TEMPORAL RESPONSES OF THE AUDITORY-NERVE FIBERS TO SINGLE-TONE AND TWO-TONE STIMULI: EXPERIMENTAL AND MODELING STUDIES

by

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In memory of my mother

Yongfeng Cai

(1946-1993)

谨以此纪念母亲蔡永凤

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Abstract

This thesis reports a study of the temporal responses of single auditory-nerve (AN) fibers of cats to single-tone (low-frequency) and two-tone stimuli. *Chapter 1* deals with the responses to single-tones. Two main issues are addressed: "peak-splitting" and the phase of AN fiber responses relative to the phase of basilar membrane (BM) motion. Peak-splitting was observed mostly in fibers with lower characteristic frequencies (CF < 2 kHz) and with lower frequency stimulation (<= 500 Hz). The occurrence of peak-splitting, the number of peaks occurring in each cycle of the low frequency tone, and the distances between the peaks were dependent upon the stimulus frequency. Comparison of the temporal patterns of peak-splitting with "simultaneously" recorded two-tone suppression patterns (Chapter 2) suggests that the outer hair cell (OHC) function is not directly involved in the generation of peak-splitting. The phase response of an AN fiber to a low-frequency tone was a complex function of the stimulus frequency, intensity, and the fiber's CF. For lower frequency stimuli, the phase lag increases with increasing intensity for fibers with lower CFs while phase lag decreases for fibers with higher CFs. The CF division was dependent on the stimulus frequency and was about 1, 2 and 4 kHz for stimulus frequencies of 50, 100 and 200 Hz, respectively. The amount of phase change with intensity was generally small (< ~50 degrees) at the intensities used (<= 95 dB SPL), although abrupt larger phase changes (e.g., ~180 degrees) can sometimes be seen for higher frequency stimuli. Assuming the maximum negativity of cochlear microphonics recorded near the round window is in phase with the peak displacement of the BM towards scala tympani, the phase of the neural response in the basal region roughly corresponds to the maximum velocity of the BM towards scala tympani,

at 50 and 100 Hz.

Chapter 2 deals with the main temporal aspects of two-tone suppression (2TS) that we observed, using suppressor frequencies (50-2000 Hz) well below fiber CF. We found that the response to the CF tone was suppressed in a phase-specific manner, attaining one or two minimums in each cycle of the suppressor tone. The *phase lead* (defined as the amount by which the phase of suppression led the phase of the response to the suppressor-tone alone) was about 1/4 cycle for lower frequency suppressors (50, 100 and 200 Hz), and was close to half a cycle for higher frequency suppressors (500, 1000 and 2000 Hz). Both the phase of suppression and the phase lead are independent of the spontaneous rate (SR) of the fiber. Some fibers also show a secondary (minor) suppression at higher suppressor intensities, which is always approximately half a cycle away from the first (major) one. Fibers with higher CFs (> 2 kHz) are more likely to show a secondary suppression than those with lower CFs. The threshold difference between the major and minor suppression is CF-dependent: lower CF fibers usually show differences 10 dB or greater, while higher CF fibers show smaller differences. The secondary suppression, when it occurs, is usually restricted to lower frequency suppressors (<= 200 Hz). No fibers showed a secondary suppression with a suppressor frequency of 1000 Hz or greater. The phases of suppressions (both the major and minor suppressions) are not affected by the intensity of the CF tone. Non-excitatory, low-frequency suppressors can give rise to significant suppression. Of all the various types of thresholds measured, the threshold of synchronization to the suppressor tone in the two-tone part was always the lowest (most sensitive), while the SUP-alone rate threshold was always highest. The threshold of synchronization in the SUP-alone segment and threshold of rate suppression were intermediate. In some low-SR fibers, complete suppression was observed.

In *Chapter 3*, we examine differences between the two-tone responses of AN fibers with different SRs, as a function of suppressor intensity. The *relative-response index*, defined as the ratio of the peak response level in the two-tone segment to the response level in the CF-alone segment, at or near the intensity of maximum suppression (i.e., where the two-tone rate was lowest), was dependent on the fiber's SR. For all the suppressor frequencies used, lower-SR fibers almost always showed values less than unity, while high-SR fibers almost always gave values near or greater than unity. In one experiment, a pair of low- and high-SR fibers with the same CF (12 kHz) were recorded consecutively in the same electrode penetration, and were studied with the same stimulus parameters. Their temporal responses showed dramatic resemblance, and their phases of suppression and phases of responses to the suppressor alone were the same. But the relative-response indexes were different. The similarities in the lower- and high-SR fibers support the idea that the basic response *patterns* and suppression *patterns* in all fibers are formed at or before the inner hair cell (IHC) stage, while the differences suggest that processes more central than the IHC receptor potential are important in determining the *magnitudes* of suppression in the lower-SR fibers (see Chapter 4).

In *Chapter 4*, we use a phenomenological model of cochlear function to simulate two-tone suppression. The model uses the output of the OHC to control the gain of the "cochlear amplifier", which affects only frequencies near the CF. Among other things, the model can simulate the 1/4 cycle relationship between the phase of suppression and the phase of excitation by the suppressor-tone alone, which is observed in lower-CF auditory-nerve fibers (Chapter 2). Without any changes, it is also able to simulate the low-frequency biasing data and the suppression of the LF component by the high-frequency CF tone in the OHC outputs (Cheatham and Dallos, 1994). These successful simulations support the basic

assumption of the model, that is: the saturation of the OHC transduction current produces two-tone suppression. Using only the IHC stage, the model also produces suppressions. These are characterized by a half-cycle relationship between phase of suppression and phase of excitation due to the suppressor-tone alone, similar to that observed in high-CF fibers. Therefore, we suggest that the basic *temporal* suppression patterns of two-tone suppression can be accounted for by saturation of OHC and/or IHC currents. However, the fact that the *amplitude* behavior of the model fits only data from auditory-nerve fibers with *high* SRs but not with *lower* SRs, suggests that other mechanism(s) more central than the IHC potential determined the response rates occurring at the neural level.

Two-tone suppression requires the characteristic-frequency (CF) tone and the suppressor tone act simultaneously. In *Chapter 5*, we report a novel phenomenon that the responses to the CF tone *alone* were "suppressed" by a preceding high-intensity low-frequency suppressor tone. Such suppression occurred for repetition intervals of up to 3 seconds. The magnitude of this "long-term" suppression was not dependent upon fiber CF, but fibers with low SRs generally showed more suppression than high-SR fibers did. The threshold of suppression was not dependent upon fiber SR. This suppression affected neither the phases of responses to the CF tone and the suppressor tone, nor the phase of suppression. Controls showed that this phenomenon is not due to adaptation or fatigue. The efferent system, particularly the "slow effect", might be responsible for it.

Abbreviations

2TS	two-tone suppression
AM	amplitude-modulated
AN	auditory nerve
AW	analysis window
BM	basilar membrane
CAP	compound action potentials
CF	characteristic frequency
CM	cochlear microphonic
EPSP	excitatory post-synaptic potential
IHC	inner hair cell
LF	low frequency
LTS	long-term suppression
MER	middle ear muscle reflex
OHC	outer hair cell
PST	post-stimulus time
RW	round window
SR	spontaneous rate
ST	scala tympani
SUP	suppressor
SV	scala vestibuli
TH	threshold