Auditory-Nerve Responses to Clicks at Low Levels, and the Initial Peak at High Levels, are Suppressed at Opposite Bias-Tone Phases

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Abstract. Apical auditory nerve (AN) fibers show two click-response regions that are both strongly inhibited by medial olivocochlear (MOC) efferents: (1) ringing responses from low- level (LL) clicks that are thought to be enhanced by a "cochlear amplifier," and (2) AN initial peak (ANIPr) responses from moderate-to-high level (~70–100 dB pSPL) rarefaction clicks. Since MOC fibers synapse and act on outer hair cells (OHCs), the MOC inhibition of these responses indicates that OHC processes are heavily involved in the production of both LL and ANIPr responses. Using AN recordings in anesthetized cats, we explored the role of OHC stereocilia position in the production of these click-response regions by presenting rarefaction clicks at different phases of 50 Hz, 70–110 dB SPL bias tones. Bias effects on LL responses followed the traditional biasing pattern of twice-a-bias-tone-cycle suppression with more suppression at one phase than the other. This suppression is attributable to the bias tone moving the OHC stereocilia toward low-slope, saturation regions of the mechano-electric transduction function with the rest position being closer to one saturation region. A somewhat similar pattern was found for ANIPr responses except that the bias phases of the largest suppressions were different in ANIPr versus LL responses, usually by ~180 degrees. The data are consistent with the LL and ANIPr responses both being due to active processes in OHCs that are controlled by OHC stereocilia position. The different phases of the LL and ANIPr suppressions indicate that different mechanisms, and perhaps different vibration patterns in the organ of Corti, are involved in the production of LL and ANIPr responses.

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INTRODUCTION

Apical cochlear mechanics is poorly understood and difficult to study. Insight into the complex mechanical drives to inner-hair-cell (IHC) stereocilia can be obtained from auditory-nerve (AN) responses. In response to moderate-to-high-level rarefaction clicks (~75–100 dB pSPL), the AN initial peak (ANIPr) response is strongly inhibited by medial olivocochlear (MOC) efferents while much later peaks are not [4]. This indicates that the ANIPr response is due to active processes in outer hair cells (OHCs). Traditional cochlear amplification of low-level responses is also due to OHC active processes and depends on the slope of the OHC stereocilia conductance vs. angle function (the "OHC I/O" function) [2]. Here we inquire if the active process that produces the ANIPr response depends on OHC stereocilia angle in the same way as traditional cochlear amplifier gain.

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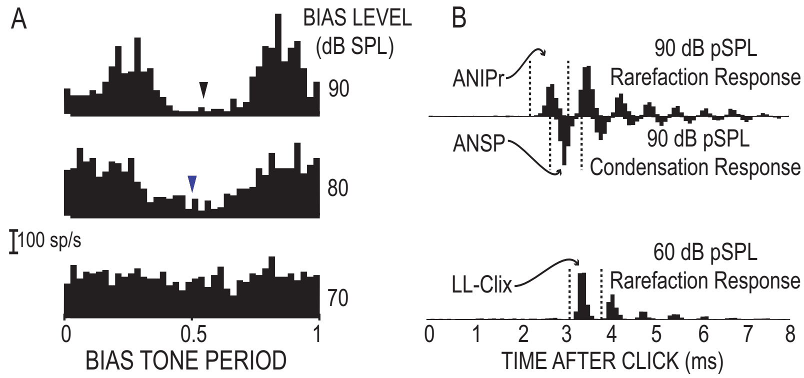

FIGURE 1. A: Responses to a CF (2.59 kHz) tone modulated by 3 levels of a 50 Hz bias-tone. The phase reference was the peak voltage to the DT48. Triangles show the major suppression phases. B: Responses to clicks showing the analysis windows used for each (a different fiber than A).

METHODS

The operating point that determines the slope of the OHC I/O function can be changed by adding a low-frequency "bias" tone (BT). Suppression of cochlear amplification is caused by the BT moving the OHC stereocilia into low-slope "saturation" regions of the OHC I/O function [2]. If the OHC I/O function rest point is asymmetrically located, the result will be greater suppression in one saturation region [1, 2, 6]. This results in BT suppression of cochlear amplifier gain twice each BT period, with one suppression greater than the other. Here we focus on the BT phase that produces the largest suppression.

Recordings were made from >50 AN fibers in 8 anesthetized cats using methods described previously [4,5,7] and approved by our institutional animal review committee. To minimize ringing, clicks were produced by a reverse-driven condenser earphone. 50 Hz bias tones were produced by a DT48 coupled through hollow ear bars.

For the "BT-alone" and "BT-on-CF-tone" paradigms, a BT level series 70 to 120 dB SPL was presented alone, and together with a continuous tone at the characteristic frequency (CF) which was 10 to 20 dB above threshold. Spikes from the BT-alone and BT-on-CF-tone paradigms were binned re the BT period (e.g., Fig. 1A). Directional data analysis [7] on the period histograms allowed calculation of the excitation phase from the BT-only runs and the suppression phase from the 1st and/or 2nd harmonic phase of the period histogram from the BT-on-CF-tone runs. Before suppression phase was measured, we excluded BT levels at which the BT alone excited the fiber (determined as the BT level at which the rate exceeded the fiber spontaneous rate (SR) by 2 times the standard deviation of the SR). Phase errors were calculated [7] and on each fiber we used only the point at the lowest BT level for which the standard error of the phase estimate was less than 20 degrees.

For clicks, an initial set of data were obtained from a randomized level series (typically 30–115 dB pSPL) of interleaved rarefaction and condensation clicks presented at 50/s. From these we determined the threshold for low-level clicks, the ANIPr response and the Auditory-Nerve Second Peak (ANSP) response (see Fig. 1B) which is the first

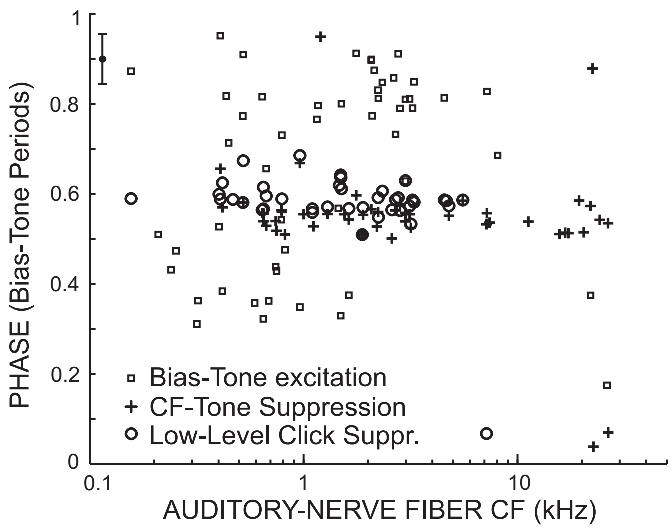

FIGURE 2. The bias-tone phase of the major suppression of low-level CF tone responses (+) and low-level click responses (o). For reference, the small squares show the phase at which the bias tone alone excited each fiber. Suppression points are only shown if they were from a bias level lower than the bias level that caused excitation.

response to condensation clicks in the 70–100 dB pSPL range. The ANSP response was looked at because it shows weak MOC inhibition [4]. Since MOC inhibition is not seen for peaks following ANSP, it has been suggested that ANIPr and ANSP could be one complete cycle of a decaying oscillatory motion generated by an active mechanism which is distinct from the active mechanism involved in traditional cochlear amplification [4]. After obtaining the thresholds, clicks were then presented at 10–20 dB above these thresholds. For BT effects on clicks, 100 us clicks of appropriate polarity were presented at a repetition interval of 18 ms together with 50 Hz bias tones. The time slip of the click repetition interval against the BT period of 20 ms resulted in click bursts at 10 phases of the BT period.

Analysis of the click-response data started by obtaining a 180-ms-long histogram which covered the 18 ms duration click responses of the clicks presented at the 10 distinct phases of the bias tone period. This histogram was separated into the responses at the 10 distinct BT phases and the peak appropriate to the response being measured was obtained by averaging all the spikes in the appropriate window as shown in Figure 1B. These 10 rates then formed a 10-point histogram over the BT period on which period histogram analysis was done in the same was as for the more- closely-binned tone data (e.g., Fig. 1A). In the click BT period histogram, the phase delay of the analysis window was taken to be the delay at the center of the window.

RESULTS

For most fibers, the responses to low-level tones at CF and to low-level clicks were suppressed at approximately the same bias-tone phase (Fig. 2). In contrast, for most fibers ANIPr and ANSP responses were suppressed at a bias phase approximately

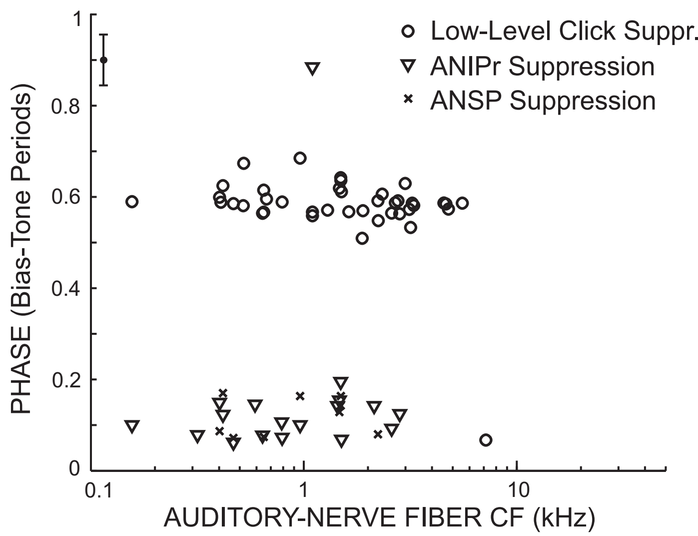

FIGURE 3. The bias-tone phase of the major suppression of low-level click responses (o) and high-level ANIPr and ANSP responses (triangle, ×). Note that the ANIPr and ANSP responses were suppressed at bias-tone phases that were approximately 1/2 bias-tone period from the phase at which low-level click responses were suppressed.

opposite the phase that suppressed the responses to low-level tones and clicks (Fig. 3). Suppression of ANIPr responses typically required an ~10 dB higher bias-level than suppression of low-level click and tone responses. Suppression of ANSP responses required the highest bias levels (~10 dB higher than for ANIPr).

DISCUSSION

Bias tone suppression of click responses has not been previously studied. We found that AN responses to low-level tones and clicks both show the greatest suppression at approximately the same bias-tone phase (Fig. 2). This is consistent with both being due to motion amplified by the same mechanism, i.e. by the traditional cochlear amplifier that amplifies low-level sound responses of any kind.

In contrast, AN responses to low-level and high-level clicks were suppressed at opposite bias-tone phases (Fig. 3). The fact that the initial peaks of the high-level click responses were suppressed by the bias tones (at these click levels, later peaks were not substantially suppressed) is consistent with the conclusion from their MOC inhibition that the initial peak (ANIPr and ANSP) are strongly influenced by active processes in OHCs. The fact that the suppression was twice each bias-tone cycle indicates that the OHC influence depends on the slope of the OHC stereocilia I/O function. However, since the phase of the major suppression is opposite for the low-level and high-level click responses, different OHC processes, or different coupling of OHC processes to IHC stereocilia, must be involved.

The ANIPr and ANSP responses (from rarefaction and condensation clicks at the same high level) are suppressed at the same bias-tone phase. Similar to the ANIPr response, the ANSP response is also MOC inhibited, but more weakly [4]. A hypothesis that fits these data is that high-level clicks evoke a short-latency, quickly- decaying, oscillatory mechanical response that produces the ANIPr response by itself, and that the ANSP response is produced by a combination of this early mechanical response and the earliest part of the traveling wave (which at this high level receives little cochlear amplification). The result is that suppressing (or MOC inhibiting) the early mechanical response strongly reduces the ANIPr response and only partly reduces the ANSP response—thus, to get significant ANSP suppression (and an angle error of <20 degrees) requires a higher bias-tone level.

CONCLUSIONS

The earliest part of the auditory-nerve response to high level clicks is produced by a mechanical motion from an active process in OHCs that depends on the OHC stereocilia I/O slope and is distinct from the process that produces traditional cochlear amplification at low sound levels.

ACKNOWLEDGMENTS

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