CROSS-FIBRE INTERSPIKE INTERVAL PROBABILITY DISTRIBUTION IN ACOUSTIC STIMULATION—A COMPUTER MODELLING STUDY

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1   Introduction

Electrical stimulation strategies for cochlear implants may be improved by studying temporal frequency coding in single auditory fibres and across fibres in acoustic stimulation [1]. In single nerve fibres, phase locking between action potentials and the acoustic stimulus can only be maintained at frequencies below 600 Hz. At these frequencies, the time interval between successive action potentials, called Interspike Interval (ISI), is the same as the period of the stimulus, and it can therefore be used to code frequency within single fibres. At higher frequencies, the phase locking of individual nerve fibres diminishes but it may still be possible to retain phase locking properties by combining the action potentials in an ensemble of nerve fibres. In an ensemble of fibres innervating different regions in the cochlea, the ISI in each nerve is affected by factors such as the spectral shape of the stimulus, the characteristic frequency, and the maximum firing rate of the nerve. The ISI between the fibres, however, is further affected by the propagation or phase delay of the travelling wave. It is therefore uncertain how these factors would affect frequency coding across fibres. It is possible that the propagation delay between the fibres may lower the phase locking in an ensemble of nerves—because the probability that the majority of nerves in an ensemble will fire simultaneously may be low. It is also possible that the combined firing statistics of the fibres in an ensemble may result in a higher degree of synchrony such that the predominant intervals in an ensemble is preserved over a wider frequency range than in a single fibre. Are these accurate postulations of the physical system? In a future electrical stimulation strategy that incorporates temporal frequency coding, is it necessary to mimic the spatial-temporal delay in the firing patterns caused by the travelling wave? These are important questions that need to be studied and answered.

To try to shed some light on these questions, this paper investigates the statistical relationship of spike events between pairs of nerve fibres with different spatial separations and propagation delays by using a mathematical model of the cochlea, a hair cell/auditory neuron transduction model and an integral expression for the Cross-Fibre Interspike Interval Probability Distribution (CFISI). Given a time-varying acoustic stimulus, the cochlear model simulates the propagating waves in the cochlear fluid resulting in the vibrations on the basilar membrane and the shearing movements on the hair cells. The auditory neuron model then takes the hair cell shearing displacements and converts them into the fluctuating firing probabilities of the neurons. The CFISI probability distribution is then calculated from the firing probabilities using the integral expression. The effect of the propagation delay on the CFISI is studied and its implications for cross-fibre temporal frequency coding are discussed.

2   The Cochlear Model

The cochlear model is a linear, active, time-domain model which is based on a frequency-domain model published by Neely and Kim [2]. The cochlea is modelled as a fluid-filled rectangular box with rigid boundaries, and it is separated into upper and lower halves by a flexible cochlear partition. The endocochlear fluid is assumed to be inviscid and incompressible, and the propagation of waves in the fluid is restricted to one-dimension in order to simplify the solution. The cochlear partition is modelled as a 4th order spring-mass-and-damper vibration system shown in Fig 1. It is driven by the fluid pressure difference across the partition P_d and a frequency dependent active feedback pressure source P_a which is proportional to the hair bundle displacement given by the relative motion of the two masses. A simplified middle ear model is also included to provide the
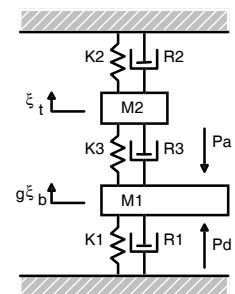

Fig. 1 Micromechanical model with 2-DOF [2].

air-to-fluid coupling from the eardrum to the stapes, so that the input stimulus may be specified as the sound pressure at the eardrum or the acceleration of the stapes. The output of the model is the basilar membrane displacement or the hair cell shearing displacement. The frequency domain response of the model at 5 different frequencies from 500 Hz to 10 kHz is shown in Fig 2.

According to [3], the boundary condition at the stapes is solved in the time-domain using spatial integration to conserve the volume of fluid in the cochlea. However, computer simulation shows that this causes stability problems when the waves are reflected from the apex due to the inaccurate model of the helicotrema. To overcome this problem, the present model uses temporal integration to solve the boundary condition at the stapes, and the helicotrema can either be modelled as zero pressure difference across the apical wall or as a vibrating apical wall with a pure damping impedance.
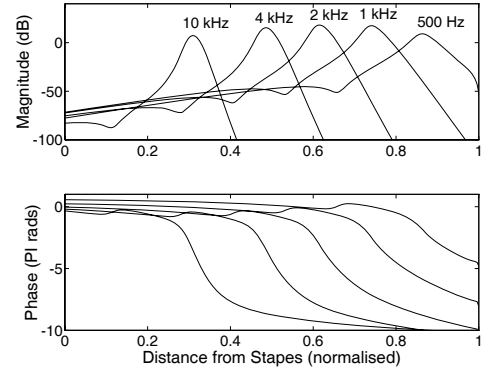

Fig. 2 Hair bundle displacement vs normalised distance from stapes with eardrum pressure at 0 dB SPL.

3   The Hair Cell/Auditory Neuron Model

The vibration pattern on the basilar membrane is converted to the fluctuating probability of an action potential using an auditory synapse model based on a model published by Meddis et.al. [4]. The input to the model is the instantaneous shearing displacement on the hair cell at any one position on the basilar membrane, and the output is the fluctuating firing probability of the auditory nerve. However, this firing probability does not take into account the refractory period after the nerve has been fired. It simply represents the instantaneous probability of an action potential irrespective of the last action potential. To simulate the effect of an absolute refractory period, the Meddis model generates nerves spikes by comparing the instantaneous firing probability with a random number, and suppresses all action potentials when the nerve is in the refractory period. With such a model, a post-stimulus time histogram can be obtained by feeding the same stimulus through the model repeatedly until a reasonable number of spikes are obtained, which may require a lot of computational time when the probabilities are small. Even more iterations may be required if one wants to estimate the firing probabilities after they have been modified by the refractory period. To overcome this problem, the present model has been altered to calculate directly the modified firing probabilities according to Eqn. 22 in [5]. For a step refractory function with no relative refractory period, the equation can be simplified to

$$p_k = s(k\,\delta t)\delta t - s(k\,\delta t)\delta t \sum_{i=1}^{n} p_{k-i} \qquad (1)$$

where p_k is the modified firing probability of the kth time-bin including refractory effect, s_k is the unmodified rate, δt is the size of each bin, and n is the number of bins in the absolute refractory period. A 1 ms absolute refractory period is used in the present model.

4   Cross-Fibre Interspike Interval Probability Distribution

Neural firing response can be modelled as a self-exciting point process which for many applications is well approximated by an inhomogeneous Poisson process [6]. The most obvious technique for evaluating the statistical relationship between action potentials is to use cross-correlation. However, cross-correlation measures the probability of the interval between any two nerve spikes and not just the interval between successive spikes. The following describes an improvement on the cross-correlation method that measures the probability of only successive nerve spikes. First, define the Poisson rate of nerve i as λ_i. Then the probability that nerve i fires between time $t - d$ and $t - d + \delta t$ but not again in the next d seconds is:

$$\lambda_i(t-d)\,\delta t\, e^{-\int_{t-d}^{t}\lambda_i(s)\,ds} \tag{2}$$

Similarly, the probability that nerve j fires between time t and $t + \delta t$ but has not fired in the last d seconds is:

$$\lambda_j(t)\,\delta t\, e^{-\int_{t-d}^{t}\lambda_j(s)\,ds} \tag{3}$$

Using (4) and (5), we can derive an integral expression which provides the normalised probability of intervals of d seconds between action potentials of nerve i and nerve j:

$$\text{Normalised Pr}(d) \;=\; \frac{\int_d^T \lambda_i(t-d)e^{-\int_{t-d}^{t}\left(\lambda_i(s)+\lambda_j(s)\right)ds}\lambda_j(t)dt}{T-d}, \;\text{ where } T \to \infty \tag{4}$$

The auditory models provide the probability of neural firings in small time-bins. When the bins are sufficiently small such that the firing probability of each bin is small, the probability divided by the bin size approximates the Poisson rates of the action potentials. Eqn. 6 can therefore be used to calculate the Cross-Fibre Interspike Interval (CFISI) Probability Distribution.

5   Results

The CFISI distribution for several pairs of nerve fibres with various spatial separations and corresponding phase delays are calculated from the model for 5 frequencies from 500 Hz to 10 kHz. The Cross-Fibre Synchronisation Indices are then calculated and compared. The results are summarised in Fig. 3(a)–(d).
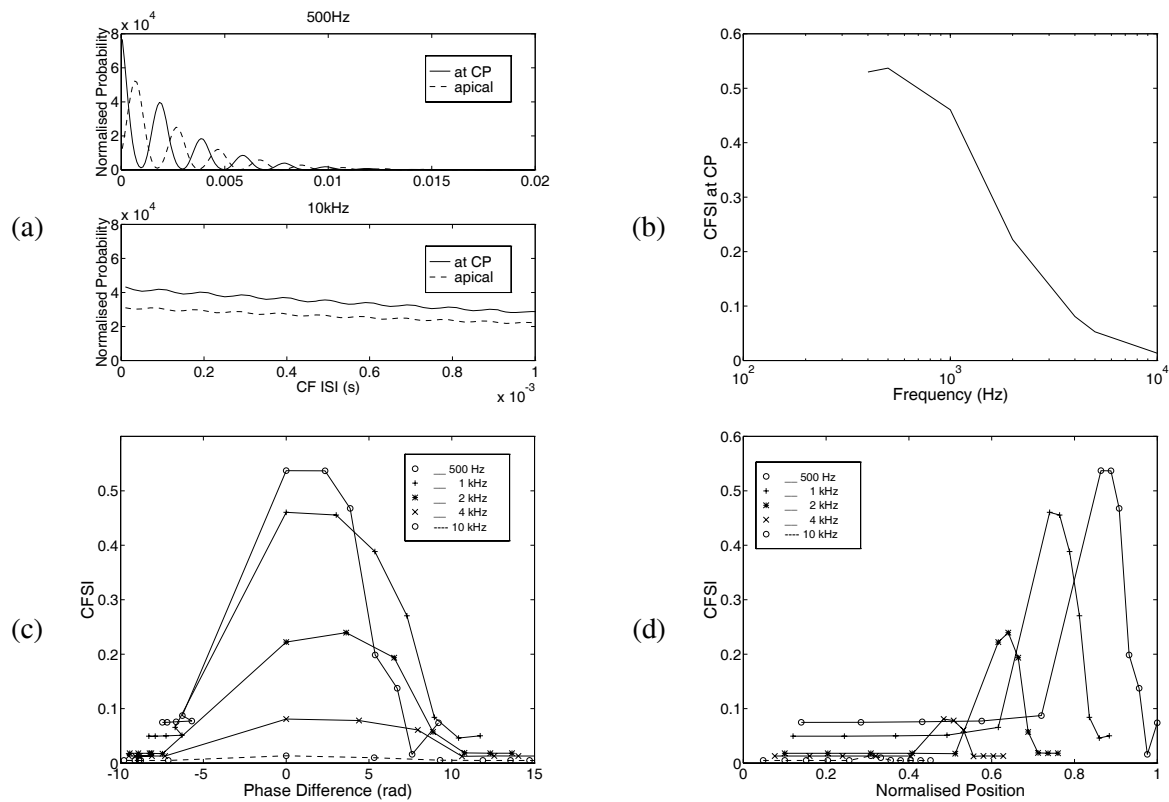
Fig. 3   (a) Cross-fibre interspike interval probability distribution for 500 Hz and 10 kHz.   (b) Cross-fibre synchronisation index (CFSI) vs characteristic frequency.   (c) CFSI vs phase difference between the fibres.   (d) CFSI vs normalised distance from stapes.

Fig. 3(a) shows the CFISI distribution at 500 Hz and 10 kHz for 2 scenarios: (i) both fibres at the characteristic place (solid curve), and (ii) one fibre at the characteristic place and the other at a more apical position (dashed curve). For the solid curve, the first and highest peak is at zero firing delay, meaning there is a high probability for both nerves to fire simultaneously. The fast decay of the curve indicates that the CFISI is likely to be a small multiple of the period. Also, the high peak to trough ratio is indicative of good phase locking to the positive phase of the sine wave. For the dashed curve, the fibres are separated and the probabilities are smaller. The position of the first peak is now shifted to the right to a position determined by the propagation delay of the travelling wave, but the difference between the peaks remains the same as the period of the stimulus. At 10 kHz, the distribution is flatter for both scenarios such that the probabilities for more cycles between nerve spikes are now comparable with fewer cycles. In other words, the rate of decay of the probability with respect to the number of cycles between nerve spikes at 10 kHz is significantly lower than at 500 Hz. The phase locking between the fibres is also poor as indicated by the low peak to trough ratio.

In order to obtain a measure for the synchronisation between the fibres, the Cross-Fibre Synchronisation Index (CFSI) is defined as the quotient of the fundamental component of the Fourier transform of the distribution with the DC component. Fig. 3(b) shows a plot of the CFSI against the input frequency with both fibres at the characteristic place. At low frequencies, the CFSI is high. But for frequencies above 1 kHz, the CFSI drops rapidly reaching almost zero at 10 kHz. This suggests that temporal frequency coding across fibres may be limited to frequencies below 1–2 kHz.

The effect of the propagation delay of the travelling wave on the cross-fibre synchronisation is also investigated. A plot of the CFSI against the phase difference between the fibres for 5 frequencies from 500 Hz to 10 kHz is shown in Fig. 3(c). In this figure, one fibre is fixed at the characteristic place and the other is moved from basal positions

to apical positions. The results show that for all 5 frequencies, the CFSI is good only for phase differences smaller than 6–8 radians on the basal side and 8–10 radians on the apical side, suggesting that only fibres with phase difference within this range can participate in cross-fibre temporal frequency coding.

To investigate the cross-fibre synchronisation in the spatial domain, the CFSI is replotted against the normalised distance from stapes, and this is shown in Fig. 3(d). It shows that the spread of fibres that are in synchrony is narrower in the basal region but wider in the apical region. This can be explained by the different slopes in the phase response of the basilar membrane in the basal and apical regions of the cochlea.

6   Conclusion

This computer modelling study shows that temporal frequency coding can take place across fibres, but it can be affected by factors such as the frequency of the stimulus and the phase delay due to the travelling wave. The results for the CFSI show that temporal frequency may occur across fibres only for frequencies below 1–2 kHz and for phase differences smaller than 6–8 radians. Finally, the spread of fibres that may be involved in temporal frequency coding is smaller in the basal region than in the apical region.

7   References

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