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LINEAR RESPONSE OF THE COCHLEA

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ABSTRACT

Beginning with the work of Mammano and Nobili it is shown that in the passive state the cochlear partition may be modelled as an array of modally uncoupled independent mechanical oscillators. While uncoupled modally the oscillators of the cochlear partition are strongly coupled hydraulically through the forcing fields of the stapes and all other segments of the cochlear duct. Consequently, each mechanical oscillator of the cochlear partition responds modally in forced response dependent upon the motion of the stapes and the motions of all other segments of the cochlear partition. It is shown that the oscillators of the cochlear partition are linear in passive response to sound pressure levels of 110 dB re 20 μ Pa. Evidence is presented in support of the assumption that in the case of active response undamping may be assumed to vary on a time scale which is long compared to the period of sound in the audio frequency range. In the latter case active response of the cochlea may also be described in terms of the same system of linear oscillators as in the passive case but with variable damping. It will be shown that the proposed active model is in good agreement with available data.

INTRODUCTION

In a recent paper Mammano and Nobili (1993) describe a model of the cochlear partition which is capable of responding in either a passive or an active state. In a passive state the damping factor is assumed to be constant and some large value. In an active state the damping factor is assumed to be variable and may range between large and very small as the model incorporates an undamping mechanism based upon the motility of the outer hair cells (Ashmore 1987, Ashmore & Brownell 1986, Brownell et al., 1985).

Mammano and Nobili introduce nonlinearity into their model through a variable damping term. In the latter case the damping term is time dependent which, of course, may

introduce a considerable complication in determining an appropriate wave equation and an exact solution. In fact, sufficient information for the purpose of producing such a wave equation does not exist. However, in the passive state the damping term, $h(z)$, is constant and the solution is well known.

Mammano and Nobili describe the passive state response of the cochlea with a second order differential equation with constant damping. They describe their proposed undamping mechanism and introduce it into their model as an addition to the constant damping term with the implication that the active state may also be described by the same second order differential equation as proposed to describe the passive state. The authors suggest no other modification of their wave equation.

In considering the active state a great simplification is possible if it may be assumed that the time scale for variation in $h(z)$ is long compared to the period of variation of the acoustic signal, $1/f$, where f is the frequency under consideration. In the latter case of slowly varying damping, relative to the time scale of the acoustic signal, $h(z)$ may be treated as a constant in determining a solution for the wave equation of Mammano and Nobili. In this case the second order differential equation describing the passive state is assumed also to describe the active state. It may then be assumed that to a first approximation the solution for the passive state also applies to the active state and the case of active undamping. As will be shown observed nonlinear cochlear response may readily be explained in terms of a linear model with variable damping.

In support of the proposal that the time scale of variation in the cochlear damping term $h(z)$ is long compared to the period of the sound which is detected, $1/f$, is the observation that whereas about 10% of the afferent nerves run from the outer hair cells about 50% of the efferent nerves run directly to the outer hair cells in their respective connections with the brain (Spoendlin, 1972, 1978). Strong intervention of the brain in response to signals sent to it is clearly implied in the function of the outer hair cells. In turn a time delay sufficient to account for the proposed slow response also is implied.

In the guinea-pig the time constant $1/f$ is about .007 seconds and in humans it is about .05 seconds at the lowest frequencies of their respective ranges of audibility. At the lowest frequency of audibility a periodic signal ceases to sound like a tone to humans and becomes a series of discrete events. It will be assumed that the guinea-pig probably would find the same effect to be true. This observation suggests that a processing time characteristic of the brain that is long compared to $1/f$ is required to recognize separate periodic events. Review of psychophysical data suggests temporal integration times an order of magnitude greater than $1/f$ in agreement with the proposal made here (Moore 1982). Here it is postulated that the time required for processing of signals from the ear to the brain and return of instructions to the ear will be subject to the same constraints as those controlling temporal integration times and the change from recognition of tones to discrete events. In turn these observations are consistent with the postulated slow response of the outer hair cells.

Mammano and Nobili consider two possible forms of coupling between segments of the cochlear partition. Coupling, which takes place through the fluid of the cochlea between the sections of the cochlear partition, produces a force on any typical segment of the cochlear partition in addition to that due to motion of the stapes at the oval window. Such coupling will be referred to as fluid coupling. The resulting total force determines the phase and amplitude of response but has no effect upon the characteristic frequency of a typical segment. By contrast, coupling which takes place at the junctions between segments will have the effect of perturbing the modal responses of the adjacent segments. Such coupling will be referred to as modal coupling. However, as will be shown the

coupling between adjacent segments is negligible and thus any effect upon frequencies of maximum velocity and displacement also is negligible.

In the absence of modal coupling the wave equation of Mammano and Nobili describing wave motion on the basilar membrane in the passive state, is that of a series of simple one-degree-of-freedom linear oscillators in forced response. In the passive state when the damping factor is constant the wave equation shows that a typical segment of the cochlear partition may be thought of as a linear oscillator and it will be convenient to refer to a typical segment of the cochlear partition as an oscillator. The basilar membrane travelling wave is explained in terms of the fluid coupling between all segments of the cochlear partition while the frequencies of maximum velocity and displacement of a typical segment of the cochlear duct are unaffected by any modal coupling.

In the following discussion the assumption will be explicit that both the passive and the active states may be described with the same second order differential equation of motion. It will be assumed that variation in damping takes place on a time scale which is long compared to the period of the frequency under consideration. In either the passive or the active state the system is linear and behaves as though the damping factor were constant. However, in the active state the damping factor may range in value from very small to very large.

At very high sound pressure levels it is reasonable to assume that cochlear response is passive. On the other hand, active response is to be expected at very low sound pressure levels. In their Figure 4 Johnstone, Patuzzi and Yates (1986) show the expected variation in response with variation in sound pressure level. At very low sound pressure levels, where strong active response is expected, very peaked response is observed which corresponds to very small damping in the region of resonance. For example, strong active response introduced as undamping has greatly reduced the inherent damping in the active state. As shown in the same figure in the region of resonance at very high sound pressure levels, where passive response is expected, the response is broad corresponding to large inherent damping in the passive state. In the latter case undamping is nil. The figure also shows that intermediate between very low and very high sound pressure levels undamping takes on intermediate values corresponding to intermediate damping between that of the strongly active state and that of the passive state.

As may readily be shown the frequency of maximum velocity response of a linear viscously damped oscillator is independent of damping, but by contrast, as may also be shown the frequency of maximum displacement response is dependent upon the system damping (Tse et al. 1978a). Thus variable damping through some active undamping mechanism as proposed by Mammano and Nobili will not affect the frequency of maximum velocity response but it will strongly affect the frequency of maximum displacement response. The shift in maximum displacement amplitude from high to low frequency shown in the figure of Johnstone et al. is the result of increasing damping with increasing sound level. As the frequency of maximum velocity response is independent of the damping, whether passive or active, in a system in which undamping determines active velocity response of the cochlea the "best frequency" for velocity response will remain fixed over the entire auditory dynamic range (Lighthill 1991, 1996). It will be shown that the cochlear velocity in passive response is linear to 110 dB re 20 μ Pa (110 dB SPL).

THE EFFECT OF LONGITUDINAL COUPLING

The cochlear partition may be modeled as a series of joined segments each tuned to a

lower frequency as one progresses apically from the basal end. When oscillators are coupled in such a way that their properties are dependent upon their relative responses they tend to influence each other and they are modally coupled. For example, strong modal coupling between a pair of oscillators produces resonances which are not at all those of the uncoupled pair; one resonance will always be higher and the other will always be lower than the resonances of either oscillator taken singly (Tse et al. 1978b).

The segments of the cochlear duct may be thought of as oscillators each tuned to a frequency slightly lower than the preceding oscillator as one advances apically along the cochlear duct. The observation that the cochlea responds as though each segment were tuned only slightly lower in frequency than the previous segment in progressing apically strongly suggests that the modal coupling between adjacent segments is weak. On the other hand, observed cochlear displacement response is described as a travelling wave (Pickles 1982). The large phase shifts of several wavelengths between the stapes and the point of observation reported by Rhode (1980) implies a delay of several cycle between the energy input at the stapes and its arrival at the point of observation. Such delay is only possible if there exists some energy storage mechanism along the length of the cochlea as would be provided by coupling between cochlear segments. One or the other of the coupling terms introduced by Mammano and Nobili is crucial to an explanation of Rhode's observations.

Lighthill (1991) has analysed the phase data of Rhode (1980) and he has shown that the cochlear wave group speed has the remarkable property that it rapidly decrease as the wave approaches a place of resonance where it stops and travels no further. As wave energy travels with the group speed the implication is that energy introduced at the stapes travels to the place of resonance and simply piles up and travels no further (Lighthill 1991). The observation that a wave of a given frequency travels to the place of resonance and travels no further is thus explained. For later convenience this phenomenon will be referred to as Lighthill's cut-off condition.

The implication of the observations of travelling waves in the cochlear partition is that the motions of the segments of the cochlea strongly influence each other. As may readily be shown longitudinal coupling between adjacent segments is negligible, but strong coupling exists between any typical segment and all other segments through the fluid forcing field (Lighthill 1991; Mammano and Nobili 1993).

To investigate the strength of the coupling between segments of the cochlear partition reference will be made to work of Mammano and Nobili (1993) who have provided estimates of all physical quantities involved and have proposed an analytic model of the cochlea. They begin by formulating the basic dynamical equation of motion of the passive cochlea in which they include all effects which may influence cochlear response. They show that only modal coupling between adjacent segments through longitudinal viscous shear forces may be of importance.

Mammano and Nobili begin their analysis by formulating the following differential equation to describe the displacement response of the passive cochlea to an imposed acoustic stimulus.

$$m(z) \frac{\partial^2 \xi}{\partial t^2} + H(z) \frac{\partial \xi}{\partial t} + k(z) \xi = F_s(z, t) + F_{BM}(z, t) \quad (1)$$

where

$$H(z) = h(z) + \frac{\partial}{\partial z} s(z) \frac{\partial}{\partial z} \quad (2)$$

Here the equation of Mammano and Nobili has been written in terms of an operator $H(z)$ as given by Equation (2) which incorporates both the viscous damping term, $h(z)$, and the longitudinal shear coupling term.

In Equations (1) and (2) all quantities are per unit length where z is the normalised basilar membrane longitudinal coordinate along the spiral axis of the cochlear duct in the apical direction extending from $z = 0$ at the stapes to $z = 1$ at the helicotrema and $\xi(z,t)$ is the resulting basilar displacement. $m(z)$ and $k(z)$ are respectively the effective mass including fluid inertial effects and the stiffness of the duct per unit length. $F_s(z,t)$ is the force per unit length resulting from motion of the stapes and $F_{BM}(z,t)$ is the force per unit length resulting from displacements of all other parts of the basilar membrane. These two forcing fields result in the imposed acoustical signal on any oscillator of the array. As may be shown the latter term provides the only significant coupling between segments of the cochlear partition (Lighthill 1991) and, as shown by Mammano and Nobili, it accounts for the observed travelling wave.

Straight forward analysis, which makes use of data provided by Mammano and Nobili, shows in the case of greatest possible coupling the following:

$$\frac{H(z)}{h(z)} - 1 = 3.3 \times 10^{-8} \quad (3)$$

As shown here for the case of greatest longitudinal coupling the coupling between oscillators is negligible. Consequently, the cochlea may be modelled as a linear array of viscously damped simple one-degree-of-freedom linear oscillators. Voldřich (1978) has experimentally investigated the properties of the basilar membrane of the guinea-pig and has shown that in an immediate post-mortem preparation longitudinal coupling between adjacent segments is negligible in confirmation of the latter conclusion.

DYNAMIC RANGE OF THE COCHLEA IN VELOCITY RESPONSE

In this section it will be shown that the velocity response of the cochlea is quite linear at sound pressure levels sufficient to cause physical destruction of selected portions of the cochlear partition. The demonstration will be based upon the observation that a linear model can predict the observed destruction of hair cells brought about by two hour exposure to narrow bands of noise at sound pressure levels of 109 dB and 110 dB re 20 μ Pa (Liberman and Dodds 1984a,b). It is to be noted that at sound pressure levels high enough to cause hair cell destruction it is quite reasonable to assume that the ear responds passively as otherwise the cochlea would be contributing to its own destruction.

In the audio frequency range the fluid in the cochlea is essentially incompressible thus any slight pressure variation which might result from motion of the stapes acts upon all portions of the cochlear partition at once and in phase. When a tone is introduced at the basal end all of the oscillators which sense higher frequencies will be driven below their resonant frequencies in stiffness controlled response. In the region in which the tone is sensed the oscillator response will be controlled by the system damping, while in the region of the cochlea beyond, where lower frequencies are sensed, the oscillator's response will be greatly reduced by Lighthill's cut-off condition and mass controlled.

It will be convenient to introduce the frequency ratio, x , the driving frequency, f , and the undamped resonance frequency, f_N , as follows.

$$x = \frac{f_N}{f} \quad (4)$$

$$f_N = \frac{1}{2\pi} \sqrt{k/m} \quad (5)$$

The expression for the displacement amplitude, X , of a one-degree-of-freedom oscillator takes the following form (Tse et al. 1978a) when written in terms of the driving force, F , and the damping factor, ζ , and the introduced variables.

$$\frac{X}{F/k} = \left[(1 - 1/x^2)^2 + (2\zeta/x)^2 \right]^{-1/2} \quad (6)$$

An expression for the normalised velocity amplitude, $V = 2\pi Xf$, is obtained by dividing Equation (6) by x . The resulting expression for the normalised velocity is

$$\frac{V}{2\pi f_N F/k} = \left[(x - 1/x)^2 + 4\zeta^2 \right]^{-1/2} \quad (7)$$

In the case of exposure to a narrow band of noise characterised by a band center frequency a corresponding narrow range of the cochlea about the place of stimulation of the band center frequency will be driven strongly in resonant response. At very high sound pressure levels in the narrow range of strong cochlear stimulation the response may be expected to be passive and thus well damped. All segments within the narrow range of strong stimulation will exhibit broad response and consequently the motion of any particular segment within the narrow range of stimulation will differ very little from that of all other segments within the same narrow range. Any difference in the contribution of any particular segment within the narrow range compared with the contributions of all other segments within the narrow range to the forcing term, $F_{BM}(z,t)$ must be small. Consequently, it may be assumed that the basilar membrane forcing term, $F_s(z,t) + F_{BM}(z,t)$ (see Equation 1), is essentially constant within the narrow range of strong stimulation.

The power introduced into a linear oscillator or a distribution of linear oscillators may be calculated as the integral of the product of the basilar membrane forcing term and the velocity of the cochlear partition, which here is modelled as a series of oscillators of gradually varying resonant frequency as described by Equation (7). Since the forcing term is essentially constant in the narrow range of interest the power distribution is controlled by the velocity response given by Equation (7). The normalised power distribution parameter, P , is as follows.

$$\frac{P\sqrt{km}}{F^2} = \frac{1}{2} \left[\left(x - \frac{1}{x} \right)^2 + 4\zeta^2 \right]^{-1/2} \quad (8)$$

Consideration of Equation (8) shows that if the undamped resonant frequency f_N is held constant and the frequency f is allowed to vary then Equations (6), (7) and (8) provide a description of the frequency response of an individual oscillator (cochlear section).

Alternatively, the same equations provide a description of the amplitude response along the cochlea of the displacement, velocity and power injection when the cochlear partition is modelled as a series of oscillators each resonant at a slightly lower frequency as one progresses from the basal end to the apical end.

Two investigations concerned with selective destruction of portions of the cochleas of experimental animals, by subjecting them to intense sound and subsequently determining the extent of damage to the cochleas and the associated hearing deficits, have been reported by Liberman and Dodds (1984a,b). Here attention will be given to Figure 6 of the first and Figure 8D of the second of the referenced papers. In each case the animals were subjected to narrow band noise centered at 5.5 kHz for two hours at a level in the first case of 109 dB and in the second case of 110 dB re 20 μ Pa.

It will be assumed that the induced damage is proportional to the work done and thus to the acoustic power input to the damaged area of the cochlea. While information is insufficient to calculate the actual power input, the predicted power input distribution may readily be calculated using Equation (8) and may be compared with the observed distribution of damage to the hair cells as reported by Liberman and Dodds. It will be assumed that the upper and lower bounds, f_u and f_l , of a region of destruction will be determined by corresponding input power levels. For example, as may readily be shown by use of Equation (8) the following relation is predicted.

$$f_u / f_N = f_N / f_l \quad (9)$$

Referring to Figure 6 of Liberman and Dodds (1984a) an upper bound in terms of frequency of 6.4 kHz and a lower bound of 4.8 kHz may be estimated leading to 1.15 and 1.16 for estimates of the left and right hand sides of Equation (9). In this case the agreement is very good.

Referring to Figure 8D of Liberman and Dodds (1984b), where the extent of damage is not as clear cut as in the previously cited figure, a lower bound of 4.0 kHz and an upper bound of about 9.0 kHz is estimated leading to 1.6 and 1.4 respectively for the upper and lower bounds. In view of the well known uncertainties associated with fatigue induced failure (strongly suggested by the referenced figure) the left and right estimates of the upper and lower bounds are in reasonable agreement with the prediction of Equation (9).

NONLINEARITY

Rhode (1980) investigated the possibility that the ear is nonlinear in a region of resonant response and summarised his investigation in his Figure 6. In his figure measured basilar membrane displacement over a range of frequencies at a point of observation is plotted as a function of sound intensity introduced at the test animals ear canal. In the figure coordinates are chosen so that linear response results in a straight line plot of 45 degrees positive slope. Rhode tells the reader that the observation point on the basilar membrane is characterised by resonant response of about 7500 Hz. In the frequency range well below and well above resonant response Rhode observed linear response but in the frequency range of resonant response Rhode observed slopes very much less than 45 degrees showing that in this range response was nonlinear.

It will be useful to reanalyse Rhode's data observing that when the displacement is reduced by the intensity linearity will cause all data points which lie on a straight line of positive forty five degree slope in Rhode's plot to lie on a single point as shown here in

Figure 1. For example, the data points on the extreme left at 0.62 (4636 Hz) and on the extreme right at 1.28 (9600 Hz) show linear response. In the figure the frequency ratio, $1/x = f/f_N$, has been introduced for convenience even though this presentation suffers somewhat because Rhode gives only an approximate value for the characteristic frequency ($f_N = 7500$ Hz) at his point of observation.

In Figure 1 it may be observed that the data point on the extreme right is very much lower than all other data points. To understand this it is necessary to recall that resonant response on the basilar membrane proceeds from high to low frequencies as one advances apically along the membrane. For example, sound energy at the corresponding frequency of 9600 Hz will have passed through the point where it would be resonant on the basilar membrane well before reaching the point of observation which is resonant at the much lower frequency of 7500 Hz. Consequently, sound at 9600 Hz will be subject to Lighthill's cut-off condition which was described earlier and thus will be considerably reduced.

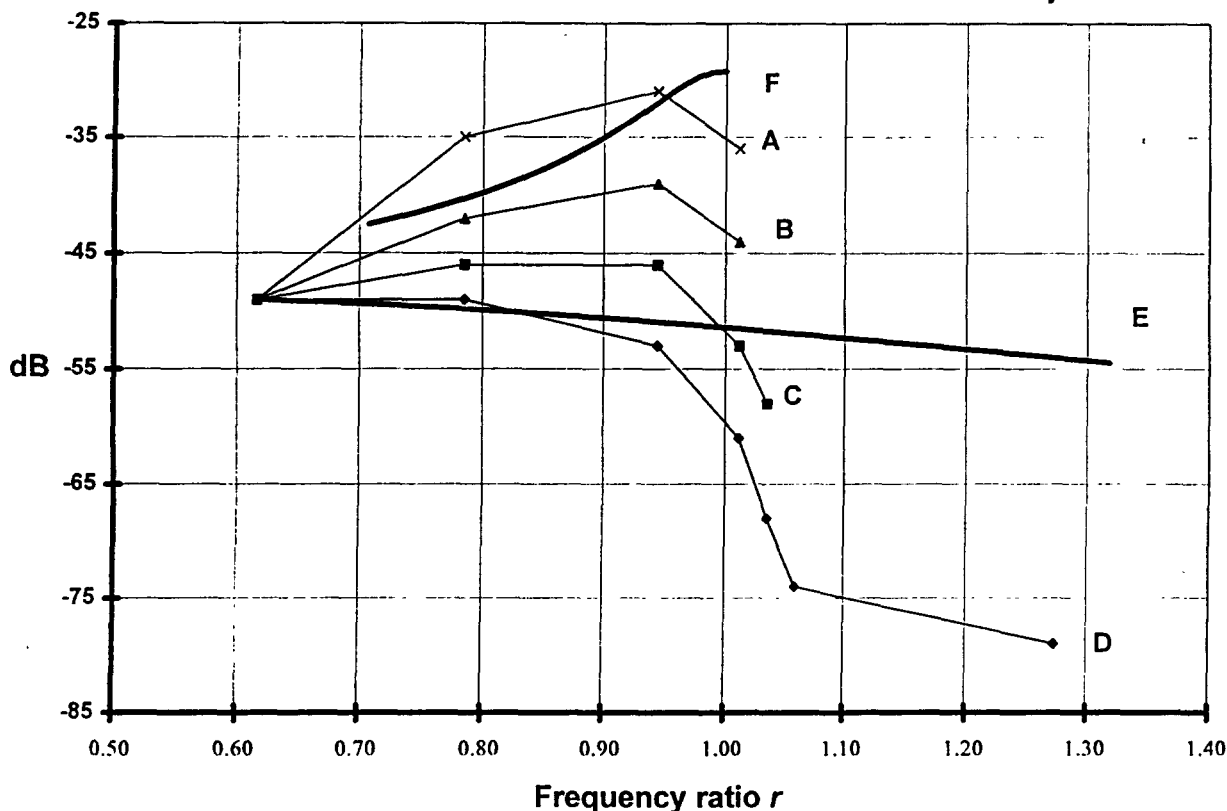


Figure 1. Analysis of Rhode's data

In the format of Figure 1 curves A to D correspond respectively to displacement response measured by Rhode at sound pressure levels of 70, 80, 90 and 100 dB re 20 μ Pa. In the figure Rhode's data should be described by Equation (6) with the reservation that the applied force at the tympanic membrane undergoes two transduction processes during transmission which are not taken into account in the formulation of the equation. The first transduction process is that of the middle ear which, however, may be assumed to have imposed negligible variation in resulting force in the restricted frequency range of one octave shown in the figure. The second transduction process occurs in transmission along the basilar membrane as described earlier and has been given the name Lighthill's cut-off condition.

All sound energy at frequencies greater than about 7500 Hz, or as shown in Figure 1 at reciprocal frequency ratios greater than 1, will be subject to Lighthill's cut-off condition

while all sound energy less than about 7500 Hz will be transmitted unaffected by the cut-off condition. Consequently, Equation (6) should describe the data of Figure 1 for frequency ratios less than $1/x = 1$ subject to use of the appropriate damping factor. The latter equation should also describe the data at values of the frequency ratio, $1/x = 1.28$ and greater where the response is again linear in the passive state.

It may readily be shown that the observed shift of about one half octave of the frequency of maximum displacement with loud sounds reported by Johnstone et al. (1986) leads to a value of the damping factor, ζ , in the passive state of 0.7. Using this value Equation (6) may be used to calculate the continuation of the predicted passive response (line E) passing through the point starting at $1/x = 0.62$. Comparison of the calculated response at $1/x = 1.28$ with the measured response shows that Lighthill's cut-off condition has resulted in a 23 dB reduction in transmitted sound energy. This corresponds to transmission of 0.5% of the incident energy at 9600 Hz. As Lighthill predicts that no energy will be transmitted this result may be due to some unknown artefact of Rhode's experiment. On the other hand, a reduction of 23 dB suggests that the energy transmitted is quite negligible in agreement with the well known observation that sound energy transmission along the basilar membrane appears to abruptly stop at a point of resonant response.

It has been proposed that in the active state the cochlea may be considered to respond as though the damping factor was constant but reduced from that which characterises passive response. While it is probably quite reasonable to assume that response at 100 dB re 20 μ Pa is passive and thus characterised by a damping factor of 0.7 as was done above it is not clear that a sound pressure level of 70 dB re 20 μ Pa may be characterised as strongly active. Nor is it clear what damping factors are to be assigned to curves A, B and C in Figure 1. Never-the-less it is instructive to compare the measured data with a prediction using Equation (6) and the damping factor estimated for the active state based on the peak bandwidth response shown in Figure 4 of the reference cited earlier (Johnstone et al. 1986). Substitution of the value 0.05 in Equation (6) has allowed calculation of curve F shown in the figure.

Comparison of curve F with the data clearly shows the same general trend indicating that the data is consistent with the model which has been proposed. For example, with decreasing sound pressure level a decreasing damping factor is expected with associated increasing response as shown in the figure. However, as mentioned earlier the plotted data suffer from the uncertainty of the characteristic frequency at the point of observation which is given by Rhode only as about 7500 Hz. If, for example, the characteristic frequency were taken as 7142 Hz then the plotted data point shown at $1/x = 0.94$ would shift right to $1/x = 1.0$ and the plotted data point at 0.79 would also shift right to 0.83 suggesting a little better agreement with the data. As it may reasonably be expected that the damping factor at a sound pressure level of 70 dB re 20 μ Pa is greater than that of the strongly active state, for example at threshold levels, 0.05 is too small so that the prediction should exceed the measured response as observed.

CONCLUSION

It has been shown that the cochlea may be modelled as a series of linear oscillators with variable damping which are only lightly coupled and thus respond independently. Strong hydrodynamic coupling exists between the oscillators of the cochlear partition which

accounts for travelling wave response but such coupling does not affect oscillator modal response. For example, oscillator resonant frequencies are unaffected.

It has been shown that the velocity response of the passive cochlea is linear at sound pressure levels, respectively, of 109 dB and 110 dB re 20 μ Pa. It has been shown that in a viscously damped linear system the frequency of maximum velocity response is independent of the damping. Thus in a system in which the damping varies with a time scale long compared to the period of the frequency under consideration, as in the model proposed here, the frequency of maximum velocity response of the active system must be the same as in the case of the passive system. It may be concluded that where the active system takes the form of undamping, as in the model proposed by Mammano and Nobili (1993), the frequency of maximum velocity response is constant. Alternatively, as the frequency of maximum displacement response is dependent upon the damping factor, as may readily be shown (Tse et al. 1978a), the frequency of maximum displacement response will be variable in a system in which the damping varies. The model provides quantitative explanation for the observations presented in Figure 4 of the paper of Johnstone, Patuzzi and Yates (1986) as well as explanation for the observations presented in Figure 6 of the paper of Rhode (1980).

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