Multicomponent stimulus interactions observed in basilar-membrane vibration in the basal region of the chinchilla cochlea

William S. Rhode\(^{a}\) and Alberto Recio

Department of Physiology, University of Wisconsin, Madison, Wisconsin 53706

(Received 8 May 2001; revised 23 August 2001; accepted 7 September 2001)

Multicomponent stimuli consisting of two to seven tones were used to study suppression of basilar-membrane vibration at the 3–4-mm region of the chinchilla cochlea with a characteristic frequency between 6.5 and 8.5 kHz. Three-component stimuli were amplitude-modulated sinusoids (AM) with modulation depth varied between 0.25 and 2 and modulation frequency varied between 100 and 2000 Hz. For five-component stimuli of equal amplitude, frequency separation between adjacent components was the same as that used for AM stimuli. An additional manipulation was to position either the first, third, or fifth component at the characteristic frequency (CF). This allowed the study of the basilar-membrane response to off-CF stimuli. CF suppression was as high as 35 dB for two-tone combinations, while for equal-amplitude stimulus components CF suppression never exceeded 20 dB. This latter case occurred for both two-tone stimuli where the suppressor was below CF and for multitone stimuli with the third component = CF. Suppression was least for the AM stimuli, including when the three AM components were equal. Maximum suppression was both level- and frequency dependent, and occurred for component frequency separations of 500 to 600 Hz. Suppression decreased for multicomponent stimuli with component frequency spacing greater than 600 Hz. Mutual suppression occurred whenever stimulus components were within the compressive region of the basilar membrane. © 2001 Acoustical Society of America.

[DOI: 10.1121/1.1416198]

PACS numbers: 43.64.Kc

I. INTRODUCTION

The operation of the cochlea has principally been studied using simple stimuli such as tones and/or clicks. This has provided an enormous amount of information about this complicated nonlinear system. However, because the cochlea is nonlinear, one cannot predict the response to a novel stimulus in a straightforward manner (e.g., Rhode, 1971; Sellick et al., 1982; Robles et al., 1986). If one wishes to understand processing of complex sounds more representative of the acoustic ecology, it is necessary to present stimuli whose spectra are more realistic than those of clicks and single tones. In particular, two-tone and multitone suppression effects are studied here.

Although the response of the auditory nerve (AN) to various stimuli largely reflects basilar-membrane response to the same stimuli, it would be beneficial to employ the same stimulus set for basilar-membrane studies that has been used to study AN behavior, as a way to understand the nature of AN responses. Some commonly used stimuli for the study of AN function are amplitude-modulated (AM) signals and harmonic complexes (Javel, 1980; Joris and Yin, 1992). The responses of auditory-nerve fibers (ANFs) to AM signals indicate an enhancement of modulation depths over a range of frequencies and intensities.

Horst et al. (1986, 1990) studied the representation of multicomponent (N = 4 to 64) octave band stimuli centered at the characteristic frequency (CF) of AN fibers in the cat. They observed that edges of the stimulus spectrum were dominant in the response with increasing N, and response to the center component was reduced under these conditions. Similar behavior is observed at the level of basilar-membrane mechanics for N as low as 3, and it appears that frequency spacing of stimulus components is the most important factor (Rhode and Recio, 2001).

Two-tone suppression has been studied at the level of the auditory nerve (e.g., Sachs, 1969; Javel, 1981; Javel et al., 1978; Javel et al., 1983; Delgutte, 1990), in cochlear mechanics (e.g., Rhode, 1977; Ruggero et al., 1992; Cooper and Rhode, 1996b; Nuttall and Dolan, 1993), and via hair-cell recording (Sellick and Russell, 1979; Cheatham and Dallos, 1990; Nuttall and Dolan, 1993). Results indicate that much of the behavior seen in the auditory nerve arises as a result of cochlear mechanics. However, there have been limited cochlear mechanical studies using more complex stimuli (cf. Recio and Rhode, 2000). To help reduce that limitation, single-, two-, three (AM)-, five-, and seven-tone stimuli were used in the present study to further explore nonlinear effects at the level of basilar-membrane vibration.

II. METHODS

Methods are essentially those detailed in Cooper and Rhode (1992). Seven chinchilla cochleas were studied at approximately the 3–4-mm location [characteristic frequency (CF) = 6.5–8.5 kHz]. All procedures were approved by the Animal Care and Use Committee of the University of Wisconsin.
Each animal was anesthetized with sodium pentobarbital using a dose rate of 75 mg/kg. Additional smaller doses were administered to maintain the animal in a deeply areflexive state. All anesthetics were administered intraperitoneally. A tracheotomy was performed to ensure an open airway. After the ear was surgically removed, four screws were implanted in the skull and fixed with dental cement, forming a rigid base. A bolt was then cemented at the base to provide a stable fixation of the skull to a head holder that has six degrees of freedom for positioning the cochlea under the microscope.

The bulla was opened widely and a silver ball electrode was positioned so as to touch the round window for the purpose of recording the compound action potential (CAP) of the auditory nerve in response to short-duration tones (16 ms) for each animal. Because we recorded only in the high-frequency region of the cochlea, the stimulus was stepped in 2-kHz increments from 2 to 20 kHz. At each frequency, a visual detection threshold for $N_1$ was determined by viewing an average of 20 repetitions as the stimulus level was varied in 1-dB steps. If thresholds were above our best threshold curve by more than 20 dB, no data were collected. High CAP thresholds equated to little or no compression in the hook region by more than 20 dB, no data were collected. High CAT levels in 1-dB steps. If thresholds were above our best threshold an average of 20 repetitions as the stimulus level was varied.

The overlying cochlear bone was shaved down using a microchisel until the overlying bone could be removed with the microelectrode pick. Gold-coated polystyrene beads 25 $\mu$m in diameter served as retroreflectors. They were placed in the perilymph and allowed to sink to the basilar membrane. They have a specific gravity of 1.05 that should minimize any loading of the basilar membrane. A glass cover slip was placed over the opening with no hydraulic seal. Perilymph wicked up to the glass, and beads could then be imaged without detrimental effects on the measurements that occur through an unstable interface between the perilymph and air.

An opening in the bony ear canal, immediately over the tympanic membrane, was made so that the probe tube of a $\frac{1}{2}$-in. Bruel & Kjaer condenser microphone could be visualized as it was positioned parallel to the tympanic membrane within 1 millimeter of the tip of the malleus, the probe was fixed in place with dental cement, forming a closed-field acoustic system. The opening was sealed with a glass cover after a 45-$\mu$m bead was placed on the tympanic membrane at the tip of the malleus (or umbo). The bead was used as a retroreflector for the interferometer and allowed measurement of the transfer function of the malleus. The sound source was a RadioShack super tweeter dynamic phone for all stimuli except two-tone stimuli. In the latter case, reverse-biased $\frac{1}{2}$-in. condenser microphones that were compensated for frequency flatness were used.

A. AM stimuli

AM signals were synthesized and presented using a TDT system (Tucker-Davis Technologies®) system [Eq. (1)]

$$S(t) = (1 + m \cdot \sin(2 \pi f_{\text{mod}} t)) \sin(2 \pi f_{\text{car}} t).$$

The carrier frequency, $f_{\text{car}}$, was set equal to the characteristic frequency of the basilar membrane. The modulation frequency was varied in 100-Hz steps from 100 to 1000 Hz, and above 1 kHz was set to 1250, 1500, and 2000 Hz. The modulation coefficient ($m$) was set to 0.5, 1.0, or 2.0 where $m = 2$ results in three equal-amplitude sine tones. Stimulus level was varied from 0 to 90 dB SPL in 5-dB steps. Stimuli were 30 ms in duration, 8 times at a rate of 10/s. A cosine envelope with 1-ms rise/fall time was used for all stimuli.

Amplitude and phase were determined using a phase-locked loop technique that computes dc and the Fourier component (sine wave fit, abbreviated as sinfit).

B. Multicomponent stimuli

A subset of these stimuli consisted of five equal-amplitude sine waves with the first, third, or fifth component frequency set equal to the CF of the basilar-membrane location under study. The frequency separation of stimulus components was varied in steps of 100 Hz up to 1 kHz and set to 1250, 1500, and 2000 Hz above 1 kHz. $f_{\text{mod}} > 2000$ Hz was not explored because ANFs do not show any AM temporal coding for this condition. Stimulus level was varied from 0 to 90 dB SPL in 5-dB steps. The stimulus level for multi-component stimuli always refers to the level of the center (CF) component. Stimuli were 30 ms in duration, repeated 8 times at a rate of 10/s. Analysis consisted of determining the amplitude of nine response components around CF using the sinfit procedure described above. The amplitude at the difference frequency was also determined but was insignificant or buried in the noise except for high levels and large frequency separations.

Another stimulus consisted of seven equal-amplitude sine waves with the middle component always set equal to CF. These stimuli had the same difference frequencies as the five-component stimuli and were analyzed in the same manner except that 11 components were analyzed using the sinfit technique. The level of the center component is specified throughout the paper.

The component amplitudes of each stimulus used (three, five, and seven-component stimuli) were compensated by the acoustic calibration.

C. Two-tone stimuli

Two-tone suppression (2TS) data were collected in order to provide a comparison for suppression effects due to multiple components. These data were also important for determining whether suppression effects are compatible with the large body of literature on 2TS in cochlear mechanics. The two-tone paradigm consisted of a 30-ms probe stimulus at CF and a 30-ms suppressor tone delayed 10 ms relative to the probe onset. Generally, eight repetitions of the combination were presented at a rate of 10/s. The probe tone was held constant while input–output (I/O) functions were collected as the suppressor tone was varied in 5-dB SPL steps from a maximum to a minimum (usually 90 to 0 dB SPL). The suppressor frequency was then changed and the process re-
peated. The probe level was varied in 10-dB steps. I/O functions for 20–40 suppressor frequencies were presented at each probe level with closer frequency spacing near CF than away from it. A Hamming window (Rabiner and Gold, 1975) was applied to the response before analysis occurred.

D. Single-tone basilar-membrane and middle-ear vibration measurements

Basilar-membrane input–output (I/O) functions were determined using 30-ms tone bursts with 1-ms raised-cosine rise and fall times and presented every 100 ms. The stimulus level covered a 100-dB SPL range in 5-dB SPL steps. A minimum of eight basilar-membrane and four middle-ear responses were averaged for each stimulus condition. Analysis consisted of Fourier decomposition of the steady-state portion of the averaged response at the stimulus frequency. Measurements of the basilar-membrane I/O function at CF were made throughout the experiment to monitor preparation stability. Vibration of the ossicles was measured at the tip of the manubrium (umbo) or at the incudo–stapedial joint or both locations before and/or after basilar-membrane measurements.

E. Displacement measurements

Mechanical responses were measured using a custom-built displacement-sensitive heterodyne laser interferometer (Cooper and Rhode, 1992). The laser was coupled to the preparation using a long working distance lens (Nikon SLWD 5X, NA 0.1). The laser was focused to a spot ~5 μm in diameter on the reflective beads. The interferometer was not sufficiently sensitive to measure basilar-membrane vibration without the gold-coated beads. Instantaneous phase was measured using two single-cycle phase meters that worked in quadrature. Phase meter outputs were sampled at 250 kHz and the phase was unwrapped using custom software. Response amplitudes were corrected for the frequency response of the recording system. The noise floor was <5 pm/Hz.

III. RESULTS

A. Two-tone interactions

Two-tone studies were conducted along with three-, five-, and seven-tone studies. They provide data needed to determine whether or not suppression or distortion effects of multitone stimuli are predictable from two-tone results. Two-tone studies involved the collection of displacement-level (I/O) functions during simultaneous presentation of a probe and suppressor tone. The probe tone was always set to the best frequency of the basilar-membrane location under study. Prior to presentation of any complex stimulus, the preparation using a long working distance lens

FIG. 1. Single- and two-tone responses for a basal cochlear region with CF=8000 Hz. Symbol key: solid symbol=x kHz, e.g., 2=2 kHz; open symbol=x dB SPL, e.g., 2=2 times 10=20 dB SPL. (A) Single-tone amplitude I/O functions at the indicated frequencies with only a subset of the data shown for clarity. Symbol exception: ■=11 kHz. (B) Normalized isolevel curves (sensitivity=amplitude at 1 Pascal frequency transfer functions) derived from the I/O curves shown in panel (A). A two-tone suppression study is shown in panels (C) through (F). (C) Probe amplitude I/O curves that have been normalized to 0 dB for a 20-dB SPL suppressor to emphasize probe suppression as a function of suppressor level; probe level=40 dB SPL and only a third of the I/O curves are shown. (D) Isolevel normalized probe amplitude curves derived from the I/O curves in panel (C). This is the normalized probe amplitude versus frequency function representation of the data in panel (C) for the full data set. (E) Suppressor amplitude I/O curves taken at the same time as the data in panel (C). (F) Normalized isolevel suppressor amplitude curves derived by subtracting the single-tone data in panel (B) from the isolevel suppression amplitudes obtained from the I/O functions in panel (D) for the condition when the level of the probe is 40 dB SPL. The arrow indicates the frequency of the probe tone. Chinchilla Ct17.
function, or growth rate, equals 1 for a linear system. Growth rates < 1 dB/dB are characteristic of a nonlinear compressive system, and greater than 1 for an expansive nonlinearity. An expansive nonlinearity is seen at 10 kHz for levels > 90 dB SPL, just beyond the notch in the I/O function, which is accompanied by a rapid change in the response phase (~180°, not shown). Compression at CF (~8 kHz) begins around 20 dB SPL with a growth rate of 0.36 (dB/dB) between 40 and 70 dB SPL.

The complete set of I/O functions can be recast as a set of transfer functions normalized by stimulus level [Fig. 1(B)] where deviation from linearity is seen by a lack of superposition of the individual isolevel functions for frequencies above 6 kHz. At CF, a reduction in sensitivity of ~45 dB occurs as sound pressure is increased from 30 to 100 dB SPL. Response amplitude to a CF tone was 1.5 nm at 20 dB SPL and was among the best of this experiment series (0.25, 0.3, 0.4, 1.0, 1.4, 1.5, 1.6 nm at 20 dB SPL). A significant portion of differences in amplitude is likely due to the variability in the radial location of the basilar-membrane measurement, as there is limited control on where the reflective bead falls. The maximum displacement is a function of the radial location of the bead on the basilar membrane.

In a two-tone suppression (2TS) paradigm, the motion in response to the probe tone (40 dB SPL at CF= ~8 kHz) is reduced as the suppressor level is increased beyond a certain threshold [a subset of I/O functions is shown in Fig. 1(C)]. Suppressor frequencies near the probe frequency exhibit the lowest suppression thresholds, <40 dB SPL or slightly below the level of the probe. As suppressor frequency increases, suppression threshold increases and the amount of suppression decreases. As the suppressor frequency decreases below CF (= probe frequency) the rate of suppression, measured as the slope of the curves in Fig. 1(C), approaches 1 dB/db. The rate of suppression decreases as suppressor frequency increases above CF. These latter relations are seen best in Fig. 1(D), where probe suppression is shown as a reduction of probe amplitude versus suppressor frequency with suppressor level the parameter (probe level=40 dB SPL). When the suppressor level is near 40 dB SPL the first signs of suppression are seen in the vicinity of CF. As the suppressor level is increased, the range of frequencies that suppresses the probe widens, and the amount of suppression increases to ~30 dB for suppressor levels >80 dB SPL. Because probe amplitude is monotonically decreasing with increasing suppressor level, it is hypothesized that probe suppression would continue to increase with higher suppressor levels than were used here. Similar maximum amounts of suppression (25–35 dB) were obtained in the other six preparations.

An alternate method of expressing the interaction of two tones is to plot the amplitude I/O functions of the suppressor tones [Fig. 1(E)] corresponding to the probe I/O functions [Fig. 1(C)]. Compared to the single-tone I/O functions [Fig. 1(A)] these are more linear and the notch in the 10-kHz function is not present. Mutual suppression of the probe and the suppressor response components can be seen by subtracting the single-tone isolevel curves shown in Fig. 1(A) from the suppressor isolevel curves obtained from the data in Fig. 1(E) with the result shown in Fig. 1(F). The 40-dB SPL probe tone at CF is shown to have a suppressive effect on the second tone that extends from 6 to 11 kHz, nearly an octave, and can be seen to suppress the second tone by more than 18 dB at 9.5 kHz. As suppressor level is increased, suppression due to the probe tone is reduced in both amplitude and frequency extent. The probe tone at CF has its strongest suppressive effect for the cochlear region basal to its location with the location of the maximum effect increasing with suppressor level. At this point it should be obvious that the terms, probe/suppressor, are merely a convenience since both the probe and the suppressor produce suppression of the other component with the caveat that both must reside in the compressive region of the basilar membrane for mutual suppression to occur.

Two-tone neural suppression in the auditory nerve has been extensively studied (e.g., Sachs, 1969; Javel et al., 1983; Delgutte, 1990). One typical display method for auditory-nerve 2TS I/O functions is to examine the effect of a suppressor tone at several levels on the I/O function at CF for a nerve fiber. This AN paradigm was used in one study of the mechanical correlate of neural 2TS when the suppressor tone was held constant while the I/O function at CF (=6.5 kHz) was measured (Fig. 2). The typical rightward shift observed in the rate-level AN I/O functions with increasing suppressor level is also seen in the mechanical I/O functions for all suppressor frequencies. Larger shifts with each level increment occur for suppressor frequencies lower than CF [4 and 6 kHz in Figs. 2(A) and (B), respectively]. As the I/O response function shifts to the right with increasing suppressor level, the probe amplitude response stays linear to proportionally higher levels. In all other studies, the suppressor

FIG. 2. I/O curves that are similar to those collected from the auditory nerve in a two-tone suppression paradigm. Probe amplitude versus probe level with suppressor level varied (CF=6500 Hz). The suppressor frequency is indicated as a parameter in each panel. Probe level was varied in 5-dB SPL steps. Responses with amplitudes less than ~28 dB re 1 nm are removed from the display since they were below the system noise level. Cb057.
sor level was decremented in 5-dB steps from 90 to 0 dB SPL to produce the I/O functions while the probe level was held constant. Results for one of these studies shown in Fig. 1 are presented in the same format as in Fig. 2, although the probe levels are fewer (six versus 19) and also the range of levels is smaller than that in Fig. 2 (20 to 70 vs 0 to 90 dB SPL). The rightward shift of the probe amplitude function for a 10-dB suppressor level increase is as much as 18 dB at 3000 Hz or a rate of suppression of 1.8 dB/dB (Fig. 3, CF = 8 kHz). The magnitude of the shift to the right of the probe response curves increases with decreasing suppressor frequencies. The shift is relatively constant, usually ~1 dB/dB, once the suppressor frequency is in the linear region of the basilar-membrane response. Probe amplitude I/O functions are linear to higher levels as the suppressor level is raised. In general, this mechanical 2TS behavior closely parallels comparable neural 2TS data.

Three views of two-tone suppression are presented in Fig. 4 for three probe levels (30-, 50-, and 70 dB SPL in rows 1, 2, and 3, respectively). Suppression thresholds of an 8-kHz, 30-dB SPL probe by a near-CF suppressor are of equal or even lower (~20 dB SPL) levels than probe levels [Fig. 4(A)]. With increasing suppressor level, the frequency extent of suppression increases until all lower frequencies suppress the probe. On the high-frequency side of the probe, suppression occurred at least up to 15 kHz, the highest frequency suppressor that was employed. It appears that suppression continues with further increases in suppressor frequency, though there is a relatively small reduction of the probe. Near CF there is a “break” in the isolevel curves for levels > 60 dB SPL (indicated by the solid line below the abscissa) that is a result of leakage in the frequency analysis routines due to the width of the Fourier filters (see the discussion below).

As the probe level is increased to 50 and 70 dB SPL [Figs. 4(B) and (C), respectively], the suppressor level that just begins to suppress the probe remains roughly 10 dB less than the probe level. The “break” in the 30-dB SPL isolevel curves near CF doesn’t occur when the probe is at higher levels (>40 dB SPL). To avoid possible damage of the cochlea by stimulus levels >95 dB SPL, the suppressor level never reached 40–50 dB above the probe level, which is necessary to see the break. For probe levels between 20 and 30 dB SPL, the suppressor level can be as much as 60 dB greater than the probe level. Another effect of increasing probe level is that the suppressor frequency that produces maximum suppression moves to lower values.

Iso-suppression curves for 1, 10, and 20 dB of suppression are compared to the single-tone 1-nm iso-amplitude curve [Figs. 4(D), (E), and (F): dashed line = 1-nm iso-amplitude curve]. Iso-suppression curves lose their “tip” as probe level increases and become nearly constant up to a cutoff frequency. It is also apparent that the high-frequency side of the suppressive region extends beyond the 1-nm iso-amplitude region. The single-tone 1-nm iso-amplitude region can be viewed as the excitatory region for an AN fiber with the same CF, essentially a frequency threshold curve.

Slopes of the probe I/O functions [cf. Fig. 1(C)] versus suppressor frequency are shown with suppressor level as a parameter [Figs. 4(G), (H), and (I)]. These slopes define the rate of suppression and (for the convenience of using the same ordinate scale) are compared to the negative of the single-tone I/O growth rates where rates < 1 dB/dB define the nonlinear or compressive region [column 3, Figs. 4(G), (H), and (I), single-tone data at 70 dB SPL indicated by the dashed line]. Suppression rates approach ~1 dB/dB for sufficiently high suppressor levels in the frequency region where single-tone growth rates are 1 dB/dB, i.e., the linear region of basilar-membrane single-tone response. In the compressive region around CF, the suppression rate is 0.3 dB/dB and decreases to 0.2 dB/dB at 11.5 kHz. Suppression rate decreases as growth rate decreases and is not equal to zero even at 15 kHz, a frequency that is beyond the single-tone response region. It is noteworthy that suppression occurs for frequencies >11 kHz, even though the single-tone displacement is less than 0.1 nm for levels <70 dB SPL. Above 70 dB SPL the single-tone vibration is complicated by the fact that there is a notch in the 10-kHz I/O function, and the compression slope is negative, zero, or greater than 1 dB/dB depending on the stimulus level. The fact that there is suppression in what has traditionally been labeled the plateau region of the basilar-membrane transfer function (e.g., Rhode, 1971; Cooper and Rhode, 1996a) suggests that the vibration of the basilar membrane is influenced by tones nearly an octave above CF and possibly more.

Perhaps a more telling relationship is the relative suppressor-to-probe amplitude that results in a fixed reduction of the probe across both frequency and probe level (Fig. 5). This relation shows that the suppressor amplitude required to produce 1 dB of suppression is near that of the probe amplitude for frequencies up to CF and is nearly inde-
dependent of the probe amplitude for frequencies <CF/2. Beyond CF, the required suppressor amplitude decreases rapidly and can be as small as 1% of the probe amplitude. This latter number is intriguing and suggests that the probe is affected by what is happening in the region basal to 8 kHz. This is consistent with the fact that there is suppression even when the suppressor frequency is beyond the single-tone upper cutoff frequency for a particular place. In order to reduce the probe amplitude by 12 dB, the suppressor amplitude has to be increased over 20 dB. The suppressor-to-probe relation as a function of frequency is seen to be similar for all probe levels employed.

**B. Multitone suppression**

Suppression effects in BM responses to AM stimuli were studied by analyzing the amplitude of the CF component of the basilar-membrane response to an AM signal relative to the single-tone response. From results shown in Fig. 6, it is clear that there is a systematic increase in probe suppression with increasing modulation depth. There is only a modest amount of suppression (1–2 dB) at 50% modulation, for which the amplitudes of sideband components are 12 dB less than the carrier amplitude [Fig. 6(A)]. However, suppression increases for 100% modulation, in which case the sideband components amplitudes are 6 dB less than carrier amplitude [Fig. 6(B)]. While suppression is dependent on both the stimulus level and the modulation frequency, the

![Graphs and diagrams](image_url)
relation is not straightforward across stimulus level. This is clearest when the AM carrier and sidebands are equal in amplitude ~200% modulation! where a nonmonotonic relation between suppression and level exists for modulation frequencies $1\ kHz$ ~Fig. 6!. While suppression increases with level from 20 to 70 dB SPL, suppression decreases regardless of modulation frequency for stimulus levels above 70 dB SPL ~Fig. 7!. This inflection in I/O curves at CF may result from a linearization of the I/O functions with level $>75\ dB\ SPL$.

Suppression of the CF component during presentation of five-component stimuli behaves somewhat similarly to that for AM stimuli. In this instance, there is a strong dependency on which of the five components is positioned at CF ~Fig. 8!. With the first component placed at CF and the remaining four components higher in frequency than CF, suppression is relatively small, $<4\ dB$ for small frequency separation of the components at 60-dB SPL stimulus level. Maximum suppression occurs when the third (center) component $=CF$ ~Fig. 8(B)!. In this case, suppression can reach 10 dB for modulation frequencies as high as 800 Hz with the maximum occurring at 70 dB SPL. Suppression decreases for frequency separations $>800\ Hz$. Finally, when the fifth component $=CF$ and the remaining four components are lower in frequency than CF, suppression reaches 7.5 dB at a frequency separation of 400 Hz and decreases rapidly for larger frequency separations ~Fig. 8(C)!. Suppression is increased somewhat over the case when the first component is set to CF but less than when the third component frequency $=CF$. Suppression as a function of level when the stimulus is centered on CF is similar to that of the AM stimulus ~Fig. 9!. Suppression increases with stimulus levels up to 70 dB SPL and decreases for higher levels. Suppression is inversely proportional to frequency separation of the components. These results replicate those from previous studies of suppression in that energy on the low side of CF is more effective in suppressing CF tones than energy of higher frequency.

Mutual suppression effects are present whenever there is more than one stimulus component. Such effects are presented in Fig. 10 for the case when component frequency separation is 500 Hz for two, three, five, and seven-component equal-amplitude stimuli. The amplitude of each component is shown in relation to the single-tone amplitude (dot-dash line). At the 30-dB SPL level (G), stimuli are in the linear response region and track the single-tone curve.

**FIG. 6.** Suppression of the CF component versus modulation frequency when the stimulus is an amplitude-modulated signal with modulation depths of 50%, 100%, and 200% for panels (A), (B), and (C), respectively. Ct17.

**FIG. 7.** Probe suppression I/O curves when the modulation depth is 200% as a function of the level of the center (carrier) component. $F_{mod}$ is indicated by the symbols, e.g., $\circ =300\ Hz$; $\bullet =1500\ Hz$. Line thickness increases with increasing $F_{mod}$.

**FIG. 8.** Suppression of the CF component is shown when the stimulus consisted of five-equal-amplitude sinewaves. The first, third, or fifth component is set equal to the CF in (A), (B), and (C), respectively. Ct17.
For two tones at 30 dB SPL there is nearly no suppression of either component regardless of whether the suppressor frequency is above or below the probe tone (at CF=8000 Hz). When the level of the tones is increased to 60 dB SPL, there is a mutual suppression of ~2 dB. The low-frequency component is least reduced, as expected, based on having the more linear I/O function for the individual components. That is, the rate of growth or slope of the I/O function decreases as the frequency increases in the compressive region. When three equal-amplitude stimuli are presented [200% modulation, Fig. 10(B)], a similar result occurs with the amount of mutual suppression increasing relative to the two-tone case. The results for the five- and seven-component cases [Figs. 10(C) and (D)] establish a trend of increasing mutual suppression with an increase in the number of components.

While there will always be some AN fibers for which CFs are located at the center of a complex stimulus, the majority will have CFs displaced relative to the frequency center of the stimulus. This latter condition was explored by positioning the first, third, or fifth component of the five-component signal at CF in order to examine the differential response to these conditions (Fig. 11). Even at 30 dB SPL there is some suppression of individual components when either the third (dashed line) or first (thin solid line) component is at CF where suppression is measured by the deviation from the single-tone response (dot-dash lines). Lower-frequency (<CF) components are least suppressed in each case. When stimulus level is increased to 60 dB SPL, there is as much as 30-dB suppression of the higher-frequency components (first=CF, thin solid line) with the CF component suppressed the least. With the third-component frequency equal to CF (dashed line) there is still 5–6-dB suppression of individual components with the lowest-frequency component nearly equal to the single-tone result. Finally, when the fifth-component frequency equals CF (thick solid line), mutual suppression is the smallest of the three conditions, and the lowest-frequency component is even slightly higher in amplitude than the tone-alone condition.

C. Unequal-amplitude components

Most natural stimuli are not composed of equal-amplitude components. Mutual suppression effects when stimulus components were not equal were studied for AM stimuli with modulation <200%. Such stimuli are analogous to a three-formant stimulus in speech signals. When $f_{\text{mod}}$ is
<200 Hz [e.g., Figs. 12(A), (E), (I)] the response to each sideband is about equal. There is an increase in suppression of both sidebands with increasing AM level up to 70 dB SPL and a decrease with further level increases. Maximum suppression of sidebands by the carrier is ~8 dB [Fig. 12(A)]. Suppression is reduced as modulation depth increases [Figs. 12(E), (I)].

As \( f_{\text{mod}} \) increases beyond 200 Hz there is a divergence of the fate of the upper and lower sideband responses. Less suppression of the lower sidebands occurred while at the same time the upper sideband response was attenuated by cochlear filtering [Fig. 12(B)]. Again, there is less sideband suppression at higher modulation depths [Figs. 12(F), (J)]. At a modulation depth of 200% [Fig. 12(J)] the lower sideband amplitude is greater than the carrier amplitude due to its suppression of the carrier. With higher \( f_{\text{mod}} \) the amplitude of the lower sideband grows faster than the other AM components, while the upper sideband amplitude is often 20–30 dB less than the lower sideband. These responses essentially consist of two components: the lower sideband and the carrier response.

Mutual suppression of stimulus response components is dependent on the relative amplitudes, frequency content, and position of the acoustic spectra relative to the characteristic frequency of each cochlear location. A near-CF component has the largest effect when it is larger than the surrounding components. When the AM modulation frequency is 100 Hz and carrier frequency set at CF, response amplitudes are all in the linear range of basilar-membrane I/O curves for low stimulus levels. Therefore, no suppression is observed (Fig. 13, 20 dB SPL). When the stimulus level is at 70 dB SPL, the sidebands are reduced relative to their expected amplitudes given the input spectra. The largest reduction occurs for a modulation depth of 25%, where there is a substantial deviation from the expected amplitudes. The magnitude of the deviation is reduced as modulation depth is increased from 50% to 100% [Figs. 13(B) and (C)]. Nevertheless, in each instance the carrier had a suppressive effect on the sideband components. In effect, the response spectra were “sharpened” up. For stimulus levels greater than 80 dB SPL the I/O curves begin to approach linearity and the response spectrum is no longer sharpened. When the input spectrum consists of equal-amplitude components \((m = 2)\), the carrier no longer suppresses the sideband response components; in fact, for small modulation frequencies the carrier is suppressed by the sidebands [Fig. 13(D)]. This spectral edge enhancement effect similar to Mach bands in vision was
shown previously for stimuli with 5 and 7 components (Rhode and Recio, 2001).

D. Phase functions

AN discharge phase has been shown to exhibit a lag/lead relative phase relation for stimulus frequencies below/above CF with increasing stimulus level (Anderson et al., 1971). Basilar-membrane phase relations are largely compatible with the neural observations. In the chinchilla midfrequency range, phase relations appear to be somewhat more complex. At low stimulus levels the results are compatible; phase lags with increasing level for stimulus frequencies below CF, and phase leads above CF [Fig. 14(A)]. However, for stimulus frequencies above CF, increasing the level above 70 dB SPL results in increasing phase lags, as there are phase lags at all stimulus frequencies at the highest stimulus levels. Phase data can also be seen for all stimulus frequencies in Fig. 14(B). For stimulus levels below 70 dB SPL, there is little phase change at CF (8000 Hz), but increasing phase lags occurred at higher levels. As much as a 130° phase lag occurred below CF and ~90° phase lead above CF.

In the presence of a second tone, phase behavior is somewhat similar but is a function of the relative levels and frequencies. A common stimulus paradigm in a 2TS experiment is to place the probe tone at CF and to vary the suppressor level and frequency while holding the probe frequency and level constant. The probe phase for a low-level probe exhibits a small lead with level for most suppressor frequencies [Fig. 15(A)]. At higher probe levels, there are mostly phase lags with increasing suppressor level regardless of suppressor frequency [Figs. 15(B), (C)]. The phase of the suppressor behaves similarly to the single-tone phase as a function of level and frequency [Figs. 15(D), (E), (F)]. One difference is that as the probe level increases (>45 dB SPL) only phase lags are seen, regardless of level or frequency. In general, there is not much difference between probe and suppressor phases.

FIG. 13. The response spectrum for AM signals with \( f_{\text{mod}} = 100 \text{ Hz} \), and modulation depths of 0.25, 0.5, 1.0, and in panels (A) through (D), respectively. The carrier is set to CF=8000 Hz. In each panel the response spectra are shown for nine harmonics of 100 Hz at two levels: 20 dB SPL in the linear portion of the I/O curve and 70 dB SPL in the compressive or nonlinear region of the response. ● symbols indicate the data points and ■ indicate the expected sideband amplitudes based on the input spectrum. The additional three values on each side of the AM response spectrum are a result of nonlinear distortion. The cochlear filter is essentially flat over this 200-Hz range of input frequencies and its equivalent linear system should not alter the input spectrum. Ct17.

FIG. 14. Phase portion of the basilar-membrane mechanical transfer function where CF=8000 Hz. (A) Phase I/O functions for selected frequencies: frequency=1000 times the symbol number; ● =7500 Hz and ■ =8500 Hz. The phase at 25 dB SPL was used to normalize each I/O curve. (B) Phase versus frequency functions at the levels indicated by the symbols: level=10 times symbol number. Phase at 20 dB SPL was subtracted from each curve to normalize them. Ct17.
Phase-versus-frequency transfer functions illustrate the phase lag/lead relation when the suppressor is the 8-kHz tone at several levels [Figs. 16(A), (B), (C)]. Increasing suppressor level reduces the phase variation with probe level [Fig. 16(C)]. There is little variation for probe levels < 70 dB SPL [Figs. 16(B) and (C)]. In the right column, the probe level is held constant at the level indicated in each panel and the suppressor level is varied. There is little phase change for low levels of the probe [Fig. 16(D)] while for high levels the lag/lead relation is present. In the latter case [Fig. 16(F)], increasing the suppressor level reduces the phase variation (cf. the 3 and 7 curves).

IV. DISCUSSION

A. Principal achievements of this study

(1) New two-tone suppression data are provided with greater detail than previously available.

(2) These data support the view that neural 2TS phenomena largely reflect cochlear mechanics as observed in the vibration of the basilar membrane.

(3) Information is provided about mutual suppression: suppression of a CF tone by a roaming suppressor and suppression of a probing tone by a fixed tone at CF.

(4) Spectral edge enhancement of multicomponent responses was observed in the vibration of the basilar membrane (cf. Horst et al., 1986). That is, suppression of the middle component(s) of a multicomponent stimulus by surrounding components for three, five, and seven equal-amplitude component stimuli is described.

(5) Suppression of individual components is described for an amplitude-modulated signal when the sideband components are 0, −6, −12, and −18 dB smaller than the carrier.

(6) Phase relations are described that are not entirely congruent with earlier observations.

This study was undertaken to determine the representation of a subset of multicomponent stimuli in the motion of the basilar membrane (cf. Rhode and Recio, 2001). How several stimulus components interact and mutually suppress each other has implications for understanding the processing of complex stimuli, such as speech and music, within the cochlea. Any cochlear nonlinearity, such as the I/O function for hair cells or the half-wave rectifier at the hair cell synapse, will result in suppression. However, the principal basis for suppression is the frequency-dependent compressive nonlinearity in the cochlea that results in differential growth rates of vibration in response to tones. The compressive region resulting from a tone at CF extends over an octave (Rhode and Recio, 2000; Russell and Nilsen, 1997). Response to tones above CF is increasingly compressed as frequency is increased until the stimulus exits the compressive region and enters what has been labeled the plateau region of the transfer function for the basilar membrane (Rhode, 1971; Cooper and Rhode, 1996a). This above-CF linear region has been associated with a second mode of vibration that corresponds to the fast wave (e.g., Olson, 1998; Rhode and Recio, 2001; Cooper and Rhode, 1996a).

B. Two-tone suppression: Slopes and magnitude

Ruggero et al. (1992) state that neural two-tone rate suppression appears to originate in mechanical phenomena at the level of the basilar membrane. However, there remains some difficulty in explaining two-tone rate suppression when the suppressor is lower in frequency than the CF of the AN fiber because the sum of the individual amplitudes of basilar-membrane vibration in response to the two tones is always at
least as large as that of the CF tone alone (Cooper, 1996; Geisler and Nuttall, 1997; also data reported here such as for frequencies below CF in Fig. 5). The complete mechanism of two-tone rate suppression in the AN under these conditions remains unexplained and likely requires an additional mechanism that provides another stage of filtering at the level of the hair cell or auditory nerve (Cai and Geisler, 1996; Temchin et al., 1997). A proposal has also been made for direct influence of cochlear potentials on excitation of afferent dendrites as a cause for suppression (Hill et al., 1989).

For high side suppressors (i.e., suppression of a probe stimulus by a tone whose frequency is higher than CF), displacement of the basilar membrane in the presence of a suppressor tone can be less than that to the probe tone alone (Ruggero et al., 1992; Cooper and Rhode, 1996b). Also, it was shown here that suppression can occur when suppressor amplitude is only 1% of that of the probe tone (Fig. 5). This result suggests that at least high-side suppression is a spatially distributed phenomenon, because the suppressor can have an effect even when the suppressor tone excitation does not or barely overlaps with the region for the probe tone. This result agrees with others who have noted that for suppressors above CF, a region of the cochlea is likely involved (Yates et al., 1989; Geisler et al., 1990; Geisler, 1992). This result also implies that cochlear models have to incorporate more than independent point representations of the cochlear partition. The spatial extent and variation of the nonlinearity as a function of suppressor frequency has not typically been adequately addressed in these models (cf. Baker, 2000).

Present results are largely compatible with previous results (Cooper, 1996; Nuttall and Dolan, 1993; Geisler and Nuttall, 1997; Ruggero et al., 1992). Suppression magnitudes of up to 35 dB were found over the range of suppressor/probe levels that were employed. There were several limitations imposed by the stimulating and measurement apparatus: (1) maximum stimulus levels were limited to <100 dB SPL either by the desire to avoid either temporary or permanent threshold shifts; (2) limitations in maximum stimulus levels that could be produced; and (3) the limited range of the interferometer. Finally, the use of relatively short (20-ms overlap of the 30-ms probe and suppressor tones) tones limited the accuracy of analysis because the width of the Fourier filter results in leakage between components. Leakage of a large component into another analysis component was seen whenever: (1) the amplitude of the suppressor was 25 to 30 dB greater than that of the probe; (2) the suppressor frequency was near to that of the probe; and (3) at low levels of the probe. It is likely that larger suppression magnitudes than those measured (~35 dB) occur in the cochlea, as there is no reason to believe that the monotonic decreasing probe I/O functions do not continue as the sup-

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FIG. 16. Probe phase versus frequency transfer functions for a suppressor tone at 8000 Hz and the levels indicated in each panel. \(L_p\) = probe level and \(L_s\) = suppressor level in dB SPL. (A) 30-dB SPL suppressor at 8000 Hz. Probe level = 10 times the symbol number. (B) 50-dB SPL suppressor. (C) 70-dB SPL suppressor. Right column. (D), (E), and (F). Probe phase at probe levels of 41, 61, and 81 dB SPL, respectively. 8-kHz suppressor at 10 times the number of the symbol in dB SPL and \(\bullet\) = 7500 Hz, \(\square\) = 8500 Hz. Ct17.
pressor level increases. For example, the probe amplitude
I/O functions in Fig. 3(B) exhibit a 40-dB rightward shift for
a 40-dB suppressor level shift. Such shifts are in line with
those recorded in AN fibers (Javel et al., 1983; Delgutte,
1990).

A number of auditory-nerve studies have shown sup-
pression slope to vary with suppressor frequency relative to
probe located at CF (Javel et al., 1983; Ruggero et al., 1992;
Delgutte, 1990). Above CF, the neural suppression slope var-
ies from −0.2 dB/dB and increases as the suppressor fre-
quency decreases so that when it is an octave lower than CF
the average slope ranges between −1 and −2 dB/dB. In an
extensive study of the suppression growth, Delgutte showed
that it varied from 0.5 to over −3 dB/dB. The larger values
occur for suppressors one to several octaves below CF. We
found up to −1.8 dB/dB for a suppressor frequency < CF/2
[Fig. 3(A)]. Mechanical suppression slopes appear to be
closely correlated with growth rate of basilar-membrane
motion. Mechanical suppression growth rates appear to be suf-
ficient to explain those observed in AN for two-tone sup-
pression. Because a second stimulus component in the
mechanical linear region produces a suppression rate of
−1 dB/dB, the shift in the CF neural curve should be pro-
portional to the reciprocal of the growth rate at the probe
frequency. For example, if the growth rate at CF was 0.33
dB/dB, then the neural curve should shift 3 dB/dB. This
value is at the upper end of the neural shifts found by any-
one. It is likely that there are several factors that enter into
producing the scatter in the neural data, but the most promi-
nant is the way the mechanical growth rate varies with CF.
For CFs < 1 kHz the mechanics exhibits much less compres-
sion than in the frequency region > 5 kHz. Also, varying
neural thresholds and gain functions of the hair cells lead to
further spread in the neural growth rates.

C. Suppression thresholds

There is some controversy about the level at which a
low-side suppressor takes effect. Cooper (1996) noted that
relatively constant suppressor amplitudes are necessary to
establish the suppression threshold in guinea pig. This con-
clusion draws support from the studies of Schmiedt (1982) in
gerbil AN, where the lower threshold boundary of a 2TS area
below CF is nearly absolute in level over a large range of
fiber CFs. Temchin et al. (1997) found AN modulation and
rate thresholds to be very similar at ~70 dB SPL in chinchilla.
In the present study, for a 30-dB SPL probe level, the
−1 dB iso-suppression curve is nearly identical to the 1-nm
isolevel curve for frequencies < CF and a suppressor level of
56 dB SPL. This compares to the 1.5–3 nm found for a 1-dB
iso-suppression in the guinea pig at suppressor levels of
80–90 dB SPL (Cooper, 1996). It was also found that the
suppressor level necessary to produce a 1-dB reduction in the
probe amplitude increases as the probe level increases at a
less than proportional rate (~12-dB increase for a 40-dB
increase in probe level). This latter response is expected be-
cause the growth rate of the CF response is ~0.3 dB/dB of
input; therefore, a 40-dB change in the input results in a
12-dB change in the output. At low-stimulus levels, the sup-
pression amplitude to produce a 1-dB suppression is approxi-
mately the same as the probe amplitude (1 nm). It is worth
noting that suppression thresholds vary 10–20 dB even
within an animal (Schmiedt, 1982).

Neural rate thresholds do not appear to be explicitly re-
lated to a fixed displacement of BM because they can vary as
much as 80 dB at a given CF in individual cats (Liberman,
1978; Cooper, 1996). However, in young cats Liberman
found that the spread of thresholds at a given CF was fairly
narrow, 10–20 dB. The spread in thresholds could be largely
due to hair-cell and AN synapse morphological differences
that are correlated with spontaneous rate in ANFs (Liberman,
1978). This suggests that the underlying reason for the in-
crease in spread with age is alterations in postprocessing of
basilar-membrane motion such as changes in the physiologi-
cal condition of hair cells. Such a hypothesis is difficult to
prove given the difference between the experimental condi-
tions for mechanics, hair-cell recording, and auditory-nerve
recording. It is entirely possible that there would be closer
agreement if all procedures were conducted under a single
regimen.

D. Mutual suppression

Mutual suppression was shown to occur with two-tone
stimulation [Figs. 1(D) and (F)]. With a tone at CF, suppres-
sion occurs with a second tone varying in frequency from an
arbitrary low value to as much as an octave above CF. Sup-
pression slope decreases rapidly for frequencies above CF
and the maximum suppression also decreases. When the
tone at CF is considered the suppressor, suppression is lim-
ited to a smaller frequency region, e.g., 6–11 kHz or roughly
±0.5 octave. Mutual suppression observed in inner hair-cell
recordings has been suggested as a mechanism that results in
sharpening the cochlear filter (Cheatham and Dallos, 1990).

E. Phase effects

Suppression by a high- or low-side suppressor results in
a phase change in the BM response to a CF probe. There is
some controversy in the literature as to behavior of phase of
the probe tone as a function of suppressor tone level (Cooper,
1996). There are studies showing phase leads with increasing
suppressor level (Rhode and Cooper, 1993; Cooper, 1996);
however, others show phase lags (Ruggero et al., 1992). Fig-
ure 14 showed that the relative phase change seen in the
probe phase is nearly always an increasing phase lag of up to
90° as the suppressor level increases regardless of suppressor
frequency. However, for relatively low probe levels and sup-
pressor frequencies just below the probe frequency (= CF),
there is initially a phase lead, never >90°, that turns into a
phase lag as high suppressor levels are attained. Concomitant
with the changes in probe phase are changes in the phase of
the suppressor that are also a function of probe level and
suppressor level, as well as phase changes in the phase of
the BM response to a CF probe. These changes are especially
prominent at the CF, and the maximum suppression
also decreases. When the tone at CF is considered the suppressor, suppression is limited to a smaller frequency region, e.g., 6–11 kHz or roughly ±0.5 octave. Mutual suppression observed in inner hair-cell recordings has been suggested as a mechanism that results in sharpening the cochlear filter (Cheatham and Dallos, 1990).
functions shift to the right with increasing suppressor level and/or cochlear location. He also found that 2TS phase changes were similar to those that occurred when single-tone levels were increased by an amount that caused an appropriate decrease in BM response sensitivity. This difference could be due to species difference and/or cochlear location.

AN studies of 2TS have demonstrated that rate/level functions shift to the right with increasing suppressor level (e.g., Javel et al., 1983). Based on cochlear mechanical studies, the underlying explanation is likely that the cochlear partition exhibits the same behavior (Figs. 3 and 4 in Nuttall and Dolan, 1993). These observations address the hypothesis that suppression is equivalent to a simple attenuation of the motion of the basilar membrane; however, one has to consider phase behavior of the two tones. For high-side suppressors Nuttall and Dolan found that the hypothesis is valid, but they noted that this conclusion differs from that obtained in hair-cell recording in the apex of the guinea pig, where Cheatham and Dallos (1989, 1990) found a phase lead during suppression, opposite to observations in the base. It was suggested that there could be different suppression mechanisms in apex and base. The mechanics in these two regions have considerable similarity (Cooper and Rhode, 1992; Rhode and Cooper, 1996) as there is a compressive nonlinearity in each region and isolevel vibration curves are very similar to auditory-nerve frequency threshold curves. In the apex, however, there is a smaller amount of cochlear amplification that exists over the entire frequency response of the apical region.

F. Multiple tones and suppression

Suppression has been demonstrated psychophysically using the pulsation threshold method with vowel-like sounds (Houtgast, 1974), for multiple-component stimuli (4–64) in an octave centered at the characteristic frequency of an auditory-nerve fiber (Horst et al., 1990), and for multicomponent stimuli such as speech in the auditory nerve (Sachs and Young, 1980). It has been suggested that suppression could be a way for the formants in speech signals to be enhanced relative to the neighboring components. Here, suppression in BM responses to AM stimuli is shown to be dependent on modulation frequency, modulation depth, and stimulus level. The amount of suppression of CF responses increased with level and modulation depth. At any of the modulation depths studied, the largest amount of suppression occurred for stimuli with modulation frequencies around 1500 Hz, and was smallest at either the lowest (100 Hz) or largest (2000 Hz) modulation frequencies. However, the magnitude of carrier suppression does not vary greatly as a function of modulation frequency.

There are prominent mutual suppression effects that occur for small modulation frequencies (see Fig. 13). The greatest suppression of the sideband response occurred when \( f_{\text{mod}} = 100 \) Hz and for small modulation depths \( (m < 0.5) \). This had the effect of sharpening the response spectrum when the response components were in the nonlinear portion of the basilar-membrane I/O curve. It was also shown when AM components were all equal \( (m = 2) \) that sideband response amplitudes were greater than the carrier. This spectral edge enhancement also occurs when the number of components is either five or seven and the component frequency separation is small \( (< 300 \text{ Hz}; \text{ see Rhode and Recio, 2001}) \). The effect is analogous to the Mach band in vision (Carterette et al., 1969).

The fact that the response amplitudes are a complex function of frequency separation, modulation depth, and stimulus level was demonstrated in Fig. 12. With \( f_{\text{mod}} \) and/or level increases the lower sideband grows faster than the carrier and in effect results in an overmodulated response (Rhode and Recio, 2001). This is due to the fact that the lower sideband is located in the linear portion of the cochlear response where the growth rate is 1 dB/dB and the carrier is at CF and is in the compressive region where growth rate is \( 0.3 \) dB/dB. Therefore, the lower sideband grows faster than the carrier and must drive the outer hair cell into its saturated region (Geisler, 1992). The result is that the CF response component is reduced. The upper sideband of the AM stimulus is largely eliminated by the cochlear filter and hence does not play a significant role.

As the number of components increases [Fig. 8(B)], the amount of suppression measured in responses to five-component stimuli with a frequency separation of 1500 Hz is approximately the same as the one measured using 200% AM stimuli [Fig. 6(C)]. However, five-component stimuli produced greater suppression at lower frequency separations (700 Hz) than measured in AM responses with similar component frequency separation. Greatest suppression occurs when more stimulus components are located relatively close to CF (but not too close).

Multitone suppression can result in larger suppression effects than those produced by two tones when components are symmetrically placed around CF. Results suggest that mutual suppression between signal components is not as large as might be expected based on summing two-tone suppression amplitudes. In fact, the net result of multiple tones on suppression of the probe tone can be less than for two tones in some circumstances. Suppression is dependent on the number, level, and frequency composition of the stimulus. Low-frequency (< CF) suppressors at high levels produce the greatest suppression. At low stimulus levels, the CF component has the strongest suppressive effect possibly because all the other components are in the linear region of basilar-membrane vibration.

V. SUMMARY

There is overall agreement that suppression largely originates in cochlear mechanics. The present results reinforce this conclusion and further show the basilar-membrane role in the processing of multitone stimuli. The effect is pervasive and a complex function of stimulus features: component amplitudes, number of components, frequency separation, and distribution of the components relative to characteristic frequency. This effect has implications for how complex signals such as speech are processed even before they enter the central auditory system.
ACKNOWLEDGMENTS

This work was supported by the National Institute of Deafness and Communications Disorders, Grant No. R01 DC 01910. Special thanks are given to C. Dan Geisler, Mario Ruggero, and Keith Klunder for reviewing an earlier version of this manuscript. We also thank Wiebe Horst and an anonymous reviewer for their comments.


