Chapter 5

A novel long-term suppression effect

Introduction

The responses of auditory nerve fibers to two-tone combinations, notably two-tone suppression (2TS), have been studied intensively (e.g. Arthur et al., 1971; Hill and Geisler, 1992). In 2TS, the response of the auditory nerve (AN) fiber to an excitatory tone, generally placed at the characteristic frequency (CF) of the AN fiber, is suppressed by a suppressor tone with frequency either above or below CF. This suppression requires both the excitatory tone and the suppressor tone to be presented simultaneously: the suppression takes effect almost immediately (< 2 ms) after the suppressor is started, and ends soon after the suppressor is stopped (Arthur et al., 1971; but see Hill and Geisler, 1992). Recently, during the study of 2TS in the cat auditory nerve fibers, we sometimes observed that the responses of AN fibers to CF tones were suppressed long after a low-frequency suppressor had been terminated. This chapter describes our observations of this phenomenon.

Methods

This study was done in the course of a larger study of 2TS in the auditory nerve fibers of

cats. The animal preparation, calibration of the acoustic system and the stimulus delivery were described elsewhere (Chapters 1 and 2). The stimuli were pure tones which had, because of the requirement of other parts of the 2TS study, an harmonic relationship, although there was no such need in this part of the study. The frequency of the suppressor was always well below CF and usually had one of the following values: 50, 100, 200, 500, 1000 or 2000 Hz. The frequency of the CF tone was then adjusted slightly to ensure the harmonic relationship. Two paradigms were used in the experiment (Fig. V-1). In paradigm 1 (Fig. V-1A), both the CF tone and the suppressor lasted 500 ms, but the suppressor was delayed about 200 ms so that three windows were available: CF alone, two-tone, and suppressor alone. The repetition interval varied from 1000 to 3000 ms for the data presented in this paper. The rise/fall time was 4 ms. The CF intensity was usually fixed at 10 to 30 dB above threshold and the suppressor intensity was varied during the experiment. The paradigm was then repeated for a number of different suppressor intensities between 65 and 95 dB SPL (usually in 5 dB steps). For each suppressor tone, the paradigm was repeated 25 or 75 times. Paradigm 2 (Fig. V-1B) was a variation of paradigm 1. In the first half of paradigm 2, the CF tone lasted 600 ms. The suppressor tone was delayed by 300 ms and lasted only 300 ms, so that both the CF tone and the suppressor tone were turned off at the same time. The second half of this paradigm differs from the first half only in the aspect that the suppressor was never turned on. The total stimulus off times for the first and second halves were the same for a 2000 ms repetition interval, which was twice the repetition interval in the case of paradigm 1.

The data presented here were obtained from 8 cats: C92101, C92106, C92116, C93030, C93036, C93146, C94009 and C94011, whose auditory-nerve characteristics are given in Chapter 1. For convenience, these cats are also referred to as cats A, B, D, E, F, H, I and J,

respectively. Most of the data collected using paradigm 1 were also used for other purposes in our larger study of 2TS. Only those collected using paradigm 2 were specific for this study.

Results

1. Decrease of the CF-alone rate

Figure V-2 shows the post-stimulus time (PST) histograms of one fiber (E11-4) using paradigm 1. The intensity of the 100-Hz suppressor was varied from 70 to 95 dB SPL in 5 dB steps. This fiber showed no response to the suppressor tone alone (500-700 ms), even at the highest suppressor intensity which we used (95 dB SPL). When the suppressor intensity was increased beyond 80 dB SPL, the responses in the middle part (two-tone window, 200-500 ms) were reduced. That is typical 2TS (e.g., Arthur et al., 1971; Hill and Geisler, 1992). But notice that the responses in the first part of the PSTs (0-200 ms), the responses to the CF tone *alone*, were also reduced when the suppressor intensity was high (90-95 dB SPL). In Fig. V-3, the response rates in the three windows vs. suppressor intensity are plotted for the data shown in Fig. V-2, so that the effects of the suppressor may be seen more clearly. For suppressor intensities of 90 and 95 dB SPL, the CF-alone response is clearly depressed. Notice that there was no response to the suppressor tone at any suppressor intensity, even the highest intensity used (95 dB SPL), yet the response rate to CF alone still decreased. This phenomenon is also evident in the Hill and Geisler (1992) data (their Fig. 2A) and in our examples shown in Figs. II-2 (Chapter 2) and III-1 (Chapter 3), where the suppressor tones were excitatory at high intensities. Since this decrease of responsiveness in AN fibers was

seen when the CF tone was acting alone, after the suppressor has been turned off for some time, this phenomenon is hereafter referred to as "*long-term suppression*" (LTS) to distinguish it from the true 2TS which requires both the CF tone and the suppressor tone to act simultaneously.

2. Long-term suppression is not due to fatigue or adaptation

To establish the role of suppressor in the decrease of CF-alone rate, or long-term suppression (LTS), we must show that it can not be (fully) accounted for by fatigue or adaptation, two known mechanisms that might cause a decrease of the discharge rate of auditory nerve fibers. By fatigue, we mean the decrease of responsiveness (and thus the decrease of discharge rate) of AN fibers due to the deterioration of the condition of the cochlea or the AN with time, or after prolonged presentation of stimuli. Since it took a relatively long time to finish one paradigm (7.5 minutes with 1000 ms repetition interval and six suppressor intensities), and the whole experiment on one fiber lasted sometimes more than 1 hour, we think that fatigue must be considered before we can establish the role of the suppressor in LTS. Adaptation generally refers to the decrease of responsiveness when the stimulus is presented over some period of time; it appears to be basically a synaptic phenomenon (Castillo and Katz, 1954; Furukawa et al., 1978; Hayashi et al., 1985). Since adaptation is so common, it must be carefully dealt with. Although the LTS phenomenon existed in cases where the suppressor was also excitatory, for the purpose of distinguishing it from adaptation at the synapse stage, the examples presented below were taken mostly from fibers where either the suppressors were non-excitatory at any intensity used or the responses to the suppressor were not strong.

In experiments presented in Fig. V-4, the suppressor intensity in the first intensity sweep

Fig. V-4 Rate-intensity curves for the CF-alone windows. The data for the 3 curves in each panel were collected successively using paradigm 1. First the suppressor intensity went from low to high (the normal order) (triangle), then from high to low in the second run (square and dashed line), and finally from low to high again (circle). A. C93036, fiber E1, CF = 17500 Hz, SR = 2.0/s, TH = -1 dB SPL. The CF tone was presented at 20 dB SPL. The suppressor frequency was 1000 Hz. B. C94011, fiber J69, CF = 725 Hz, SR = 0.5/s, TH = 16 dB SPL. The CF tone was presented at 30 dB SPL. The suppressor frequency was 100 Hz.

(triangle) went from low (70 dB SPL) to high (90 or 95 dB SPL), in the second sweep (square and dashed line) from high to low, and in the third sweep (circle) from low to high again (arrows indicate directions of intensity change). There was no change in stimulus parameters except for the change in the order of suppressor intensities used. The rates of responses to the CF-tone alone were then plotted against the intensity of the suppressor. In Fig. V-4A (fiber F1), the three rate curves are almost identical, suggesting the rate decrease at higher suppressor intensities was not due to some accumulated effect of the stimuli presented at all previous intensities (i.e., fatigue of the fiber). Otherwise, when the suppressor intensity sequence was going from high to low (square and dashed line, left-pointing arrow), the rates of response at higher intensities should have been higher than those at lower intensities. Another example from another experiment is given in Fig. V-4B (fiber J69). There, the curves for the two intensity sweeps in which the suppressor intensity went from low to high values (denoted by solid lines and right-pointing arrows) were both decreasing. Here again, even though, in the sweep denoted by the dashed line, the intensity went from high to low values, the rates at higher intensities were still lower than those at lower intensities. This phenomenon cannot be accounted for by either fatigue or adaptation. These data suggest that something happening within each high-intensity run (i.e. during the 75 or 25 repetitions at the same stimulus settings) was responsible for the decrease of the CF-alone rate at that particular intensity. Since the only difference between runs was the intensity of the suppressor, the suppressor must be responsible for the decrease of the CF-alone rates, the so-called LTS. The 300 ms off-time in the paradigm used must not have been adequate for the recovery of the fiber from the preceding stimuli, as indicated by the initial decrease of response from 95 to 90 dB SPL in Fig. V-4B (dashed line, when suppressor intensity went from high to low). However, this incomplete recovery is not the major factor responsible for the decrease of CF-alone rate at higher suppressor intensities.

To evaluate the possible role of synaptic adaptation in LTS, let us examine Fig. V-3 again. Notice that the change of rates for CF-alone and suppressor-alone from 85 to 95 dB SPL: the rate for suppressor alone did not increase, but the rate for CF alone decreased dramatically. Since the response rate to the suppressor alone did not increase from 85 to 95 dB SPL, and the responses to the two-tone combination actually *decreased*, the decrease of CF-alone rate at those intensities was not very likely due to adaptation at the synaptic stage.

To further establish the role of the suppressor in the decrease of the CF-alone rate, we turned off the suppressor, but mimicked the increase of suppressor intensity. This was achieved by changing the suppressor intensity from -3 to 0 dB SPL in 1 dB steps. Any sound presented at 0 dB SPL could have no possible effect in the low-frequency tail region of the tuning curve where the threshold is usually well above 50 dB SPL. In this way, the CF tone alone would still be repeated for the same number of trials for each "suppressor intensity" used in the normal case. The result is shown in Fig. V-5 (fiber E60). This fiber had no response to the suppressor even at 95 dB SPL. The solid line was the rate curve when the suppressor was on, and the dashed line was for suppressor intensity from -3 to 0 dB SPL. As can be seen, when the suppressor was effectively turned off, the decrease of CF-alone rate disappeared. This case clearly demonstrates that the adaptation at the synaptic stage can not account for the decrease of the CF-alone rate, for the following reasons. 1). In this case, the suppressor was not excitatory and thus would not contribute anything to adaptation. 2). Since the response of the fiber when the suppressor was turned off was bigger than that when the suppressor was present, the adaptation effect caused by the CF tone must be bigger when the suppressor was off, but there was no decrease of the response to the CF tone when suppressor was not present. 3). Since the responses to the CF tone were reduced by high-intensity suppressor tones in the two-tone segment, any adaptation effects should be less at

higher suppressor intensities than that at lower suppressor intensities.

In an attempt to gather more evidence to support the idea that it was long-term effects of the suppressor tone that caused the decreases of the CF-alone rate, and also in order to characterize the effects, we used paradigm 2. Our initial reasoning for using this paradigm was that it would help exclude any possible effects of fatigue, since both the first half and the second half of each stimulus presentation would be subject to the same factor of fatigue, if any. The second half (without suppressor) would thus serve as a built-in control for the first half (with suppressor). Since there was no suppressor preceding the CF-alone window of the first half (75-200 ms), we expected that the response at this window would not be suppressed, while the response at the corresponding window in the second half (1075-1200 ms for a 2000-ms repetition interval) would be suppressed, since there was a suppressor preceding it. The results were quite a surprise to us. In Fig. V-6A, the rates of responses in the two CF-alone windows of the same fiber as those in Figs. V-2 and V-3 (fiber E11) are plotted against the suppressor intensity. One can see that there was no difference between two curves, both were suppressed (i.e., the response rates decreased with increasing suppressor intensity). However, if we take a look at the corresponding PST histograms (Fig. V-7), we find that, although the *steady-state* portions of the CF-alone responses in the first and second halves were about the same, the *initial* onset portions were different: the initial portion in the first half was clearly bigger than that in the second half (arrows). The initial peak of the second-half response in the PST more resembles that shown in Fig. V-2 at the same intensities, the data for which were collected from the same fiber using paradigm 1 at an earlier time. In Fig. V-6B, we show the discharge rates of the initial portions of the responses (0-50 ms and 1000-1050 ms). One can see clearly that the response rates in the initial 50-ms portions for the first-half and the second-half responses were different, with the

Fig. V-6 Rate-intensity curves for CF-alone windows. Paradigm 2 was used, with a repetition interval of 2000 ms and 25 repetitions. The suppressor was a 100-Hz tone. Same fiber (E11) as in Figs. V-2 and V-3. A. Rate curves for the "*steady-state*" portion of the CF-alone segments in the first half (with an analysis window or AW of 75-200 ms, triangle) and in the second half (1075-1200 ms, square). B. Rate curves for the *initial* onset portion of the CF-alone segments in the first half (0-50 ms, triangle) and the corresponding portion in the second half (1000-1050 ms, square). The corresponding PST histograms are shown in Fig. V-7.

Fig. V-7 The PST histograms from which the rate curves in Fig. V-6 were derived (fiber E11). Compare the initial portions of the first and the second halves of each response (arrows).

response rates in the first-half higher than the corresponding rates in the second half at all intensities, although both were decreasing. This is in contrast to the lack of difference in the responses in the steady-state portions (Fig. V-6A). In Figs. V-8 and V-9, two more such examples were given (fibers E38 and E12). For comparison, the rate curves of the same CF-alone portions taken with paradigm 1 are also plotted in the figure (dashed lines). Both fibers basically showed the same phenomenon as did fiber E11. Clearly, the rate curves of the initial portions of the second-half responses were closer to the ones taken with paradigm 1 (Figs. V-8B and V-9B), while the steady state portions of the first and second halves (Figs. V-8A and V-9A) were nearly the same, both similar to the comparable data taken with paradigm 1.

In Figs. V-6 toV-9, although the total response in the second half was larger than that in the first half (since there was no suppression in the second half, cf. Fig. V-1B), the suppressive effect of the second half on the initial response of the first half was smaller than the suppressive effect of the first half on the initial response of the second half. Thus such suppressive effects can not be explained by adaptation. Since both the CF tone and the suppressor tone were turned off at the same time in paradigm 2 (Fig. V-1B), any extra excitation due to the suppressor-tone alone sometimes seen in fibers with high spontaneous rates (SRs, >= 20/s) when paradigm 1 was used (Fig. V-1A) did not exist with paradigm 2 in most cases (except at very high suppressor intensities where the SUP-alone response exceeds the CF-alone response). Yet we still see the decrease of the CF-alone rate with increasing suppressor intensity (Figs. V-6 to V-9). These results further support the idea that adaptation plays no significant role in the decrease of CF-alone response rate.

Fig. V-8 Another example of the rate-intensity curves for CF-alone windows obtained using paradigm 2, with a repetition interval of 2000 ms and 25 repetitions (C93030, fiber E38, CF = 2140 Hz, SR = 32.5/s, TH = 13 dB SPL). The CF tone was presented at 22 dB SPL. The suppressor frequency was 100 Hz. The curves are arranged as in Fig. V-6. The corresponding rate-intensity curves using paradigm 1 (with 1000-ms repetition interval) are also shown (circle and dashed lines).

3. Characteristics of LTS

The repetition interval required to elicit LTS

A natural question to ask about the decrease of CF-alone rate is what is the minimum repetition interval required to elicit this effect. In some fibers, we kept the stimulus the same as shown in Fig. V-1A for paradigm 1, but varied the repetition interval from 1000 to 4500 ms. The results from two fibers are shown in Fig. V-10. In the example shown in Fig. V-10A (fiber E11), the effect was appreciable at 1000 and 1500 ms but very small when the repetition interval was 2000 ms. Increasing the repetition interval to 3000 ms failed to elicit any LTS. In the example shown in Fig. V-10B (fiber E12), the effect was also minimal when the repetition interval was 3000 ms, although a strong suppression was present for a 2000 ms repetition interval. In a few other fibers we examined, a repetition interval of less than between 2000-4500 ms was usually required to elicit LTS.

Magnitude and threshold of suppression

In order to qualitatively characterize the LTS, we tried to measure the maximum magnitude and the threshold of LTS in all the fibers we studied. We denote the rate of response to the CF-alone at lowest suppressor intensity as R*low*, and that at highest suppressor intensity as R*high*. The magnitude of suppression is then defined as

$$1 - (R_{low} - R_{high})/R_{low} = R_{high} / R_{low}.$$

Figure V-11 shows the magnitude of suppression for all the fibers we studied, as a function of

Fig. V-10 Rate-intensity curves for the steady-state CF-alone windows (75-200 ms) using paradigm 1 with varying repetition intervals (1000 to 3000 ms). A. Fiber E11, same fiber as in Figs. V-2, V-3, V-6 and V-7. B. Fiber E12, same fiber as in Fig. V-9. There were 75 trials averaged when the repetition interval was 1000 ms, and 25 trials averaged when the repetition interval was longer. For each fiber, the LTS disappeared or diminished when a repetition interval of 3000 ms was used.

fiber CF. It can be seen that the great majority of the points fall below 40%, for both lower frequency (50, 100 and 200 Hz, Fig. V-11A) and higher frequency suppressors (500, 1000 and 2000 Hz, Fig. V-11B). There were indeed a number of fibers which showed severe suppression (> 60%), some of the points falling close to 100%. The negative numbers in the figure indicate that the response rate at the highest suppressor intensity was greater than that at the lowest suppressor intensity, presumably due to natural variations in the responsiveness of the fiber. There seems to be no indication of either CF-dependence or suppressor-frequency dependence in the data. In Fig. V-12, the same data are plotted as a function of fiber SR. It is clear that there is a SR-dependence: fibers with lower SRs (< 20/s) generally show greater long-term suppression than those with high SRs. Almost all points showing severe suppression (> 50%) were contributed by lower-SR fibers.

Due to natural variation, it is possible that the CF-alone rate might decrease somewhat without any LTS occurring. Thus we defined the threshold of LTS as the lowest suppressor intensity at which the magnitude of suppression was at or greater than 15%. The particular number chosen (15%) is purely arbitrary. By this criterion, slightly over half of the points in Fig. V-11 did not reach LTS threshold. However, it should keep in mind that in some of the cases the experiment terminated at a relatively low suppressor intensity (highest suppressor intensity used was 95 dB SPL), which was especially true for those with higher suppressor frequencies. If the suppressor intensities had been allowed to go higher, no doubt more fibers would have shown LTS.

The threshold data for the cases where LTS threshold was reached are plotted in Figs. V-13 and V-14 as functions of fiber CF and SR, respectively. For the three lower suppressor frequencies, the threshold was generally above 80 dB SPL, and there is no CF-dependence

(Fig. V-13A). For the three higher suppressor frequencies, the threshold was lower, mostly between 70-90 dB SPL, and there seems to be some CF-dependence, with higher CF fibers having slightly higher thresholds (Fig. V-13B). However, the suppression threshold seems not to be dependent upon fiber SR, regardless of suppressor frequency (Fig. V-14). The lack of SR dependence is significant since most of the high-SR fibers displayed some responsiveness to the suppressor tones. This result is also in agreement with our previous conclusion that adaptation plays at best a minor role in LTS (e.g., Figs. V-5 and V-7).

Effect on response and two-tone suppression phases

Since the LTS affects the magnitude of responses to the CF tone, it was desirable to examine its impact on phases. We used paradigm 1 and increased the repetition interval from 1000 ms to 3000 ms. Since any repetition interval of 3000 ms or more fails to elicit LTS, it is reasonable to assume that the impact of LTS on phase (if any) would also disappear with the same repetition interval. Thus, we would see phase shift, if any, as we changed the repetition interval. In Fig. V-15, the period histograms for three different analysis windows using paradigm 1 are shown. They are for the suppressor alone, two-tone (both binned on the period of suppressor tone), and CF alone (binned on the period of the CF tone). Each column is arranged with increasing repetition interval from top to bottom. The suppressor intensity was 85 dB SPL for CF-alone and two-tone cases. Due to insufficient responsiveness to the suppressor tone at 85 dB SPL, we used the data at the 95 dB SPL for the SUP-alone case. As can be seen, there was no appreciable variation in phase with increasing repetition interval. Hence we conclude that LTS does not affect the phase of responses to the CF tone, the phase of suppression, or the phase of responses to the suppressor-tone alone.

Fig. V-15 Period histograms for CF-alone, two-tone and suppressor alone. The same fiber (E12) as in Figs. V-9 and V-10B. The binning frequency was the CF (1300 Hz) for CF-alone column, and the suppressor frequency (100 Hz) for the two-tone and SUP-alone columns. The suppressor intensity was 85 dB SPL for CF-alone and two-tone columns, but was the 95 dB SPL for SUP-alone column. Paradigm 1 was used. From top to bottom, the repetition interval was 1000, 1500, 2000 and 3000 ms. There were 25 trials summed except for the case with a repetition interval of 1000 ms, in which case there were 75 trials summed. The numbers of spikes shown in the figure were normalized to the equivalent of 250-ms analysis window (as in CF + SUP column) and 75 trials summed, so that the bin heights are comparable.

Discussion

1. The suppression results with paradigm 1

We have shown that the responsiveness of cat's auditory-nerve fibers to a CF tone alone using paradigm 1 were suppressed by a low-side suppressor long after the suppressor tone was turned off. This reduction of CF-alone rate, referred as long-term suppression or LTS here, was not due to fatigue or adaptation, although in the cases where the suppressors were excitatory those effects also existed. The LTS could not be elicited when the repetition interval was longer that about 3000 ms. It did not affect the phases of the responses to the CF tone or to the suppressor tone, nor did it affect the phase of suppression. The fact that LTS only exists when the suppressor intensity is high (generally > 80 dB SPL) suggests that it might be involved in the protection of the ear from loud sounds.

2. The suppression results with paradigm 2

The *equal* response rates in the *steady-state* portions and *unequal* response rates in the *initial* portions of the CF-alone segment with paradigm 2 (Figs. V-6 to V-9) pose a dilemma. We have no satisfactory explanation for these, only to suspect that there might be two separate mechanisms involved: one is faster (< 400 ms) while the other is slower. The slower mechanism might be working all the time and be responsible for the decrease of discharge rates in the steady-state portions of the CF-alone segments in both the first and second halves, while the faster mechanism is responsible for the lower discharge rate in the initial portion of the CF-alone segment in the *second* half of the paradigm. Since the fast mechanism would have already recovered by the time the paradigm is repeated, higher

discharge rates are expected in the initial portion of the CF-alone segment in the *first* half of the paradigm.

The *equal* response rates in the *steady-state* portions of both the first and second halves of the CF-alone segment when paradigm 2 with 2000-ms repetition interval was used seem to be in conflict with the reduction of response rates at high suppressor intensities when paradigm 1 with 2000-ms repetition interval was used (Fig. V-10). We have no explanation for this apparent discrepancy, aside from noting that the CF tone in the second half of paradigm 2 must be responsible for the difference.

3. Possible mechanisms for LTS

The fact that LTS does not require the simultaneous presence of the suppressor tone and the CF tone distinguishes itself from the well known 2TS, which is a direct result of the interaction between the suppressor tone and the CF tone. We have shown that adaptation is not likely to be involved in this phenomenon. The presence of LTS some 3000 ms after the suppressor was turned off suggested that the involvement of cochlear mechanics is less likely. The long recovery time distinguishes LTS from the "offset notch" described by Hill and Geisler (1992), which has a much shorter time constant (5-20 ms). In the following, we consider two main possibilities for LTS: the middle ear reflex and the efferent system.

Middle ear reflex

The generally high threshold of LTS suggests that it might be involved in the protection of ear from loud sounds, which is a function of the middle ear muscle reflex (MER) (Borg and

Nilsson, 1984). Thus it is possible that MER is a mechanism for LTS. There are several points worth consideration. The first point concerns the threshold of suppression. Recently, the threshold of the stapedius-muscle reflex has been linked to the tail of the frequency tuning curve of AN fiber (Borg et al., 1990; Kobler et al., 1992). It is believed that the reflex is triggered by summed activity of AN fibers with both low and high CFs, and that excitation of the high-CF fibers by sounds in their tails is an important factor in eliciting the reflex. The fact that the threshold of LTS was lower with higher frequency suppressors (500, 1000 and 2000 Hz) than that with lower frequency suppressors (50, 100 and 200 Hz) seems to fit with this idea. However, the threshold for the stapedius-muscle reflex is generally high in cats (85-100 dB SPL with ipsilateral stimulation, Kobler et al., 1992). In our data, a lot of high-CF fibers showed LTS thresholds below 80 dB SPL (Fig. V-13B). The second point is the time course of suppression. In one study, Nellis and Wiley (1979) showed that in humans the average recovery time is between 400 and 2500 ms, depending upon stimulus duration and intensity. But most other studies showed that MER has a recovery time around 400-800 ms (e.g., Borg, 1982; Gorga and Stelmachowicz, 1983). Thus in general the recovery time of MER seems to be shorter than the repetition interval that elicits LTS. The third point concerns the magnitude of suppression. It is known that the MER mainly affects low frequency tones, its effect on the high frequency tones is much less (e.g. Teig, 1973; Pang and Peake, 1986). However, the magnitude of suppression produced by LTS showed no difference between low and high CF frequencies (Fig. V-11). Based on the above arguments, we conclude that MER is less likely to be a mechanism for LTS.

Efferent system

The efferent feedback loop is probably the most thoroughly studied feedback system in the

auditory system. The traditional efferent effect ("fast effect") recovers in about 200 ms, as demonstrated by Warren and Liberman (1989) in cat through contralateral acoustical stimulation, and by Art et al. (1982, 1985) in turtle through direct electrical stimulation. Recently, however, a much slower efferent effect (70-90 s) on the compound action potentials of AN fibers has been demonstrated using pulsed electrical shocks (Sridhar et al., 1994, 1995). Although it has not been fully characterized, this "slow effect" is believed to be mediated by the same efferent system. It appears to play an important role in the protection of the ear from loud sounds (Reiter and Liberman, 1995).

The SR dependence of the magnitude of suppression (Fig. V-12) is in agreement with an efferent mechanism, since it is known that the low-SR fiber terminals are preferably innervated by the lateral efferent system (Liberman, 1980b). The existence of suppression long after stimuli are turned off (as compared to the 100-200 ms offset time of fast effect) suggests that LTS is not mainly due to the fast effect. Rather, the similar ranges of repetition interval required to elicit LTS (< 2-4.5 s) and the efferent slow effect (< 4-6 s, Liberman, personal communication) suggests the role of the latter in LTS. However, the results from paradigm 2 suggest that, if the efferent system is indeed responsible for LTS, both the fast and slow effects must be involved, with the fast effect contributing only to the suppression in the initial portion in the second half and the slow effect working throughout the repetition interval (see part 2 of this section). Further studies of both LTS and the efferent slow effect are needed to address this issue.

Note: Roth and Rhode also observed strong long term suppressions with high-side suppressors in their unpublished data. (Rhode, W.S., personal communication.)