Analysis of dynamical motion of sensory cells in the Organ of Corti using the spectrogram

M. C. Teich1, C. Heneghan1, S. M. Khanna2, Å. Flock3, L. Brundin3, and M. Ulfendahl3

1 Departments of Electrical Engineering and Applied Physics, Columbia University
    500 West 120th Street, New York, NY 10027, U.S.A.
2 Fowler Memorial Laboratory, Department of Otolaryngology, College of Physicians & Surgeons, Columbia University
    630 West 168th Street, New York, NY 10032, U.S.A.
3 Department of Physiology II, Karolinska Institutet
    S-10401 Stockholm, Sweden

3 Analysis Technique

A slowly varying AM tone was chosen since this stimulus allowed us to track the response of the cell at a single frequency (the carrier frequency) over a wide range of intensities. The spectrogram [the squared magnitude of the Short Time Fourier Transform (STFT)] allows us to trace the changes in the spectral response as a function of time.

The STFT is the Fourier transform of a windowed time waveform (Oppenheim and Schafer, 1989). In the continuous domain, the STFT is written as

\[ STFT^g(t, f) = \int_{-\infty}^{\infty} [x(u)g^*(u-t)] \exp(-j2\pi fu) \, du, \tag{1} \]

where \( x(t) \) represents the time waveform being analyzed, \( g(t) \) represents a window function in time, \( t \) is the time variable, and \( f \) is the frequency variable. The Gaussian window \( g(t) = \exp(-t^2) \) is a good choice for \( g(t) \) since it maximizes the available time and frequency resolution for this transform. A discrete version of this transform can be implemented using a summation approximation to Eq. 1:

\[ STFT[n, k] = \sum_{m=0}^{N-1} x[n+m]w[m] \exp\left(-j\frac{2\pi mk}{N}\right), \quad 0 \leq k \leq N - 1, \tag{2} \]

where \( L \) is the width of the time-window in number of samples, \( n \) is the discrete time index, \( k \) is the discrete frequency index, and \( w[m] \) represents the Gaussian window sampled in the range \([-2,2]\). The value of \( N \) (which sets the number of discrete frequencies at which the STFT is sampled in the frequency domain) was chosen equal to \( L \). The spectrogram was not evaluated for all values of \( n \); sampling at values of \( n \) that were multiples of 8 usually gave a sufficiently detailed picture of the spectrogram for our purposes.

Strictly speaking, the spectrogram is defined as the squared magnitude of the STFT defined in Eq. 1, but we plot the magnitude of the STFT, since that allows both low- and high-magnitude spectral components to be represented in a more compact range. The spectrogram is presented in a 3D format. Time and frequency form the bottom plane, and the magnitude of the STFT is represented on a linear axis in the third dimension. The magnitude of the STFT is normalized so that its value can be interpreted in terms of the units of the input waveform (i.e., in spectrograms of velocity waveforms, the magnitude of the STFT can be interpreted as velocity).
Dynamical motion of sensory cells

4 Results

4.1 Response of an outer hair cell to an AM stimulus with a carrier frequency below its characteristic frequency

We report the response of an outer hair cell in the third turn of the guinea-pig cochlea. This cell has a characteristic frequency (CF) of approximately 700 Hz in its velocity response to sinusoidal stimuli of constant intensity. Figure 1 shows the response when an AM tone with a carrier frequency \( f_c = 439 \) Hz (below CF) is applied to the cochlear preparation.

In Fig. 1(a), the observed velocity response to the AM stimulus is shown. The response does not precisely follow the input; rather it exhibits distortion in the form of an asymmetry between negative and positive velocities.

The spectrogram of the velocity response [Fig. 1(b)] shows the time behavior of the spectral content in the velocity time waveform. As the acoustic intensity of the stimulus increases towards the center of the envelope, multiple harmonic components are generated. The component at \( 2f_c \) is first to appear (at \( 0.09 \) s), followed in time by \( 3f_c, 4f_c \), and \( 5f_c \). More harmonic components may be present, but the sampling rate of the data collection does not permit them to be viewed.

Figure 1(c) provides a different view on the spectrogram. It explicitly shows the time variation of the four most significant spectral components, at \( f_c, 2f_c, 3f_c, \) and \( 4f_c \). The plot is symmetrical in time about the center of the modulation envelope. The component at \( 2f_c \) is seen to appear before the component at \( 3f_c \), but their magnitudes are approximately equal for the time range 0.17–0.25 s near the center of the envelope.

4.2 Response of an outer hair cell to an AM stimulus with a carrier frequency at its characteristic frequency

Figure 2(a) shows the velocity response of the same cell to an AM stimulus with \( f_c = 706 \) Hz (at CF). Comparison with Fig. 1(a) shows that the peak velocity is higher by about a factor of 10 for the same sound pressure level.

The spectrogram of the velocity response [Fig. 2(b)] demonstrates the presence of three principal spectral components: \( f_c, 2f_c, \) and \( 3f_c \). Near the center of the envelope, the component at \( 3f_c \) is clearly dominant with respect to that at \( 2f_c \).

Figure 2(c) shows that the responses at the carrier frequency and at the harmonics do not follow the envelope of the modulating signal. There is a slight asymmetry in time about the center of the modulating envelope (at \( 0.205 \)) s, with the third harmonic not reaching a peak until \( 0.28 \) s. The response is therefore not simply a function of the instantaneous input stimulus but it also depends on past history. Note also that the component at \( 3f_c \) starts later, in time than the component at \( 2f_c \), yet it is far more significant in the response at the higher sound pressure levels, indicating that the spectrum of the response is level dependent. Since these cells also undergo displacement shifts in response to AM stimuli (Brundin et al., 1991; Brundin et al., 1992), the asymmetry in time may reflect an underlying change in the dynamical response due to the positional change of the cell.

4.3 Response of an outer hair cell to an AM stimulus with a carrier frequency above its characteristic frequency

Figure 3(a) shows the velocity response of the same cell to an AM stimulus with \( f_c = 1013 \) Hz (above CF). The magnitude of the velocity waveform is lower than...
its value at CF. The envelope of the response follows the stimulus envelope with no distortion (again the "scalloping" on this raw data carries no information).

The spectrogram of the velocity response [Fig. 3(b)] indicates a component at the carrier frequency and at its first harmonic. It is not possible to investigate the presence of a response at 3f_c since components at that frequency was removed by anti-aliasing filters in the experiment prior to sampling. The two spectral components are symmetrical in time with respect to the center of the modulation envelope [Fig. 3(c)].

5 Discussion

The use of a slowly varying AM stimulus with a range of carrier frequencies, allows us to clearly examine the level-dependent and frequency-dependent nonlinear dynamics in the responses of outer hair cells and Hensen’s cells. The results presented here are typical of the 34 data sets we investigated, taken from 8 outer hair cells and 8 Hensen’s cells from 7 different animals. Analysis of the velocity response waveforms using the spectrogram has shown the following:

(i) The nonlinearity of the dynamics increases with sound pressure level. This is evident in the spectrograms, where the generation of harmonics (a nonlinear effect) sets in at higher sound pressure levels (away from the edges of the envelope).

(ii) The patterns of harmonic generation for AM stimuli of a given peak sound pressure
level depend upon the carrier frequency of the stimulus relative to the CF of the cell. As an example, the spectral component at 3f_c is greater than that at 2f_c for carrier frequencies near CF, but these components are approximately equal in magnitude below CF. At higher sound pressure levels than those illustrated here, half-harmonic as well as harmonic components also appear.

(iii) The cellular response is not simply a function of instantaneous input, but it depends on prior events also. By tracing the time-varying spectrum of the response, we observe that precisely the same stimulus level produces differing spectral responses depending upon prior input.

In short, we have found that the spectrogram is a valuable tool for qualitatively and quantitatively analyzing the time-varying nonlinear responses of cellular structures in the organ of Corti. This analysis tool provides important information for modeling the response of these cellular structures, since it summarizes the frequency-dependent and level-dependent behavior of various elements in these structures in a single picture.

6 Acknowledgments

This research was supported by the Office of Naval Research under Grant N00014-92-J-1251, by the National Institutes of Health through NIDCD Program Project Grant DC00316, by the Emil Capita Foundation, by the Swedish Medical Research Council (02461), by the Magnus Bergvall Foundation, and by the Tysta Skolan Foundation.

References