Encoding of Rapid Amplitude Fluctuations by Cochlear-nerve Fibres in the Guinea-Pig*

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Summary. Responses of cochlear nerve fibres in the guinea-pig were measured to sinusoidally amplitude-modulated tones at fibre characteristic frequency. The modulation depth was ± 3 dB and the modulation rate was varied between 6.25 and 6400 Hz keeping the mean level of the tone constant. The resultant period histogram (locked to the modulation cycle) was used to determine the depth of modulated neural discharge. The functions showing the variation of discharge modulation with modulation frequency were, in general, low-pass. The cut-off of these functions appears to be primarily determined by the filtering properties of the fibres.

Key words: Cochlear-nerve – Amplitude-modulation

Introduction

The rate of change of amplitude of natural sounds, such as speech, varies over a wide range and it is therefore of interest to determine the way in which cochlear fibres are able to follow rapid amplitude fluctuations. Few studies have investigated the dynamic properties of fibre responses to rapid fluctuations in signal envelope. Those studies which have investigated dynamic responses have often used sinusoidal amplitude modulated stimuli to elucidate adaptation mechanisms, to make comparisons with psychophysics or to make comparisons with steady-state responses (Javel 1980; Smith and Brachman 1980a, b; Evans and Palmer 1980; Yates 1981). The present study investigates the ability of cochlear nerve fibres to follow sinusoidal amplitude modulation as a function of modulation rate. Moller (e.g., 1972, 1974) has extensively reported the responses of cochlear nucleus cells to sinusoidal amplitude modulation but has only reported similar data for cochlear nerve fibres obtained by another technique (Moller 1976). From Moller's data it appeared that the major
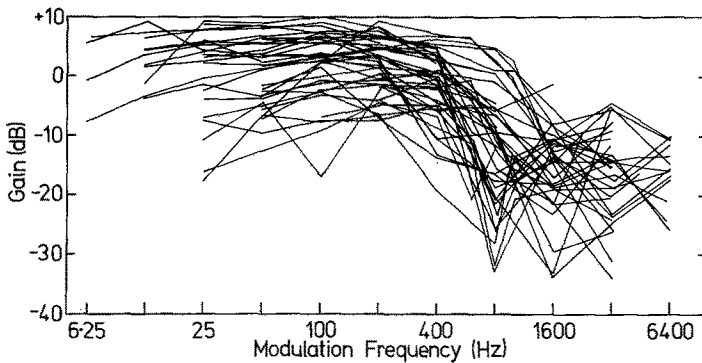

Fig. 1. Functions relating the gain of the discharge modulation with respect to the stimulus modulation to modulation frequency for guinea-pig cochlear nerve fibres

elements of the cochlear nucleus response were determined at the cochlear nerve level and this is confirmed in the present study. The present study was also intended to test Yates (1978) hypothesis that the limitation on a fibre's ability to follow rapid amplitude fluctuations is determined by its filtering properties.

Methods

Recordings were made from adult guinea-pigs anaesthetised using the neuroleptic technique of Evans (1979a). Detailed methods of surgical preparation etc. are as described by Evans (1979b).

Characteristic frequency (CF), minimum threshold and bandwidth at 10 dB above minimum threshold [and complete frequency threshold curves (FTCs) when time permitted], were measured with 50 ms tone bursts (5 ms rise/fall time repeated every 130 ms). To obtain the amplitude modulated (AM) signals, continuous tone signals at CF were sinusoidally modulated (± 3 dB) by a second oscillator via a two quadrant multiplier, gated with 5 ms rise/fall time and 100 ms duration and presented every 330 ms. Stimulus, response and synchronization signals were recorded on magnetic tape. Responses were measured for 30−40 s (of which 9−10 s were driven activity) at a single level for each fibre (7−25 dB above fibre threshold) and over a range of modulation frequencies from 6.25 to 6400 Hz. After the experiment the taped data were replayed and period histograms were generated using an averager locked to the modulation waveform and only triggered during stimulus presentation. The depth of modulation of the neural discharge was quantified (using the method of Goldberg and Brown 1969), and was related to the stimulus modulation by calculation of the 'gain' in decibels of the discharge modulation with respect to the stimulus modulation as a function of modulation frequency (as in Moller 1972, 1974).

Results and Discussion

Figure 1 shows gain functions for 39 guinea-pig cochlear-nerve fibres. Although there is interfibre variability, several common features are readily distinguishable. All but one of the functions shown are essentially low-pass, as the average low-frequency slope is only a few dB/octave. Above a certain modulation frequency all of the curves show a rapid decrease in gain. In many, but not all, of
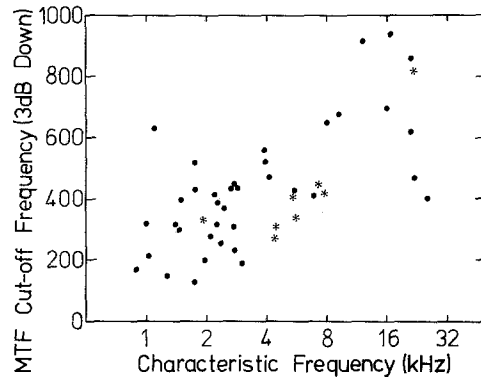
Fig. 2. Variation of cut-off of cochlear nerve gain functions with fibre CF. Dots show guinea-pig data, asterisks show cat data

the functions there appears to be a second peak occurring at modulation rates of 1000 to 3200 Hz. This latter feature only occurred in fibres with low CF. The general low-pass shape is consistent with the functions reported for certain cochlear-nucleus neurones and for cochlear-nerve fibres by Moller (1972, 1974, 1976), although other cochlear-nucleus cells had band-pass gain functions. The second peak at high modulation rates has not been previously reported, which is probably because most studies were on high CF neurones and modulation rates exceeding 1000 Hz were seldom employed.

Ignoring the peak at high modulation frequencies the interfibre variability is due to different pass-band modulation depths and variation in the the low-pass cut-off frequency (i.e., the frequency at which the gain had decreased by 3 dB from the maximum). The major factor producing the variable pass-band modulation depth is the arbitrary choice of stimulus level. In general only one function at a fixed stimulus level was measured in a single fibre. The mean level at which this was measured ranged from 7 to 25 dB above fibre minimum threshold. As the mean level of the AM signal is increased the discharge modulation increases to a maximum and then falls again as the fibre approaches saturation (Evans and Palmer 1979; Smith and Brachman 1980a, b; Yates 1981). The levels in the present study were selected to fall on or near the peak discharge modulation. Since recording time was limited and all analyses were performed off-line it was not possible to optimize the level.

A second factor was indicated in unpublished data of Palmer and Evans who measured gain functions for eight cochlear nerve fibres in a single cat at stimulus levels which did coincide with the previously determined peak modulation for each fibre. These data suggested that the peak depth of discharge modulation was not equal in all fibres, but was greater in fibres with higher CF. However, plots of gain versus CF at each modulation frequency for the present data failed to reveal any such relation: presumably this effect if present in the guinea-pig data was masked by the variability discussed above.

The data of Palmer and Evans also indicated that the cut-off of the gain functions depended on fibre CF as is also found in the present data as shown in Fig. 2. The dots indicate the present guinea-pig data and the asterisks show the cat data of Palmer and Evans. There is a definite increase of the cut-off with fibre
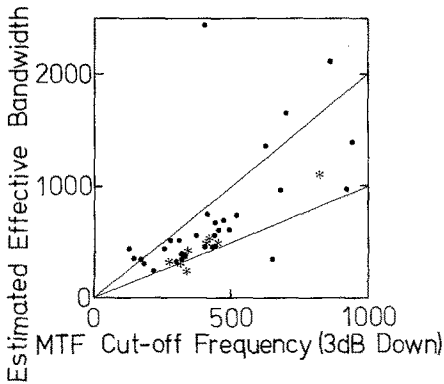
Fig. 3. Variation of cut-off of cochlear nerve fibre gain functions with estimates of fibre effective bandwidth. Dots show guinea-pig data, asterisks show cat data

CF; the guinea-pig data have a correlation coefficient of 0.69. Several characteristics of cochlear fibre responses vary with fibre CF (see Kiang et al. 1965; Evans 1975) including the absolute width of the fibre FTC which increases with CF. It seems reasonable to infer that a primary cause of the variation of cut-off with CF would be the underlying variation of cut-off with fibre tuning (as suggested by Yates 1978). Sinusoidal amplitude modulation results in a stimulus having a power spectrum with a carrier frequency component (chosen to be at fibre CF in this case) and an upper and lower side-band each separated from the carrier by an amount equal to the modulation frequency. Amplitude variations of the carrier can be considered as interactions between these constant amplitude components. At low modulation rates all three components will fall within the cochlear fibre filter and result in effective amplitude fluctuations. As modulation rate is increased the fibre will reject the side-band components and eventually only respond to the constant level carrier frequency. Thus discharge modulation will decrease rapidly when the width of the three component stimulus exceeds the width of the fibre FTC. The cut-off frequency of the gain function is plotted against estimates of the fibres' effective bandwidth in Fig. 3. These estimates were obtained by taking 46% of the measured 10 dB bandwidth. Again a relationship between these two measured variables is evident (correlation coefficient = 0.62). A slope of two between these variables would be expected since for a given increase in modulation frequency 'x' the width of the AM spectrum increases by '2x'. The slope of the data in fact is less than two (slopes of one and two are shown by the straight lines in Fig. 3): linear regression gives a value for the slope of 1.54. The slope of less than two is probably due to several factors such as (1) a fixed stimulus set (of modulation rates) was employed thus resulting in limited resolution which in some cases results in poor accuracy in the cut-off frequency estimation; (2) asymmetry of FTC slopes will result in unequal removal of the side-band components; (3) use of the fibre effective bandwidth assumes linear filtering (for which there is evidence see for example Evans and Wilson 1973) at least over the range of levels used to determine the gain functions and this assumption may not be justified (see Pfeiffer and Kim 1973).

These considerations aside, it would appear that the data allow the conclusion that the shape of the gain function of cochlear nerve fibres and particularly the cut-off frequency are predominantly a result of the fibres filtering properties. A similar conclusion was reached by Javel (1980) although from his very detailed analyses he identified other factors which may contribute to the decrease in modulation depth with modulation rate.

The extra peak occurring in some fibres (with CFs below 3 kHz) beyond the cut-off frequency is a severe problem for such an interpretation. The stimulus set used contained modulation frequencies up to 6400 Hz to ensure that the cut-off of the high frequency fibres was exceeded. When such high modulation rates were employed for low CF fibres the modulation rate exceeded the carrier frequency. Under these conditions the lower side-band component on reaching zero (carrier = modulation frequency) then increases in frequency. At modulation rates of at and near twice the carrier frequency the lower side-band is once again within the FTC of the fibre and will produce amplitude fluctuations which will be at a frequency determined by the difference between the lower side-band and the carrier frequency. The period histograms, however, demonstrate locking to the modulation frequency. The locking indicated must therefore represent a higher frequency distortion product generated by the carrier and side-band. There are two prominent sources of such distortions; combination tones and products of the rectification which takes place in transducing sound into nervous impulses (for detailed discussion see Young and Sachs 1979). Since in these experiments only a single cochlear place was examined in response to a particular carrier frequency the distortion products presumably resulted from rectification. Higher frequency distortion products of the rectification will also be present at low modulation rates but will not be visible in histograms locked to the lower rate. The distortion only occurs when both the carrier and lower side-band are within the fibre FTC since discharge modulation again decreases as the lower side-band passes beyond the high frequency extreme of the FTC. If this interpretation is correct the extra peak adds further weight to the suggestion the filtering properties of the fibre determine the shape of the gain function.

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