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How Broadband Speech May Avoid Neural Firing Rate Saturation at High Intensities and Maintain Intelligibility

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Abstract

While broadband speech may remain perfectly intelligible at levels exceeding 90 dB, narrowband speech intelligibility (e.g., 2/3-octave passband centered at 1.5 kHz) may decline by 25% or more at moderate intensities (e.g., 75 dB). This “rollover” effect is substantially reduced, however, when a speech band is accompanied by flanking bands of white noise [J.A. Bashford, R.M. Warren, & P.W. Lenz, 2005, *J. Acoust. Soc. Am.* 117, 365–369 (2005)], suggesting that lateral suppression helps preserve broadband speech intelligibility at high levels. The present study found that when noise flankers were presented individually at a low spectrum level (–30 dB relative to the speech) only the higher-frequency flanker produced a significant intelligibility increase. However, the lower-frequency flanking noise did produce an equivalent increase when its spectrum level was raised 10 dB. This asymmetrical intensity requirement for noise flankers links the effective dynamic range of speech intelligibility to reported characteristics of both lateral (two-tone) suppression of auditory nerve (AN) fiber activity and lateral inhibition of secondary cells of the cochlear nucleus. These and other observations will be discussed in the broader context of how various auditory mechanisms help preserve speech intelligibility at high intensities by reducing firing rate saturation. [Supported by NIH.]

INTRODUCTION

The auditory system operates very effectively over an extraordinarily broad range of intensities, with a difference limen (DL) of only about 1 dB for signal levels up to 100 dB and a DL of only about 1.5 dB at a signal level of 120 dB (for a review, see Viemeister, 1988). Yet, the large majority of auditory nerve (AN) fibers have far narrower ranges (20 to 40 dB) over which their firing rates can vary with signal level before they reach rate-saturation. This interesting “dynamic range problem” (Viemeister, 1988) is also manifest in the perception of speech, which may remain nearly perfectly intelligible at levels exceeding 90 dB (e.g., Studebaker, Sherbecoe, McDaniel, & Gwaltney, 1999) despite the fact that most AN fibers reach their firing-rate limits at conversational speech levels of about 65 dB, and at higher intensities are unable to provide a firing-rate-based encoding of either the fine spectral details (Sachs & Young, 1979) or amplitude envelope fluctuations (Palmer & Evans, 1979) that encode the critical features of speech.

Viemeister (1983) has examined intensity discrimination limits under conditions that excluded as likely cues both the spread-of-excitation to unsaturated AN fibers and neural

synchrony with temporal fine-structure. He obtained compelling behavioral evidence that the dynamic range of rate-based discrimination does extend to 100 dB, with an acuity of 1 dB, despite the limited ranges of most individual AN fibers. He has also provided a theoretical account of discrimination at high signal intensities (Viemeister, 1983, 1988) that relies on firing-rate information provided by the small population of AN fibers known to have high thresholds and wide dynamic ranges. He has argued that these fibers are sufficient to account for rate-based processing at the upper end of the dynamic range if input from the larger population of readily saturated, low-threshold fibers is excluded from analysis at high signal intensities (see also Siebert, 1968). Physiological models have been proposed (Eriksson & Robert, 1999; Winslow, Barta, & Sachs, 1987) that attribute this exclusionary process to mechanisms of lateral suppression, which reduce input from AN fibers when sufficient stimulation occurs in spectral regions adjacent to their best frequencies. These mechanisms of mutual suppression may include both mechanical (two-tone) suppression within the cochlea (Rhode, 1971) and a substantially more effective neural inhibition of AN input to cells of the cochlear nucleus (Rhode & Greenberg, 1994). In addition, Eriksson and Robert (1999) and Winslow, Barta, and Sachs (1987) have proposed that, at high intensities, lateral inhibition within the cochlear nucleus selectively attenuates input from low-threshold, readily saturated AN fibers, producing a shift in the weighting of intensity analysis to favor input from high-threshold unsaturated fibers.

Behavioral predictions from this lateral inhibition hypothesis were initially tested by Bashford, Warren and Lenz (2005), who used a steeply filtered 2/3-octave band of “everyday” sentences centered at 1500 Hz and found that the narrowband speech was much more vulnerable than broadband speech to a decline, or “rollover” of intelligibility as intensity was increased. A significant intelligibility loss was obtained when speech intensity reached 65 dB, a level at which, as discussed above, most AN neurons are incapable of providing rate-based speech cues. This intelligibility rollover at moderate signal levels was considered to be due to the absence of lateral suppression that would normally be evoked by speech components spectrally adjacent to the 2/3-octave band. Bashford et al. (2005) then tested the conjoint prediction that adding flanking bands of white noise would restore intelligibility of the speech band, by restoring lateral inhibition, but only at a speech intensity sufficient to produce rollover. Listeners were presented with the narrowband sentences at either 45 or 75 dBA slow-peak SPL, without flanking noise, which yielded average intelligibility scores of about 80% vs. 60%, respectively, indicating a substantial rollover effect. When flanking noise bands were added to the 75-dB speech at relative spectrum levels ranging from -40 to -20 dB, intelligibility increased, with a maximum recovery of 13% with noise presented at a level of -30 dB (see stimulus in Figure 1 below). As predicted, however, flanking noise did not increase the intelligibility of the sentences presented at 45 dB.

In a subsequent study, Bashford, Warren, and Lenz (2011) conducted a series of experiments designed to better specify the likely mechanism and site in the auditory pathway responsible for the noise-induced recovery of intelligibility from rollover. They reasoned that if recovery is produced by lateral interactions in the cochlear nucleus, then the effectiveness of the flanking noise bands should not be influenced by binaural lateralization cues processed more centrally in the superior olivary complex. Their test employed an MLD

paradigm in which 75-dB speech was accompanied either by narrowband noise matching the spectral limits of the speech (and producing within-band masking), or by broadband noise (producing both within-band masking and out-of-band reduction of rollover). The noise was presented at a relative spectrum level of -20 dB to ensure that some masking would occur. On half of the trials in the experiment the noise added to the diotic (interaurally identical) sentences was also diotic, and on the remaining trials was interaurally uncorrelated. Decorrelation of the noise was found to produce a binaural release from masking exerted by the within-band noise components in both the narrowband and broadband noise conditions: Intelligibility was about 5% higher in the uncorrelated conditions regardless of noise bandwidth. Crucially, intelligibility was about 13% higher in the broadband noise conditions, regardless of interaural noise correlation, suggesting that the processing responsible for the observed protection against rollover occurs below the level of the superior olivary complex. Bashford et al. (2011) also used the contrasting narrowband and broadband noise conditions to determine whether an adaptation effect peripheral to the cochlear nucleus might also contribute to the effect of flanking noise on rollover. Adaptation, which is a shifting of the operating point of a neuron's dynamic range of firing rates under sustained stimulation, has been observed throughout the auditory pathway, including the auditory nerve (Wen, Wang, Dean, & Delgutte, 2009), midbrain (Dean, Harper, & McAlpine, 2005), and cortex (Watkins & Barbour, 2008). While the lack of a binaural influence on the effects of flanking noise would appear to rule out central adaptation effects, classical firing-rate adaptation in AN fibers might have been produced by the spread of excitation from the flanking noise into the frequency range of the speech band, shifting the operating ranges of the fibers to include higher signal levels (e.g., Gibson, Young, & Costalupes, 1985). To test this hypothesis, 75-dB rectangular 2/3-octave speech was accompanied by either spectrally matching narrowband noise or broadband noise at -20 dB relative spectrum level, and on half of the trials the noise was continuous while on the remaining trials it was gated on and off with individual sentences. As expected, an "overshoot" of within-band masking did occur with the gated noise: Intelligibility was about 5% lower in that condition, whether the noise was spectrally matching or broadband. Importantly, however, intelligibility was about 11% higher with broadband rather than narrowband noise, regardless of gating, ruling out peripheral adaptation as a contributor to the flanking noise effect on rollover.

Bashford et al. (2011) also examined the possible role of two additional mechanisms that might contribute to the intelligibility enhancing effect of flanking noise at high speech intensities: the middle ear (aural) reflex and the medial olivocochlear (MOC) reflex. Aural reflex contractions of the tensor tympani and stapedious muscles stiffen the joints of the middle ear and produce an increase in mechanical impedance and reduced input to the cochlea. This attenuation, typically ranging from 5 to 10 dB but found in some studies to be as great as 20 to 30 dB (Durrant & Lovrinic, 1995), is believed to be primarily protective in function, and can be evoked by either ipsilateral or contralateral sound input. The MOC reflex also produces mechanical attenuation of cochlear vibration, evoked equally well by ipsilateral or contralateral input (Guinan, 2006), but it does so in a different fashion. Neurons in the olivary complex form a feedback loop, receiving input from the cochlear nucleus and sending efferent projections back to both cochlea, which hyperpolarize the outer

hair cells, especially in response to wideband noise, and turn down the gain of the cochlear amplifier (e.g., Lilaonitkul & Guinan, 2009). In addition to providing a protective function for the delicate structures of the cochlea (Cody & Johnstone, 1982), the MOC reflex is also thought to improve the auditory nerve's signal-to-noise ratio by reducing its response to background noise (e.g., Dolan & Nuttall, 1988). An effective attenuation of 10 dB or more may be produced with ipsilateral or contralateral presentation of broadband noise (Warren & Liberman, 1989). In order to examine the possible role of the aural and MOC reflexes in reducing rollover, Bashford et al. (2011) contrasted the effects of ipsilateral vs. contralateral flanking noise bands on the intelligibility of narrowband sentences presented monaurally at 75 dB. When ipsilateral flanking noise was added to the speech band at -30 dB relative spectrum level a significant intelligibility increase was obtained relative to a no-noise baseline condition (64.6% vs. 57.5%). However no increase occurred when the flanking noise bands were presented contralaterally at levels ranging from -30 to -10 dB; intelligibility in those conditions ranged from 55.7 to 57.6%, strongly indicating that neither the aural nor MOC reflex contribute to the reduction of rollover under these conditions.

With a number of possible alternative mechanisms now eliminated from consideration, the present study focuses on a specific prediction from the CN lateral inhibition hypothesis. Lateral interactions observed between cells of the cochlear nucleus show a striking asymmetry: Higher-frequency inhibitors are generally effective at substantially lower intensities (often by 20 dB or more) than lower-frequency inhibitors (e.g., Rhode & Greenberg, 1994). The present study tested for a corresponding asymmetry in the effects of high- vs. low-frequency flanking bands on the rollover of intelligibility for narrowband speech presented at 75 dB. In experiment 1, flanking bands of white noise were presented at a relative spectrum level of -30 dB. It was expected that this low level of noise stimulation would reveal the higher activation level for suppression by the low frequency noise band. In experiment 2, the spectrum level of the noise required to reduce rollover was determined separately for the lowpass and highpass flanking noise bands, using separate groups of listeners. Experiment 3 employed flankers derived from speech-shaped (USASI) noise, which boosted the noise-power per unit bandwidth of the low frequency noise band by roughly 20 dB relative to the higher noise band, and permitted an evaluation of the compatibility between the asymmetrical thresholds of activation for lateral inhibition and the spectral tilt of speech.

METHODS

Listeners

The 88 listeners in this study (24 each in Experiments 1, and 3, and two groups of 20 in Experiment 2) were undergraduate students at the University of Wisconsin-Milwaukee who were paid for their participation. They ranged in age from 18 to 30 and were native monolingual English speakers who reported having no hearing problems and had normal bilateral hearing, as measured by pure tone thresholds of 20 dB HL or better at octave frequencies from 250 to 8,000 Hz.

Stimuli

The formal test stimuli were the 100 (10 lists of 10) CID "everyday" sentences (Silverman and Hirsh, 1955). They were derived from a broadband digital recording (44.1 kHz sampling, 16-bit quantization) used previously by Bashford et al. (2005). An additional 25 practice sentences were drawn from the high predictability sublist of the revised Speech Perception in Noise (SPIN) test (Bilger, Nuetzel, Rabinowitz, & Rzeczkowski, 1984; Kalikow, Stevens, & Elliott, 1977). The recordings were produced by the same male speaker who had no evident regional accent and an average voicing frequency of 100 Hz. Prior to filtering, the sentences were digitally matched to within 0.2 dBA in slow-rms peak level, and then passed through two successive stages of 4000-order band-pass FIR filtering, using the `fir1` function in MATLAB, to produce a 2/3-octave narrow band of speech, centered at 1500 Hz (passband from 1191 Hz to 1890 Hz), with both low-pass and high-pass filter slopes exceeding 3000 dB/octave. White noise, low-pass filtered at 20 kHz, was used to produce the lowpass and highpass flanking noise bands employed in experiments 1 and 2 and a band of USASI speech noise, also lowpass filtered at 20 kHz was used to derive the flankers presented in Experiment 3. The low-pass and high-pass flankers were each produced through two successive stages of 4000-order FIR filtering, as with the speech band, yielding a rolloff of more than 3000 dB/octave). The low-frequency limit of the lower flanking band and the high-frequency limit of the higher flanking band matched those of the broadband noise. Separate pairs of flanking noise bands were prepared for each noise spectrum-level employed in the present study (−10, −20, −30, and −40 dB relative to the speech spectrum-level). Noise cutoff frequencies for each pair were adjusted so that the filter skirts of the flanking noise bands intersected the skirts of the speech band at an average level 60-dB below that of the speech cutoff frequencies.

GENERAL PROCEDURE

The design of each experiment incorporated repeated measures. Before receiving a given stimulus condition listeners were presented with 5 practice sentences, which were first presented broadband and then presented bandpass filtered, along with noise when appropriate, in the same manner as the test sentences that followed. The different experimental conditions presented to a given group of listeners were assigned to separate sets of the "everyday" test sentences. This assignment varied pseudorandomly, so that, across listeners in a group, each condition was applied an equal number of times to each set of sentences.

Experiment 1: Extent of Rollover Recovery Produced by Lowpass vs. Highpass Flanking Noise Bands Presented at Matched Levels

Experiment 1 examined the relative effectiveness of lowpass and highpass flanking bands of white noise when presented at the −30 dB relative spectrum level previously found optimal for matched flanker levels by Bashford et al. (2005). The 24 listeners in this experiment were presented with separate sets of 25 "everyday" sentences in each of four flanking noise conditions: 1) a no-noise baseline condition; 2) a lowpass noise condition; 3) a highpass noise condition; and 4) a condition in which both flanking noise bands were added to the 75-

dB speech. Table 1 presents the mean percent repetition accuracy for the sentence keywords in each condition, along with standard errors.

The main effect of noise conditions was significant [$F(3,69) = 5.1, p < 0.004$], and a set of orthogonal, single-df contrasts comparing the "no-noise" baseline condition with the remaining conditions indicated that the highpass noise flanker ($F = 4.6, p < 0.04$) and the combination of highpass and lowpass flankers ($F = 23.4, p < 0.001$) did produce a significant recovery from rollover, whereas the lowpass flanker alone did not ($F = 0.46, p > 0.5$). Performance in the two effective conditions did not differ by Tukey test ($p > 0.05$). These results provide preliminary evidence of a difference in the level requirements for rollover reduction by lowpass vs. highpass flanking noise that is generally consistent with the asymmetry in activation thresholds for lateral inhibition evoked by lower vs. higher frequency suppressors. Experiment 2 replicated and extended this finding by providing a more detailed examination of the range of levels over which the lowpass and highpass flanking bands of white noise effectively reduce rollover.

Experiment 2: Effects of Level on the Effectiveness of Lowpass vs. Highpass Flanking Noise Bands in Reducing Speech Intelligibility Rollover

In this experiment separate groups of 20 listeners each were employed to determine the spectrum levels required for lowpass vs. highpass flanking noise bands to reduce intelligibility rollover of the 75 dB 2/3-octave sentences. Both the lowpass- and highpass-flanker groups were presented with 20 sentences in each of five conditions, which included a no-noise baseline condition and four conditions presenting the flanking noise band at spectrum levels of $-40, -30, -20$, and -10 dB relative to the speech band. Table 2 presents the mean percent repetition accuracy for the sentence keywords in each condition, along with their standard errors.

Significant main effects of level were obtained for both the lowpass [$F(4,76) = 3.2, p < 0.02$] and highpass [$F(4,76) = 3.0, p < 0.03$] flanking noise bands. For the lowpass flanker, orthogonal contrasts comparing baseline intelligibility with that obtained with noise present indicated that only the -20 dB spectrum level lowpass flanker condition produced a significant recovery from rollover [$F = 10.1, p < 0.005$]. In contrast, the highpass flanking noise produced a reliable recovery at -30 dB [$F = 7.4, p < 0.02$] and -20 dB [$F = 11.8, p < 0.003$], as well as a marginally significant recovery of intelligibility at -40 dB [$F = 4.2, p < 0.06$], which provides tentative behavioral evidence of a roughly 20-dB difference in minimal level requirements for the lowpass vs. highpass flankers. This difference is consistent with typical physiologically measured differences in activation thresholds for low-side vs. high-side inhibition in the cochlear nucleus (e.g., Rhode & Greenberg, 1994). However, given the pronounced spectral tilt of the speech signal, results obtained with white noise flankers may not provide the best estimate of potential benefits from lateral inhibition evoked by adjacent speech components. In particular, the contribution of low-side inhibition to speech intelligibility might be compromised by a greater upward spread of masking. To evaluate this possibility, Experiment 3 employed flanking bands derived from USASI speech-noise, with spectral components of the flanking noise directly contiguous with the

speech band adjusted to the –20 dB relative spectrum level found effective for both bands in Experiment 2.

Experiment 3: Extent of Rollover Recovery Produced by Lowpass vs. Highpass Flanking Bands of USASI Speech-Shaped Noise Presented at –20 dB Spectrum Level Relative to the 75 dB Speech Band

Experiment 3 employed the same design as that used in Experiment 1, with listeners presented 25 sentences in each of the four conditions: the no-noise baseline condition, lowpass noise alone, highpass noise alone, and both flanking bands. Mean percent repetition accuracy and standard errors are presented in Table 3.

The main effect of noise condition was significant [$F(3,69) = 12.0$, $p < 0.001$], and orthogonal contrasts indicated that intelligibility increased significantly with the addition of lowpass flanking noise alone [$F = 17.4$, $p < 0.001$], highpass flanking noise alone [$F = 6.3$, $p < 0.02$], and also when both noise bands were added [$F = 38.4$, $p < 0.001$]. Intelligibility in the lowpass and highpass conditions did not differ by Tukey test, but the dual flanker condition produced higher intelligibility than the highpass flanker alone ($p < 0.05$).

The results of Experiments 1–3 are consistent with characteristics of lateral inhibition and its proposed function in reducing rate-saturation by high-intensity signals. The results of Experiment 3 further indicate that the asymmetrical thresholds for low- and high-side inhibition are well suited to the spectral tilt of speech, at least in the midrange of the spectrum. A functional role of inhibition evoked by noise 40 dB below the speech signal, as found in Experiment 2, is also consistent with the wide dynamic ranges of some CN interneurons (e.g., onset-choppers) thought to mediate lateral inhibition (Winter & Palmer, 1995). What remains to be determined is whether a significant subset of such neurons are strictly ipsilateral in operation, as is the reduction of intelligibility rollover produced by flanking noise in our paradigm (Bashford et al., 2011).

It should be pointed out that two additional apparently ipsilateral mechanisms might make some contribution to intelligibility rollover reduction under some conditions. Two-tone suppression within the cochlea may provide limited control over rate saturation, but available evidence suggests those effects would be negligible for signals of 75 dB, even with suppressors of equal intensity (e.g., Humes, 1980; Ruggero, Robles, & Rich, 1992), and would not likely be evoked at all by suppressors as much as 40 dB lower in level, as was found for rollover reduction evoked by flanking highpass noise in the present study. Another mechanism believed to act only ipsilaterally is the lateral olivary complex (LOC) reflex, which provides both excitatory and inhibitory innervation to AN neurons synapsed with inner hair cells. This rather poorly understood reflex is believed to be involved in balancing the response of the auditory nerves from the two ears for accurate localization (Darrow, Maison, & Liberman, 2006). The fact that the efferent LOC fibers projecting to the cochlea are nonmyelinated, suggests that their effects would be too diffuse to provide the selective attenuation of low-threshold, readily saturated AN fibers required by theory (Siebert, 1968; Viemeister, 1983; Eriksson & Robert, 1999; Winslow, Barta, & Sachs, 1987).

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FIGURE 1.

Spectral plot of stimuli used by Bashford et al. (2005). A 2/3-octave rectangular band of everyday sentences was presented either alone or along with flanking bands of white noise.

TABLE 1

Mean percent intelligibility scores and standard errors (N = 24) for 2/3-octave narrowband sentences presented at a slow-rms peak level of 75 dBA along with either: no flanking noise bands; lowpass flanking noise; highpass flanking noise, or both lowpass and highpass flanking bands of white noise presented at –30 dB spectrum level relative to the speech.

No Noise	Lowpass Noise	Highpass Noise	Both Noise Bands
64.0 (1.9)	66.0 (2.7)	70.1 (2.2)	73.2 (1.8)

TABLE 2

Mean percent intelligibility scores and standard errors for 2/3-octave narrowband sentences presented at a slow-rms peak level of 75 dBA along with either no flanking noise, or with noise at one of four spectrum levels relative to the speech: -40, -30, -20, or -10 dB. Separate groups of 20 listeners received the lowpass and highpass flanking noise conditions.

Flanking Noise	No Noise	-40 dB Noise	-30 dB Noise	-20 dB Noise	-10 dB Noise
Highpass Group	64.5 (1.7)	69.4 (1.5)	71.4 (2.1)	71.2 (1.1)	70.8 (2.1)
Lowpass Group	65.0 (1.5)	65.7 (1.1)	67.0 (1.7)	71.8 (1.8)	64.7 (1.8)

TABLE 3

Mean percent intelligibility scores and standard errors (N = 24) for 2/3-octave narrowband sentences presented at a slow-rms peak level of 75 dBA along with either: no flanking noise bands; lowpass flanking noise; highpass flanking noise, or both lowpass and highpass flanking bands of white noise presented at –30 dB spectrum level relative to the speech.

No Noise	Lowpass Noise	Highpass Noise	Both Noise Bands
65.1 (2.2)	72.7 (1.8)	70.5 (2.2)	76.0 (2.1)