Dynamic Range Compression in the Cochlea: Experiments and Models

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ABSTRACT

Experimental results from this and other laboratories have demonstrated that com-
pression of dynamic range exists at the level of the basilar membrane mechanics
and is clearly reflected in the response characteristics of auditory nerve fibres. We
have previously shown that plots of the rate of generation of nerve action potentials
against sound pressure level (rate-intensity functions, or RI functions) range over a
continuum, reflecting the existence of fibres extending from rapidly saturating with
dynamic range around 20 dB sound pressure level (SPL) to non-saturating types
with dynamic ranges in excess of 60 dB SPL. Together, these two types have been
shown to cover a range of at least 100 dB. We have also used the neural RI func-
tions to show that the degree of compression appears to extend from around 0.3
(dB/dB) in the low-frequency region of the cochlea to around 0.12 at high frequen-
cies. This suggests that the cochlea compresses a 60 dB range of sound pressure
levels into as little as 8 dB of basilar membrane movement. Now we have applied
the boundary element technique of solving velocity-potential equations to a two-
dimensional model of the cochlea, and have produced solutions which match
extremely well with direct observation of basilar membrane mechanics. By including
a nonlinearity in the modelled active process, a process of mechanical positive
feedback widely believed to operate in the cochlea, we have also shown compres-
sion of the modelled basilar membrane input-output function. Slopes as low as 0.12
have been calculated from a simple Boltzmann operating characteristic assumed to
be driving the positive feedback through the cochlear outer hair cells. We now
believe we have an explanation for the cochlea's ability to process input signals
varying over a very wide range of intensities.

INTRODUCTION

Recent research, both experimental and theoretical, has demonstrated a continuously variable
gain control operating in the mammalian cochlea in the form of a highly-nonlinear, compressive
input-output function integrated with the cochlea's filtering mechanisms. Direct measurement of
basilar membrane responses have shown that a degree of compression exists at the mechanical
level in the cochlea and it may be that the wide dynamic range of the nerve fibres simply reflects
the underlying mechanical drive. The degree of compression is, however, quite remarkable;
detailed experiments on the responses of auditory nerve fibres (Sachs and Abbas, 1972; Winter,
Robertson and Yates, 1990) suggest that the compression may be as much as 0.2 dB/dB of SPL,
but few direct measurements of basilar membrane motion have shown compressions of this or-
der in the mechanics. Robles, Ruggero and Rich (1986) show one basilar membrane input/output
(I/O) function with a slope of 0.2 but all others appear to be steeper. Some recent results
derived from auditory nerve measurements (Cooper and Yates, 1994) have suggested that
slopes of as little as 0.12 occur in the high-frequency regions of the cochlea, with a rapid switch
to greater slopes of around 0.3 in the apical, lower-frequency regions.
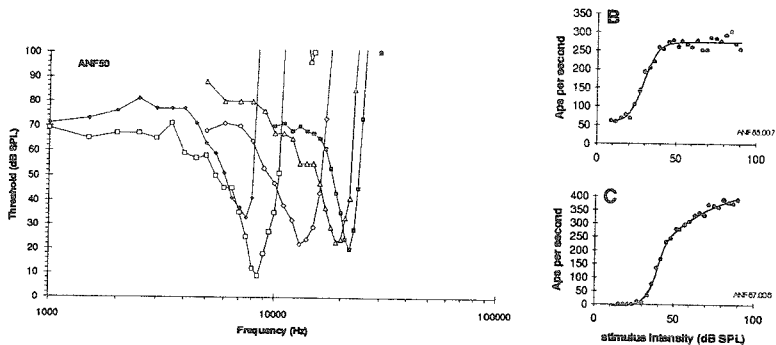
Auditory nerve responses

Fig.1. (A) Frequency versus threshold curves for five auditory nerve fibres from different points along the cochlea of a guinea pig. The abscissa is the stimulus frequency, the ordinate the sound pressure level necessary to produce a just-detectable increase in nerve firing rate. (B) RI function at CF for a sensitive auditory nerve fibre. (C) RI function at CF for a less-sensitive fibre.

The SPL at which a given nerve fibre will just begin to respond to a tone depends upon the frequency of the tone: typically, each fibre has a (different) frequency, known as its *characteristic frequency*, or CF, to which it most sensitive (fig.1A). The shape of the frequency response curves, however, changes with the intensity of the stimulus, becoming broader and shifting to lower frequencies with increasing SPL. This nonlinearity can be displayed in another way, as I/O curves which plot the neural discharge rate against SPL. Fig.1B shows a typical rate-vs-intensity function (RI function) measured from a guinea pig auditory nerve at a CF of 20kHz. This fibre is particularly sensitive, responding to sounds as low as 20 dB SPL. It is an example of a *saturating* RI function: it is s-shaped and saturates at about 280/sec. Similar CF data in fig.1C is from another fibre of similar CF in the same species. It has a higher threshold SPL and the RI function is quite different. Up to approximately 45-50 dB SPL the shape is the same, but at higher intensities the RI function flattens to a slower slope before eventually approaching saturation. This type is known as a *sloping saturation* RI function and is capable of responding differentially up to very high SPLs. For frequencies well below CF, all RI functions are of the saturating type. The different shapes of RI functions are believed to be due to nonlinearity of the basilar membrane.

Basilar membrane responses

Direct measurements of the vibration of the basilar membrane, the stimulus to the auditory nerve, have shown similar frequency selectivity in its responses. It has the same peak in sensitivity at the same frequency, for a given place along the cochlea, as the nerve fibres and a nonlinearity which is constrained to frequencies close to the amplitude peak. I/O functions are compressive, but reported slopes are generally not as great as those we have seen in the neural recordings. One exception (Robles et al, 1986) has a slope of 0.2, but whether it, or all the others, are the exception is unclear. Measurement of the frequency response of the basilar membrane requires considerable interference with the cochlea and it is known that this can damage the sharp tuning, so it is quite possible that the published results are not representative of the true physiological situation.

Derived bm input/output curves

In a recent paper Nigel Cooper and I (Cooper and Yates, 1994) used a technique of deriving a presumed basilar membrane I/O function from a set of neural RI functions by comparing the responses at CF with responses at other frequencies far from CF (Yates, 1990) Both of these papers implied that the basilar membrane was linear at very low SPLs, then became nonlinear at intermediate SPLs with I/O slopes of as low as 0.12 for high frequency fibres, while the former

paper also implied flatter slopes, of around 0.3, at frequencies below 4 kHz. These figures have been challenged as being too flat and await confirmation by more direct measurements. It would be helpful, however, if modelling could shed some light on how these slopes might come about and if they are reasonable.

The cochlear amplifier

It is now generally accepted, on evidence reviewed elsewhere, that the outer hair cells of the cochlea are capable of acting as sources of mechanical power which operate as part of a positive feedback loop synchronised to the motion of the basilar membrane. Its effect is to amplify the motion of the basilar membrane. Displacement of the membrane causes shearing between the tops of the hair cells and the tectorial membrane, a gelatinous mass which sits over the hair cells. The shearing displaces the tops of the stereocilia, resulting in an increased probability of opening of the mechanically-sensitive ion-channels located there. The channel gates are in (almost) thermodynamic equilibrium and their actual states at any instant are best described by a probability function which is approximately Boltzmann. The ionic current which then flows somehow triggers mechanical activity in the outer hair cells and results in mechanical energy being fed back into the wave motion. Because the impedance of the membrane is great everywhere but close to resonance, the power fed back influences the membrane only close to the characteristic frequency, however.

It has been proposed (Mountain and Hubbard, 1983; Patuzzi et al 1989) that the Boltzmann-like gating function is a major cause of nonlinearity in the motion of the membrane: poitive feedback is extremely sensitive to loop parameters and even slight saturation of the ionic current through the hair cells leads to reduced loop gain and reduced amplitude of vibration (Yates, 1990).

Modelling the nonlinear cochlea

Many models of the active cochlea have appeared in the literature over the past fifteen years but most have been hampered by approximations made to improve calculation efficiency. I have now adapted the boundary element method of solving numerically boundary condition problems in Laplace's equation, the equation governing the motion of the basilar membrane. Mechanical aspects of the model are similar to early models (Lesser and Berkley, 1972) with the inclusion of a negative resistance component to function as the active gain element. The negative resistance is constrained to fall off at a rate of 6 dB/octave with the -6 dB point being 0.8 octaves below the frequency of membrane resonance.

The nonlinear element was modelled as multiplier of the negative resistance component taking the form of a Boltzmann function of the instantaneous basilar membrane displacement. Thus, as the amplitude of the membrane increased, the negative resistance component was reduced. Harmonic distortion of the negative resistance was ignored, since experiments and other theoretical studies have shown that the basilar membrane does not respond to harmonics. The nonlinear problem was solved iteratively (Kanis and de Boer, 1983) by first solving the linear problem, then using the results to calculate the degree to which saturation of the negative resistance reduced its feedback. The solution was then recalculated, using the adjusted negative resistance feedback, and the saturation again calculated. The process converged to a self-consistent state, i.e., one where the hydrodynamic equations were satisfied and the amplitudes along the basilar membrane were consistent with the degree of saturation calculated.

Calculations were run on a Digital Equipment Corporation Alpha model 3000. Boundary element specifications were prepared on a personal computer using Microsoft Excel and then transferred to the Alpha for the calculations. Raw output from the Alpha was then returned to the personal computer for analysis and graphical display with Excel. Each calculation gave an excitation pattern along the cochlea for a single frequency; frequency response curves required recalculation for each frequency of interest. Parameters appropriate to the guinea pig cochlea were used in
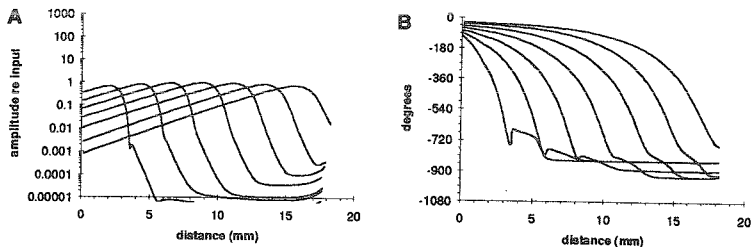
Fig.2 Calculated basilar membrane responses for a linear, passive cochlea. (A) Excitation pattern magnitude. (B) Excitation pattern phase. Stimulus frequencies were 20 kHz, 10 kHz, 5 kHz, 2.5 kHz, 1.25 kHz, 625 Hz, 312.5 Hz.

the calculation since our laboratory has a great deal of data relating to direct measurements on guinea pig ears.

RESULTS

Linear responses without active gain

Fig.2 shows a set of excitation patterns for a range of frequencies. For each frequency the phase shows a travelling wave to be propagating from the stapes (input) end towards the apex of the cochlea. As the wave travels, its amplitude rises at a rate of approximately 9 dB/octave (2.5 mm) to reach a broad peak about one half octave before the place of membrane resonance. At that place the phase accumulation abruptly changes, typically to approach a steady value which indicates that the wave is no longer propagating as a wave but is decaying exponentially. The high frequency slope falls smoothly from the maximum down to the plateau region, the membrane resonance place, where it changes to a smooth, exponential decay suggested by the phase data. These curves match up well with experimental data from the guinea pig using the Mössbauer technique (Johnstone and Yates, 1974).

Linear responses with active gain

Fig.3 shows similar excitation patterns but this time with active gain present. The negative resistance near the base was set to 9 times the value of the (conventional) damping in the membrane, It was rolled off at -6 dB/octave with the -6dB point being 2 mm below the membrane resonance place. At the basal (left) end, the responses are similar to those of Fig.2, rising smoothly at about 9 dB/octave. Within 1 octave of the resonance place, however, the responses increase rapidly in amplitude, rising by as much as 55 dB to a sharply defined peak before falling rapidly, with steeper slopes, to the plateau region. The gradual change in peak height with frequency is due to the reduction in damping and active feedback towards the apex (right) end, in order to match the known variation in the real cochlea.

Nonlinear excitation patterns

The same parameters as in Fig.3 are now shown in Fig.4 for the nonlinear condition and for one frequency only (8 kHz) but for a range of input intensities. At the lowest intensity the excitation pattern is the same as for the linear case of Fig.3. For higher stimulus intensities, however, the vibration in the basal region grows in proportion to the stimulus, but the response near to and beyond the maximum amplitude place does not. Moreover, the place of maximum amplitude shifts towards the base with increasing intensity, as is seen in the physiological case (the 'half-octave shift'). At the highest intensity the response looks much the same as for the passive case
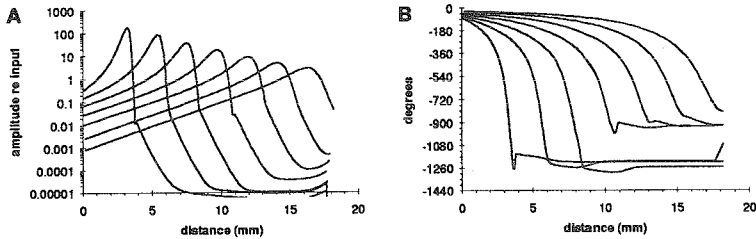
Fig.3 Calculated basilar membrane responses for a linear, active cochlea. (A) Excitation pattern magnitude. (B) Excitation pattern phase. Stimulus frequencies were 20 kHz, 10 kHz, 5 kHz, 2.5 kHz, 1.25 kHz, 625 Hz, 312.5 Hz.

(Fig.2), as is to be expected when the forward gain is completely saturated and the feedback loop is rendered ineffective.

Input/output functions
Since we are interested in the I/O functions for a given frequency, it is appropriate to take vertical slices through the data of Fig.4 to generate plots of response magnitude against stimulus intensity for a given place along the model cochlea. Fig.5 shows such a plot. At 1 mm from the basal end the I/O function is quite linear, reflecting the fact that the feedback is ineffective because of the high impedance of the membrane. At the place of maximum sensitivity, at 5 mm, the response is at its most sensitive and initially is linear up to 100 before entering a highly compressive region with a slope of bout 0.2.

CONCLUSION
The cochlea's remarkable sensitivity is due to a positive feedback loop which feeds mechanical energy, derived from metabolic sources, into the mechanical motion of the basilar membrane. One element of the feedback loop is the mechanical to electrical transduction stage at the top of the stereocilia of the outer hair cells. The transduction is nonlinear, the transfer between displacement and electrical current approximating a Boltzmann function. Incorporating such a nonlinearity into a numerical model of the cochlea travelling wave produces exactly the type of nonlinear I/O functions observed on the basilar membrane with slopes as flat as those suggested by more indirect but less invasive experimental techniques. The calculated I/O functions show the initial linear region at low stimulus levels, leading into a highly compressive region where the basilar membrane amplitude is virtually clamped over a very wide range of input levels. In vivo,
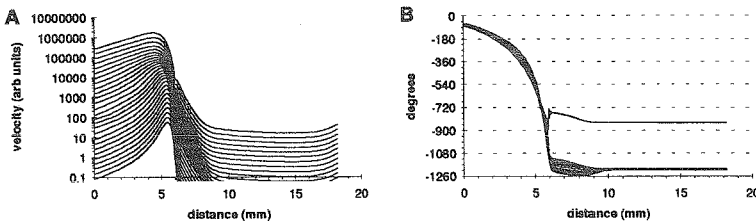

Fig.4. Magnitude (left) and phase (right) of the excitation patterns formed in the nonlinear, active model for different input amplitudes. Note the progressive shift (bottom to top) of the magnitude curves from sharply tuned (as in Fig.3) to broadly tuned (as in Fig.2).The phase curves round off slightly but do not change much.
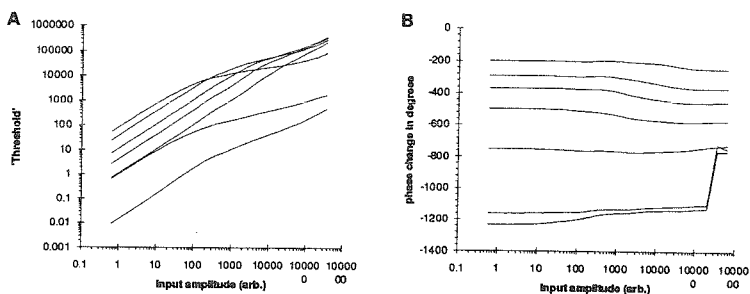
Fig.6. Calculated I/O functions for the nonlinear model. (A) magnitude. (B) phase.

this corresponds to the range of speech intensities, implying that speech is received by the cochlear nerve at almost constant intensity regardless of quite wide variations in the sound pressure level at the eardrum.

ACKNOWLEDGEMENTS

REFERENCES

Cooper, N.G. and Yates, G.K. (1994). Nonlinear input-output functions derived from the responses of guinea-pig cochlear nerve fibres: Variations with characteristic frequency. Hear.Res. 78, 221-234.

Johnstone, B.M., Patuzzi, R. and Yates, G.K. (1986). Basilar membrane measurements and the travelling wave. Hear.Res 22, 147-153.

Kanis, L.J. and De Boer, E. (1993). Self-suppression in a locally active nonlinear model of the cochlea: a quasilinear approach. J.Acoust.Soc.Am. 94, 3199-3206.

Lesser, M.B. and Berkley, D.A. (1972). Fluid mechanics of the cochlea. Part I. J.Fluid.Mech. 51, 497-512.

Mountain, D.C., Hubbard, A.E. and McMullen, T.A. (1983). Electromechanical processes in the cochlea. In, Mechanics of Hearing, E. de Boer and M.A. Viergever, eds. Martinus Nijhoff Publishers, Delft University Press, The Hague., 119-126.

Patuzzi, R.B., Yates, G.K. and Johnstone, B.M. (1989). Changes in cochlear microphonic and neural sensitivity produced by acoustic trauma. Hear.Res 39, 189-202.

Robles, L., Ruggero, M.A. and Rich, N.C. (1986). Basilar membrane mechanics at the base of the chinchilla cochlea. I. Input-output functions, tuning curves, and phase responses. J.Acoust.Soc.Am. 80, 1364-1374.

Sachs, M.B. and Abbas, P.J. (1974). Rate versus level functions for auditory-nerve fibres in cats: tone-burst stimuli. J.Acoust.Soc.Am. 56, 1835-1847.

Yates, G.K. (1990). Basilar membrane nonlinearity and its influence on auditory nerve rate-intensity functions. Hear.Res. 50, 145-162.

Yates, G.K., Winter, I.M. and Robertson, D. (1990). Basilar membrane nonlinearity determines auditory nerve rate-intensity functions and cochlear dynamic range. Hear.Res 45, 203-220.