Am J Otolaryngol
3:408–416, 1982

Comparison of Psychophysical and Evoked-potential Tuning Curves in the Chinchilla

RICHARD J. SALVI, PH.D., WILLIAM A. AHROON, PH.D., JOHN W. PERRY, PH.D., ADELE D. GUNNARSON, M.S., AND DON HENDERSON, PH.D.

Frequency selectivity was examined in normal-hearing chinchillas using psychophysical and evoked-potential tuning curves. The acoustic conditions and masking procedures used for the evoked-potential and psychophysical studies were nearly identical. Frequency selectivities as measured by psychophysical and physiologic techniques were quite similar across different probe frequencies. The results suggest that the relatively efficient evoked-potential procedure may be substituted for the time-consuming psychophysical paradigm. Furthermore, the results are consistent with the view that tuning takes place primarily at the auditory periphery. (Key words: Evoked response; Frequency selectivity; Tuning curves.)

Brainstem electrical responses (BSER) have become popular metrics for estimating thresholds in both humans and animals. Generally, the responses have been measured with clicks or tone pips with fast rise–fall times, since these signals are the most suitable for synchronizing the underlying neural activity. Tone pips have the added advantage that thresholds may be assessed at different frequencies in order to obtain an "audiogram."[1–3]

One of the important issues surrounding the interpretation of the BSER data concerns the degree of frequency-specific information contained in the response. Frequency specificity is suggested by several properties of the response. The latency of the BSER decreases as stimulus frequency increases[4] in a manner consistent with the mechanics of the basilar membrane.[5] Furthermore, the "threshold" of the BSER varies with frequency in roughly the same manner as the behavioral threshold.[2]

From the Callier Center for Communication Disorders, University of Texas at Dallas, Dallas, Texas. Received May 14, 1982. Accepted for publication July 12, 1982.

Supported in part by grants from the National Institute of Health (1-R01-NS1676), the National Institute of Occupational Safety and Health (1-R01-OH-00364), and the U.S. Army Medical Research and Development Command (DAMD 17-80-C-0133).

Address correspondence and reprint requests to Dr. Salvi: Callier Center for Communication Disorders, 1966 Inwood Road, Dallas, Texas 75235.

More refined techniques have been used to demonstrate the frequency-specific nature of the BSER. Don and Eggermont[6] and Terkildsen et al.[7] used a masking paradigm to derive the frequency-dependent components of the BSER response. Both studies demonstrated that frequency-specific information is contained in the BSER; however, it is difficult to relate the set of frequency-dependent components of the BSER to psychophysical measures of frequency selectivity.

A more direct way of assessing the degree of frequency specificity of the BSER response is to measure tone-on-tone masking patterns or tuning curves (TCs). In psychophysical studies, the subject's task is to detect a low-level probe tone that is fixed in level and frequency. The assumption is that the low-level probe excites a limited number of neurons having best frequencies in the vicinity of the probe tone. A masking tone then is introduced and adjusted in level until it abolishes the response to the probe. The masking procedure is carried out over a range of frequencies around the probe. Masked thresholds are lowest in the vicinity of the probe and then increase with frequency separation between probe and masker.[8]

The same tone-on-tone masking paradigm has been employed in physiologic studies to obtain tuning curves for the compound action potential (AP) of cranial nerve VIII of man, guinea pig, and chinchilla[9–12] and Wave I and Wave V of the

0196-0709/82/1100/0408 $01.80 © W. B. Saunders Co.

BSERs from humans and guinea pigs.[12,13] These physiologic TCs are qualitatively similar to those obtained psychophysically; however, it is difficult to compare the results since many of the stimulus conditions used to obtain the psychophysical and physiologic data are different. For example, most psychophysical studies employ tones with relatively long rise–fall times in order to minimize spectral spread,[8,14–18] whereas physiologic studies use short-duration signals with rapid rise–fall times to maximize neural synchrony.[10,12,13] Comparing TCs from animals can also be difficult because the psychophysical measurements are frequently performed under free-field conditions[10] while the physiologic data are generally collected with a closed acoustic system and with the middle ear space vented.[11,12]

Recently, Klein and Mills[13] used identical stimulus conditions to collect both psychophysical and physiologic TCs (brainstem Wave I and Wave V) from humans. Although the TCs were qualitatively similar there were some important quantitative differences. For example, the bandwidth of the TC 10 dB above the tip was smallest for the Wave V TCs, followed by Wave I and the psychophysical TCs. However, when the TCs were compared at a fixed sound pressure level (SPL), 76 dB, the psychophysical bandwidths were smaller than the physiologic ones. While the results of Klein and Mills[13] show that the BSER can provide a reasonable estimate of frequency selectivity, the results are limited to one probe frequency. Since the shape of psychophysical tuning curves systematically changes with probe frequency,[16,18] it is important to assess the full range of neural tuning, particularly at low frequencies, where it is difficult to synchronize the onset response. In guinea pigs, Mitchell and Fowler[12] found a progressive broadening of the physiologic tuning curves with decreasing probe frequency. However, no behavioral measures were obtained, so it is unclear how well these physiologic tuning curves approximate the behavioral measures.

Psychophysical, AP, and single auditory nerve fiber tuning curves of the chinchilla have been measured,[11,14,19] but TCs from the brainstem have not yet been obtained. The dominant component of the brainstem potential in the chinchilla is a large positive wave which arises primarily from the inferior colliculus.[1] One practical reason for measuring the brainstem TCs is that the potentials can be easily and reliably recorded from awake chinchillas over many months using chronically implanted electrodes[2]; similar AP measurements are more difficult to obtain because of the possibility of middle ear infections. Furthermore, the time and effort required to collect the evoked-potential measures are considerably less than the time and effort involved in obtaining similar behavioral measures. Thus, if the evoked-potential tuning curves can be shown to approximate the behavioral tuning curves, one might consider substituting the evoked response for the psychophysical method when time and effort are important experimental variables. The objective of this study was to measure the brainstem TCs of the chinchilla over a broad range of probe tone frequencies. In order to compare the degrees of frequency specificity, the physiologic and psychological TCs were collected under similar acoustic conditions; however, the two sets of TCs were obtained from different animals because the behaviors required in the two procedures were mutually incompatible (i.e., jumping in the behavioral paradigm versus remaining stationary during evoked-potential testing).

METHOD

Subjects

Four chinchillas were used in the psychophysical experiment and another four were used in the physiologic study. The animals weighed between 400 and 800 g. Each animal was anesthetized and made monaural by surgical destruction of the left cochlea.[7] The probe tone was presented 15 dB above either the evoked response or the behavioral threshold; thus, the absolute SPLs of the probe varied a small amount from animal to animal and were slightly higher (approximately 5 to 15 dB) for the evoked potential than for the psychophysical conditions. It is important to note that both psychophysical and physiologic studies indicate that the shapes of the tuning curves are not substantially altered when the probe levels are varied over a 25- to 35-dB range above threshold.[10,16,17] By presenting the probe tone near threshold one reduces the effects of combination tones. Furthermore, the masker frequencies near the tip of the tuning curve were at least 20 Hz above or below the probe frequency to minimize the effects of beats.

Behavioral Testing

Audiograms and psychophysical TCs were obtained using a shock-avoidance conditioning paradigm and a modified method of limits (for

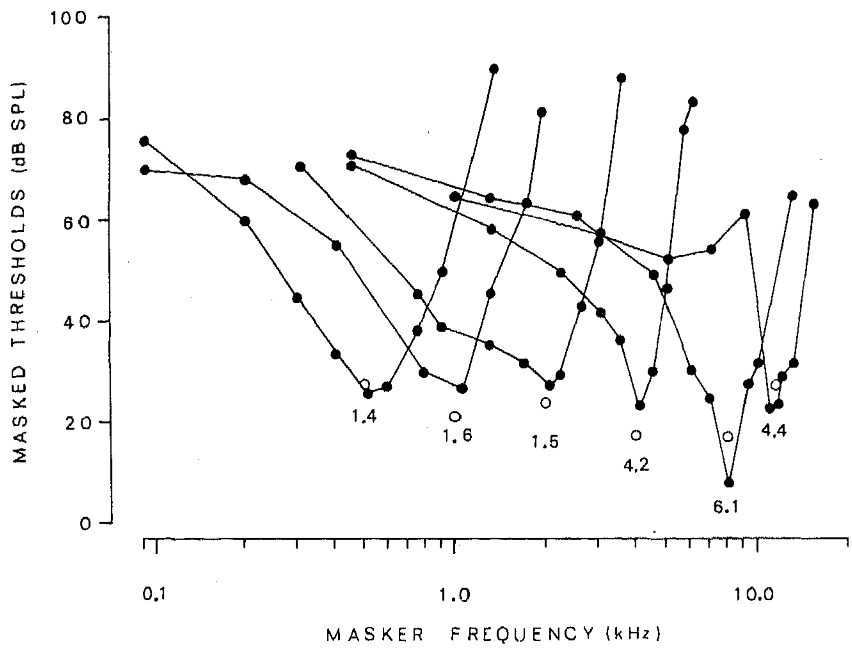


Figure 1. Psychophysical tuning curves obtained for one animal. The value of Q_{10} dB is indicated below the tuning curve tip for each probe-tone frequency. Open circles indicate the probe tone level.

details, see references 19–21). The chinchilla was placed in a restraining yoke which fixed the orientation of its head in the sound field, but allowed a slight upward motion of the body so that the animal could register a response. A stimulus trial consisted of a train of eight tone bursts (20 ms duration between half-power points; 5 ms rise–fall time, 2 bursts/s). A response during bursts 1 to 4 was registered as a "hit" and was followed by the presentation of a safety light for 7.5 seconds. If the animal failed to respond by the onset of the fifth tone, mild pulsed shock was delivered to the animal's tail, except at near-threshold intensities. A response to tone bursts 5 through 8 or no response was scored as a "miss."

Tone Threshold

Testing began at clearly audible levels. After each correct response, the signal was reduced in 10-dB steps until a "miss" occurred; then the signal was increased in 10-dB steps until a "hit" occurred. At that point, the step size was reduced to 5 dB and four additional threshold crossings were obtained. The data were accepted as valid if the threshold crossings differed by 10 dB or less. A total of 48 to 72 threshold crossings were used to estimate the threshold of the 20-ms probe tone.

Psychophysical Tuning Curves

The procedures for obtaining psychophysical TCs are similar to those outlined earlier.[19] Tuning curves were obtained with the probe tone at a 15-dB sensation level (SL). A continuous tone then was introduced at a low level so that the probe, which was presented randomly, was clearly audible. The animal was trained to ignore the continuous masking tone and to respond to the probe.

The procedures for determining the level of the continuous tone necessary to mask the probe were similar to those used to estimate quiet threshold, except that masker level was varied. A total of at least 12 threshold crossings were used to compute each point on the psychophysical TCs.

Evoked Response Testing

Chronic electrodes were implanted in the vicinity of the inferior colliculus in four chinchillas using procedures outlined in a previous report.[2] The animals were tested using the same restraining yoke and acoustic equipment employed in the behavioral experiments. The acoustic signals were identical to those in the behavioral experiments except that the probe tone was presented at the rate of 10/s throughout the averaging session. The electrical potential from the electrode was filtered (300 to 1,500 Hz), amplified (20,000 to 50,000 times) and led to a signal averager (Fabri-Tek 1070) with artifact-reject capability. The data were sampled at 25 kHz over 512 points to obtain a window of 20.48 ms. Normally, 512 samples were collected. However, if a clear evoked response was present with fewer samples, the averaging was terminated. No effort was made to measure the actual

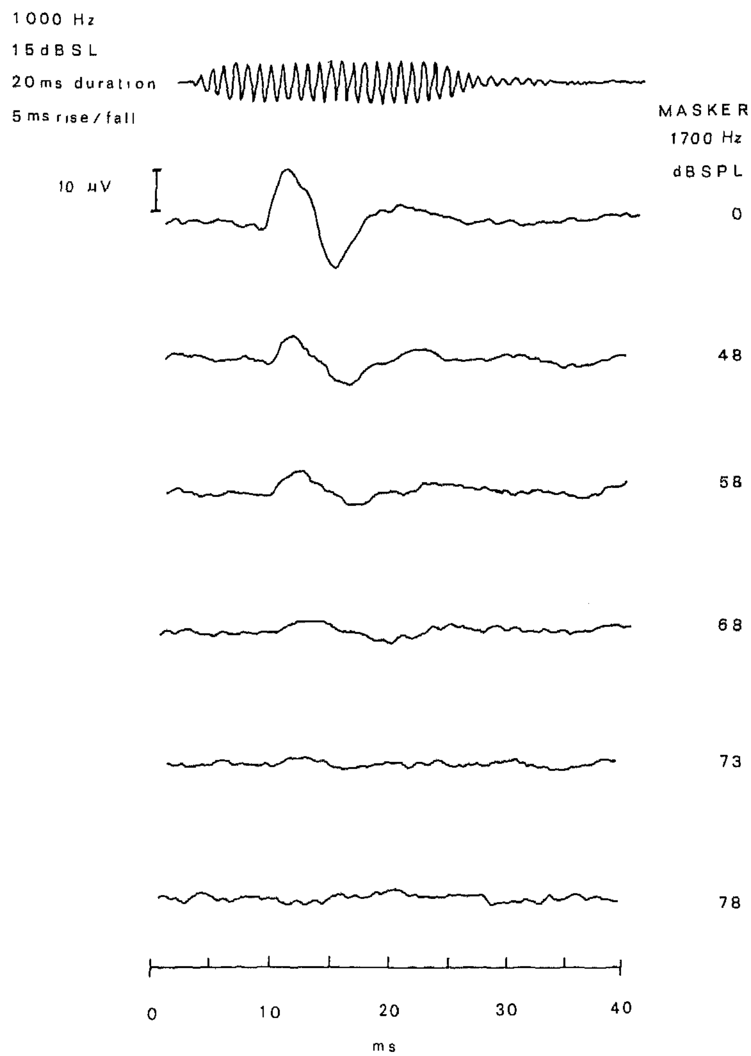


Figure 2. Examples of evoked responses from one chinchilla. The top trace represents the acoustic output of the speaker. The second trace is the evoked response to the 1-kHz probe tone at a level of 15 dB above the animal's threshold. Successive traces represent the evoked responses to the 1-kHz probe with a simultaneous 1.7-kHz masker increasing in intensity.

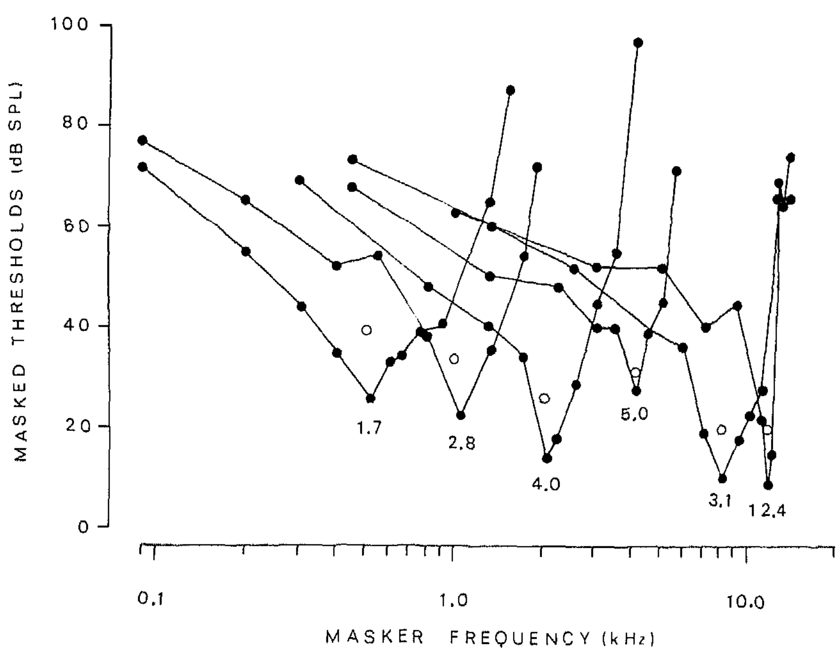


Figure 3. Evoked-response tuning curves obtained for one animal. The value of Q_{10} dB is indicated below the tuning curve tip for each probe-tone frequency. Open circles indicate the level of the probe tone.

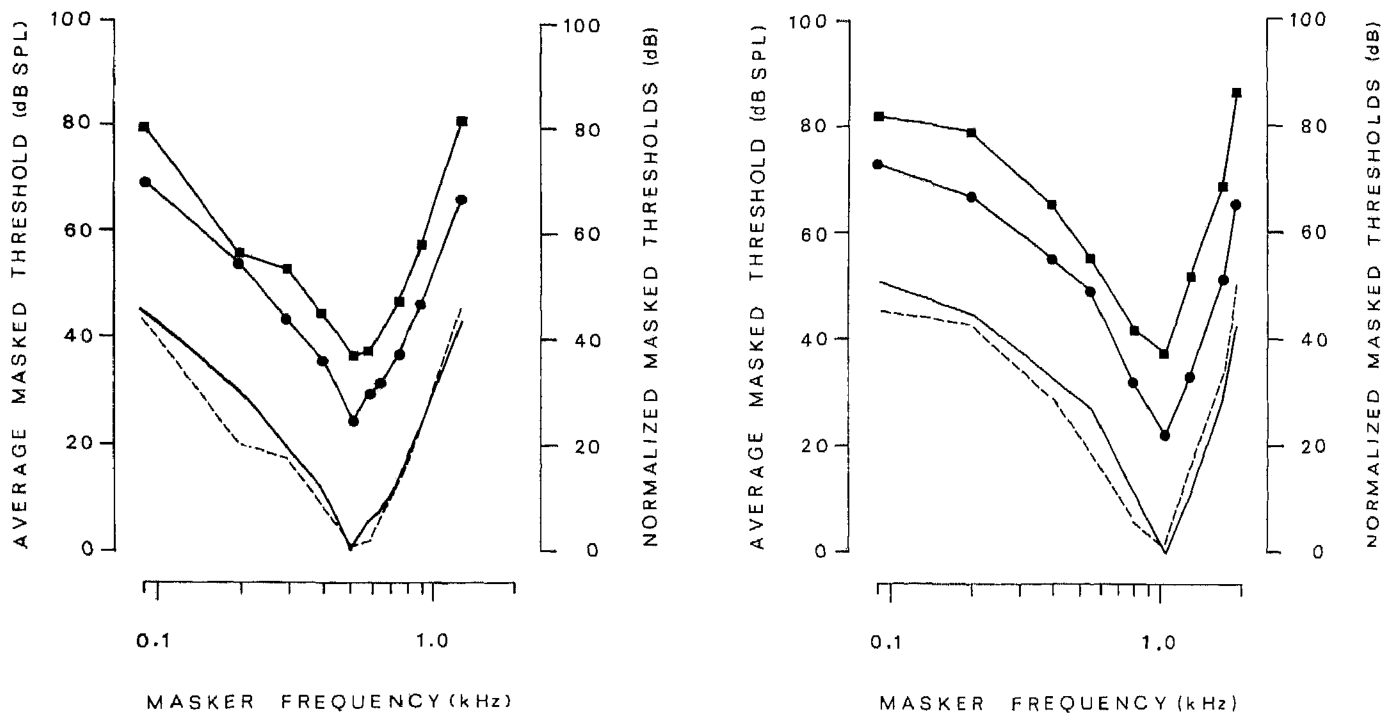


Figure 4, A–F (above and facing page). Comparison of average psychophysical and evoked-response tuning curves. Filled circles and filled squares are the average psychophysical and average physiologic tuning curves presented in dB SPL. The psychophysical (*solid line*) and physiologic (*dashed lines*) tuning curves have been normalized to 0 dB at their tips.

amplitude of the evoked response waveforms, since only the transition from the presence to the absence of the evoked response was used to make a judgement regarding the absolute and masked thresholds.

Physiologic Threshold

Thresholds were determined with a 20-ms probe tone with random starting phase and 5 ms rise–fall times. Testing began at an intensity that produced a clear and unambiguous response. Then the signal level was reduced in 10-dB steps until the response was slightly above the background noise. At this point, the intensity step was reduced to 5 dB and additional samples were collected. Threshold was the point midway between the highest intensity where the response was absent and the lowest intensity where the response was present.

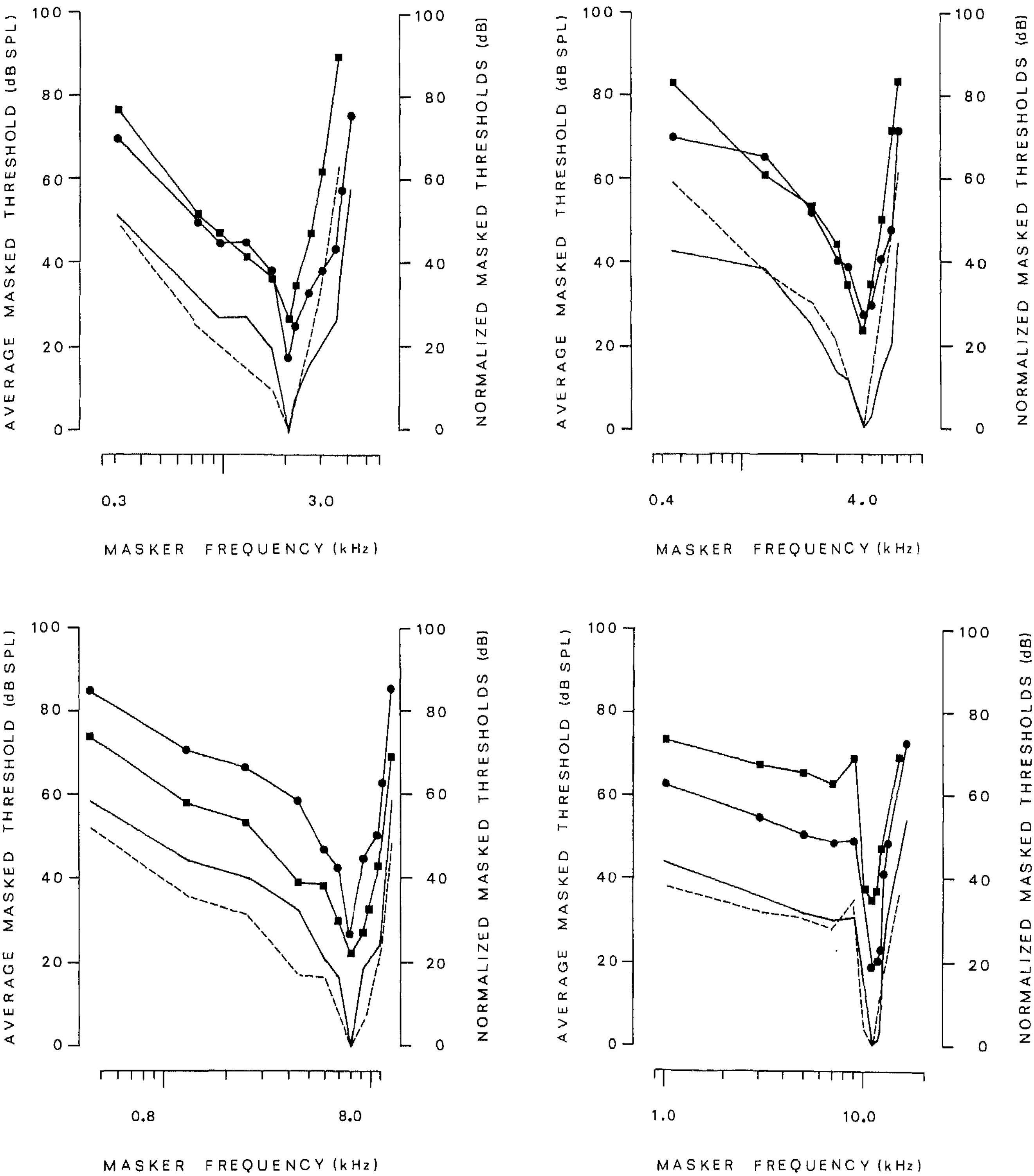
Physiologic Tuning Curves

Immediately following the determination of a threshold, a tuning curve was collected for that frequency. The probe tone was presented at a level 15 dB above the evoked-potential threshold. A continuous masker then was introduced at a level low enough so that a clear evoked potential was obtained. Masker level was subsequently increased in 10-dB steps until the evoked response was nearly obliterated; then the step size was reduced to 5 dB and additional samples were collected. Masked threshold was the intensity midway between the lowest intensity where the response was present and the highest intensity where the response was absent. Masking was employed at frequencies above and below the probe tone in order to obtain a TC that could be compared with the psychophysical data.

RESULTS

Individual Psychophysical Tuning Curves

Figure 1 shows six psychophysical TCs obtained from one chinchilla at six probe frequencies from 0.5 to 11.2 kHz. At probe frequencies above 2 kHz, the psychophysical TCs tend to be asymmetrically shaped on a log-frequency plot, while those below 2 kHz are nearly symmetrical. In general, the psychophysical TCs are characterized by a low masked-threshold region near the probe sandwiched between a steep high-frequency slope and a somewhat shallower low-frequency slope. The "tail" segment of high-frequency psychophysical TCs refers to the region where the low-frequency slope becomes



extremely shallow, usually 1–2 octaves below the probe. The transition to the tail segment can be easily identified in the 11.2-kHz psychophysical TC because of the high threshold notch at 9 kHz that separates the tip from the tail segment. The transition to the tail segment occurs much more gradually at lower probe frequencies.

A popular and useful measure of quantitatively assessing the frequency selectivity of tuning curves is to compute the Q_{10} dB value, defined as the center frequency of the tuning curve divided by the bandwidth 10 dB above the minimum threshold. Generally, Q_{10} dB values increase with probe frequency. A similar trend

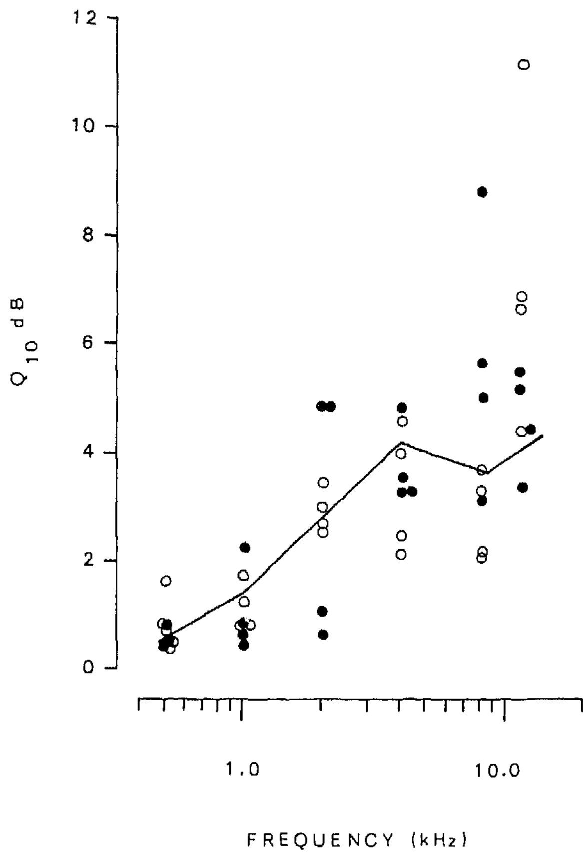


Figure 5. Values of Q_{10} dB for psychophysical (*solid circles*) and evoked-response (*open circles*) tuning curves. The solid line represents Q_{10} dB values for single auditory nerve fibers, from Salvi et al.[19]

occurs in Figure 1, where the Q_{10} dB values range from 1.4 at a probe frequency of 0.5 kHz to 6.1 at a probe frequency of 8.0 kHz.

The psychophysical TCs shown in Figure 1 are representative of the four animals and are similar to psychophysical TCs reported in an earlier study.[19] However, the psychophysical TCs of our chinchillas did not appear to be quite as sharply tuned as those reported by McGee et al.[14]

Individual Evoked-potential Tuning Curves

Before presenting the evoked-potential tuning curve data, it is important to identify the evoked-response waveforms obtained with the tone-on-tone masking paradigm. The top trace in Figure 2 shows the voltage–time waveform of the acoustic signal, while the second trace represents the evoked potential obtained with a 1-kHz tone pip at 15 dB above the evoked-response threshold. In the absence of the masker, the response consists of a large positive wave at approximately 11 ms, followed by a negative wave at 17 ms. Traces 3 through 7 illustrate how the evoked response is affected by a 1.7-kHz masker. As the masker intensity is increased, amplitude decreases and latency increases. There is a remnant of the positive wave with a masker of 68 dB SPL; however, the evoked potential is completely obliterated at 78 dB SPL. Response waveforms similar to those were obtained at other frequency–intensity combinations of the probe and masker; the waveform closely resembles those obtained from microelectrodes in the inferior colliculus.[1]

Shown in Figure 3 are the six evoked-potential TCs from a single chinchilla. The evoked-potential TCs are remarkably similar to those obtained behaviorally. While the overall similarity is encouraging, a much more comprehensive assessment can be made by comparing the average behavioral TC and the average evoked-potential TC at each probe frequency.

Psychophysical versus Evoked-potential Tuning Curves

The intersubject variability was quite small, generally less than 8 dB, so that it is reasonable to average the tuning curves from each condition. The average evoked-potential and the average psychophysical tuning curves are shown in Figure 4. In order to aid the comparison further, the tuning curves were normalized at their tips to compensate for differences in sensitivity and then plotted in the lower portion of each panel.

When the data are normalized, four of the six pairs of tuning curves (0.5, 1, 4, and 11.2 kHz) are essentially the same. The bandwidths are similar for the curves at 2 kHz, except that the evoked-potential TC has a steeper high-frequency skirt, while the psychophysical TC has a steeper low-frequency skirt. The 8-kHz evoked-potential TC is broader than the psychophysical TC; this difference is somewhat difficult to explain given the fact that the 4-kHz and 11.2-kHz evoked-potential TCs are essentially the same as their psychophysical counterparts.

A standard metric for comparing TCs is the Q_{10} dB value. Figure 5 shows the individual Q_{10} dB values plotted as a function of the center frequency of the probe for both the evoked-potential and the psychophysical measures. The median Q_{10} dB values for single auditory nerve fibers in the chinchilla also are presented to aid the analysis.[19] It should be noted that the acoustic conditions for the single-unit data are different from those in the present experiment; however, this should not significantly influence the comparison, since the Q_{10} dB values are computed over a relatively narrow range of frequencies. The Q_{10} dB values are in good agreement up to 4 kHz, and still show considerable overlap at higher frequencies. At 8 kHz, the Q_{10} dB values obtained with the evoked response tend to be somewhat smaller than the psychophysical data. Conversely, the evoked-potential Q_{10} dB values tend to be larger than those obtained psychophysically at 11.2 kHz. Note that the median Q_{10} dB values of single auditory nerve fibers (solid line) provide a reasonably good fit to the psychophysical and evoked-response data.

DISCUSSION

Since masked thresholds increase rapidly with increasing separation between probe and masker, it seems reasonable to conclude that the evoked potential elicited by the probe tone synchronizes the response of a limited number of single units with best frequencies in the vicinity of the probe. Furthermore, the response appears to contain considerable frequency-specific information.

The present results also indicate that the evoked-potential TCs provide a reasonable approximation of the psychophysical TCs in the normal-hearing chinchilla over a broad range of probe frequencies; the only difference between the two is a 5–15-dB difference in sensitivity. The evoked-potential TCs can be obtained easily in a matter of a few weeks from awake chinchillas using the procedures outlined above, but months of training and testing are needed to obtain the psychophysical TCs. Consequently, when time and effort are critical experimental factors, it would be advantageous to use the evoked-potential TC as an estimate of tuning in normal chinchillas. While the evoked-potential TC appears to offer a promising technique for assessing frequency selectivity, its application to hearing-impaired subjects needs to be explored more fully before its use is justified completely.

One important issue in hearing concerns the origin(s) of tuning within the auditory pathway, i.e., which structures or processes set the limits of frequency selectivity of the final detector represented by the psychophysical TC. There is some evidence to suggest that tuning is primarily set at the level of the cochlea and that no further sharpening takes place centrally.[22,23] Other data, however, suggest that the central auditory pathway may provide additional frequency selectivity beyond that seen at the cochlea.[24–26] One way of evaluating this issue is to compare the Q_{10} dB values at different levels of the auditory pathway with the psychophysical data. Figure 5 shows that the median Q_{10} dB values of single auditory nerve fibers in the chinchilla correspond closely to the Q_{10} dB values of the evoked potential that arises in the inferior colliculus. Thus, one might argue that the brainstem nuclei do not substantially alter the tuning properties established at the cochlea, but this interpretation should be made with caution, given that the acoustic conditions and testing procedures for the two conditions are somewhat different. However, at a more central level, one finds that the evoked-potential Q_{10} dB values show considerable overlap with the psychophysical data, implying that little or no sharpening takes place beyond the colliculus. Recall that the acoustic conditions for this comparison are nearly identical. Thus, the present data provide support for the view that tuning originates primarily at the auditory periphery.

Acknowledgments. The authors thank Patricia L. Robinson and Harley Willet for technical assistance and G. and D. Clemmer, J. and O. Mooneyham, E. and K. Rockwood and N. and M. Sifford for their generous support.

References

1. Rothenberg S, Davis H: Auditory evoked response in chinchilla: application to animal audiometry. Percep Psychophys 2:443–447, 1967
2. Henderson D, Hamernik RP, Woodford C, et al: Evoked response audibility curve of the chinchilla. J Acoust Soc Am 54:1099–1101, 1973
3. Mitchell C, Clemis JD: Audiograms derived from the brainstem response. Laryngoscope 87:2016–2022, 1977
4. Klein AJ, Teas DC: Acoustically dependent latency shifts of BSER (Wave V) in man. J Acoust Soc Am 63:1887–1895, 1978
5. von Bekesy G: Experiments in Hearing. New York, McGraw-Hill, 1960.
6. Don M, Eggermont JJ: Analysis of the click evoked brainstem potentials in man using the high pass noise masking. J Acoust Soc Am 63:1084–1092, 1978
7. Terkildsen K, Osterhammel P, Huis in't Veld F: Far field electrocochleography: frequency specificity of the response. Scand Audiol 4:167–172, 1975
8. Chistovich LA: Frequency characteristics of masking effect. Biofizika 2:749–755, 1957
9. Eggermont JJ: Compound action potential tuning curves in normal and pathological human ears. J Acoust Soc Am 62:1247–1251, 1977
10. Dallos P, Cheatham MA: Compound action potential tuning curves. J Acoust Soc Am 59:591–597, 1976
11. Harris M: Action potential suppression, tuning curves and thresholds: comparison with single fiber data. Hearing Res 1:133–154, 1979
12. Mitchell C, Fowler C: Tuning curves of cochlear and brainstem responses of the guinea pig. J Acoust Soc Am 68:896–900, 1980
13. Klein AJ, Mills JH: Physiological (waves I and V) and psychophysical tuning curves in human subjects. J Acoust Soc Am 69:760–768, 1981

14. McGee T, Ryan A, Dallos P: Psychophysical tuning curves of chinchillas. J Acoust Soc Am 60:1146–1150, 1976
15. Small AM: Pure tone masking. J Acoust Soc Am 31:1619–1625, 1959
16. Vogten LLM: Pure tone masking: a new result from a new method, *in*: Zwicker E, Terhardt E (eds.): Facts and Models in Hearing. New York, Springer, 1974, pp 142–155
17. Wightman FL, McGee T, Kramer M: Factors influencing frequency selectivity in normal and hearing impaired listeners, in: Evans EF, Wilson JP (eds.): Psychophysics and Physiology of Hearing. London, Academic Press, 1977, pp 295–306
18. Zwicker E: On a psychoacoustic equivalent of tuning curves, *in:* Zwicker E, Terhandt E (eds.): Facts and Models in Hearing. New York, Springer, 1974, pp 132–141
19. Salvi R, Perry J, Hamernik RP, et al: Relationships between cochlear pathologies and auditory nerve and behavioral responses following acoustic trauma, *in:* Hamernik RP, Henderson D, Salvi RJ (eds.): New Perspectives on Noise-induced Hearing Loss. New York, Raven Press, 1982, pp 165–188
20. Blakeslee EA, Hyson K, Hamernik RP, et al: Asymptotic threshold shift in chinchillas exposed to impulse noise. J Acoust Soc Am 63:876–882, 1978
21. Salvi R, Hamernik RP, Henderson D: Discharge patterns in the cochlear nucleus of the chinchilla following noise induced asymptotic threshold shift. Exp Brain Res 32:301–320, 1978
22. Moller AR: Coding of sounds in lower levels of the auditory system. Q Rev Biophys 5:59–155, 1972
23. Pickles JO: Psychophysical frequency resolution in the cat as determined by simultaneous masking and its relation to auditory nerve resolution. J Acoust Soc Am 66:1725–1732, 1979
24. Dallos P, Harris D: Properties of auditory nerve responses in the absence of outer hair cells. J Neurophysiol 41:365–383, 1978
25. Dallos P, Ryan A, Harris D, et al: Cochlear frequency selectivity in the presence of hair cell damage, *in:* Evans EF, Wilson JP (eds.): Psychophysics and Physiology of Hearing. London, Academic Press, 1977, pp 249–261
26. Pickles JO: Role of centrifugal pathways to cochlear nucleus in determination of critical bandwidth. J Neurophysiol 39:344–400, 1976