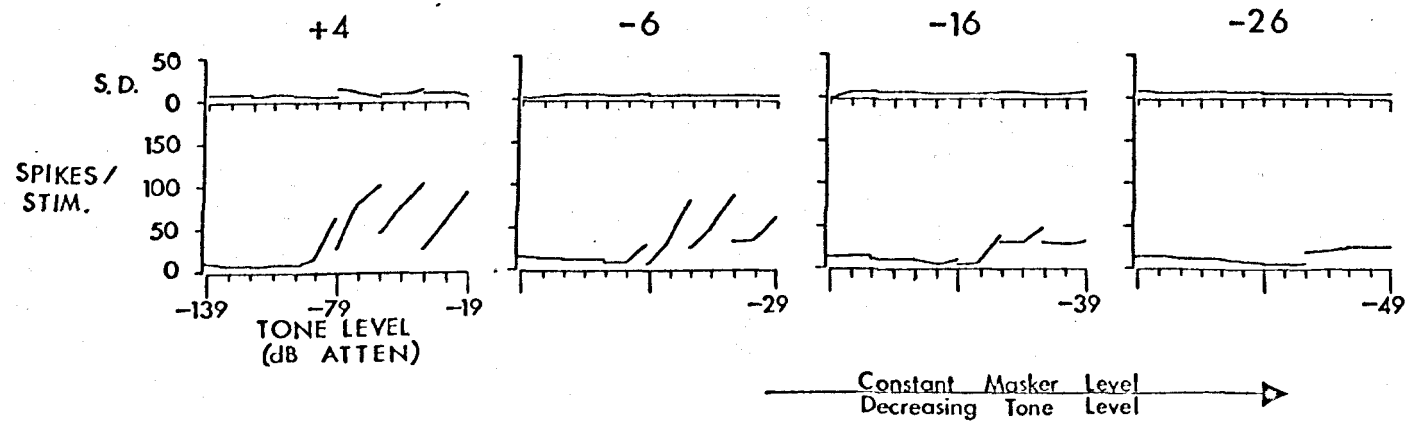
Figure 71

This figure shows rate versus intensity functions of unit 570.03 in response to either a tone signal alone or to a tone signal in bandstop noise masker (stop band 3 human critical bandwidths) at different signal to masker intensity ratios. The signal-to masker intensity ratio is defined as the ratio of the energy of the signal to that of a white noise (of spectral density equal to that of the passband of the bandstop noise) within a human critical band at the unit's CF, and is indicated in dB above each rate versus intensity function. At the top of each rate versus intensity function is shown the standard deviation of the individual spike counts about the mean value. In all rate versus intensity functions, except that to the tone alone, the continuous lines join the responses to the three tone levels at each masker level. The numbers on the +4 dB rate versus intensity function are referred to in the text.

Figure 71

COCHLEAR NUCLEUS UNIT 570.03





responses at masker level 1 in the top row at +4 dB are so much less than at masker level 1 at +4 dB in the lower row since the two rows differ only in overall level. One would only expect a shift of the response by 10 dB along the intensity axis.) When the S/M ratio is increased to +14 dB, the biassing begins to disappear beginning at the masker level 4 and the slopes of the lines joining the three responses to the tone at masker levels 1, 2 and 3 are decreased. At +24 dB S/M ratio only masker level 1 produces any biassing and at +34 dB S/M ratio the response looks very like the response to the CF tone presented alone.

Decreasing the S/M ratio to -6 dB results in a slight increase in the slopes of the lines joining the responses to the tones at masker levels 2 and 3. At -16 dB S/M ratio the noise inhibition becomes dominant and the tone only produces an increase in the discharge rate at its highest level relative to the masker level. When the S/M ratio is further decreased to - 26 dB, the only observable responses are those to the bandstop noise masker, which is inhibitory at low intensity levels and excitatory at high intensity levels. This again is despite the fact that at the highest level in the -26 dB S/M ratio rate versus intensity function, the tone is exciting the unit at about 50 dB above threshold. This effect, also noted for unit 473.09 is discussed later.

A final example of this type of analysis on a unit which showed a wide dynamic range (i.e. of category 2 above) is shown in Fig.72 for unit 473.21 using a wideband noise signal. The features described above using CF tone signals are readily discernible.

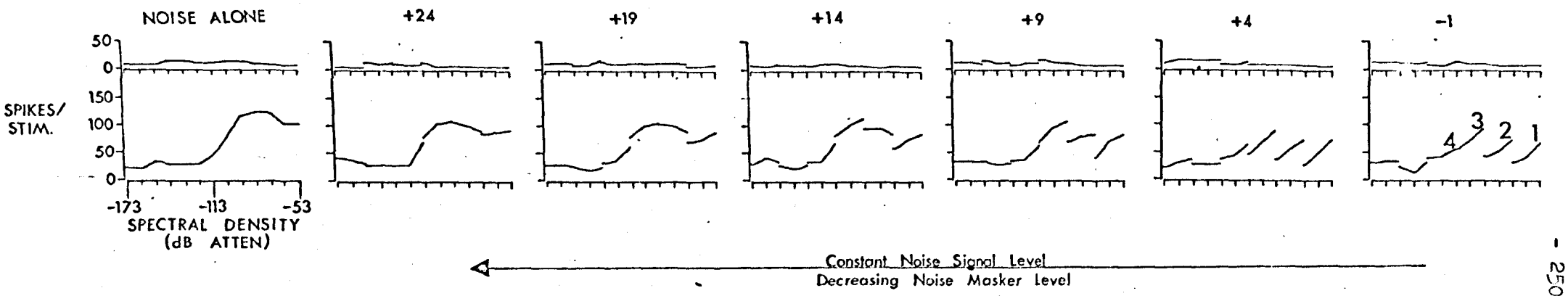
At a S/M ratio of -1 dB this unit shows a 'monotonic' response to signal level changes over a range of 70 - 80 dB. As the S/M ratio is increased the biassing effects initially become more pronounced

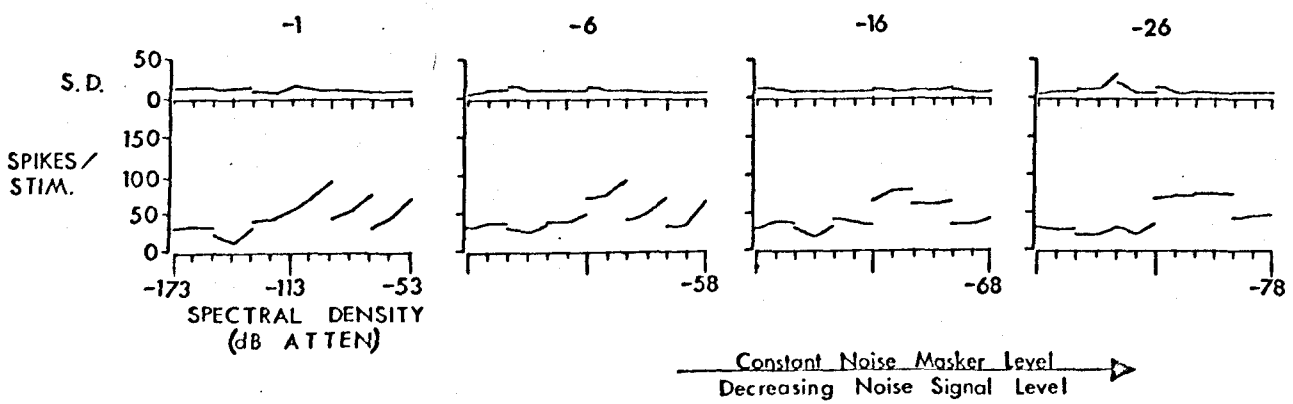
Figure 72

Rate versus intensity functions of unit 473.21 in response to either a wideband noise signal alone or to a wideband noise signal in bandstop noise masker (stop band 3 human critical bandwidths) at different signal to masker intensity ratios. The signal-to masker intensity ratio is defined as the ratio of the energy of the signal to that of a white noise (of spectral density equal to that of the passband of the bandstop noise) within a human critical band at the unit's CF, and is indicated in dB above each rate versus intensity function. At the top of each rate versus intensity function is shown the standard deviation of the individual spike counts about the mean value. In all rate versus intensity functions, except that to the tone alone, the continuous lines join the responses to the three tone levels at each masker level. The numbers on the -1 dB rate versus intensity function are referred to in the text.

Figure 72

COCHLEAR NUCLEUS UNIT 473.21





(at S/M +4 dB). At a S/M ratio of +9 dB the biassing effects disappear at masker levels 3 and 4 and the slope of the lines joining the responses to the signal at masker levels 1 and 2 is reduced. At a S/M ratio of +19 dB only the masker level 1 produces any biassing and at +24 dB the response shows no biassing and looks like the response to the white noise presented alone.

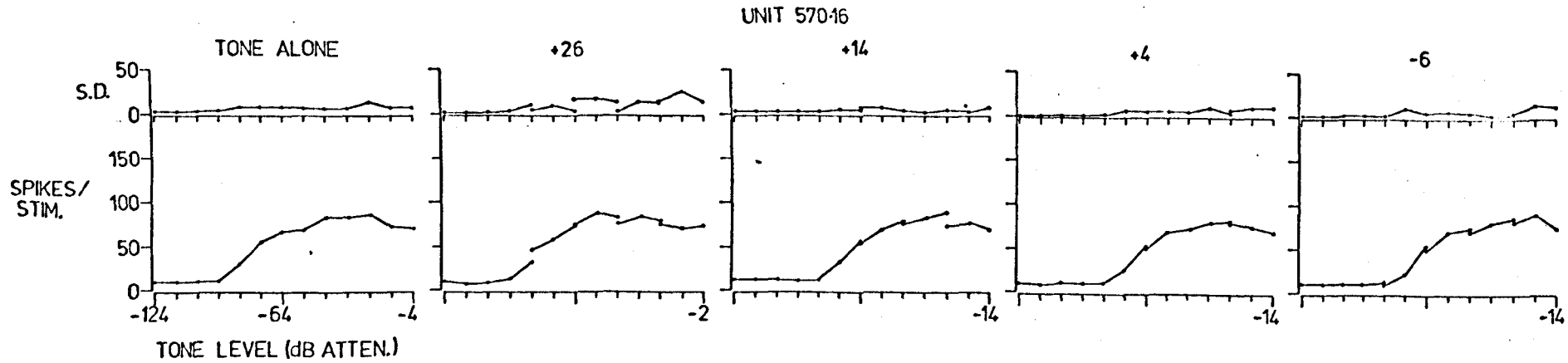
As the S/M ratio is decreased the masker begins to dominate the unit's response. At -6 dB S/M ratio the 'signal' only produces a discharge rate increase at its highest level relative to the masker. At -16 dB S/M ratio the increases in discharge rate caused by the noise 'signal' intensity steps are further reduced and at -26 dB S/M ratio the only discernible response is that due to the masker even though the noise signal is some 45 dB above threshold at its highest level.

The effect of varying the S/M ratio was studied for only one unit of category 1 (i.e. which responded 'monotonically' only over a limited range of masker levels). The results of this analysis on unit 570.16 are shown in Fig. 73 plotted in a similar manner to Figs. 69 - 71. This unit shows no prominent biassing effects for S/M ratios of -6, +4 or +26 dB. For a S/M ratio of +14 dB the highest masker level does produce a biassing effect which is, however, insufficient to produce 'monotonic' responses to the signal. Thus, for this unit, manipulation of the S/M ratio did not change the response observed from a category 1 to a category 2 type response. Since, however, many of the neurones of category 1 had response characteristics such as inhibitory side bands and complex PSTHs which are shared by category 2 neurones it seems likely that suitable manipulation of parameters such as stop bandwidth and signal to masker ratio might have changed the type of response observed.

Figure 73

Rate versus intensity functions of unit 570.16 in response to either a tone signal alone or to a tone signal in bandstop noise masker (stop band 3 human critical bands) at different signal to masker intensity ratios. The signal to masker intensity ratio is defined as the ratio of the energy of the signal to that of a white noise (of spectral density equal to that of the passband of the bandstop noise) within a human critical band at the unit's CF, and is indicated in dB above each rate versus intensity function. At the top of each rate versus intensity function is shown the standard deviation of the individual spike counts about the mean value. In all rate versus intensity functions, except that to the tone alone, the continuous lines join the responses to the three tone levels at each masker level.

Figure 73


UNIT 570·16
TONE ALONE
+26
+14
+4
-6
S.D.
50
0
SPIKES/
STIM.
150
100
50
0
-124
-64
-4
-2
-14
-14
-14
TONE LEVEL (dB ATTEN.)

In general, for units in category 2 (i.e. having a wide dynamic range when the signal is presented in bandstop noise), the effect of altering the signal to masker ratio are consistent with the suggestion that the biassing effect is a result of lateral inhibition due to the noise.

5.4 Discussion

In the first part of this discussion some features of the responses described above are considered and, where appropriate, comparisons are drawn with previously reported studies. The later part of the discussion deals with the implications of the present work for intensity encoding in the cochlear nerve and the nature of the input to the cochlear nucleus neurones.

5.4.1 Some Aspects of the Present Data and Comparison with Previous Studies

Greenwood and his colleagues have extensively studied the responses of cochlear nucleus neurones to tone + noise stimuli and the present data shows many similarities with that of the earlier studies (Greenwood and Maruyama, 1965; Goldberg and Greenwood, 1966; Greenwood and Goldberg, 1970).

Fig. 74 from Greenwood and Goldberg (1970) shows the responses of a DCN neurone to a CF tone and a narrow band noise. The narrow band noise is presumably located in the inhibitory side bands since its effect when presented alone is inhibitory (Fig. 74a). The response to the CF tone presented alone at the three different levels shown is excitatory (Fig. 74b). Fig. 74c shows three responses to the tone + noise which are analogous to responses measured in the present study in that the level of the noise band is kept constant and the tone level is varied over 20 dB. At its least intense relative to the noise the response to the tone is suppressed (compare lower PSTHs in columns b and c, Fig. 74), while at the two higher levels relative to the noise the response to the tone is augmented (compare PSTHs to tone levels 20 and 30 dB SPL in columns b and c, Fig. 74). Similar effects have been found in the present experiments using bandstop

Figure 74

PSTHs of responses to CF tones and narrow-band noises alone or presented together.

(From Greenwood and Goldberg, 1970.)

Figure 75

Responses of a neurone to a tone as a function of the level of a band of noise either below CF (a and b) or above CF (c and d).

(From Greenwood and Goldberg, 1970.)

Figure 74

Average-response histograms of response of unit 63-334-3 (a) to a band of noise outside the response area, (b) to best frequency tones, and (c) to combinations of the two. Stimuli were 200 msec in duration, coincident in time when combined, and presented at a rate of 1/sec. Ordinate scale is 50 spikes per time bin; time bin is 5 msec. Duration of stimuli is represented by horizontal bar, and total time on the abscissa is 500 msec. Column (a): response to a 500 Hz band of noise alone at 6.1 Hz center frequency at 60 dB SPL. Noise largely suppresses spontaneous activity during stimulus but not after stimulus. Column (b): response to a best-frequency tone of 9.8 kHz alone at three intensities. Tone excites strongly and suppresses spontaneous activity immediately after stimulus at all intensities shown. Column (c): response to combination of band of noise and tone; noise intensity remains *constant*; tone intensity increases. Noise partially suppresses tone response when tone is 10 dB and eliminates tone's slight suppression of spontaneous activity after the stimulus At two higher intensities of *tone*, same noise augments response and does not eliminate suppressive effect of tone on spontaneous activity immediately after stimulus *Location of unit*: uncertain, but probably dorsal cochlear nucleus

Figure 75

noise as for example in unit 343.19 (Fig. 76B); the response to a tone of level 46 dB SPL (at -6 dB relative to the masker) is suppressed below the response to a similar tone presented alone; the response to tone levels 56 and 66 dB SPL in the same level of masker are greater than when the tone was presented alone. A more common finding in the present study was, however, a response to the masker + tone which was below the response to the tone alone at the two lowest levels relative to the masker, and approximately equal to the tone alone at its highest level relative to the masker (e.g. unit 323.06, Fig. 61; unit 473.21, Fig. 63).

Fig. 75, also from Greenwood and Goldberg (1970), illustrates further similarities with the present data. The open squares in this figure show the responses to a band of noise centred either above or below the CF (as indicated in the figure) when presented alone. The noise is situated in the inhibitory sidebands (at least for graphs b, c and d, Fig. 75) and as its intensity is increased it reduces the discharge below spontaneous rate and then at higher intensities drives the unit (in a, b and c but not in d, Fig. 75). If the same sequence of noise levels is presented in the presence of a CF tone the observed response of the unit depends upon the level of the CF tone. If the CF tone is weak, the noise first suppresses the response (maximum suppression occurring at noise levels causing spontaneous rate suppression when presented alone), and at higher intensity the noise dominates the response and drives the unit as it would have in the absence of the tone. If the CF tone is more intense, the noise (at least for some centre frequencies) first augmented the response to the tone and then reduced the response towards and sometimes to exactly the value of response of the unit to the noise presented alone.

In the study of the effects of varying the signal to masker intensity ratio, similar domination of the response by the noise was also noted. For units 473.09 at a S/M of -26 dB (Fig. 70), 570.03 at a S/M of -26 dB (Fig. 71) and 473.21 at a S/M of -16 dB (Fig. 72) the only observable response was that due to the bandstop noise masker. In the rate versus intensity functions cited above, the signal at its most intense was 50, 50 and 45 dB above the threshold of the three units respectively. Signals at such levels, when presented alone, produce a higher firing rate than that observed when the signal is presented in bandstop noise. Thus it can be seen that, as in the study of Greenwood and Goldberg, the noise is dominating the response and driving the unit at a lower rate than would the tone presented alone. Thus the narrow bands of noise of Goldberg and Greenwood (1970) appear to have similar effects on the responses of cochlear nucleus cells as the bandstop noise used in the present study. One may speculate that any signal, whether wideband, narrow band or bandstop noise or even single tones, which has sufficient energy within the inhibitory regions of a unit's response area may produce the biassing effects seen in the present study.

Wideband noise 'signals' when presented alone did not drive the majority of units as effectively as the CF tone 'signal'. At the CN this is presumably because the noise simultaneously activates both excitatory and inhibitory regions of the response area.

The finding for cochlear fibre 327.50 of a lower slope of the rate versus level function for noise compared with that for CF tones (see Fig. 55) is in agreement with the findings of Greenwood and Goldberg (1970) for narrow bands of noise. These authors attributed the lower slope in large part to the amplitude fluctuations in the

narrow band noise, but suggested that other factors might also be involved. Since amplitude fluctuations are much less for white noise than for narrow bands of noise, explanations of the lower slope of the rate function in such terms seems less tenable. It seems reasonable to suppose that at the level of the cochlear nerve, noise signals not only cause excitatory effects but also produce suppression (see Evans, 1975a for review of two tone suppression effects). Thus the differences between responses to tones and noise seen at this level may also reflect simultaneous activation of excitatory and suppressive influences by the noise signal.

At the cochlear nucleus the existence regions of the biassing effects in both signal:masker intensity ratio and stop bandwidth of the masker dimensions are also different for the two signals (tone and wideband noise). For both signals the biassing effects disappear when the reject bandwidth is made so wide that no masker energy falls within the inhibitory regions of the response area. However, as the reject bandwidth is decreased the biassing effects for the tone signal, although not as pronounced as in bandstop masking, are still evident and persist when the tone is presented in a wideband noise masker. In contrast, as one would predict from the rate versus intensity function to white noise (see Section 5.3.1.4 and Fig. 63) the wideband noise in wideband noise masker does not show monotonic responses over a wide range of intensity (although this has only been studied in one unit).

Data for comparing the existence regions of the biassing effects in terms of the S/M ratio are sparse since few studies of the effect of varying the S/M ratio were completed with noise signals. The indications are, however, that the biassing effects to tone 'signals' in bandstop noise masker are evident over a wider range of S/M ratios than for wideband noise 'signals' in bandstop masking. For example,

in Fig. 70 the biassing effects to tone signals are observable over a range of S/M ratios of 40 dB (from +24 to -16 dB), in Fig. 71 this range is again 40 dB (from +24 to -16 dB). However, in Fig. 72 the range over which biassing occurs for noise signals is only 25 dB (from +19 to -6 dB). A second cell for which such data was obtained also showed biassing using a white noise signal over a range of S/M ratios of 25 dB. These differences could of course be unit to unit variation not due to the different signals, but for unit 473.21 (Figs. 63, 72) data were obtained using both noise and tone signals in bandstop noise masker which clearly showed a response to the tone 'signal' over a wider range of S/M ratios than for noise 'signals'.

The existence region for the observance of biassing effects of the masker in terms of both reject bandwidth and S/M ratio therefore appears to be more restricted for noise 'signals' than for tone 'signals'. Since the settings of these parameters were initially chosen somewhat arbitrarily (+4 dB S/M ratio and three human critical bandwidths) for some units the values may have been inappropriate to show biassing effects of the masker using a white noise signal while showing such a response to tones. This may at least in part explain why several units responding monotonically to tones at all masker levels failed to do so for wideband noise 'signals'.

5.4.2 Implications of the Present Study for Encoding of Intensity Differences in the Cochlear Nerve

It is apparent from both the psychophysical experiments and the responses of cochlear nucleus cells described above that information concerning differencesin 'signal' level in bandstop noise masking is being transmitted by the cochlear nerve over a very wide dynamic range. What is not at all clear from the present data is which aspect

of the single cochlear fibre discharge is carrying the intensity information. Over the usually defined single fibre dynamic range the mean rate is capable of encoding differences in the intensity of a signal. At higher intensity levels, however, for signals presented alone, the mean rate of the majority of cochlear fibres is saturated and incapable of encoding small level differences.

Fig. 76 illustrates the deficiency of mean discharge rate as a means of encoding intensity differences over a wide enough range. In this figure are shown the responses of cochlear fibre 343.16F (Fig. 76A) and of DCN unit 343.19 (Fig. 76B) which have CFs of 12.8 and 12.6 kHz respectively. These neurones were recorded in the same experiment from the same ear thus enabling a direct comparison of the responses at the two neural levels at approximately the same frequency. The nerve fibre (Fig. 77A) only responds 'monotonically' to the changes in signal level in the presence of bandstop noise masker over a range of some 45 dB. Beyond about 65 dB SPL this neurone's discharge is saturated and shows no systematic changes as the tone level is varied at each masker level. The DCN unit, however, responds 'monotonically' to the CF tone level changes at all of the masker levels at which the tone is suprathreshold, and therefore has a dynamic range under these conditions of about 100 dB. The cochlear fibre thus ceases to signal small level changes 55 dB or so below the level at which the DCN unit still responds to signal level changes. The thresholds of both 343.16F and 343.19 are quite similar (about 18 dB SPL). It has been shown in Chapter Three, however, that at any frequency the thresholds of a single animal may vary by up to 20 dB. Even assuming that cochlear fibres exist with thresholds 20 dB above that of 343.16F that still leaves a considerable discrepancy of some 35 dB unaccounted for. It should also be noted, that as in the responses of many of the neurones in category 2, 343.19 (Fig. 76B) may be capable of

Figure 76A

Rate versus intensity function for cochlear fibre 343.16F (CF 12.8 kHz) in response to a CF tone signal presented in bandstop noise. The sets of three filled circles joined by the continuous lines represent the responses to the three tone levels at each masker level. The inset is a photograph of the responses of this neurone to the tone + bandstop noise at the level indicated.

Figure 76B

Rate versus intensity functions for DCN unit 343.19 (CF 12.6 kHz). The dashed line is the response to the CF tone presented alone. The sets of three circles joined by continuous lines are the responses to the three tone levels at each masker level. The filled circles were obtained as the intensity was progressively increased and the open circles as the intensity was progressively decreased. The inset is a photograph of the responses of this neurone to the tone + bandstop noise at the level indicated.

Figure 76A

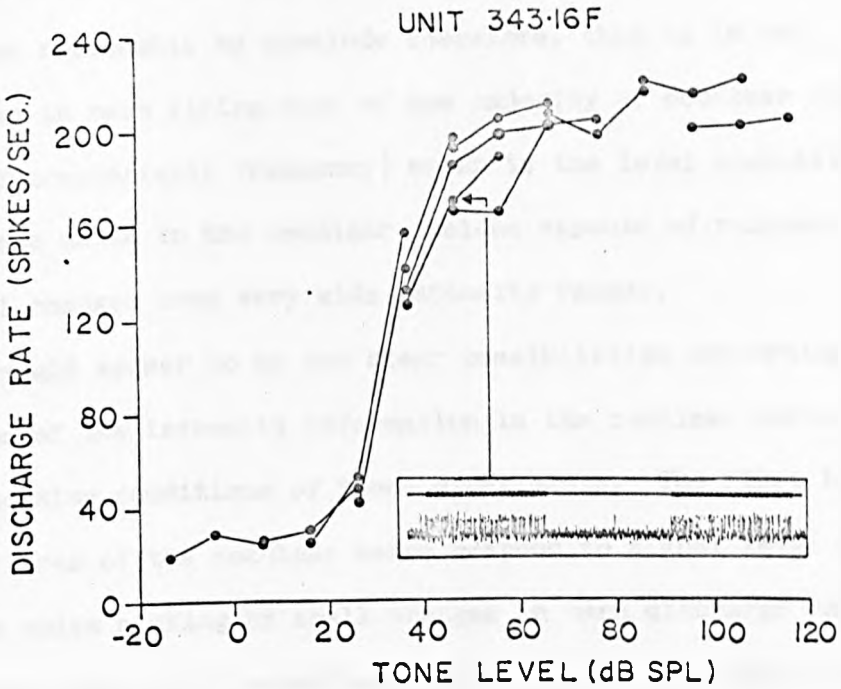
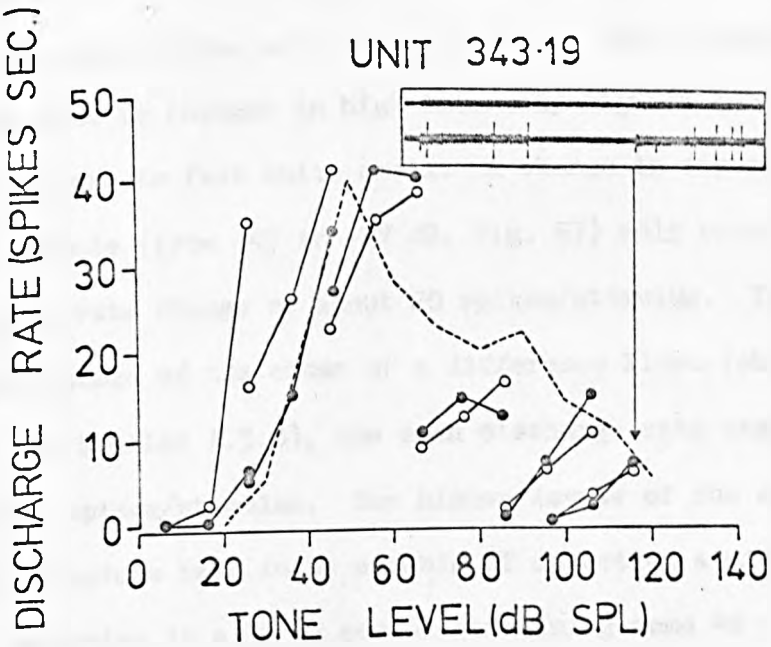


Figure 76B



responding to signal level changes at even higher intensities which could not be tested due to equipment limitations.

It seems reasonable to conclude therefore, that it is not large changes in mean firing rate of the majority of cochlear fibres (of common characteristic frequency) which is the level signalling input to those units in the cochlear nucleus capable of responding to signal level changes over very wide intensity ranges.

There would appear to be two clear possibilities concerning the transmission of the intensity information in the cochlear nerve, under the masking conditions of these experiments. The first is that some fibres of the cochlear nerve respond to signal level changes in bandstop noise masking by small changes in mean discharge rate at levels beyond those which cause saturation to the tone signal alone, as for example fibre 570.83 (Fig. 57). These small discharge rate changes would then be the input to the category 2 cochlear nucleus cells.

The system could of course be able to utilise similar small changes across a number of fibres, but for the present we are only considering the capabilities of a single neurone. The changes in mean discharge rate to changes in high intensity signals for fibre 570.83 (Fig. 57) are in fact quite small. A change in signal level of 20 dB for example (from -47 to -27 dB, Fig. 57) only results in a mean discharge rate change of about 20 spikes/stimulus. Thus for a signal level change of the order of a difference limen (about 2 dB for the cat, see Section 1.3.3), the mean discharge rate changes only by about 2 spikes/stimulus. The higher levels of the auditory system would therefore have to be capable of detecting a difference of 2 spikes occurring in a 50 ms period containing some 40 - 60 spikes despite the fact that tone evoked cochlear fibre activity is

characteristically irregular (e.g. Kiang et al., 1965a; Kiang, 1968).

It should be stressed that fibre 570.83 is the only example we have found of responses to the tone in bandstop noise over a wider range than to the tone presented alone, and further that the data of Fig. 57A consists of only two repetitions of the stimulus. If the responses shown by this unit are typical of a minority population of fibres in the cochlear nerve upon which discrimination depends, then one might expect a discontinuity in the DL function; at low levels of stimulus, changes of 10 dB will be signalled by large discharge rate changes in many fibres whilst at high stimulus levels a similar change will only result in a small discharge rate change in a few fibres. Thus the cue which the animal uses to detect the change would be different and one might expect a discontinuity in the DL function as one cue was abandoned in favour of the second; no such discontinuity is found (see Section 1.2.5).*

Secondly, if the small mean rate changes are not sufficient to provide the input to the cochlear nucleus cells which respond monotonically over very wide intensity ranges then one must postulate that intensity is encoded along another dimension of the cochlear fibre discharge. The most attractive alternative to mean rate coding is encoding by means of the fine time structure of the fibre's discharge. Certainly, phase locking in low frequency fibres occurs to all suprathreshold signals including those for which the discharge rate is saturated (Rose et al., 1967). It is, however, difficult to see how such a mechanism could be of importance at frequencies of 20 kHz (e.g. unit 323.06, Fig. 61) since phase locking is not obvious beyond about 5 kHz. A second possible temporal coding mechanism would be changes in the interspike interval distributions of cochlear fibres without change in the discharge rate. As this has not been

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* See footnote on page 144.

studied under the masking conditions of these experiments, it is not possible at this time to form any conclusions on this point.

A third possible mechanism involves a combination on two or more primary inputs. Since many cochlear fibres innervate a single IHC (see Section 1.5.2) it is not unreasonable to suppose that their discharge patterns, which depend upon the same receptor potential, may not be entirely independent. Thus while the fine time structure of the discharge of a single fibre may bear no relation to signal intensity, the temporal structure of the discharge of a group of fibres from a single IHC might well vary systematically with intensity. If this were the case then the category 2 CN cells might be combining the outputs of several cochlear fibres and performing some kind of cross correlation in order to obtain an excitatory input which increased with intensity over a very wide range. This possibility is obviously highly speculative at present since no data are available to test the hypothesis.

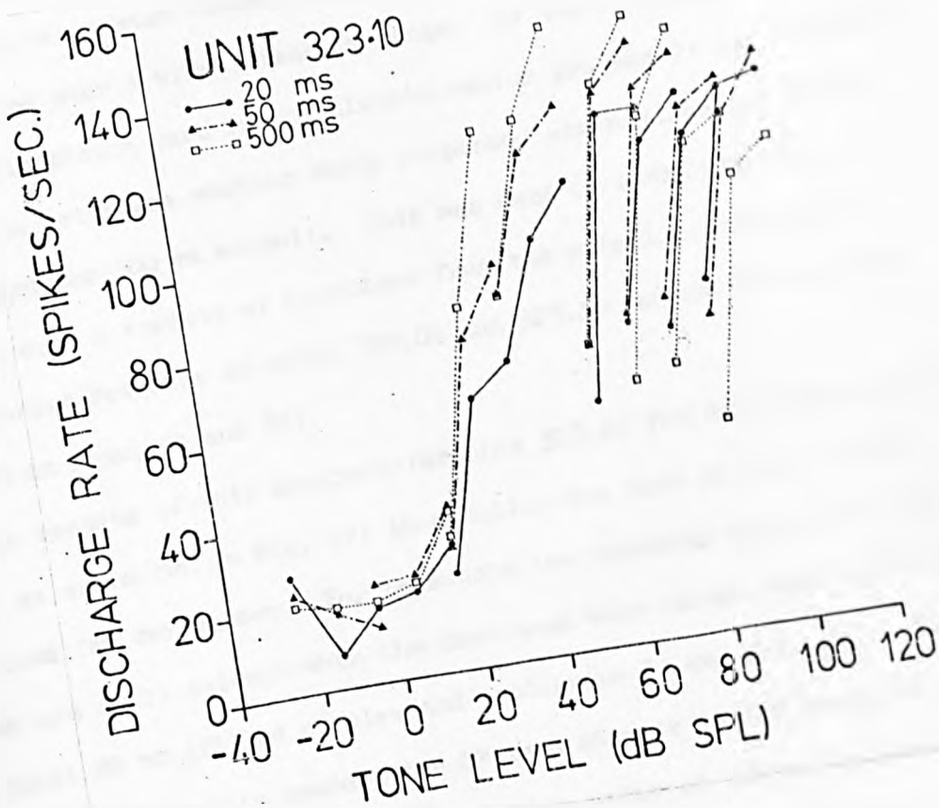
An alternative to such a suggestion is that not all cochlear fibres are completely saturated under conditions of bandstop masking noise. The shoulders of the noise could, for example, produce suppression of some cochlear fibres, since suppression is known to occur in the cochlear nerve when two or more stimulus components are present (see Evans, 1975a for review). Thus a 'biassing' might occur at the cochlear nerve level analogous to that found at the cochlear nucleus. However, preliminary experiments of Dr. E. F. Evans to test this hypothesis have failed to find any such responses in the cochlear nerve (these experiments are discussed in Section 6.3).

In Chapter Three attention was drawn to the considerable proportion of cochlear fibres which had sloping saturations, some of which as a result had dynamic ranges up to 80 dB. In Chapter Four it was suggested

Figure 77

Rate versus intensity functions for DCN unit 323.10 (CF 8.7 kHz) in response to a CF tone signal in bandstop noise masker. The filled circles joined by continuous lines represent the responses to the three tone levels at each masker level as measured over the first 20 ms of the discharge. The filled triangles and dot-dash lines, and open squares and dotted lines represent the same responses measured over the first 50 ms and 500 ms respectively.

Figure 77


UNIT 323·10
20 ms
50 ms
500 ms
DISCHARGE RATE (SPIKES/SEC.)
160
140
120
100
80
60
40
20
0
-40
-20
0
20
40
60
80
100
120
TONE LEVEL (dB SPL)

that this wider range might reflect the contribution of the discharge some hundreds of milliseconds after the stimulus onset and that the onset discharge had a more restricted dynamic range. It was further noted that in the available psychophysical data, no deterioration in discrimination of even short duration signals was evident and thus the onset discharge must contain all the information necessary for discrimination over a wide intensity range. If the category 2 cochlear nucleus cells play a part in the discrimination process it is therefore necessary to determine whether their responses are similar for short duration and for 500 ms stimuli. This was done by measuring the discharge over a variety of durations from the stimulus onset from tape recorded raw data of units 323.06 and 323.10 (whose 500 ms data is shown in Figs. 61 and 62).

The results of this analysis for unit 323.10 for durations of 20 and 50 ms are shown in Fig. 77; in addition the data of Fig. 62 are replotted for comparison. For this unit the biassing effects of the masker are still evident when the discharge rate is measured only over the first 20 ms (filled circles and continuous lines, Fig. 77). The dynamic range of this neurone for CF tone signals in the presence of bandstop noise masker is therefore of the order of 110 dB even when using only 20 ms signal durations. For the second unit analysed (323.06) the biassing effects of the masker were evident for signal durations of 50 ms but biassing effects were not seen when the discharge was measured only over 20 ms. Thus the wide dynamic range of cochlear nucleus cells for signals in bandstop noise masker, is found when using stimulus durations as short as 50 ms and for some neurones for stimulus durations as short as 20 ms.

5.5 Summary

1. The majority of fibres of the cochlear nerve respond 'monotonically' to signal level changes in the presence of bandstop noise masker over ranges of intensity which are equal to their dynamic range to stationary tonal stimuli.

2. There are cells in the cochlear nucleus which respond 'monotonically' to signal level changes in the presence of bandstop noise masker at all masker levels for which the signal is suprathreshold. The dynamic range for some neurones under these conditions are up to 110 dB.

3. The wide dynamic range of the cochlear nucleus cells is due to the bandstop masker acting on inhibitory side bands biassing the cells discharge rate, thereby maintaining its sensitivity to small signal level changes.

4. Parametric studies of the effects of changing the signal:masker intensity ratio and the masker reject bandwidth, confirm that it is the action of the inhibitory side bands which is responsible for the very wide range over which the cochlear nucleus cells encode small intensity changes.

5. Cochlear nucleus cells have been shown to have very wide dynamic ranges under conditions of bandstop noise masking for both CF tone and wideband noise 'signals'.

6. Large mean rate changes do not appear to occur in the cochlear nerve over a sufficient intensity range to account for the responses observed at the cochlear nucleus. The following alternatives were therefore considered: 1. Not all cochlear fibres were completely saturated at the highest intensities used and therefore small changes in their mean discharge could occur when the intensity was altered.

2. The masking noise may release some fibres from saturation by 'two-tone' suppression. 3. The fine time structure of the discharge may convey intensity information. Preliminary experiments by E.F. Evans failed to find any evidence in support of the first two alternatives. Of the three most obvious time codes (phase-locking, interspike intervals and a cross correlation of the discharge of two or more fibres) the first two appear to be unlikely candidates since phase-locking and the presence of resolvable peaks in interspike interval histograms are only evident up to about 5 kHz.

CHAPTER SIX: GENERAL DISCUSSION

It was in an attempt to resolve the discrepancy between the range of intensity over which single fibres can encode intensity differences and the range of intensity over which humans can detect small intensity differences that the experiments reported in this dissertation were undertaken.

It has been suggested (e.g. Simmons, 1959; Borg, 1972; Borg and Zakrisson, 1973; Suga and Jen, 1975) that the middle ear reflex might extend the range over which single neurones could signal intensity changes by compressing the amplitude of the input stimulus. From a review of the literature in Section 1.4, however, it was concluded on the grounds of i) the wide range of intensity over which humans discriminate small intensity differences even for frequencies not atten-

uated by the reflex and ii) that the growth of loudness of sounds too short to activate the reflex was not restricted at very high intensities, that the middle ear reflex was an insufficient mechanism to account for the wide dynamic range for intensity discrimination observed psychophysically.

In Chapter Three, the range over which single neurones in cochlear nerve and cochlear nucleus responded to differences in the intensity of stationary tonal stimuli was re-examined. The dynamic range of cochlear nerve fibres of the present report (the majority of which were measured by Dr. E. F. Evans) extended up to only 60 dB and therefore was in reasonable agreement with previously reported values (e.g. Kiang et al., 1965a). Dynamic ranges for the majority of monotonic cochlear nucleus cells also ranged from 20 - 60 dB but the dynamic ranges of a few cells were found to extend up to 80 dB. The limited number of cochlear nucleus cells with such wide dynamic ranges had rate versus intensity functions of the type described by Sachs and Abbas (1974: for cochlear fibres) having sloping saturations (see Section 3.1.2). Almost half of the cochlear fibres of Evans (Section 3.3.4) also had sloping saturations but were all completely saturated by stimuli 60 dB above threshold. Sachs and Abbas, however, did find a minority of cochlear fibres with dynamic ranges as wide as 80 dB (a result of the sloping saturation). Thus in Chapter Three it was concluded that there was no significant difference between the dynamic ranges of single cochlear fibres and those of monotonic cochlear nucleus cells. The majority of cochlear fibres are therefore completely saturated at levels of 80 dB or so above threshold. Inclusion of those neurones with rate versus intensity functions of the sloping saturation type does bring the single neurone dynamic range closer to that shown psychophysically but a discrepancy still exists.

The remaining experiments reported in Chapter Three explored the possibility that a hitherto undetected high threshold population of neurones might exist. Measurements of single neurone minimum thresholds in both cochlear nerve (by Evans) and in cochlear nucleus, revealed that in a single animal the thresholds at any frequency span only 20 - 30 dB, the most sensitive of which approach the cat's behavioural audiogram.

This finding is in good agreement with the previously reported data of Kiang (1968) and of Evans (1972). However, some very recent data suggest that at least in a restricted frequency band the range of thresholds may be wider. Kiang, Liberman and Levine (1976) measured the thresholds of cochlear nerve fibres in normal animals which were distributed over 30 - 40 dB for most of the frequency range. This range is wider than that found in the present study but may merely reflect sampling differences: the number of thresholds measured from a single ear in the present study was very limited compared with the 176 fibres from a single ear measured by Kiang et al. (1976). Over a band of frequencies (from 3 - 9 kHz), however, Kiang et al. (1976) found threshold differences of up to 80 dB between the least and most sensitive fibres. They attributed this wide range to the effects of environmental noise and suggested that it may be difficult to find cats with undamaged hearing.

Against this interpretation is the finding of Liberman (1977) who reported that units differing in sensitivity by 70 dB could be found, even when the cats were born and raised in a soundproof chamber. The frequency range over which such a threshold distribution is found is not indicated. Liberman used electric shocks to locate the high threshold fibres which all had zero spontaneous rate. It is therefore conceivable, as suggested in Chapter Three, that if such units do

indeed exist we would have overlooked them with our present techniques. However, we would have definitely found the large numbers of neurones (which Kiang et al. (1976) reported) with thresholds within 40 dB of those of the most sensitive neurones since our search stimuli were typically 50 dB above the most sensitive thresholds.

Since the FTCs of the high threshold units are not shown by either Kiang et al. (1976) or Liberman (1977) it is not possible to decide whether the high thresholds represent units of low sensitivity but are otherwise normal (i.e. sharply tuned) or whether they are very broadly tuned and likely to be the result of cochlear pathology (Evans, 1972) as indeed, was suggested by Kiang et al. (1976). Further evaluation of these data awaits their publication in a more complete form. For the remainder of this discussion the range of thresholds (20 - 30 dB) reported in Chapter Three is assumed.

If one combines even the limited threshold range of 20 - 30 dB with the dynamic range of some cochlear fibres showing sloping saturations (and hence dynamic ranges of 80 dB or so), it would appear that a small number of cochlear fibres would be capable of responding to signal level changes over a range of intensity comparable with the psychophysically determined dynamic range. It should be remembered, however, that few neurones have thresholds as much as 30 dB above those of the most sensitive neurones (even in the data of Kiang et al. (1976)) and few of those fibres with sloping saturations have dynamic ranges of as much as 80 dB. Thus the number of fibres not only of relatively high threshold but also of wide dynamic range will be extremely limited. This is evident in Fig. 37 in which even taking <u>no</u> account of the wide variation of thresholds between animals, nearly all of the neurones are saturated at 90 dB SPL. Thus it seems doubtful that neurones with sloping saturations which still respond

at levels of 100 dB above absolute threshold would be sufficiently numerous to account for i) the fine intensity discrimination observed psychophysically at such high stimulus levels, and ii) the large proportions of cochlear nucleus neurones which have very wide dynamic ranges (up to 110 dB) under conditions of bandstop noise masking. Furthermore, if fibres with sloping saturations are important for discrimination at the high intensities, the cue which the animal uses to discriminate a change in intensity must change as intensity is increased; at low levels an increase of a few dB causes a large increase in the discharge rate of many fibres, whereas at levels at which only a few sloping saturation fibres are still unsaturated a similar change in intensity will result in only a small change of the discharge rate in a few fibres. Thus, as has been argued, at the changeover from one cue to the other, one might expect a discontinuity in the DL versus intensity function* which is not the case and in fact remains smooth to the highest intensities tested.**

It was therefore concluded in Chapter Three that since few cochlear fibres are capable of responding to intensity differences at the highest levels at which fine intensity discrimination is maintained in humans, the dynamic range of neurones to stationary tonal stimuli was insufficient to account for the psychophysically determined dynamic range. The experiments of Chapter Four therefore examined two possibilities: i) that the adaptation process occurring in primary neurones and monotonic cochlear nucleus cells might serve to extend their dynamic range, and

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** The contribution of fibres with sloping saturations to intensity discrimination at high intensity is discussed further later in the light of the findings of Chapter Four.

* But see footnote on page 144.

ii) that neurones might have a wider dynamic range to incremental intensity changes than to stationary stimuli.

It was found that for some cochlear nucleus units (labelled Type B in Chapter Four) the dynamic range of the firing rate measured after adaptation (180 ms after onset) did indeed exceed the dynamic range of the firing rate before adaptation (measured at the stimulus onset). This wider dynamic range of the firing rate measured at 180 ms after the stimulus onset was a result of a reduction in the amount of relative adaptation* occurring as a function of stimulus level. The widest dynamic range to stationary tonal stimuli, even measuring the firing rate at 180 ms after the stimulus onset, was still only of the order of 70 dB.

In those units for which the dynamic range of the firing rate measured at the stimulus onset was narrower than that measured 180 ms after the onset, the rate versus intensity function for the firing rate measured over the whole duration of the stimulus was of the sloping saturation type. Complete saturation of the rate versus intensity functions so obtained occured at the intensity at which the firing rate at 180 ms after the onset saturated. Thus measuring the discharge over the whole duration of a stimulus appears to take account of the wider dynamic range which results from changes in the relative adaptation occurring with increase in stimulus level. This explanation of the sloping saturation type of rate function, if correct, has a further consequence. If discrimination at high intensity depends on fibres with sloping saturation (i.e. dynamic ranges of 80 dB or so) and dynamic ranges of 80 dB are only found for stimuli in excess of 50 ms (since dynamic ranges of only 60 dB were found by Evans) then

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* The relative adaptation is defined as the ratio of the onset to the 180 ms firing rate (see Chapter Four).

one should expect a deterioration in the intensity discrimination of short duration signals for which the dynamic range of neurones is limited. The available psychophysical data, however, indicate that the discrimination of sounds of only 20 ms duration continues to improve with intensity up to at least 80 dB above threshold (Campbell and Lasky, 1967). It is unfortunate that these psychophysical data were only collected over an 80 dB range since combination of the dynamic ranges found by Evans (up to 60 dB, Section 3.3.4) with the range of neural sensitivities could account for such data. However, Evans' data were collected using 50 ms tones and the explanation of sloping saturations would suggest that the dynamic range for 20 ms tones might be more restricted. Thus it would appear, that cochlear fibres with dynamic ranges of the order of 80 dB, as a result of a sloping saturation, are neither necessary nor sufficient to account for fine intensity discrimination at high intensities for short duration stimuli.

A few cochlear nucleus cells responded to small intensity increments occurring 180 ms after the stimulus onset over ranges of intensity which were wider than predictable from their response to stationary tonal stimuli (Type C, Chapter Four). The widest dynamic range to intensity increments found in the, albeit limited, sample of such neurones was 80 dB. Such responses to intensity increments are apparently not found in the cochlear nerve (Smith, personal communication).* If no such responses occur in the cochlear nerve then the wider dynamic range of some cochlear nucleus cells to intensity increments must result from re-encoding the information carried by cochlear nerve fibres.

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* Although this is not clear from the available published data (Smith, 1973; Smith and Zwislocki, 1975) since these studies were only performed over a restricted range of intensity.

The extended dynamic range to intensity increments was only found when the increment occurred at some delay from the stimulus onset. Thus, as with neurones exhibiting sloping saturation it is difficult to see how such cells could contribute to the discrimination of sounds of short duration. In addition two alternative forced choice discrimination experiments do not involve incrementing a pedestal (the intensity is constant throughout the stimulus) and it is doubtful whether Type C neurones could contribute to discrimination of intensity changes under these conditions.

According to our data, a single low threshold population of neurones exists in the cochlear nerve and cochlear nucleus, and (given the qualifications outlined above) the dynamic ranges of neurones innervating a limited region of basilar membrane (with CFs at the stimulus frequency) appear inadequate to account for the psychophysical data. Nevertheless under conditions of bandstop noise masking, which limits the spread of activity across the frequency continuum, neurones in the cochlear nerve innervating a limited expanse of basilar membrane are apparently capable of signalling intensity changes over a wide dynamic range. Thus in the experiments reported in Chapter 5, the responses of neurones in cochlear nerve and cochlear nucleus under conditions analogous to the psychophysical bandstop noise experiments, were examined.

Under bandstop noise masking conditions a substantial proportion of cochlear nucleus neurones had very extensive dynamic ranges. Dynamic ranges of up to 110dB were found with no indication that the neurones would fail to respond to signal level changes at even higher stimulus levels if our equipment were capable of producing such intense stimuli (in excess of 120 dB SPL). The very wide dynamic range at the cochlear nucleus was interpreted as resulting from a 'biassing' of the neurone's discharge by lateral inhibitory action of the bandstop masking noise. Thus at the level of the cochlear nucleus, neurones were found which, under conditions of bandstop noise masking, responded to signal level changes over an

intensity range comparable with the dynamic range for intensity discrimination observed psychophysically. What is not at all clear from these experiments is what aspect of the single cochlear fibre discharge is encoding intensity changes over such a wide range and is providing the input to the cochlear nucleus cells.

In only one cochlear nerve fibre was any indication found of a wider dynamic range to the CF tone in bandstop noise than to the CF tone alone. The vast majority of cochlear nerve fibres saturate at the same intensity to a CF tone, whether or not a bandstop masking noise is present. Thus the extensive dynamic ranges of large numbers of cochlear nucleus cells under conditions of bandstop noise masking are found despite saturation of the mean discharge rate of all but a small proportion of cochlear nerve fibres under the same conditions.

Although the masking experiments of Chapter Five used the same stimulus duration as in the psychophysical experiments (i.e. 500 ms) it was shown that the firing rate measured over the first 50 ms (or even 20 ms in some units) of the stimulus had similar wide dynamic ranges.

The explanation of the sloping saturation presented in Chapter Four was based on recordings from cochlear nucleus cells. It remains to be determined whether the lack of cochlear fibres with dynamic ranges of more than 60 dB in the data of Evans reflects either differences in sampling or the use of a shorter stimulus (50 ms compared with, for example, 400 ms of Sachs and Abbas (1974)). If sufficient numbers of sloping saturation fibres with dynamic ranges of 80 dB or more are found using short duration stimuli, it is possible that the cochlear nucleus cells with wide dynamic ranges are sensitive to the small differences in mean discharge rate which occur at high intensities in such cochlear nerve fibres. If, however, the fibres with sloping saturation and hence wide dynamic ranges are

not found for short duration (50 ms) stimuli, then one must conclude that in cochlear nerve fibres, under conditions of bandstop masking, intensity information at high stimulus levels is carried in some form other than mean discharge rate.

Finally, therefore, in Chapter Five it was suggested that the fine time structure of the cochlear fibres discharge might provide an alternative means of encoding intensity over a wide dynamic range. Phase-locking in primary fibres was not considered an adequate encoding mechanism since it is not obvious beyond frequencies of 5 kHz; cochlear nucleus cells of CFs of up to 2o kHz have been studied which had wide dynamic ranges under conditions of bandstop noise masking. Changes in the distribution of interspike intervals was considered to be a possible mechanism but no data are presently available under bandstop noise masking conditions. A second possibility suggested in Chapter Five was that the cochlear nucleus cells might be able to cross-correlate the discharge patterns from two or more cochlear fibre inputs. This suggestion could be tested by simultaneous recording from two cochlear fibres.

As was pointed out in the introduction, the limited dynamic range of single cochlear fibres poses a problem not only for the encoding of intensity differences of a stimulus, but also for the representation of its loudness.

The basis of all population models (such as those described in section 1.7) is that the total activity of the cochlear nerve might signal the level of a stimulus (whether in terms of the total discharge or of the number of active fibres). Such a representation of intensity implies that it should be possible to grossly modify the judgement of the loudness of a simple tonal stimulus by using masking signals which limit the recruitment of neural responses of fibres with CF

above the stimulus frequency. This prediction is not, however, supported by the masking data of Scharf (1964) or Hellman (1974): loudness judgements are hardly affected by high frequency masking. Thus the encoding of the intensity of a stimulus appears not to require a spread of activity across frequency.

Since, at least in our data, the mean discharge rate of cochlear fibres of common CF appears to be incapable of encoding high stimulus intensities, the alternative codes hypothesised for intensity differences may also apply to the representation of absolute intensity at high stimulus levels.

6.2 Implications of the Present Work for the Place Coding of Frequency Information

Although the experiments reported in this dissertation were directed specifically at the problem of how fine intensity discrimination is maintained at high intensities, they also have direct relevance for the place coding of frequency information and hence for the maintenance of frequency resolving ability at high intensities.

At low stimulus levels, differences in the discharge of neurones across the frequency continuum provide sufficient basis for the separation of the components of complex stimuli: it has been shown that the effective bandwidth and frequency resolution of cochlear fibres matches the analogous psychophysical measures, the critical band and frequency resolution (Evans and Wilson, 1973). At high stimulus levels, however, in response to complex stimuli the cochlear fibres are saturated and small variations in energy across the frequency spectrum cannot be signalled by differences in cochlear fibre mean discharge rate. The following two sets of data from cochlear fibres support this conclusion. Firstly, Kiang and Moxon (1972, 1974) showed that at low stimulus levels, cochlear fibres responded to complex waveforms such as speech in a way predictable from the frequency selectivity indicated by their FTC. However, at higher levels (40 - 60 dB above threshold) fibres of very different CFs display similar responses to complex waveforms: responses which appear to be determined by the amplitude fluctuations rather than the frequency content of the waveform. Thus for speech signals 40 - 60 dB above threshold, the ability of single fibres to selectively signal different frequency components is much reduced. Secondly, Evans (1977) measured the ability of cochlear fibres to resolve the frequency components of comb-filtered noise as a function of level. He found that no

cochlear fibre was able to resolve the peaks in the comb-filtered noise spectra at levels above those at which they were saturated (70 dB SPL).

The limited dynamic range of cochlear fibres is therefore a severe problem for the classical 'place' theories, which suggest that the resolvable frequency components of a stimulus are signalled in terms of the mean discharge rate of the neurones tuned to those frequencies. If differences between the discharge of cochlear fibres across the fibre array were the means by which components of a complex sound are separated, subjects should be unable to resolve frequency components at intensities above those at which the cochlear fibres become saturated. Yet psychophysical measurements of the ear's frequency selectivity are relatively unchanged up to 70 dB above threshold and only show a small but significant deterioration at higher levels (Zwicker and Feldtkeller, 1967; Scharf, 1970; Pick, 1977; Scharf and Meiselman, 1977; Wilson and Seelman, unpublished experiments).

It would appear that since relatively fine frequency selectivity is maintained at intensities beyond those at which cochlear fibres are saturated, the information necessary for the separation of components of a complex sound is carried in the cochlear nerve in some form other than mean discharge rate. Some recent experiments of Evans (1977) support this suggestion. Evans measured the tuning properties of cochlear fibres as a function of stimulus level using a reverse correlation technique and demonstrated that the filter characteristics so obtained, remained unchanged up to levels of 70 dB SPL, but deteriorated slightly at higher levels. The cochlear fibres were able to transmit the cochlear filtering properties in the time structure of their discharge patterns at stimulus levels well above these producing saturation of the mean discharge rate.

The reverse correlation technique depends upon phase locking of the discharge to the stimulus waveform and hence can only be used for fibres of CFs of 5 kHz and below. It is not obvious what aspect of the fine time structure could be signalling the frequency selective properties at higher frequencies. It is, however, evident from further experiments of Evans (1977) that, over a very wide range of intensities, information regarding frequency selectivity is certainly reaching the cochlear nucleus even at frequencies in excess of 5 kHz. The finding of the present study: that cochlear nucleus cells had a wider dynamic range than cochlear fibres under conditions of bandstop noise masking, prompted Evans to compare the ability of cochlear fibres and cochlear nucleus cells to resolve frequency components of comb-filtered noise. He measured the threshold of a 100 ms CF tone in the presence of comb-filtered noise with progressively finer peak spacings and found that DCN cells, which had extensive inhibitory side bands, were capable of resolving comb-filtered noise over a very wide range of noise levels. The frequency selectivity of the DCN cells showed no obvious deterioration up to 70 dB SPL; thereafter a progressive deterioration took place but relatively fine frequency selectivity was still evident at noise levels of 105 or even 115 dB SPL. In contrast no cochlear fibre in the same animal was able to resolve the comb-filtered noise spectra at levels above 70 dB SPL.

It was concluded in the bandstop noise masking experiments, that the unit's discharge was biassed by the shoulders of the noise producing lateral inhibitory effects (see Chapter Five). Similarly in the case of the comb-filtered noise peaks of the noise falling in the inhibitory side bands of the DCN unit could be biassing the cells' discharge below saturation

It would appear, subject to the qualifications outlined in Section

6.1, that information pertaining to intensity, intensity discrimination, and frequency selectivity at high intensities may be transmitted by cochlear fibres in some form other than large changes in their mean discharge rate. In section 5.4.2 alternative codes were discussed in detail. These alternatives may be summarised as 1) not all cochlear fibres are completely saturated under the bandstop noise masking conditions and 2) the fine time structure of the discharge may convey intensity information.

As far as the first alternative is concerned, few fibres in our material had dynamic ranges in excess of 60 dB. Furthermore preliminary experiments of Dr. E. F. Evans did not find any evidence to support the suggestion that release from saturation might result from two-tone suppression (see section 5.4.2). Of the most obvious time codes, phase-locking and information carried in the distribution of interspike intervals seem unlikely candidates since this information is only evident up to about 5 kHz.

6.3 Some Unanswered Questions Arising from the Present Work

1. Although, from our experiments, it seems unlikely that a high threshold population of units has been overlooked, the data of Kiang et al. (1976) and Liberman (1977) discussed above, suggest that hitherto undetected high threshold neurones do exist in the cochlear nerve. Kiang et al. (1976) used 'moderate intensity' clicks as search stimuli and concluded that the high threshold neurones were due to cochlear pathology caused by environmental noise. Liberman (1977), however, found similar high thresholds even when cats were raised in soundproof enclosures. The full evaluation of Liberman's data awaits their publication in a complete form, but taken at face value they indicate a wide range of thresholds in a single animal which is contrary to the findings of the present study and to those of earlier studies (e.g. Kiang, 1968). Evans (1972) did in fact find nine fibres with thresholds above 70 dB SPL in otherwise normal guinea-pig cochleae. He later suggested (Evans, 1975b) that these could relate to sporadic hair cell loss which occurs in normal guinea-pigs. The possibility remains, however, that these high threshold fibres had CFs above the high frequency limit (40 kHz) of Evans's sound system as suggested by Evans (1972). Excluding these nine fibres, Evans (1972) concluded that, in optimal preparations, the range of minimum thresholds at a common CF is less than 20 dB. Liberman's study differed from the present study apparently only in his use of direct electrical stimulation to locate the neurones. Thus in order to resolve this discrepancy it would be necessary to measure the thresholds of large numbers of neurones from a single ear using electrical search stimuli.

2. It is clear, both from the present study and from a study of the literature, that cochlear fibres exist which have wide dynamic ranges

as a result of rate versus intensity functions of the sloping saturation type: as the stimulus intensity is increased the fibre's discharge increases rapidly over 20 - 30 dB and then more slowly over as much as another 50 dB or so (e.g. Sachs and Abbas, 1974). It is not known whether the discharge over the whole duration of a stimulus continues to increase with intensity over approximately 80 dB or whether (as was shown to be the case for some cochlear nucleus neurones in chapter four) the sloping saturation reflects the contribution to the total firing rate, of the firing rate some hundreds

of milliseconds after the stimulus onset. Therefore, a study of the rate versus intensity function of cochlear fibres as a function of stimulus duration is required. Even if such a study revealed that the firing rate at the onset also had a wide dynamic range, it would be necessary to determine whether fibres with wide dynamic ranges occur in sufficient numbers over the whole frequency range to account for a) the psychophysical dynamic range, or, b) the very wide dynamic ranges found in the cochlear nucleus under bandstop noise masking conditions.

3. Throughout the bandstop noise masking experiments (both psychophysical and physiological) it has been assumed that fibres with CFs falling in the pass band of the noise are saturated by the masking noise and are therefore unable to signal energy changes of the tone in the stop band by changes in discharge rate. It is possible that this assumption is not justifiable and that the masking noise does not in fact cause complete saturation of the fibre's surrounding the stimulus frequency. In which case spread of excitation could still provide a means of intensity discrimination even in bandstop noise masking. Evans (unpublished experiments) has demonstrated that two tone suppressive effects are strong enough to release a fibre from saturation under certain restricted conditions, and the possibility cannot be ruled out that such mechanisms could release fibres from saturation under conditions of bandstop noise stimulation. These possibilities may be tested directly by using a bandstop masker and tone which are not centred at the neurone's CF. Ideally one should use just one setting of the bandstop noise and tone, and measure the responses of fibres with different CFs. In practice it is easier to move the masker stop band and tone frequency relative to the response area of a single neurone. Thus the responses of

fibres with CFs in the noise pass band can be measured at any desired frequency separation from the CF. Pilot experiments of Dr. E. F. Evans on cochlear fibres suggested that both of the above possibilities are unlikely. The frequency 'steps' by which the masker stop band could be shifted were, however, not sufficiently small (due to equipment limitations) to be able to completely eliminate the possibility that suppressive effects of the masker might release fibres from saturation. Further experiments using a filter with finer frequency resolution are therefore required.

4. From experiments in which the width of the masker stop band was progressively widened, it was concluded that the wide dynamic range of some cochlear nucleus neurones (under conditions of bandstop noise masking) resulted from lateral inhibitory effects of the masker. In some neurones the extent of the lateral inhibition due to the masker was in qualitative agreement with the inhibitory sidebands shown by presentation of single tones. In other neurones, however, the inhibition due to the masker appeared to contain a component which is only observed when more than one stimulus is presented simultaneously. It was not possible to decide from our present data whether the inhibition to more than one stimulus component, reflected two-tone suppression in the cochlear nerve or two-tone inhibition in the cochlear nucleus. A study of the region over which such inhibition occurs might provide a means of distinguishing between these alternatives since there is some indication in the present data that the inhibition occurs over a wider frequency range at low intensities than two-tone suppressive effects.

5. Finally, if a single low threshold population of neurones exists and sloping saturation rate functions and suppressive effects in the cochlear nerve do not sufficiently extend the range over which the

mean discharge rate can encode intensity (see 1, 2 and 3 above), then alternative 'codes' by which intensity is signalled under conditions of bandstop noise masking must be considered. The most likely alternative to mean rate coding of intensity changes is some form of fine time structure coding of intensity. Three alternatives were discussed (see Sections 5.4.2 and 6.1): i) phase locking; ii) interspike intervals, and ; iii) cross-correlation between channels, but phase locking was rejected due to the limited frequency range over which it occurs.

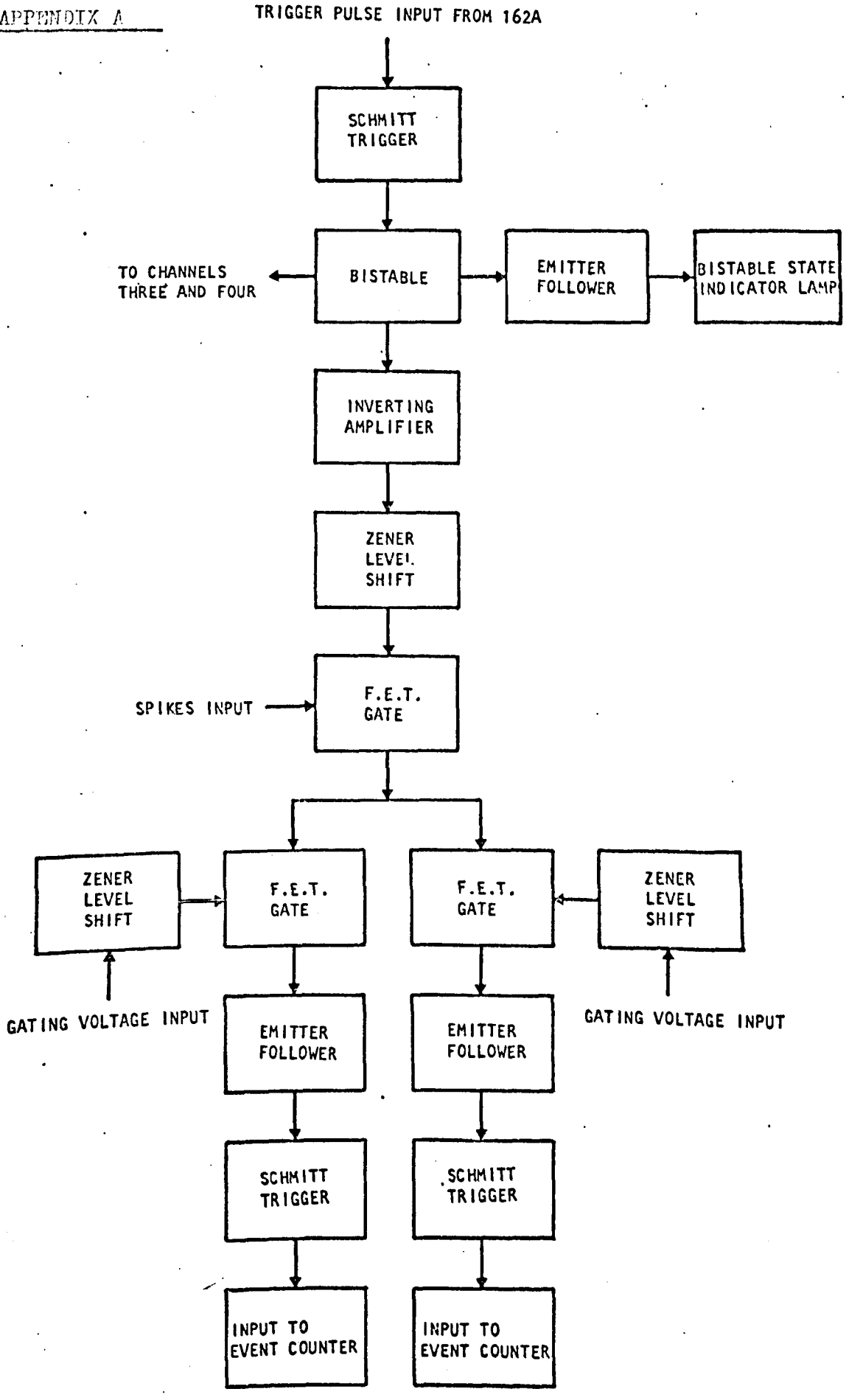
Perkel and Bullock (1968) discussed the viability of interspike interval distributions as a means of encoding stimulus parameters. They gave several examples (none from the auditory system) which indicated that the responses of some cells did depend on the intervals between spikes. They concluded, however, that although an inter-spike interval code could be 'read' by some cells that there was no indication of whether it was actually used. Measurement of the distribution of interspike intervals as a function of intensity would serve either to confirm or to eliminate interspike intervals as possible means of encoding intensity.

The third mechanism (which has already been discussed in section 5.4.2, p. 264) involves a combination of two or more primary inputs. Since many cochlear fibres innervate a single IHC it seems reasonable to assume that their discharge patterns which depend upon the same receptor potential will not be entirely independent. Thus the excitatory input to the cochlear nucleus cells, which varies over a wide dynamic range, might be achieved by some kind of cross-correlation of several primary fibre inputs. The only way to test this somewhat speculative suggestion is by simultaneous recording of the discharge of primary fibres from the same receptor cell and measuring the variation of the cross-correlation function with intensity.

Appendix A

The network for gating the spike counts consisted of six Field Effect Transistors (FETs). The discriminated spikes were fed into the first two FETs in parallel. The Q and $\bar{Q}$ outputs of a bistable triggered on every stimulus presentation were used to gate the first pair of FETs, thus feeding the spike signals into the parallel output pairs of FETs on alternate stimulus presentations. One of the output FETs was gated during the first 20 ms of a stimulus and the other during the last 20 ms. Thus spikes occurring at the onset and after 180 ms of an incremented and non-incremented pedestal were accumulated by separate counters (see Section 4.2).

APPENDIX A



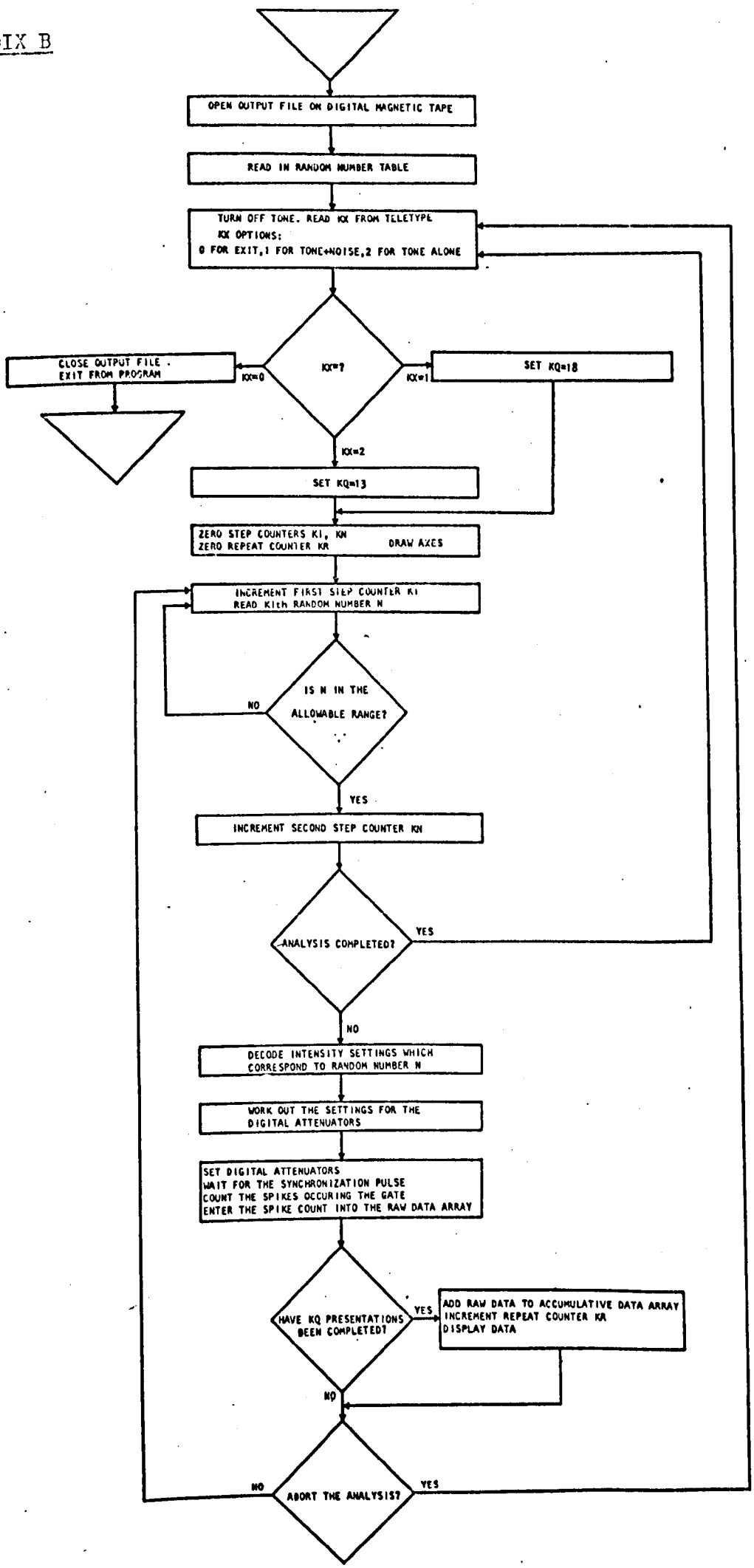
BLOCK DIAGRAM OF THE EVENT COUNTER GATING NETWORK USED

IN THE INCREMENTED TONE BURST EXPERIMENTS

Appendix B

Flow diagram of the computer program used to present tones either alone or in bandstop noise masker. The stimuli were presented in a pseudorandom sequence and the discharge evoked by each presentation was counted and displayed.

APPENDIX B


OPEN OUTPUT FILE ON DIGITAL MAGNETIC TAPE
READ IN RANDOM NUMBER TABLE
TURN OFF TONE. READ KX FROM TELETYPE
KX OPTIONS:
0 FOR EXIT,1 FOR TONE+NOISE,2 FOR TONE ALONE
KX=?
KX=0
CLOSE OUTPUT FILE .
EXIT FROM PROGRAM
KX=1
SET KQ=18
KX=2
SET KQ=13
ZERO STEP COUNTERS KI, KN
ZERO REPEAT COUNTER KR
DRAW AXES
INCREMENT FIRST STEP COUNTER KI
READ KIth RANDOM NUMBER N
IS N IN THE
ALLOWABLE RANGE?
NO
YES
INCREMENT SECOND STEP COUNTER KN
ANALYSIS COMPLETED?
YES
NO
DECODE INTENSITY SETTINGS WHICH
CORRESPOND TO RANDOM NUMBER N
WORK OUT THE SETTINGS FOR THE
DIGITAL ATTENUATORS
SET DIGITAL ATTENUATORS
WAIT FOR THE SYNCHRONIZATION PULSE
COUNT THE SPIKES OCCURING THE GATE
ENTER THE SPIKE COUNT INTO THE RAW DATA ARRAY
HAVE KQ PRESENTATIONS
BEEN COMPLETED?
YES
ADD RAW DATA TO ACCUMULATIVE DATA ARRAY
INCREMENT REPEAT COUNTER KR
DISPLAY DATA
NO
ABORT THE ANALYSIS?
NO
YES

Appendix C: Comparison of Sharpness of Tuning of Single Units at Different Levels of the Auditory System

Møller (1972c), in comparing the sharpness of tuning of single units at different levels in the auditory system, computed the bandwidths of the single unit frequency threshold curves (FTCs) at 10 dB above threshold both from his own data and from data reported in the literature. Instead of plotting all the individual points in the form of a scattergram, he partitioned the data into half octave groupings and plotted the mean value within each half octave against CF (Fig. 78). From these mean values Møller concluded that FTCs of single units in the cochlear nucleus (of rat and cat - solid circles, dotted lines and open squares, dot-dash lines (Fig. 78) respectively) and in the superior olive of the cat (solid triangles and continuous lines, Fig. 78), are wider than those of the primary fibres in the cat (solid squares and dashed lines, Fig. 78) by an almost constant factor of two. However, this conclusion takes no account of the variance of the individual data points about the mean value.

The cochlear nucleus data from the present study have been treated in a similar manner and plotted along with their standard deviation about the mean values in Fig. 78 (open circles and continuous lines for the mean values and horizontal bars for the standard deviations). Merely considering the mean data, the present data would appear to confirm Møller's conclusion since the agreement of the present cochlear nucleus data with that of Pfeiffer (1963) from the cat (open squares) and with that of Møller (1970) from the rat (solid circles) is very good. However, if one considers the scatter indicated by the standard deviation the cochlear nucleus data overlap the cochlear nerve data to a large extent.

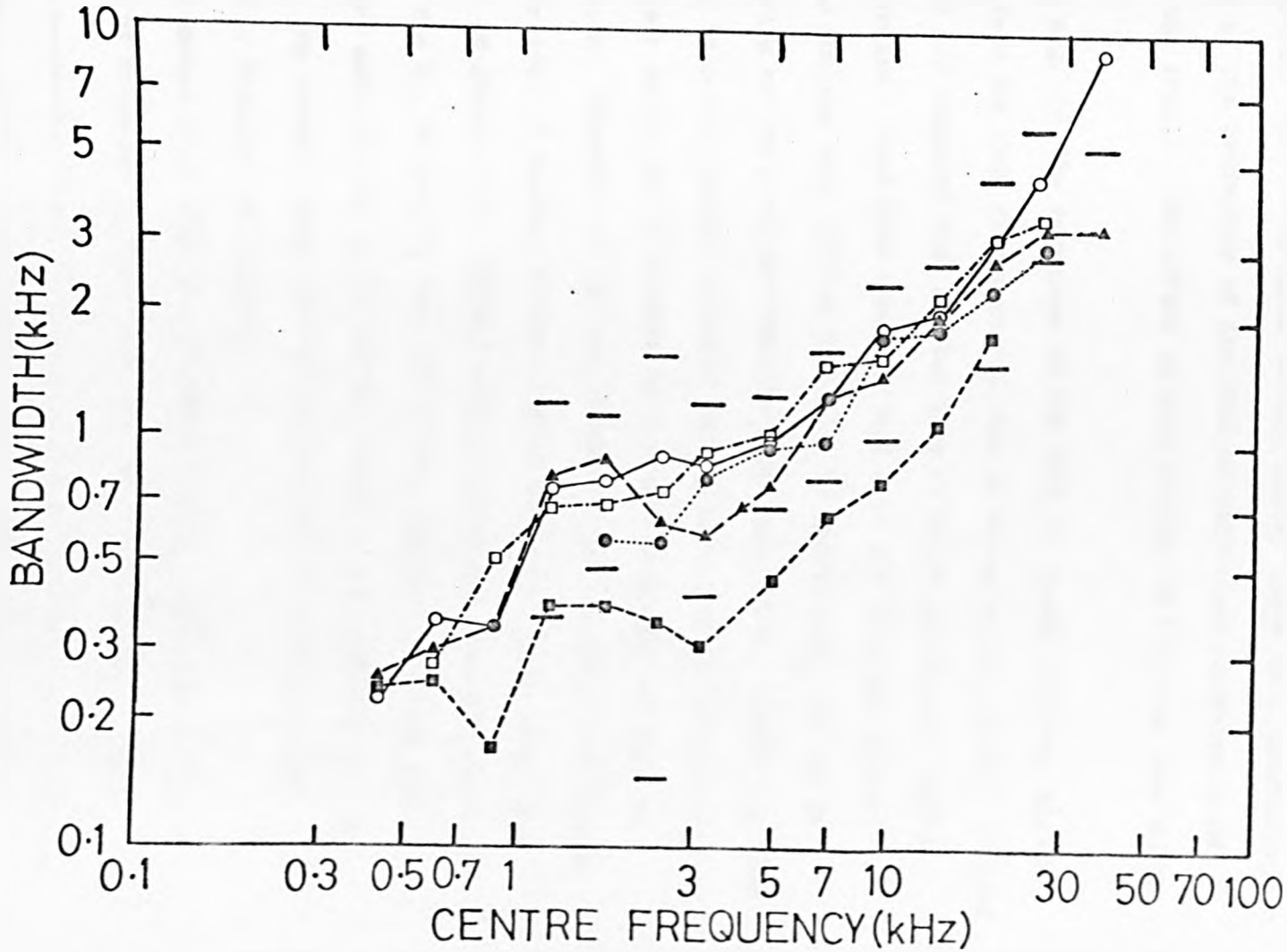
Figure 78

Bandwidth of tuning curves measured at 10 dB above the threshold at CF plotted against CF. The data were divided according to CF into half octave groups and the bandwidth of each group was averaged.

Filled squares - cat cochlear nerve (Kiang et al., 1965a).
Open squares - cat cochlear nucleus (Pfeiffer, 1963).
Filled circles - rat cochlear nucleus (Møller, 1970).
Filled triangles - cat superior olive (Tsuchitani and Boudreau, 1967).
Open circles - cat cochlear nucleus data from the present study.
The bars indicate the standard deviation of the individual values about the mean.

(After Møller, 1972a.)

Figure 78


BANDWIDTH(kHz)
10
7
5
3
2
1
0·7
0·5
0·3
0·2
0·1
0·1
0·3
0·5
0·7
1
3
5
7
10
30
50
70
100
CENTRE FREQUENCY(kHz)

Furthermore, the nerve data in Fig. 78 were derived from a plot of 'Q_{10}'* against CF from Kiang et al., 1965a. These data are shown in Fig. 79, and also show great scatter. Thus, although when only considering mean values, the cochlear nerve FTC bandwidths do appear to be narrower than those of cochlear nucleus cells, there is a considerable overlap of the bandwidths of the FTCs of individual neurones found at the two levels. The extent of this overlap is explored more fully below.

In Fig. 79 the sharpness of the FTCs of single cochlear nerve fibres from the four anaesthetised cats of Kiang et al. (1965a) (filled squares) are compared with similar data of Evans and Wilson (1973) (open circles), also from anaesthetised cats and with the present cochlear nucleus data (filled circles), by plotting Q_{10} versus CF. The overlap of the cochlear fibre data of Kiang et al. (1965a) (filled squares) with the present cochlear nucleus data (filled circles) is quite clear as is the difference in the mean sharpness of the two populations. However, if one considers the data of Evans and Wilson (open circles), a similar discrepancy is evident between their data and that of Kiang et al. (1965a) both of which are from the cochlear nerve. The Q_{10} values for cochlear fibres measured by Evans and Wilson are more similar to the values measured for cochlear nucleus cells in the present study than to the values for cochlear fibres measured by Kiang et al. (1965a).

The dashed lines show the regression of Q_{10} onto the CF for the data of Evans and Wilson (large dashes) and for the cochlear

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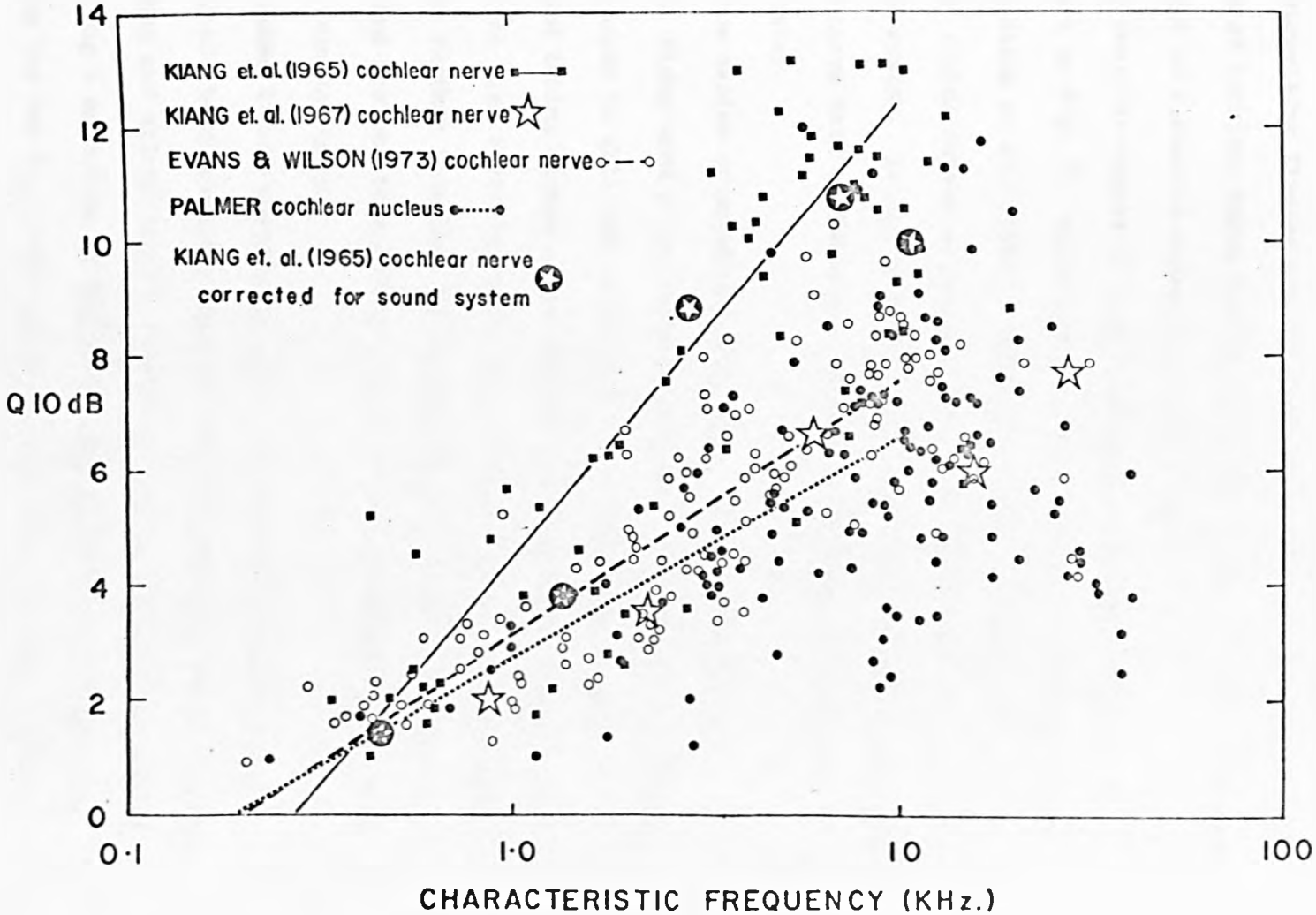
* The quantity 'Q' is used as a measure of sharpness of tuning used in characterisation of filters and is defined as centre frequency divided by the bandwidth at 3 dB below peak response. A similar measure used for auditory FTCs is the 'Q_{10}', or the centre frequency (in this case the characteristic frequency) divided by the bandwidth at 10 dB above threshold. This measure is used in preference to Q since the bandwidth at 10 dB above threshold is more accurately determinable than that at 3 dB.

Figure 79

Relative sharpness measured as Q_{10} dB i.e. CF/bandwidth of FTC at 10 dB above minimum threshold. The symbols are as indicated in the figure. The lines are regression lines through the three sets of data calculated for all the data points to 10 kHz.

Figure 79


KIANG et. al. (1965) cochlear nerve
KIANG et. al. (1967) cochlear nerve
EVANS & WILSON (1973) cochlear nerve
PALMER cochlear nucleus
KIANG et. al. (1965) cochlear nerve corrected for sound system
Q 10 dB
0
2
4
6
8
10
12
14
0·1
1·0
10
100
CHARACTERISTIC FREQUENCY (KHz.)

nucleus data (small dashes). The two regression lines are almost coincident, but no attempt was made to assess the statistical significance of the slight difference due to the complications introduced by the much wider variance of the cochlear nucleus data.

A surprising finding was the very large discrepancy between the two sets of cochlear nerve tuning characteristics. In the following an attempt to reconcile these findings is made.

One possible source of this discrepancy was suggested by the open stars on Fig. 79 which indicate tuning data taken from a later paper of Kiang et al. (1967). These 5 points represent the only published tuning curves of Kiang et al. which have been corrected for the sound system. It can be seen that these 5 points agree very well with the nerve data of Evans and Wilson and the present cochlear nucleus data.

In the series of experiments in which the nerve data were collected, Kiang used a condenser microphone, the frequency response of which began to fall off at about 3 kHz. This would result in uncorrected tuning curves appearing sharper than they actually are, since on the high frequency slope the intensity of the signal would have to be further increased to compensate for the falling response of the sound system, thus giving a greater high frequency slope and a sharper tuning curve.

It seemed likely therefore, that this correction might account for a part of the discrepancy between the data of Kiang et al. (1965a) and of Evans and Wilson (1973). However, this hypothesis was tested by correcting a selection of raw FTCs from Kiang et al. (1965a) and calculating the new Q_{10}. The new Q_{10} values were not very different from the original values, as can be seen in Fig. 79 . At low frequencies the corrected data (shown by the encircled stars, Fig.79)

agrees with the data of Evans and Wilson, but at high frequency where the discrepancy between the data of Kiang et al. (1965a) and that of Evans and Wilson is greatest, the correction for the sound system clearly cannot account for all of the discrepancy. Another possible source of the discrepancy may be choice of animals. Throughout my experiments and those of Evans (Evans, 1972; Evans and Wilson, 1973, Fig. 11) it has become evident that the FTCs of individual animals are sharper or broader than the average values, that is, a single animal can yield a selection of very sharply tuned FTCs and another animal a selection of broad FTCs. This variation appears to be natural and not linked to any pathology of the ear which as Evans has shown (Evans, 1972) may well produce very broad high threshold FTCs. It is possible then, that the four cats of Kiang et al. (1965a) may represent a selection of sharply tuned cats which would account for the discrepancy in tuning characteristics between this data and that of Evans and Wilson (1973).

If we now consider the small but possibly significant difference in tuning between cochlear nerve data of Evans and Wilson (1973) and the present cochlear nucleus data, it is not possible, in the light of the large differences in tuning from animal to animal, to decide whether this represents a real difference in the tuning of nerve and nucleus or is merely due to the limited sampling.

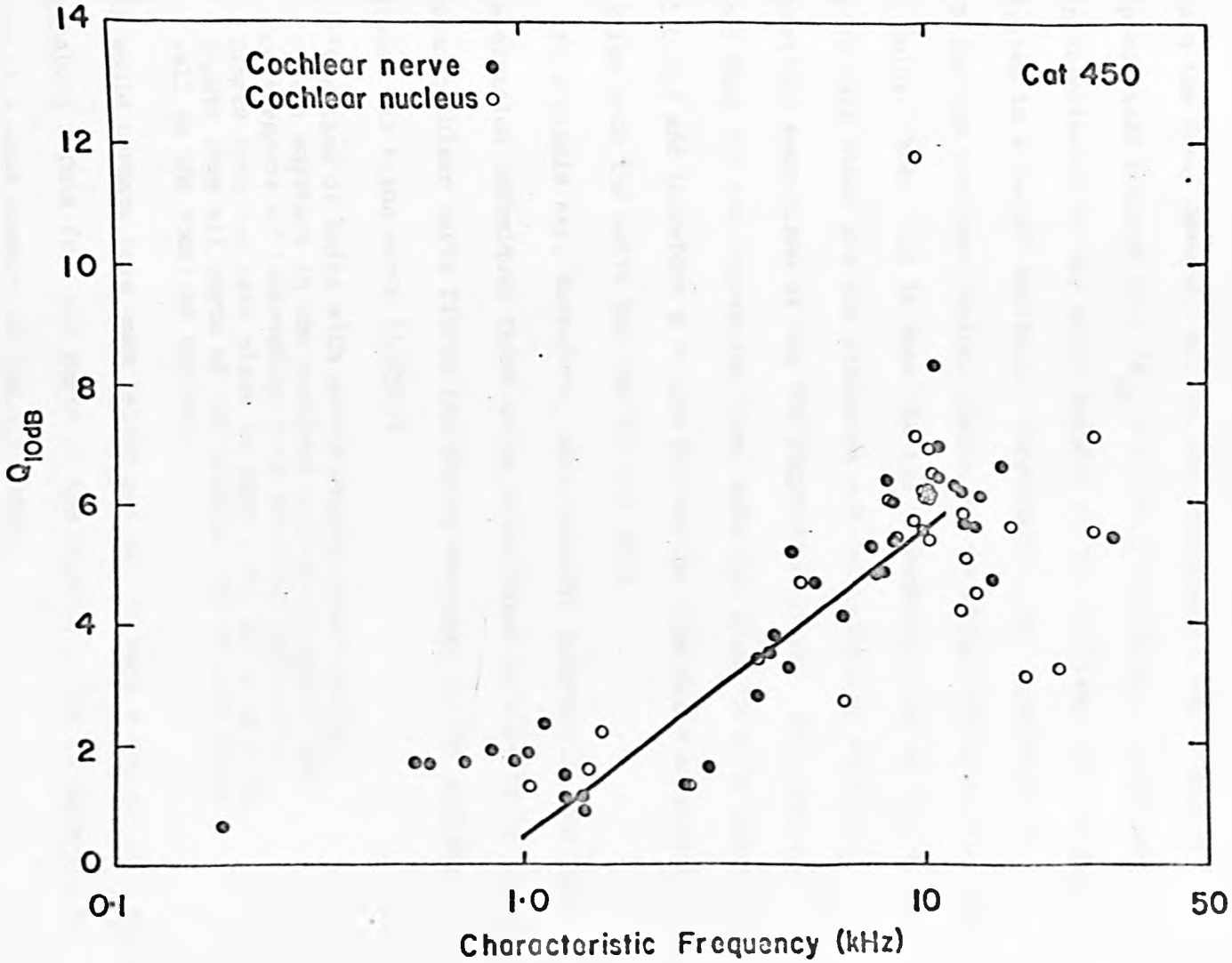
Sufficient FTC data were therefore obtainedfrom both cochlear nerve (by Evans) and cochlear nucleus of a single ear in order to eliminate any discrepancy due to inter-animal tuning differences. The data so obtained are plotted in Fig.80 as Q_{10} dB versus CF. All the data were obtained using an automatic frequency threshold curve tracing method (see Section 2.8.3).

Visual examination of the raw data would suggest that there is

Figure 80

Relative sharpness of FTCs at the cochlear nerve and cochlear nucleus from a single ear, measured as Q_{10} dB i.e. CF/bandwidth of FTC at 10 dB above minimum threshold. The continuous line is the best fit regression line for the nerve data.

Figure 80


Cochlear nerve ●
Cochlear nucleus ○
Cat 450
Q_{10dB}
14
12
10
8
6
4
2
0
0·1
1·0
10
50
Characteristic Frequency (kHz)

no significant difference between the two populations. If separate regression lines are drawn through the cochlear nerve and nucleus data using all of the data from 1.0 - 11 kHz (these limits were taken since below 1.0 kHz Q_{10} differed little with CF and above 11.0 kHz Q_{10} appears to decline with increasing CF), there is little difference between the two. However, due to the inclusion of one unusually sharp cochlear nucleus unit (Q_{10} = 11.761) statistical comparison is again complicated by the wider scatter of the cochlear nucleus data reflected in a larger variance. Consequently the regression of Q_{10} on CF for the cochlear nucleus points was recalculated excluding this data point. When this is done the two regression lines of Q_{10} on CF overlie each other and the variances are very similar, enabling statistical comparison of the two regression lines. The analysis showed that the two regression lines were not significantly different ($p < 0.01$) and therefore a single regression line would adequately describe both the nerve and the nucleus data.

In a single ear, therefore, using similar anaesthetic and FTC determination techniques there is no significant difference in tuning between cochlear nerve fibres and single neurones in the cochlear nucleus. As Kiang wrote (1965b):

> 'The lack of units with exceptionally broad tuning curves anywhere in the cochlear nucleus suggests that convergence of innervation from many auditory nerve fibres does not take place in such a way as to provide inputs from all parts of the cochlea to an individual cell in the cochlear nucleus.'

This would perhaps have been better put as 'in such a way as to provide <u>excitatory</u> inputs from all parts of the cochlea', but in general it is still a good summary of the situation.

Several authors have considered the relative sharpness of tuning between dorsal and ventral divisions of the cochlear nucleus (Kiang

et al., 1965b; Mast, 1970a;Goldberg and Brownell, 1973; Gisbergen et al., 1975a)and have found no marked differences between them. As has been suggested, however, one difference between nerve and nucleus data is the increased scatter in the latter (e.g. Rose et al., 1959; van Gisbergen, 1974). Similarly, when one compares DCN and VCN tuning one finds a similar situation; the DCN data has greater scatter than that from the VCN (Goldberg and Brownell, 1973; van Gisbergen, 1974). The wider scatter of the Q_{10} values for DCN units compared to VCN units can be seen in Fig.81 in which the present cochlear nucleus data are replotted using different symbols for DCN and VCN. This leads one to suggest that it is the inclusion of the DCN tuning data which results in the difference in scatter between the nerve and nucleus tuning data.

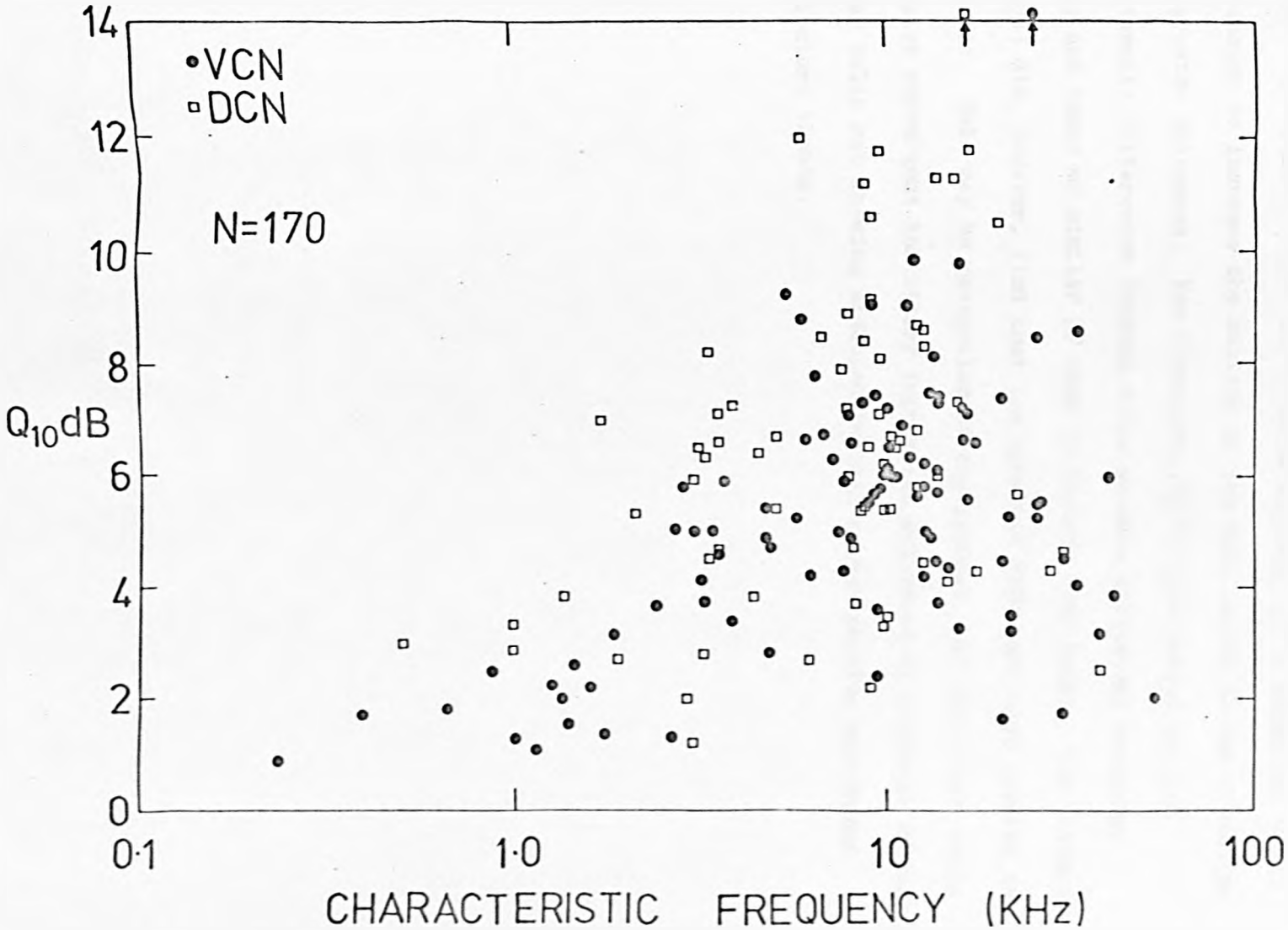
That the dorsal units show wider scatter is perhaps not surprising for two reasons. The first is that the DCN receives its predominant sensory input via internuncial neurones and the direct input from the cochlear nerve must represent only a small proportion of the DCN sensory input (Evans and Nelson, 1973b). The VCN receives its input directly from the cochlear nerve and it is not surprising therefore that single units in the VCN closely resemble cochlear fibres in their response properties.

A second reason why there is a greater variability in the sharpness of tuning of DCN neurones is the presence in large proportions of DCN units of response regions in which single tones inhibit spontaneous activity (Greenwood and Maruyama, 1965; Mast, 1970a;Evans and Nelson, 1973a). In an attempt to determine whether this inhibition produced a 'sharpening' of the FTCs of single cochlear nucleus units, Mast (1970a)compared bandwidths of neurones which showed such inhibition with those in which it was absent. The difference between the groups was very small; neurones with inhibitory areas had bandwidths with a

Figure 81

Relative sharpness of the FTCs of cochlear nucleus units from VCN and DCN (symbols as indicated) measured as Q_{10} dB i.e. CF/bandwidth at 10 dB above minimum threshold.

Figure 81


•VCN
▫DCN
N=170
Q_{10}dB
14
12
10
8
6
4
2
0
0·1
1·0
10
100
CHARACTERISTIC FREQUENCY (KHz)

median of 0.5 octaves and a range of 0.16 - 0.72 octaves. Those without inhibitory areas had a median of 0.52 octaves and a range of 0.24 - 2.0 octaves. Such differences although quite small may well be enough to increase the scatter of the data points in the direction of greater sharpness. Van Gisbergen (1974) also failed to find systematic differences between cells showing excitatory responses only and those of similar CF with inhibitory side bands. Van Gisbergen (1974) did, however, find that the broadest FTCs were also located in the DCN. This may be reconciled if one assumes that while some cells receive convergent inhibitory inputs (as evidenced by sideband inhibition) other cells not showing sideband inhibition may receive convergent excitatory inputs.

APPENDIX D

An Unsuccessful Attempt at Determining the Anatomical Location of Single Units

An attempt was made to determine the exact anatomical location of units by using dye deposits. The dye filled electrodes used (see Section 2.4.1), when connected to a DC voltage, left a deposit of blue dye when a current of 15 μA was passed through them for 2 minutes (Hellon, 1971). Injections of dye were routinely made at the end of the electrode track and at the site of any particularly interesting single unit. However, no dye spots were found in the tissue when it was sectioned. When dye spots were present, they were readily seen as the block of tissue is sectioned; on only one occasion was such a blue spot seen.

It is conceivable that in some experiments dye was successfully deposited only to be washed out of the tissue before fixation, during the course of prolonged recording.

In cases in which dye was presumed to have been deposited (by passage of 15 μA of current for 2 minutes) the electrode was removed completely. This created considerable difficulty in some experiments in locating the electrode track in the stained sections, when it was discovered that the dye deposit was not in fact present in the tissue. As a safeguard, therefore, electrodes were snipped off and left in situ until after fixation, thereby leaving a clear track in the cochlear nucleus sections. However, leaving the electrode in position eliminated any possibility of locating any dye deposits which might have been present.

Since no dye deposits were successfully recovered, and the dye electrodes produced a low yield of single units and frequently became

blocked during a penetration, the use of these electrodes was discontinued in favour of electrodes filled with 4M sodium chloride.

The sodium chloride electrodes were less susceptible to blockage, gave greater signal to noise ratio and were simpler to produce. When using sodium chloride electrodes the tapering portions (some 1 - 2 cm) were routinely left in situ during fixation.

Several of the later experiments were investigations of cochlear nerve and nucleus in the same animal (e.g. cat 450); these experiments required a recording time of up to 48 hours. Even when dye deposits are successfully produced they do not survive beyond 18 hours or so (in auditory cortex: J. E. Jolley, personal communication). Sodium chloride electrodes were therefore used in any prolonged experiments.

Locations of units were determined histologically whenever possible by reconstruction of the electrode track and use of both micrometer depth readings and measurements of single unit CFs (see Section 2.4.1).

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