EFFECTS OF COCHLEAR COMPRESSION AND EFFERENT FEEDBACK ON AMPLITUDE MODULATION DETECTION

by

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STATEMENT OF DISSERTATION APPROVAL

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ABSTRACT

Amplitude modulation (AM) detection measures a listener's sensitivity to temporal envelope fluctuations. AM signals are ecologically relevant because the amplitude of speech fluctuates over time. The post-cochlear representation of AM may be influenced by processes that occur in the cochlea, where signals are subject to cochlear compression and adaptive mechanisms that modulate the cochlear response such as the medial olivocochlear (MOC) reflex. Specifically, cochlear compression may reduce the difference between high-intensity peaks and low-intensity valleys (i.e., effective modulation depth) of AM. Furthermore, gain reduction of the cochlear amplifier via the MOC reflex is hypothesized to decompress the cochlear input-output function and thus improve the AM effective modulation depth at moderate levels. To test these hypotheses, AM detection was measured for a narrow-band, high-frequency carrier (5000 Hz) for conditions that do or do not elicit the MOC reflex. These conditions take advantage of the sluggish onset of the reflex, which exhibits an onset delay ($\sim$25 ms) upon stimulation. Specifically, AM detection was measured as a function of level for a 50 ms carrier in the presence and absence of a long ipsilateral notched-noise precursor. A longer carrier (500 ms) without a precursor was also included. For no-precursor condition, AM detection thresholds at moderate carrier levels are poorer compared to low and high levels, consistent with a reduced effective modulation depth due to cochlear compression. In the precursor condition, AM thresholds improved monotonically with carrier level, with the largest improvements seen at moderate levels. This improvement is consistent with decompression of the cochlear input-output function via the MOC reflex. For 500 ms carriers, AM detection thresholds improved by a constant (across all carrier levels) relative to AM thresholds with a precursor, consistent with the longer carrier providing more "looks" to detect the AM signal. In a second experiment, AM thresholds were measured as a function of modulation frequency to examine whether the effects of the precursor depend on the modulation frequency. The results showed that the improvement in AM detection with

compared to without a precursor is limited to low modulation frequencies (<60 Hz).

The experiment in Chapter 3 was designed to examine the effects of cochlear compression on the inherent fluctuations of narrow-band noise carriers. To test this, AM detection was measured for short and long, high- and low-fluctuating noise carriers as a function of carrier level. The results showed that AM thresholds for short, low-fluctuating noise carriers worsened as carrier level increased from low to mid carrier levels and then improved with further increases in carrier level, as found in the previous experiment. This is consistent with greater cochlear compression at moderate levels. For high-fluctuating carriers, AM thresholds were roughly constant across carrier levels. For high-fluctuating carriers, low-level linear and mid-level compressive cochlear response growth may have resulted in constant envelope signal-to-noise ratios, due to the cochlear response growth equally affecting the target modulation and inherent carrier fluctuations. Thus, AM detection for high-fluctuating carriers is constant as a function of carrier level.

CONTENTS

CHAPTERS

LIST OF FIGURES

LIST OF TABLES

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CHAPTER 1

INTRODUCTION

1.1 Background

The intensity resolution of the auditory system plays an important role for processing complex signals such as speech. Several psychophysical studies have shown that the auditory system is sensitive to small changes in intensity over a wide range of sound levels ∼120 dB (Viemeister, 1988). This wide perceptual dynamic range occurs despite the dynamic range of most auditory nerve fibers (i.e., high spontaneous rate [SR] fibers) being limited to ≤35 dB (Evans & Palmer, 1980). The ability of the auditory system to encode changes in intensity over the dynamic range of hearing is crucial for identifying, discriminating, and understanding environmental sounds (Green, 1983). The intensity resolution of the auditory system can be measured psychophysically using tasks such as intensity discrimination (Florentine et al., 1987, Jesteadt et al., 1977, Miller, 1947), increment detection (Viemeister & Bacon, 1988), and amplitude modulation (AM) detection (Long & Cullen, 1985; Zwicker & Fastl, 1990). Intensity discrimination experiments measure the smallest difference in intensity between a test signal and a standard signal (i.e., "pedestal") that the listeners can perceive. In this paradigm, the test and pedestal signals are identical in all aspects except intensity. Increment detection experiments measure the ability of a listener to detect a short-intensity increment within a longer pedestal. AM detection experiments measure the modulation depth necessary to just detect amplitude modulation occurring in a noise or sinusoidal carrier.

Psychophysical studies have shown that intensity resolution depends heavily on stimulus parameters such as intensity (Florentine & Buus, 1981; Jesteadt et al., 1977; McGill & Goldberg, 1968; Rabinowitz et al., 1976), frequency (Carlyon & Moore 1984; Florentine, 1983; Florentine et al., 1987) , and duration (Carlyon & Moore, 1984; Florentine, 1986; Nizami, 2006; Nizmie et al., 2001). For long wide-band and narrow-band pedestals ($\geq$ 500 ms), intensity resolution is constant (Miller, 1947) or improves with sound level (Jesteadt et al., 1977; McGill & Goldberg, 1968; Rabinowitz et al., 1976), respectively. However, for short (≤30 ms), narrow-band pedestals, intensity resolution deteriorates at moderate pedestal levels (Carlyon & Moore, 1984; Nizami; 2006; Roverud & Strickland, 2015a). This deterioration has been termed the “mid-level hump” (Nizami, 2006; Zeng et al., 1991) and is consistent with basilar membrane mechanics, which exhibit compressive nonlinearity at moderate to high levels for tones presented at the characteristic frequency (CF) (Heinz et al., 2001; Pienkowski & Hagerman, 2009; Roverud & Strickland, 2015a). Moreover, recent studies have shown that the mid-level hump is reduced, due to improved performance at moderate pedestal levels when a short pedestal (≤30 ms) is preceded by long (150 ms) ipsilateral or bilateral noise precursors (Roverud & Strickland, 2015a,b). This improvement at moderate levels is consistent with a reduction in cochlear gain over the course of the precursor (Roverud & Strickland, 2015b), perhaps via the medial olivocochlear (MOC) reflex. This explanation is based on the temporal and physiological properties of the MOC reflex, which regulates the outer hair cell (OHC) gain, resulting in decompression of the cochlear response (Guinan, 2006; Russel & Murugasu, 1997). Decompression of the cochlear response is expected to improve the difference between the test and pedestal signal at the output of the cochlea. The MOC reflex exhibits an onset delay of 25 ms, followed by a build-up in response strength with a time constant of about 70-100 ms (Backus & Guinan, 2006) . This suggests that listeners are more sensitive in detecting the target when preceded by a precursor that is assumed to activate the MOC reflex.

In addition to intensity discrimination experiments, intensity resolution can be assessed by measuring AM detection. Much of the semantic information contained in speech and animal vocalization is carried by gross amplitude fluctuations over time, known as the stimulus envelope (Rosen, 1992). Laboratory AM signals consist of a carrier (Figure 1.1A) whose amplitude is modulated at a specific frequency (i.e., modulation frequency, Figure 1.1B). The resulting modulated signal is characterized by gross fluctuations of the carrier’s amplitude over time (Figure 1.1C). In psychophysical experiments, AM detection thresholds reveal the amount of modulation depth (indicated by the double arrow in Figure 1.1C) needed for a listener to discriminate between the modulated and an unmodulated carrier. AM detection thresholds are usually expressed as 20*log m, where m is the modulation

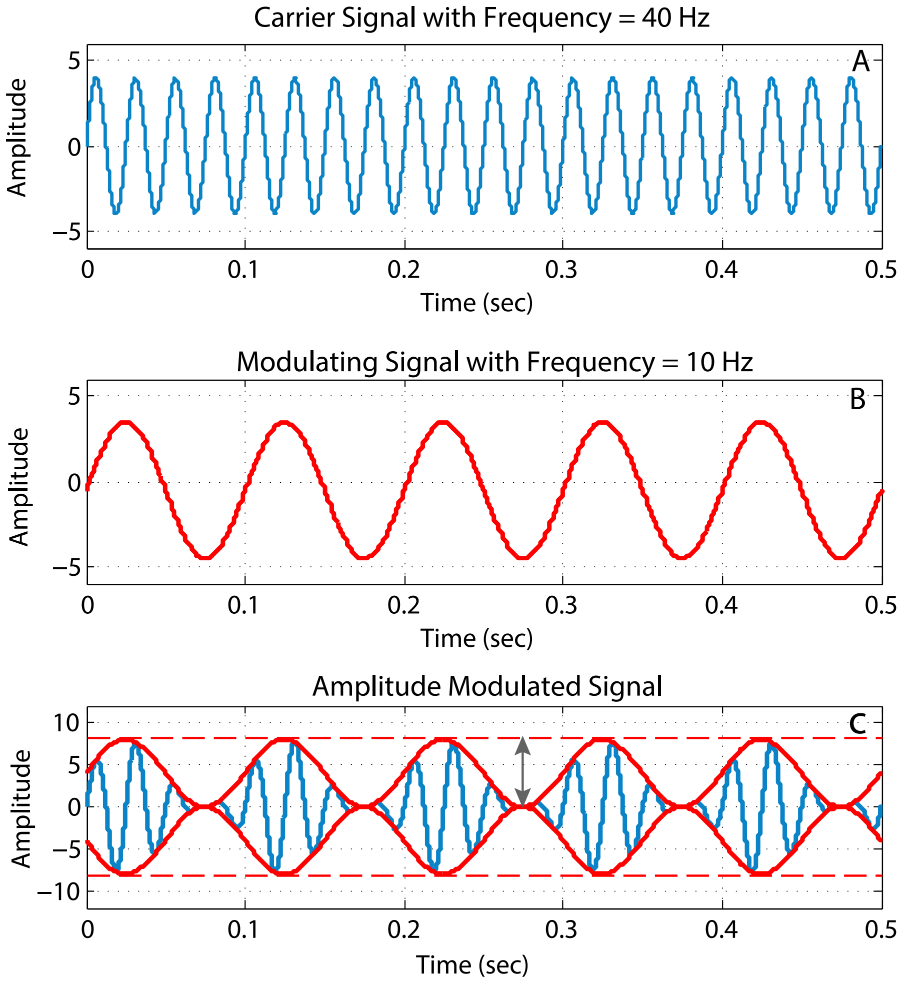

Figure 1.1. Laboratory amplitude modulated (AM) signal. Illustration of the carrier, modulator, and modulated signal. A sinusoidal carrier (A) is modulated at 10 Hz (B) producing an amplitude modulated signal (C). The double arrows indicate the modulation depth for this fully modulated AM signal.

index (m = 0 corresponds to no modulation and m = 1 corresponds to 100% modulation). An illustration of a fully modulated waveform is shown in Figure 1.1C. The experiments presented in this manuscript use AM detection to examine the hypothesis that AM detection for short narrow-band noise carriers is relatively poorer at moderate levels than at lower or higher levels, consistent with cochlear compression. Furthermore, this study tests whether the presence of a precursor preceding a short narrow-band noise carrier or long carriers without a precursor improves AM detection thresholds at moderate carrier levels, consistent with a reduction in cochlear gain, perhaps via the MOC reflex.

1.2 Effects of level on intensity discrimination and AM detection

Intensity discrimination thresholds for long ($\geq$500 ms) wide-band noise are roughly constant over a wide range of stimulus levels (Figure 1.2, closed triangles, 10-65 dB SPL), and therefore follow Weber's law (Miller, 1947; Viemeister, 1974). Weber's law states that the smallest detectable change in intensity between a standard and a test signal is proportional to the intensity of the standard. For long pure tones presented in quiet, intensity discrimination improves monotonically with level, resulting in the "near miss" to Weber's law (Figure 1.2, open triangles) (Florentine & Buus, 1981; Florentine et al., 1987; Jesteadt et al., 1977; Rabinowitz et al., 1976). Florentine and Buus (1981) showed that the near miss to Weber's law is consistent with the recruitment of off-frequency auditory filters via upward spread of basilar membrane excitation. Evidence for this interpretation is supported by studies showing that intensity discrimination of long tones is constant at higher pedestal levels when the spread of excitation is blocked by presenting noise at frequencies surrounding the pedestal frequency (Moore & Raab, 1974; Plack & Viemeister, 1992), or through the use of very-high-frequency pedestals (Florentine et al., 1987).

For short narrow-band stimuli ($\leq$30 ms), intensity discrimination thresholds are better at low and high levels than at moderate levels (Figure 1.3). The worsening of thresholds at moderate levels has been termed the "severe departure from Weber's law" (Carlyon & Moore, 1984) or the "mid-level hump" (Nizami, 2006; Zeng et al., 1991). This mid-level hump increases in size (higher peak) when off-frequency listening is blocked by gating a notched-noise with the pedestal (Carlyon & Moore, 1984), suggesting that the mid-level hump originates from processes within an auditory filter centered on the pedestal frequency.

Intensity resolution of the auditory system can also be revealed by examining a listener's ability to detect AM. Sinusoidal AM signals are ecologically relevant because the amplitude of speech fluctuates over time. A modulated carrier fluctuates over time and that these experimentally imposed fluctuations can be applied over a range of modulation frequencies, which may approximate speech signals. These fluctuations can be divided into two components including the envelope and fine structure. Based on the Rosen (1992) classification of speech temporal information, the envelope represents slow modulations (e.g., 2-50 Hz) and fine structure represents rapid modulations (e.g., 600-10000 Hz).

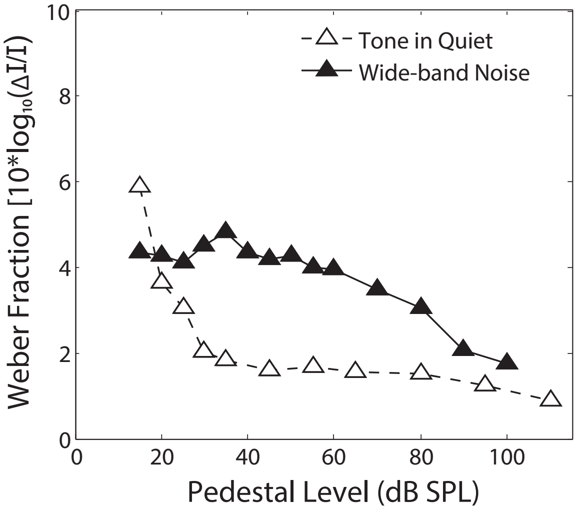

Figure 1.2. Intensity discrimination data expressed as 10*log$_{10}$(ΔI/I) as a function of pedestal level in dB SPL. Closed triangles represent data for detecting an increment in continuous wide-band noise from Miller (1947) where Weber fraction is constant over a wide range of pedestal levels and thus follows Weber's law. Open triangles represent data for pure tones in quiet replotted from Viemeister and Bacon (1988) showing improvement in Weber fraction as the pedestal level increases, reflecting the "near miss" to Weber's law.

The effects of carrier level on AM detection have been examined using wide-band noise carriers (Bacon & Gleitman, 1992; Bacon & Viemeister, 1985; Viemeister, 1979) and sinusoidal carriers (Kohlrausch et al., 2000; Millman & Bacon, 2008; Moore & Glasberg, 2001; Zwicker & Fastl, 1990). For long wide-band noise carriers, AM detection thresholds are generally constant as a function of carrier level regardless of modulation frequency (Bacon & Gleitman, 1992; Bacon & Viemeister, 1985; Viemeister, 197). Thus, Weber's law holds for AM detection measured with long, wide-band noise carriers. For long sinusoidal carriers, AM detection thresholds improve monotonically with increasing carrier level (Kohlrausch et al., 2000; Millman & Bacon, 2008; Moore & Glasberg, 2001), which is reminiscent of the "near miss" to Weber's law. As with intensity discrimination, improved AM detection thresholds as a function of tonal carrier level may be facilitated by recruitment of off-frequency auditory filters via spread of excitation cues (Millman & Bacon, 2008). For long, high-frequency (>4000 Hz), tonal carriers, AM detection thresholds at low modulation frequencies (<8 Hz) are worse at moderate levels than at lower or higher levels (Long & Cullen, 1985), reminiscent of the mid-level hump. This suggests that AM detection and intensity discrimi-

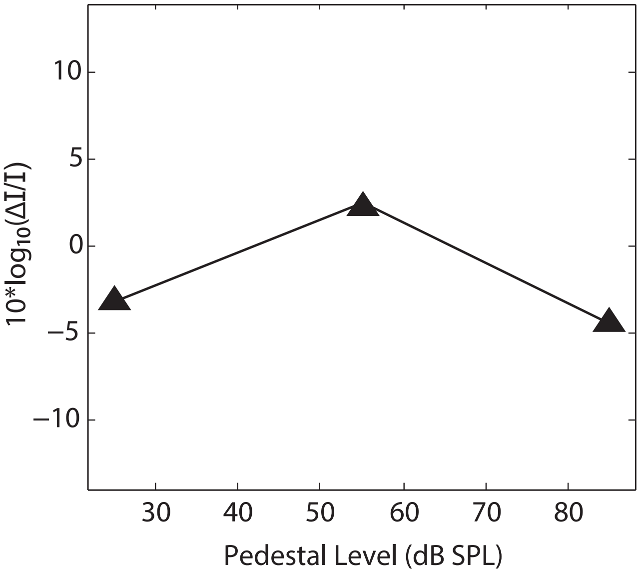

Figure 1.3. Intensity discrimination data expressed as 10*$\log_{10}(\Delta I/\mathrm{I})$ as a function of pedestal level in dB SPL replotted from Carlyon and Moore (1984). The stimulus was a 6.5 kHz, 26 ms pure tone. Intensity discrimination thresholds are poorer at moderate levels than low and high pedestals levels, reflecting the mid-level hump.

nation are sensitive to the same processes, which may determine the intensity resolution of the auditory system (Wojtczak & Viemeister, 1999).

1.3 Explanation of the mid-level hump

1.3.1 Coding gap in the firing rate of auditory nerve fibers

Several hypotheses have been proposed to explain the presence of the mid-level hump in intensity discrimination for short narrow-band stimuli (Plack, 1998). Carlyon and Moore (1984) and Zeng et al. (1991) suggested that the mid-level hump is consistent with the finding that at moderate levels, high- and low-SR fibers are saturated or near/below threshold, respectively, consistent with poorer intensity discrimination at moderate levels than at higher or lower levels. Heinz et al. (2001) found that this "two-fiber population" hypothesis was not supported by computational model simulations because the transition between high- and low-SR populations occurred at levels higher than the mid-level hump (80-90 dB SPL), and because the presence of medium SR fibers (Liberman, 1978) covered the supposed gap in sound-level coding.

1.3.2 Cochlear compression

Recently, studies have shown that the mid-level hump in intensity discrimination is consistent with cochlear compression at moderate levels (Heinz et al., 2001; Pienkowski & Hagerman, 2009; Roverud & Strickland, 2015b). By definition, cochlear compression refers to the progressively slower rate of cochlear response growth with increasing stimulus level. Cochlear compression is a by-product of the cochlear amplifier (Cooper, 2004), which is associated with the OHCs. The cochlear amplifier provides gain to the passive response of the basilar membrane, especially at low sound levels (Davis, 1983). This gain can be as much as 60 dB at the base of the cochlea (Ruggero et al., 1997). Cochlear compression is best illustrated by considering the cochlear input-output (I/O) function (Figure 1.4), which is measured by observing the response of the basilar membrane to tone pips as a function of level. For tones presented at or near the characteristic frequency (CF), basilar membrane responses are linear (1 dB/dB) at low stimulus levels and compressive (<1 dB/dB) at moderate to high stimulus levels (Rhode, 1971; Ruggero et al., 1997; Sellick et al., 1982), as shown by the solid I/O function in Figure 1.4. Thus, a given change in sound intensity (e.g., from 30 to 80 dB SPL) will result in a smaller change (10 dB) in basilar membrane motion. This compressive nonlinearity is expected to decrease the effective (i.e., post-cochlear) ratio between standard and test pedestals. Conversely, the response growth of the basilar membrane to tones whose frequencies are well below the CF is linear across all stimulus levels (Ruggero et al., 1997) as shown by the dashed line in Figure 1.4. To examine whether the mid-level hump is consistent with cochlear compression, Roverud and Strickland (2015a) measured (1) psychophysical intensity discrimination for short (30-ms), high-frequency tones (6 kHz) in quiet and (2) growth of forward masking for off-frequency maskers from the same listeners. Off-frequency growth of forward masking provides a behavioral estimate of basilar membrane compression (Oxenham & Plack, 1997). Roverud and Strickland (2015a) found a significant correlation for most subjects (7/10) between intensity discrimination thresholds for short pedestals and the slope of growth-of-masking. Specifically, intensity discrimination thresholds from low-to-moderate levels were significantly higher (poorer) for subjects with the shallowest growth-of-masking slopes (i.e., the most compression). Furthermore, using a roving-level paradigm, Pienkowski and Hagerman (2009) compared intensity discrimination of 4 kHz, 300 and 4 ms tones between listeners with normal hearing

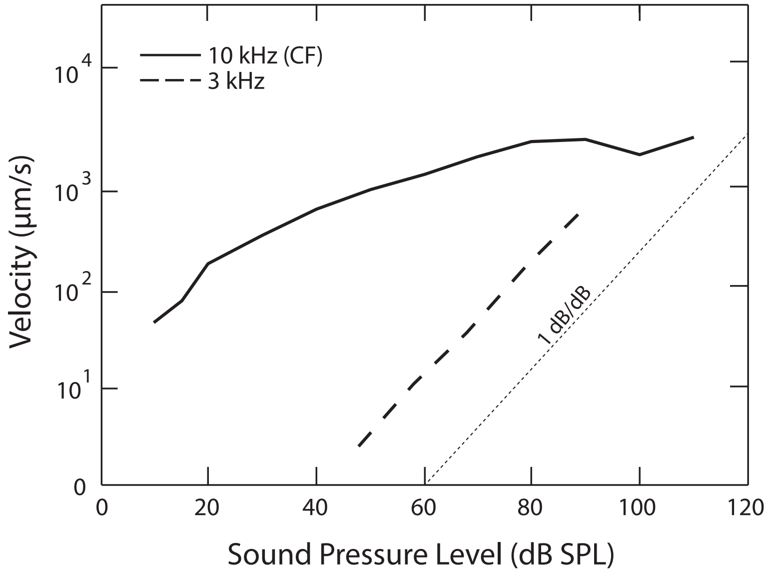

Figure 1.4. Basilar membrane input-output (I/O) functions measured from the cochlea of a healthy chinchilla. This function was obtained from measurements made at a basilar membrane location corresponding to a 10 kHz characteristic frequency (CF). The dashed line represents measurements obtained with low-frequency tone pips (3 kHz). The dotted line represents a linear reference (1 dB/dB). Figure is adapted from Ruggero et al. (1997).

and listeners with mild-to-moderate sensorineural hearing loss, who are expected to have relatively more linear I/O function slopes. In normal-hearing listeners, they observed a mid-level hump for intensity discrimination of 300-ms tones with pedestal levels roved over a wide range. For the same conditions, intensity discrimination thresholds for hearing-impaired listeners improved monotonically with pedestal level and were equal to or slightly better than those of normal-hearing listeners, consistent with more linear cochlear response growth in hearing-impaired compared to normal-hearing listeners. Finally, Heinz et al. (2001) compared model predictions with psychophysical intensity discrimination thresholds using linear and nonlinear versions of an analytical model of the auditory periphery. A mid-level hump in intensity discrimination was predicted by the nonlinear model due to strong compression whereas the linear model predicted monotonically decreasing intensity discrimination thresholds with increasing pedestal level. In summary, these studies provided psychophysical and modeling support for the interpretation of the mid-level hump in terms of cochlear compression. Below, this framework is extended to an AM detection task.

1.4 A framework based on cochlear input-output function framework

The deterioration of AM detection thresholds for short carriers at moderate carrier levels compared to low levels is predicted based on a theoretical model of the cochlear I/O function (Figure 1.5). This framework applies only to short carriers, as the cochlear response is hypothesized to grow differently in response to long tones or in the presence of preceding stimulation. Specifically, for short carriers, cochlear response growth is expected to be linear at low levels and highly compressive at moderate to high levels (Ruggero et al., 1997). Conversely, for long carriers for which the MOC reflex may have been elicited, the cochlear response may have been decompressed at moderate levels (Russel & Murugasu, 1997). Figure 1.5 shows an I/O function for an auditory filter centered on the carrier frequency. This figure also shows a schematic of a short AM signal where the input modulation depth is displayed by the horizontal double arrows and the effective modulation depth is shown by the horizontal dashed lines and vertical double arrows. Assumptions of this framework for predicting AM detection thresholds are: (1) listeners detect the modulated carrier using an auditory filter centered on the carrier center frequency, (2) listeners detect the modulated carrier at a constant effective modulation depth at the output of this auditory filter. Based on these assumptions, the I/O function framework predicts AM detection thresholds to worsen from low to moderate carrier levels due to cochlear compression (Figure 1.5B); however, this framework does not predict the mid-level hump. This framework can be modified to predict the mid-level hump in AM detection by allowing for off-frequency listening. As the carrier level increases, the listener attends to the output of auditory filters centered away from the carrier frequency. The response growth of the basilar membrane in these off-frequency filters is less compressive and thus the effective modulation depth would be greater, leading to improved AM detection thresholds at high carrier levels compared to moderate levels (Kohlrausch et al., 2000; Millman & Bacon, 2008; Strickland & Viemiester, 1997). Experiments in Chapter 3 examine these predictions by measuring AM detection for narrow-band noise carriers with short (50 ms) and long (500 ms) durations as a function of carrier level.

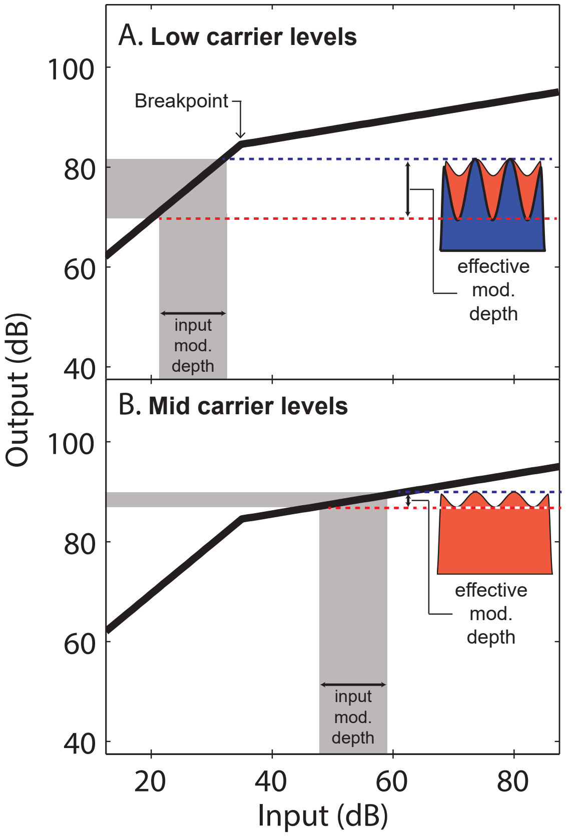

Figure 1.5. Schematic of the expected effects of cochlear compression on the effective modulation depth. Cochlear response growth through an auditory filter centered on the carrier frequency grows linearly at low carrier levels, and compressively at moderate to high carrier levels (solid line), where linear and compressive regions intersect at a breakpoint. For low-level carriers, the input modulation depth is maintained at the output of the cochlea. For moderate-level carriers, the effective modulation depth is smaller than the input modulation depth due to cochlear compression. Horizontal double arrows show the input modulation depth. Horizontal dashed lines and vertical double arrows show the effective modulation depth.

1.5 Preceding stimulation improves intensity discrimination and AM detection

Several psychophysical experiments have shown that intensity discrimination (Carlyon & Moore, 1986) and AM detection at low modulation frequencies (Forrest & Green, 1987; Sheft & Yost, 19990; Viemeister, 1979) are better when the stimulus is presented against a continuous background pedestal or carrier compared to gated stimuli. Moreover, intensity discrimination is improved when the pedestal is preceded by a precursor (Micheyl et al., 1997; Roverud & Strickland, 2015b). For example, Roverud and Strickland (2015b) examined the effects of ipsilateral, contralateral, and bilateral wide-band noise precursors on intensity discrimination conditions that give rise to the mid-level hump (30 ms, 6 kHz pedestal). In all conditions, the precursor was either short or long. The results showed that intensity discrimination thresholds improved compared to no precursor at the mid-level hump whenever the precursor is presented in the ipsilateral ear. Greater improvements were observed for long precursors compared to short precursors for some listeners.

Intensity discrimination for short-duration pedestals is improved at moderate pedestal levels when the pedestal is preceded by a notched-noise precursor (Roverud & Strickland, 2015a). Some previous studies used notched noise to restrict off-frequency listening in intensity discrimination tasks (Carlyon & Moore, 1984; Plack, 1998; Plack & Viemeister, 1992). If the notched noise restricts off-frequency listening, it is expected that intensity discrimination thresholds will worsen compared to no-notched-noise conditions as level increases, due to forcing listeners to detect the pedestal in an on-frequency filter where the response growth is compressive. However, different configurations of the notched noise relative to the pedestal lead to different findings, as discussed by Roverud and Strickland (2015a). When the notched noise was gated on and off with the pedestal, the mid-level hump increased in size (Carlyon & Moore, 1984; Oxenham & Moore, 1995), suggesting that notched noise may have restricted off-frequency listening. However, when the notched noise started 50 ms prior to the pedestal onset and continued until the pedestal offset, the mid-level hump was reduced in size (Plack, 1998; Plack & Viemeister, 1992). In addition to their wide-band precursors study, Roverud and Strickland (2015a) measured intensity discrimination thresholds at the mid-level hump in the presence of notched-noise precursors. The notched noise was either short or long. Roverud and Strickland (2015a) showed that intensity discrimination thresholds improved at the mid-level hump for long, but not short, notched-noise precursors compared to those measured in quiet. In summary, the mid-level hump is abolished for intensity discrimination of long-duration pedestals or of short-duration pedestals presented after a wide-band or notched-noise precursor. It appears that ipsilateral precursors are more effective in reducing the mid-level hump compared to contralateral precursors. This greater effect of ipsilateral precursors is consistent with the findings from animal studies showing that the ipsilateral MOC reflex is twice as strong as the contralateral MOC reflex (Guinan, 2006).

1.5.1 Effects of carrier duration

As discussed above, the mid-level hump is reduced or eliminated as the pedestal duration is increased (Nizami, 2006). The expected greater effects of the longer pedestals at moderate levels compared to low and high levels may be, in part, related to the combined effects of cochlear compression and multiple looks. Multiple looks theory states that detection thresholds improve with increases in stimulus duration due to the availability of more "looks" in long compared to short stimuli. Based on the combined effects of multiple looks and cochlear compression, at low-level pedestals where the cochlear response growth is linear, the improvement in threshold for long compared to short pedestals is expected to be equal to what is predicted from multiple looks. At moderate levels, the pedestal will undergo compression for both short and long pedestals, but due to multiple looks the difference between the test and standard signals is larger for longer pedestals, leading to improved thresholds. Alternatively, longer pedestals may elicit the MOC reflex during the forward fringe of the pedestal and thus decompress part of the cochlear I/O function. This decompression is expected to result in better intensity discrimination thresholds at moderate levels (Roverud & Strickland, 2015b).

1.6 Mechanisms for precursor/duration effects on the mid-level hump

1.6.1 Effects of a precursor

As discussed above, intensity discrimination is improved when the pedestal is preceded by a precursor (Roverud & Strickland, 2015b). This suggests that the acoustic stimulation preceding the pedestal may result in better intensity resolution. Potential mechanisms of this improvement include, (1) neural adaptation, (2) a reduction in cochlear gain via the MOC reflex (Kawase et al., 1993). Neural adaptation refers to the reduction of the firing rate of auditory nerve fibers to a steady-state rate shortly after the onset of the stimulus (Smith & Zwislocki, 1975). Neural adaptation has been proposed as a common explanation of better intensity discrimination (Bacon & Viemeister, 1994) and AM detection thresholds (Viemeister, 1979) in continuous compared to gated carriers. In the context of AM detection, this explanation posits that the neural onset response of auditory nerve fibers interferes with the response to the test modulation (Sheft & Yost, 1990; Viemeister, 1979). As discussed by Sheft and Yost (1990), this "onset insufficiency" would result in a masking effect of the first few cycles of a short-duration low frequency modulated carrier compared to high modulation frequencies where more cycles are available for "multiple looks" (Viemeister, 1979).

An alternative explanation for the improvement of performance in the presence of precursors is consistent with a reduction in cochlear gain (Roverud & Strickland, 2015b). A potential mechanism for this gain reduction is the MOC reflex, which forms part of the auditory efferent system and connects directly to OHCs (Cooper & Guinan, 2006; Guinan & Gofford, 1988). Physiological studies have shown that activation of the MOC reflex reduces cochlear gain at low-to-moderate sound levels (Figure 1.6, gray dashed line) (Cooper & Guinan, 2006; Russell & Murugasu, 1997). This reduction in gain shifts the cochlear I/O function to the right. Thus, activation of the MOC reflex decompresses the I/O function. This is shown in Figure 1.6, which shows cochlear I/O functions measured at the CF with (gray dashed line) and without (black solid line) eliciting the MOC reflex (Guinan & Cooper, 2006). Furthermore, the MOC reflex has a sluggish onset of about 25 ms after the elicitor onset followed by a gradual growth and decay of effect with a time constant of approximately 70-100 ms (Backus & Guinan, 2006). This sluggish onset of the MOC reflex has important implications for the design of psychophysical experiments. For example, several masking studies have studied the influence of the MOC reflex on auditory perception by comparing performance under stimulus conditions where the MOC reflex is either active or inactive based on a technique that takes advantage of the sluggish start of the reflex (Jennings et al., 2009; Krull & Strickland, 2008; Strickland, 2001; Strickland, 2004). Specifically, short signals were used to control for MOC effects in one condition, and and a short carrier preceded by a long precursor, where the precursor is used to stimulate the MOC reflex. These masking studies demonstrated that the presence of the precursor influences behavioral estimates of frequency selectivity (Jennings & Strickland, 2012; Jennings et al., 2009), growth of masking (Jennings et al., 2009; Krull & Strickland, 2008), overshoot (Bacon & Healy, 2000; Bacon & Liu, 2000), and intensity discrimination (Roverud & Strickland, 2015a,b).

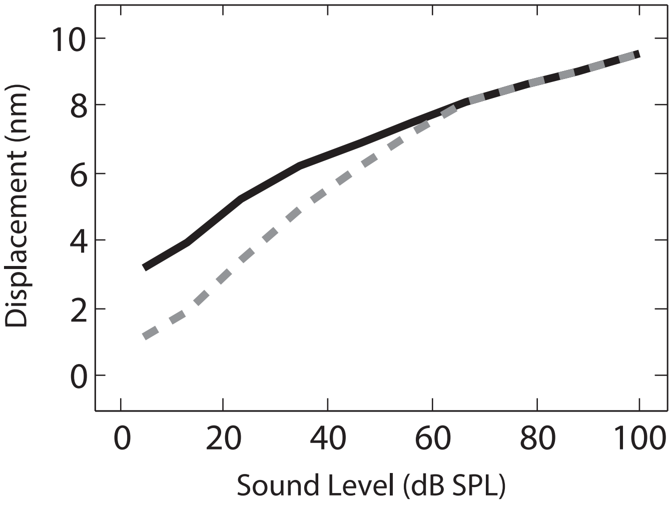

Figure 1.6. Basilar membrane input-output (I/O) function for a tone at the characteristic frequency (CF) without (solid line) and with (dashed line) MOC reflex stimulation. Activation of the MOC reflex results in a gain reduction at low levels, which decompresses the cochlea's response. Figure is adapted from Guinan and Cooper (2006).

1.7 Precursor effects: A framework based on reduction of cochlear gain

The expected influence of a reduction of cochlear gain on AM detection can be illustrated by considering a conceptual model of the cochlear I/O function. Figure 1.7 displays a schematized I/O function for a short carrier without a precursor (Figure 1.7A) and with a precursor (Figure 1.7B). It is expected that cochlear gain reduction is minimal for short carriers without a precursor and larger for short carriers with a precursor. For short carriers without a precursor (Figure 1.7A), the cochlear I/O function is linear at low levels, and compressive at moderate-range levels. In the compressive region of the cochlear I/O function, the effective AM depth is expected to be smaller than the input modulation depth, which requires a large input modulation to achieve a constant criterion at the output of the filter. For short carriers with a precursor (Figure 1.7B), part of the moderate level compressive portion of the I/O function is decompressed, as schematized by red and blue horizontal lines. This decompression increases the effective modulation depth of AM, as schematized by the red and blue amplitude envelopes in Figure 1.7B. According to the framework, it is hypothesized that the reduction in cochlear gain due to the presence of the precursor will be level-dependent such that there will be no improvement at low carrier levels, large

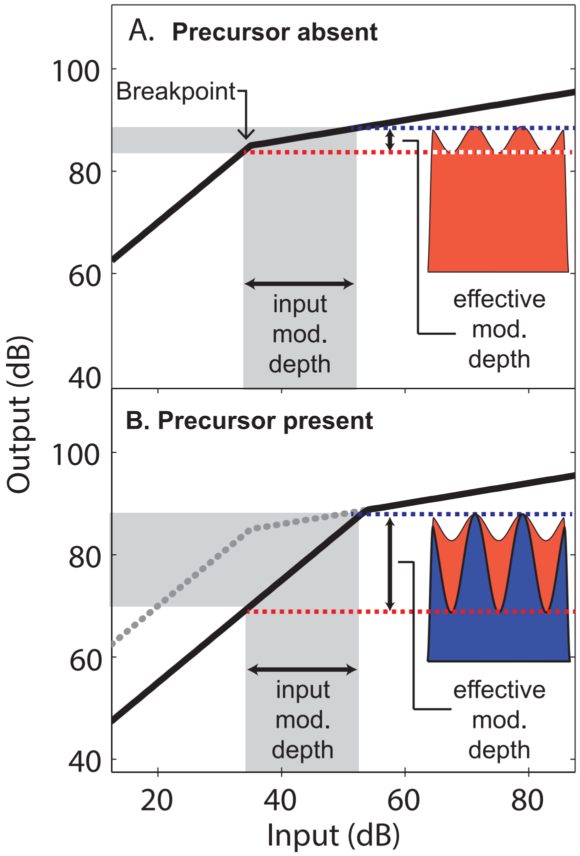

Figure 1.7. Schematic of the expected effects of a reduction in cochlear gain on effective modulation depth. Cochlear response growth through an auditory filter centered on the carrier frequency grows linearly at low carrier levels, and compressively at moderate to high carrier levels (solid line), where linear and compressive regions intersect at a breakpoint. The presentation of a precursor is assumed to reduce cochlear gain, resulting in a rightward shift in the compression breakpoint. For moderate-level carriers preceded by silence (A, precursor absent) or by a precursor (B, precursor present), the effective modulation depth is smaller or roughly equal to the input modulation depth, respectively. The solid line in A is replotted in B as a gray dotted line. Horizontal double arrows show the input modulation depth. Horizontal dashed lines and vertical double arrows show the effective modulation depth.

improvements at moderate carrier levels, and relatively smaller improvements at high carrier levels unless upward spread of excitation is assumed. Experiments in Chapter 3 examine these predictions by measuring AM detection in the presence of a precursor preceding a short narrow-band noise carrier as a function of carrier level (Experiment I) and as a function of modulation frequency (Experiment II).

1.8 Cochlear compression/gain reduction and inherent fluctuations of noise carriers

The cochlear compression/gain reduction framework presented in the preceding section is based on sinusoidal stimuli. This framework can be expanded to include narrow-band noise with additional considerations regarding the fluctuations in the envelope of narrow-band noises. Narrow-band Gaussian noises are characterized by prominent inherent temporal fluctuations. The average rate of these fluctuations depends on the noise bandwidth. In order to examine the extent to which these inherent fluctuations in noise influence detection, previous psychophysical experiments have used noises with high "high-fluctuating noise" and low "low-fluctuating noise" degrees of fluctuations. Results from previous studies indicate that masking (Hartman & Pumplin, 1988), increment detection (Gallun & Hafter, 2006), gap detection (Glasberg & Moore, 1992; Hall & Grose, 1997), and amplitude modulation detection thresholds (Dau et al., 1999) are better for low-fluctuating than for high-fluctuating noise. The poorer thresholds for high- compared to low-fluctuating stimuli are likely due to the increased modulation masking arising from the inherent fluctuations of high-fluctuating stimuli. The concept of the modulation filters was introduced by Dau et al. (1997a,b) to account for modulation masking. Dau and colleagues suggested that the auditory system performs a decomposition of the stimulus to the different modulation frequencies in a similar fashion to the well-established model of auditory filterbank to simulate cochlear frequency decomposition (Fletcher, 1940). For narrow-band noise carriers, the detectability of the target modulation is determined by the effective modulation depth of the target and the spectral density of the carrier's inherent fluctuations falling through the modulation filter centered on the target modulation frequency.

Considering the I/O function framework presented earlier, it is expected that inherent fluctuations in narrow-band noise carriers are influenced by cochlear compression. As stated earlier, the second assumption of the I/O function framework states that listeners detect the modulated carrier at a criterion modulation depth at the output of the cochlea. This can be modified to account for the effects of cochlear compression on the carrier-inherent fluctuations. First, the "acoustic" envelope signal-to-noise ratio ("acoustic SNR_{ENV}") is defined as the ratio of target modulation power to the power of the inherent fluctuations of the carrier. The acoustic SNR_{ENV} passing through the modulation filter is called the "effective SNR_{ENV}" at the output of the modulation filter. Second, AM detection is determined by the effective SNR_{ENV} that is necessary to detect the modulated carrier (i.e., criterion effective SNR_{ENV}).

For high-fluctuating carriers, the effective SNR_{ENV} at the output of the modulation filter centered at the target's modulation frequency is expected to be constant as a function of carrier level. Specifically, for high-fluctuating carriers, the envelope power of the carrier and the envelope power of the target modulation passing through the modulation filter are expected to be equally reduced (low effective SNR_{ENV}) by cochlear compression, resulting in a constant effective SNR_{ENV}; thus predicting constant AM thresholds as a function of level.

For low-fluctuating carriers, the envelope power is less than the power required to detect a carrier with a flat envelope such as sinusoidal carriers; thus, detection is primarily determined by the effective modulation depth of the target. Consequently, a linear cochlear response at low carrier levels is expected to maintain the target effective modulation depth; thus, we predict better AM thresholds at low levels. At moderate carrier levels where the cochlear I/O function is highly compressive, the target effective modulation depth is expected to be reduced due to cochlear compression, leading to poorer AM detection thresholds. When off-frequency listening is considered, the target effective modulation depth at high carrier levels is expected to be large and consequently improved AM thresholds. Chapter 4 of this dissertation includes experiments designed to examine these predictions by measuring AM detection thresholds for high- and low-fluctuating narrow-band noise carriers as a function of carrier level.

1.9 Aims and organization of the dissertation

This dissertation describes a series of experiments, based on results from preliminary experiments (see Appendix), designed to examine if carrier level effects for short carriers are consistent with cochlear compression and whether the introduction of constant-level notched noise precursors improve AM detection thresholds due to a reduction in cochlear gain via the MOC reflex. Chapters 2 and 3 are self-contained papers; thus, information from the Introduction may be repeated in the introductory paragraphs of these chapters. The aims and hypotheses of the experiments can be defined as:

Aim 1 (Chapter 2): To evaluate whether the effects of carrier level in AM detection for short carriers are consistent with expected effects of cochlear compression. AM detection was measured as a function of carrier level for short carriers because physiological studies have shown that basilar membrane growth is linear at low levels and becomes progressively more compressive with increasing level (Ruggero et al., 1997). ***Hypothesis:*** AM detection will worsen as the carrier level is increased from low- to moderate-levels due to cochlear compression and then improve as level is increased from moderate to high carrier levels due to off-frequency listening.

Aim 2 (Chapter 2): To evaluate whether the presence of a long precursor preceding a short carrier improves AM detection, an effect consistent with a reduction in cochlear gain via the MOC reflex. AM detection was measured for short carriers preceded by silence or by ipsilateral precursors. These conditions are based on the sluggish onset of the MOC reflex. When stimulated, the MOC reflex exhibits an onset delay of ∼25 ms and reaches maximum strength by ∼200-ms (Backus & Guinan, 2006). ***Hypothesis:*** AM detection at moderate-to-high levels will improve in the precursor condition compared to the no-precursor condition.

Aim 3 (Chapter 3): To evaluate whether the effects of carrier level on AM detection with fluctuating narrow-band noise carriers is consistent with cochlear compression. AM detection was measured using narrow-band, high- and low-fluctuating noise carriers. ***Hypothesis:*** For high-fluctuating carriers, AM detection thresholds will be constant as a function of carrier level due to the constant effective SNR_{ENV} at the output of the modulation filter centered on the target modulation frequency. For low-fluctuating carriers, AM detection thresholds will worsen from low to moderate levels primarily due to the reduced effective modulation depth of the target expected from cochlear compression.

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CHAPTER 2

NOTCHED-NOISE PRECURSORS IMPROVE DETECTION OF LOW-FREQUENCY AMPLITUDE MODULATION

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2.1 Abstract

Amplitude modulation (AM) detection was measured with a short (50 ms), high-frequency carrier as a function of carrier level (Experiment I) and modulation frequency (Experiment II) for conditions with or without a notched-noise precursor. A longer carrier (500 ms) was also included in Experiment I. When the carrier was preceded by silence (no-precursor condition), AM detection thresholds worsened for moderate-level carriers compared to lower- or higher-level carriers, resulting in a “mid-level hump”. AM detection thresholds with a precursor were better than those without a precursor, primarily for moderate-to-high level carriers, thus eliminating the mid-level hump in AM detection. When the carrier was 500 ms, AM thresholds improved by a constant (across all levels) relative to AM thresholds with a precursor, consistent with the longer carrier providing more “looks” to detect the AM signal. Experiment II revealed that improved AM detection with compared to without a precursor is limited to low modulation frequencies (<60 Hz). These results are consistent with 1) a reduction in cochlear gain over the course of the precursor, perhaps via the medial olivocochlear reflex, or 2) a form of perceptual enhancement which may be mediated by adaptation of inhibition.

2.2 Introduction

The auditory system is sensitive to small changes in intensity over a wide range of sound levels [$\sim$120 dB, (Viemeister, 1988)]. This wide perceptual range occurs despite the dynamic range of most auditory nerve fibers (i.e., high spontaneous rate [SR] fibers) being limited to $\leq$35 dB (Evans & Palmer, 1980). The ability to encode changes in intensity over the dynamic range of hearing is crucial for identifying, discriminating, and understanding environmental sounds (Green, 1983). For long ($>$100 ms) wide-band and narrow-band pedestals, intensity discrimination is constant (Miller, 1947) or improves with sound level (Florentine & Buus, 1981; Jesteadt et al., 1977; McGill & Goldberg, 1986; Rabinowitz et al., 1976), respectively. However, for short ($\leq$30 ms), narrow-band pedestals, intensity resolution deteriorates at moderate pedestal levels (Carlyon & Moore, 1984; Nizami, 2006; Roverud & Strickland, 2015a). This deterioration has been termed the "severe departure from Weber's law" (Carlyon & Moore, 1984) or the "mid-level hump" (Nizami, 2006; Zeng et al., 1991) and is consistent with basilar membrane mechanics which exhibit compressive nonlinearity at mid-to-high levels for tones presented at the characteristic frequency (CF) (Heinz et al., 2001; Pienkowski & Hagerman, 2009; Roverud & Strickland, 2015a). Moreover, recent studies have shown that the mid-level hump is reduced (i.e., performance improves at moderate pedestal levels) when a short pedestal is preceded by a long (e.g., 150 ms) ipsilateral or bilateral noise ("precursor"), consistent with a reduction in cochlear gain over the course of the precursor, perhaps via the medial olivocochlear (MOC) reflex (Roverud & Strickland, 2015b).

In addition to intensity discrimination experiments, intensity resolution can be assessed by measuring amplitude modulation (AM) detection. Much of the semantic information contained in speech is carried by gross amplitude fluctuations over time, known as the stimulus envelope (Rosen, 1992). AM detection assesses the sensitivity of the auditory system to a range of envelope frequencies. Based on intensity discrimination studies (e.g., Roverud & Strickland, 2015a,b), the first experiment of this study tested the hypothesis that AM detection with short carriers is relatively poorer at moderate compared to lower or higher levels, consistent with cochlear compression. Furthermore, this study tested whether the presence of a precursor improves AM detection thresholds at moderate carrier levels, consistent with a reduction in cochlear gain, similar to what has been used to describe other precursor effects in masking (Bacon & Savel, 2004; Jennings et al., 2009; Schmidt & Zwicker, 1991; Strickland, 2001), and intensity discrimination (Roverud & Strickland, 2015a,b). The second experiment assessed whether AM detection with and without a precursor depends on modulation frequency by measuring temporal modulation transfer functions (TMTFs).

The expected improvements in AM detection as a result of a reduction in cochlear gain are illustrated in Figure 2.1, which displays a schematized input-output (I/O) function for an auditory filter centered on the carrier frequency. For short carriers (e.g., 50 ms) preceded by silence (Figure 2.1A), cochlear compression limits the effective (post-cochlear) modulation depth when the carrier is presented at moderate-to-high levels. For short carriers preceded by noise precursors (Figure 2.1B), cochlear gain is expected to decrease over the course of the precursor, resulting in a local increase in I/O function slope and an improvement in effective modulation depth. Inherent to the theoretical framework presented in Figure 2.1 is the assumption that AM detection depends only on the output of the auditory filter centered on the carrier frequency (i.e., off-frequency listening does not occur), and that the decision variable for detecting AM is based only on the effective AM depth. Thus, the model makes the following predictions: 1) for short carriers preceded by silence (Figure 2.1A), AM detection thresholds should worsen as the carrier level is increased from low to mid levels due to the compressive I/O function at moderate-to-high levels; 2) for short carriers preceded by a precursor or for long carriers (e.g., 500 ms) preceded by silence (Figure 2.1B), AM detection thresholds are expected to improve at moderate levels due to decompression (linearization) of the I/O function via a reduction in cochlear gain over the time course of the precursor.

2.3 General methods

2.3.1 Apparatus and stimuli

Stimuli were digitally generated using custom-built MATLAB (The MathWorks, Natick, MA) software (Bidelman et al., 2015) and output through a LynxTWO-B (Lynx Studio Technology, Costa Mesa, CA) sound card (sampling rate, 44.1 kHz; 24-bit resolution) to listeners' right ear via a ER-2 (Etymotic Research Inc., Elk Grove, IL) insert earphone driven by a headphone buffer (Tucker-Davis-Technologies [TDT], HB7, Alachua, FL). AM detection thresholds were measured using a low-fluctuating, narrow-band-noise (bandwidth

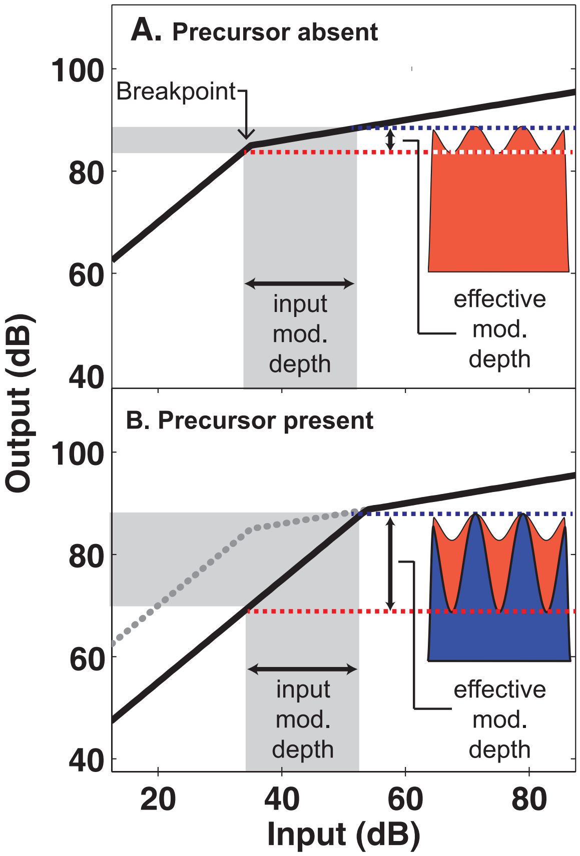

Figure 2.1. Schematic of the expected effects of a reduction in cochlear gain on effective modulation depth. Cochlear response growth through an auditory filter centered on the carrier frequency grows linearly at low carrier levels, and compressively at mid-to-high carrier levels (solid line), where linear and compressive regions intersect at a breakpoint. The presentation of a precursor is assumed to reduce cochlear gain, resulting in a rightward shift in the compression breakpoint. For moderate-level carriers preceded by silence (A, precursor absent) or by a precursor (B, precursor present), the effective modulation depth is smaller or roughly equal to the input modulation depth, respectively. The solid line in A is replotted in B as a gray dotted line. Horizontal double arrows show the input modulation depth. Horizontal dash lines and vertical double arrows show the effective modulation depth.

= 100 Hz) carrier, whose spectrum was arithmetically centered on 5000 Hz (fc). Low-fluctuating noise was generated by iteratively (10 iterations) dividing filtered noise by the Hilbert envelope as described by Kohlrausch et al. (1997). Narrow-band noise carriers were used because this study was part of a larger set of experiments that involved comparing AM thresholds for fluctuating- and flat-envelope carriers. High-frequency carriers were used because cochlear amplifier gain is greatest in the base of the cochlea (Cooper & Rhoode, 1995) and previous studies have shown the largest mid-level effects on AM detection at high carrier frequencies (>4000-6000 Hz, Long & Cullen, 1985). Sinusoidal AM was applied in cosine phase over the duration of the carrier as follows

$$x(t) = [1 + m * cos(fm * t)] * yt \qquad (2.1)$$

where m is the modulation index, fm is the modulation frequency, and y(t) is the noise carrier. Modulated carriers were scaled to the desired root-mean-square (rms) level after applying AM. Carriers were 50 ms (Experiments I and II) or 500 ms (Experiment I), excluding 2 ms onset/offset ramps. The precursor was a 40 dB SPL (overall level) notched noise, where low- and high-frequency noise bands extended from 1500-4500 Hz and 5500-8500 Hz, respectively. Notched-noise precursors were used because pilot studies were consistent with forward masking in the modulation domain (Wojtczak & Viemeister, 2005) from precursors with spectral energy at the carrier frequency. Precursor duration was 200 ms, including 5 ms onset/offset ramps. There was no delay between the offset of the precursor and the onset of the carrier. Off-frequency listening (Johnson-Davies & Patterson, 1979; O'Loughlin & Moore, 1981) was restricted by gating an additional notched noise simultaneously with the carrier, where the noise level was 50 dB/Hz below the carrier spectrum level (Nelson et al., 2001). The spectral notch of the off-frequency listening noise extended from 0.9*fc to 1.2*fc (i.e., 4500-6000 Hz), similar to Oxenham and Plack (1997). The outer frequency cutoffs of the off-frequency listening noise were 2000 and 8000 Hz. Figure 2.2 shows the time waveform (top panel) and spectrogram (bottom panel) of the 50-ms AM carrier preceded by the 200-ms, notched-noise precursor.

2.3.2 Procedure

Subjects participated in the experiment in a sound-attenuating booth. The dependent variable was AM detection threshold, expressed as modulation depth (m) in dB. AM detection thresholds were measured using an adaptive three-interval, three-alternative forced-choice (3AFC) task. During a trial, the carrier was presented in each interval separated by 500 ms and marked by lighted squares on a computer monitor. The carrier and precursor (when present) noises were independently generated for each observation interval (i.e., frozen noises were not used). In order to eliminate level cues, the power of the carrier was the same in all observation intervals (Viemeister, 1979). During a randomly-chosen interval, the carrier was sinusoidally amplitude modulated. The subject pressed a button on a keyboard

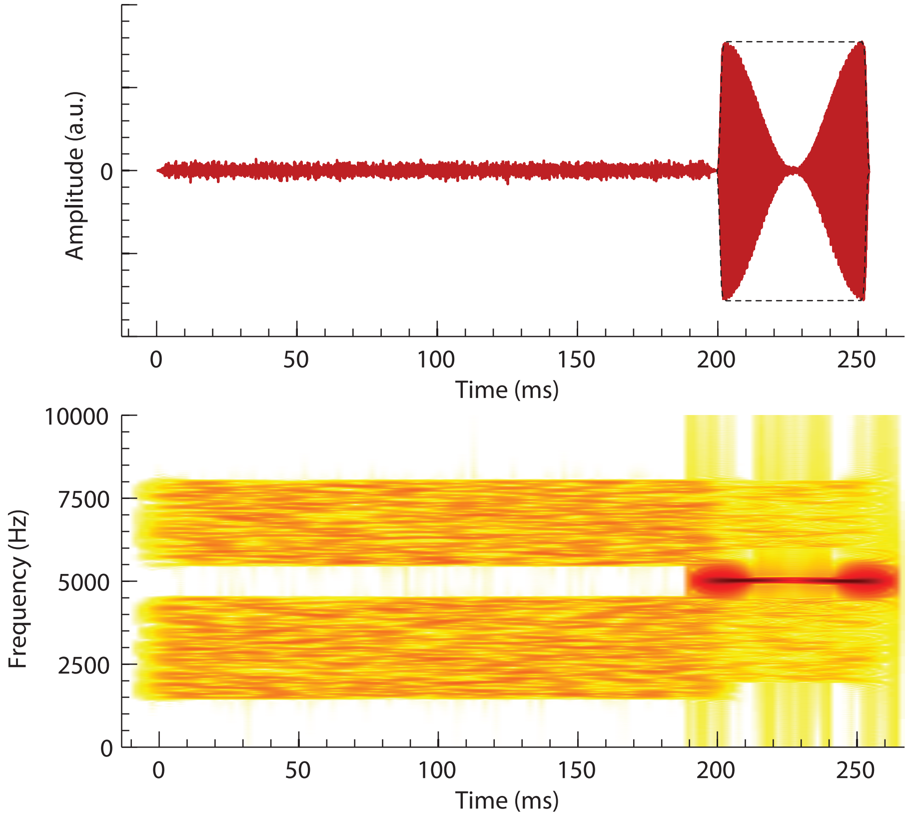

Figure 2.2. Time waveform (top) and spectrogram (bottom) of the 200 ms, notched-noise precursor, followed by the 50 ms (plus 2-ms rise/fall ramps) narrow-band, amplitude-modulated carrier. The dashed line in the top panel shows the envelope of the unmodulated carrier. Off-frequency listening was limited by gating an additional notched noise with the carrier. For the spectrogram, dark colors represent relatively higher amplitudes, while light colors represent relatively lower amplitudes. (a.u.: arbitrary units).

to indicate the interval in which the modulation was perceived. Visual feedback was provided to indicate a correct or incorrect response.

During a threshold run, the modulation depth was adjusted using a two-down, one-up rule which measures the modulation depth necessary to achieve 70.7% correct on the psychometric function (Levitt, 1971). The initial 8-dB step size was decreased to 2 dB after the second reversal. Twelve reversals were obtained and the mean modulation depth of the last eight reversals was defined as the AM threshold for that run. Thresholds from four runs were averaged to compute the final threshold of each condition. Runs with a standard deviation greater than 5 dB were discarded and the run was repeated. The need to obtain an additional threshold occurred a total of 9 times of the measured experimental thresholds

(1.7% of thresholds in Experiment I; 3.7% of thresholds in Experiment II).

Learning was measured by calculating the change in threshold per repetition (i.e., slope) across these four runs. If the slope was greater than 3 dB/repetition, an additional threshold was obtained and the slope was recalculated. This process was continued until the slope fell below 3 dB/repetition. Although learning effects were monitored, none of the subjects exceeded the 3 dB/repetition criterion; therefore, only the initial four thresholds were averaged to compute the final threshold[1]. Experimental sessions were limited to 1.5-2 hours. Total number of sessions was about 8 sessions/subject. Training lasted at least 2 hours and involved measuring two consecutive AM thresholds from a representative sample of conditions from Experiment. I including several carrier levels, two carrier durations, and the presence/absence of the precursor. Thresholds measured during training were discarded.

2.4 Experiment I: AM detection with and without a precursor as a function of carrier level

This experiment investigated the effects of carrier level with and without a notched-noise precursor to test two hypotheses: (1) AM detection thresholds will be poorer at moderate levels, compared to low levels, consistent with the effects of cochlear compression on the effective modulation depth of the carrier; (2) AM detection thresholds for short carriers with a precursor or for long carriers will be better than those measured with short carriers without a precursor, particularly at moderate carrier levels. This hypothesis is based on the assumption that cochlear gain decreases during the presentation of the precursor or during the forward fringe of the long carrier, resulting in an improved effective modulation depth as schematized in Figure 2.1.

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[1] S5 reported difficulty hearing the target modulation for the 85 dB SPL carrier with a precursor. For this condition, S5 reported correctly guessing the target several times despite not actually perceiving it. Although this subject did not meet the criterion for learning (i.e., slope greater than 3 dB/repetition), four additional threshold runs for the 85 dB SPL carrier were obtained and averaged to determine the final threshold for this condition in this subject. To verify the stability of the data, one or two threshold runs were obtained for all subjects at several carrier levels. On average, these additional thresholds were within 1.28 dB (σ=2.17 dB) of the original thresholds, suggesting that the data were stable. These additional thresholds were not included in the average thresholds for the experiments.

2.4.1 Method

2.4.1.1 Subjects

Seven subjects (ages 20 to 32 years, 5 males) participated in the experiment. Subjects had thresholds $\leqslant$20 dB HL at audiometric frequencies between 250 and 8000 Hz, and normal middle ear function based on tympanometry. The right ear of each subject was tested. Subjects were inexperienced with psychoacoustic tasks except subject 1 (S1), who is the first author. All subjects, except S1, were paid hourly for their participation. Due to time constraints, two subjects (S6, S7) could not participate in the long-carrier condition and one subject (S2) participated in only three of five carrier levels for the long carrier condition.

2.4.1.2 Stimuli

A modulation frequency of fm = 20 Hz was used because previous studies show that, compared to gated carriers, improvements in AM thresholds with continuous carriers or the presentation of a forward fringe of noise are greatest at low modulation frequencies (2-20 Hz, Sheft & Yost, 1990). Carrier levels were 50, 55, 60, 65, 75, and 85 dB SPL. In the short-carrier conditions, AM detection thresholds were measured with and without a precursor (6 carrier levels * 2 precursor conditions = 12 conditions), while in the long-carrier conditions, AM detection thresholds were measured without a precursor (6 conditions). Conditions were randomized by carrier level. For a given carrier level, AM thresholds were first obtained for short carriers without a precursor, followed by thresholds for short carriers with a precursor. After measuring thresholds for short carriers with and without precursors, AM detection thresholds were measured for 500-ms carriers.

2.5 Results and discussion

2.5.1 50-ms carrier without a precursor

AM detection thresholds improved and then worsened as the level of the 50-ms carrier was increased to 65 dB SPL, above which thresholds improved monotonically, except some subjects showed a slight (S7) or modest (S3, S5) increase in thresholds at the highest carrier level (Figure 2.3, open circles). The significantly poorer AM detection thresholds at mid, compared to lower or higher carrier levels [$t(6)=6.9$, $p<0.001$] is similar to results from Long and Cullen (1985), who concluded that this nonmonotonic behavior may be a general characteristic of intensity processing at high frequencies (4000-6000 Hz and above). For

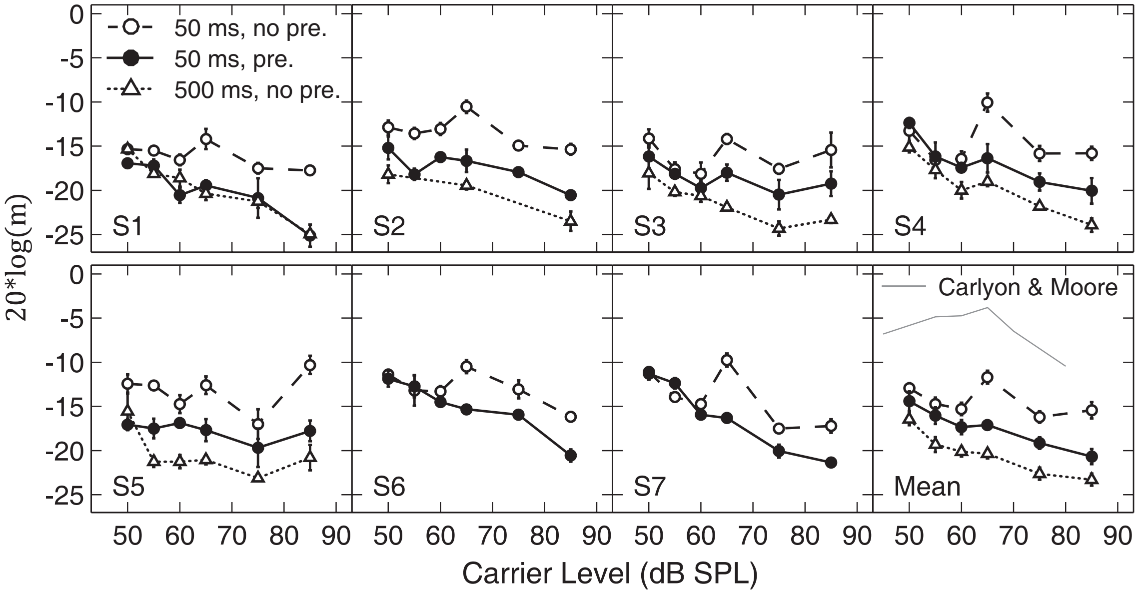

Figure 2.3. Modulation depth at threshold as a function of carrier level for short (open circles) and long (open triangles) carriers preceded by silence, or for short carriers preceded by a notched-noise precursor (closed circles). Lower values represent better AM detection (i.e., lower modulation depth (m) at threshold). Panels are results for individual subjects except the lower right panel, which displays the mean data. The modulation frequency was 20 Hz. Mean data from Carlyon and Moore (1984) are shown by the gray line in the lower right panel to illustrate the mid-level hump observed in some intensity discrimination experiments. Error bars are the standard error of the mean. The smallest error bars may be covered by data markers.

comparison, intensity discrimination thresholds (ΔI in dB) from Carlyon and Moore (1984) were converted to modulation index values based on the equation by Long and Cullen (1985) where

$$m = [10^{\frac{\Delta I_{dB}}{20}} - 1]/[1 + 10^{\frac{\Delta I_{dB}}{20}}]. \tag{2.2}$$

These thresholds are shown as the thin gray line in the lower right panel of Figure 2.3. AM detection thresholds for 50-ms carriers without a precursor, and the intensity discrimination thresholds from Carlyon and Moore (1984) are qualitatively similar, with thresholds peaking at 65 dB SPL. The relatively higher thresholds from Carlyon and Moore (1984) are likely due to differences between AM detection and intensity discrimination and due to their pedestal being roughly half the duration of the 50-ms carrier. The mid-level hump seen in intensity discrimination studies (e.g., Carlyon & Moore, 1984; Zeng et al., 1991) was originally hypothesized to be due to a threshold gap between low- and high-SR fibers. A quantitative evaluation of this hypothesis (Heinz et al., 2001) showed that 1) the transition in coding from high- to low-SR fibers occurs at higher levels than those associated with the mid-level effects observed psychophysically, and 2) the presence of medium-SR fibers (Liberman, 1978) eliminated the putative threshold gap, casting doubt on this hypothesis.

More recent studies have shown that poorer intensity discrimination thresholds at moderate compared to lower stimulus levels are consistent with cochlear compression (Heinz et al., 2001; Pienkowski & Hagerman, 2009; Roverud & Strickland, 2015a). For example, Heinz et al. (2001) compared model predictions of psychophysical intensity discrimination thresholds using linear and non-linear versions of an analytical model of the auditory periphery. A mid-level hump in intensity discrimination was predicted by the non-linear model due to strong compression whereas the linear model predicted monotonically decreasing intensity discrimination thresholds with increasing pedestal level. Furthermore, Roverud and Strickland (2015a) found a significant correlation for most subjects (7/10) between intensity discrimination thresholds for short (30 ms), 6000-Hz pedestals and psychophysical estimates of cochlear compression. Specifically, intensity discrimination thresholds from low-to-moderate levels were significantly higher (poorer) for subjects with the shallowest I/O function slopes (i.e., the most compression). Finally, using a roving-level paradigm and a 4000 Hz pedestal, Pienkowski and Hagerman (2009) compared intensity discrimination of 300-ms and 4-ms tones between listeners with normal hearing and listeners with mild-to-moderate sensorineural hearing loss, who are expected to have more linear I/O functions (i.e., less compressive slopes). In normal-hearing listeners, they observed a mid-level hump for intensity discrimination of 300-ms tones with pedestal levels roved over a wide range. For the same conditions, intensity discrimination thresholds for hearing-impaired listeners improved monotonically with pedestal level and were equal to or slightly better than normal-hearing listeners, consistent with more linear response growth in hearing-impaired than in normal-hearing listeners.

The improvement in AM detection thresholds with carrier level for levels above 65 dB SPL (Figure 2.3, open circles) is reminiscent of the “near miss” to Weber’s law, which has been modeled by assuming greater spread of excitation at higher compared to lower stimulus levels (Florentine & Buus, 1981). For example, at low-to-moderate levels where spread of excitation is likely minimal (Nelson et al., 2001), intensity discrimination is expected to be mediated by auditory filters near the pedestal frequency, where response growth may be compressive. At higher pedestal levels, spread of excitation results in the recruitment of auditory filters centered on frequencies remote from the pedestal frequency where responses are expected to grow more linearly. Thus, as discussed by Heinz et al. (2001), better intensity discrimination thresholds at higher than at more moderate levels is consistent with recruitment of additional off-frequency auditory filters, some of which have a more linear response growth than the filter centered on the pedestal frequency. In the current experiment, off-frequency listening was restricted by presenting a notched noise simultaneously with the carrier; however, as discussed later this noise may not have been effective at the highest carrier levels. Poorer thresholds at the lowest carrier levels than at slightly higher levels may be due to near-threshold effects (Plack & Skeels, 2007) where the effective AM is reduced after being mixed with internal noise.

2.5.2 50-ms carrier with a precursor

AM detection thresholds with a precursor (Figure 2.3, closed circles) improved monotonically with carrier level (S6, S7) or had a small "bump" between 60-70 dB SPL (S1-S5). For two participants, thresholds worsened slightly at the highest carrier level (S3, S5). A repeated measures analysis of variance (rmANOVA) was performed on data collected with a short carrier with and without a precursor. Condition (precursor/no precursor) and carrier level (50, 55, 60, 65, 75, 85 dB SPL) were submitted as within-subject repeated measures. The main effects of condition [$F(1,6)=64.5$, $p<0.001$] and carrier level [$F(5,30)=11.6$, $p<0.001$] were significant, as was the condition*carrier level interaction [$F(1,6)=14.4$, $p<0.001$]. Post-hoc analyses revealed that thresholds for the 50-ms carrier were similar with and without a precursor at low carrier levels [50, and 55 dB SPL, $t(6)=1.8$, $p=0.12$]; whereas, at mid-to-high levels (60 dB SPL and above) thresholds were significantly better with than without a precursor [$t(6)=15.1$, $p<0.001$]. These findings are consistent with Roverud and Strickland (2015b), who showed that intensity discrimination thresholds for mid-level pedestals improve when the pedestal is preceded by an ipsilateral broad-band noise precursor than when preceded by silence.

2.5.3 500-ms carrier

AM detection thresholds were lower (better) for long carriers (Figure 2.3, triangles) than for short carriers (i.e., with or without a precursor), with the exception of S1, for whom thresholds were similar for long carriers and short carriers with precursors (compare filled circles and open triangles in Figure 2.3). An rmANOVA was performed on AM thresholds with long carriers and short carriers with a precursor. This analysis was chosen because the total durations of the precursor and long carrier conditions were similar, thus revealing the effect of increasing the number of modulation cycles without also increasing total duration. Condition (long carrier vs. short carrier with a precursor) and carrier level (50, 55, 60, 65, 75, 85 dB SPL)[2] were submitted as repeated measures. The main effects of condition [$F(1,4)=12.7$, $p=0.02$] and carrier level [$F(1,4)=16.7$, $p<0.005$] were significant. The condition*carrier level interaction did not reach significance [$F(5,20)=1.59$, $p=0.21$]. These findings indicate that thresholds for long carriers improved by a constant compared to those for short carriers with precursors, regardless of carrier level. A parsimonious explanation for this improvement is the 10-fold increase in the number of modulation cycles for long compared to short carriers, leading to the opportunity for "multiple looks" (Viemeister & Wakefield, 1991). Sheft and Yost (1990) presented a simple multiple looks model for predicting the improvement in AM detection thresholds based on the assumptions that (1) detectability increases by the square root of n (Green & Swets, 1966) and (2) an exponential relationship exists between d' (sensitivity) and modulator power. Based on their equation (1) with k = 1 (see Sheft & Yost, 1990), predicted thresholds for the long carrier are as follows

$$20 * log_{10} m = \theta - 5 * log_{10} n \tag{2.3}$$

where θ is the threshold in the short carrier condition with a precursor, and n is the ratio of modulation cycles for the long carrier to that of the short carrier (i.e., 10/1 cycles). When averaged across carrier levels and subjects, the improvement in AM detection thresholds for long carriers compared to short carriers with a precursor was 2.1 dB for the current experiment, which is appreciably smaller than the 5 dB improvement predicted by multiple

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[2] Due to time constraints, S2 did not complete data collection for long carriers at 55 and 75 dB SPL; thus, for the statistical analysis thresholds for this subject at these carrier levels were imputed using linear interpolation.

looks. Lee and Bacon (1997) reported a critical duration of ∼4 cycles for AM detection using sinusoidal carriers modulated at 20 Hz. This suggests that although 10 cycles of the long carrier were available to listeners, only 4 of these cycles contributed to improvements in thresholds compared to thresholds for short carriers with a precursor. Based on a 4-cycle critical duration for detection of 20 Hz AM, predicted improvements in thresholds with long carriers relative to those with short carriers with precursors are 3.01 dB, which are closer to the 2.1 dB observed from the current data.

2.5.4 Interpretation of precursor/carrier duration effects based on reductions in cochlear gain

A significant precursor effect at mid, but not low carrier levels is consistent with decompression of the cochlear I/O function via a reduction in cochlear gain. At low carrier levels, the effective modulation depth is expected to be roughly equal to the input modulation depth regardless of the presence/absence of the precursor, due to linear basilar membrane response growth. At moderate levels, where the basilar membrane growth is compressive, a reduction in cochlear gain over the course of the precursor is expected to decompress a portion of the cochlear I/O function (see Figure 2.1), consistent with better AM detection with compared to without the precursor (Figure 2.3).

The theoretical framework presented in Figure 2.1 predicts that AM thresholds without a precursor should worsen from low to high carrier levels due to the transition between linear and compressed regions of the cochlear I/O function. Similarly, this model predicts that improvements in AM detection thresholds with the introduction of a constant-level precursor (precursor-no precursor difference) should be largest for mid carrier levels, and smaller for low or high carrier levels. The smaller precursor-no precursor difference at high-carrier levels is expected based on the framework in Figure 2.1 because (1) detection is assumed to depend only on the auditory filter centered on the carrier frequency (Viemeister, 1983), (2) the constant-level precursor is assumed to produce a constant reduction in gain for all carrier levels (Warren & Liberman, 1989), and (3) cochlear gain is minimal at high levels (Robles & Ruggero, 2001). For the average data, the precursor-no precursor difference was largest at 65 dB SPL and decreased at higher levels, as expected based on the theoretical framework. Despite this, the precursor-no precursor difference was larger for 85 dB SPL than 75 dB SPL carriers, which is inconsistent with the theoretical framework in Figure 2.1. A caveat in using this theoretical framework to interpret the data obtained with high carrier levels is the finding that AM detection for short carriers without a precursor improves with increasing carrier level above 65 dB SPL (Figure 2.1). This finding is consistent with the detection of AM in remote auditory filters via the upward spread of excitation (Florentine & Buus, 1981), which is a violation of the first assumption of the theoretical framework (i.e., AM detection depends only on the auditory filter centered on the carrier frequency). Moreover, this finding suggests that the noise used to restrict off-frequency listening was not effective at the highest carrier levels. The advantage of listening off frequency is the expectation that basilar membrane growth is more linear through off- than through on-frequency auditory filters (Oxenham & Plack, 1997). It is beyond the scope of this study to speculate about the degree to which AM stimuli are compressed (no precursor condition) and decompressed (precursor condition) in these off-frequency auditory filters. In other words, the interpretation of the precursor-no precursor difference at high carrier levels in terms of a reduction in cochlear gain through an auditory filter centered on the probe frequency is encumbered by evidence consistent with off-frequency listening.

For moderate carrier levels, which avoid near-threshold effects and off-frequency listening, the precursor-no precursor difference is consistent with decompression of the cochlear I/O function. The degree of decompression for moderate carrier levels can be estimated by assuming that AM is detected at a constant effective modulation depth (Viemeister, 1979), expressed in decibels (k_{dB})

$$k_{dB} = \Delta I_{dB} \cdot c \tag{2.4}$$

where $\Delta I\ _{dB}$ is the change in intensity in decibels of the AM stimulus at threshold, and c is the average compression slope of the cochlear I/O function for the range of intensities spanned by ΔI_{dB}. Assume k $_{dB}$ is constant for no precursor and precursor conditions and let subscripts 0 and p represent these conditions, respectively. The ratio of compression slopes can be solved by substitution and simplification of Eq. (2.4) to yield:

$$c_0/c_P = \Delta I_{pdB}/\Delta I_{0dB} \tag{2.5}$$

where ΔI_{pdB} and ΔI_{0dB} were calculated from the modulation index (m) using the formula described by Long and Cullen (1985). The ratio in Eq. (2.5) indicates the fraction of the compression slope in the precursor condition needed to yield the compression slope in the no precursor condition. Values less than 1 indicate steeper compression slopes in the precursor compared to the no-precursor condition, while values greater than 1 indicate shallower slopes. Table 2.1 displays the ratio of compression slopes for each listener and for the mean data.On average, the ratio of compression slopes was 0.53, indicating that slopes are nearly twice as steep in the precursor condition than in the no precursor condition, consistent with decompression of the cochlear I/O function. For example, if the compression slope in the precursor condition was 0.7 dB/dB, the corresponding slope for the no precursor condition is 0.7*0.53 = 0.37 dB/dB. These numbers are for illustrative purposes only, as the absolute compression slopes cannot be determined without additional (and potentially invalid) assumptions.

A reduction in cochlear gain via the MOC reflex is traditionally thought of as a within channel process. This comes from early studies in laboratory animals showing that the MOC reflex is a frequency-specific feedback loop (Liberman & Brown, 1986). In other words, MOC neurons with a given CF feed back on auditory nerve fibers with roughly the same CF. Given this frequency specificity, it is expected that precursors with energy away from CF (such as the notched-noise precursors used in this study) would not reduce cochlear gain at the CF centered on the carrier frequency. However, recent otoacoustic emission (OAE) studies in humans (Lilaonitkul & Guinan, 2009) and neural labeling studies (Brown, 2014; Brown, 2016) in laboratory animals suggest that MOC feedback may be less frequency specific than previously thought. These OAE and neural labeling studies are consistent with the interpretation that MOC feedback may partially account for improvements in intensity discrimination (Roverud & Strickland, 2015b) and AM detection (current study) in the presence of a notched-noise precursor, compared to no precursor. Gain reduction via the MOC reflex shifts the dynamic range of individual auditory nerve fibers, thus producing a form of dynamic range adaptation (Chintanpalli et al., 2012; Kawase et al., 1993). The theoretical framework described in Figure 2.1 explicitly assumes that cochlear compression is responsible for poorer effective modulation depths at moderate compared to higher or lower levels and that improved modulation depth with the introduction of a precursor results from a decrease in cochlear gain. It is equally likely that mechanisms such as neural saturation, and dynamic range adaptation in the auditory nerve (Wen et al., 2009)

Table 2.1. The ratio of basilar membrane compression slopes for the precursor and no-precursor conditions (co/cp) estimated from amplitude modulation (AM) detection thresholds. AM detection thresholds were converted to intensity difference limens in dB (ΔI_{dB}). co/cp was estimated by taking the ratio of intensity difference limens in the precursor (ΔI_{pdB}) and no-precursor conditions (ΔI_{0dB}). See text for details.

Subject	ΔI_{0dB}	ΔI_{0dB}	$\Delta I_{pdB}/\Delta I_{0dB}$
S1	3.43	1.86	0.54
S2	5.32	2.57	0.48
S3	3.44	2.20	0.64
S4	5.64	2.66	0.47
S5	4.15	2.28	0.55
S6	5.35	3.01	0.56
S7	5.87	2.67	0.46
Mean	4.63	2.44	0.53
s.d	1.05	0.38	0.06

or inferior colliculus (Dean et al., 2005) could account for the mid-level deterioration in AM detection and improved AM detection thresholds with a precursor. Distinguishing between cochlear and more central mechanisms of dynamic range adaptation could be difficult since signal transformations in the cochlea are carried upstream to central auditory nuclei. Studies on the effects of contralateral stimulation on otoacoustic emissions, or cochlear microphonics elicited by ipsilateral amplitude-modulated stimuli, may verify the putative role of the MOC reflex in dynamic range adaptation. To our knowledge, no such studies have been conducted. Thus, although Experiment I was motivated by cochlear mechanisms, better AM detection with than without a precursor may be due to dynamic range adaptation in more central auditory mechanisms.

2.5.5 Other interpretations

The precursor-no precursor difference observed in Experiment I may also be explained by mechanisms other than a reduction in cochlear gain. Two potential mechanisms are discussed here. First, the precursor may have facilitated AM detection by serving as a reference for the absence of amplitude modulation. In other words, AM detection with a precursor may be mediated by detecting the change from a flat to a fluctuating temporal envelope. According to this interpretation, AM detection is better with than without a precursor because the precursor provides a more salient reference of an unmodulated stimulus than the comparison stimulus presented in the other two observation intervals of the forced choice task. The drawback to this interpretation is the lack of a clear explanation for why the effect of the precursor is smaller at lower than at mid-to-high levels.

A second alternative explanation is based on the finding that thresholds for detecting a target harmonic within a harmonic complex are better if a precursor is presented containing all harmonics except the target harmonic (Viemeister, 1980). This general phenomenon is often referred to as “perceptual enhancement” and has many variations including signal enhancement (Viemeister, 1980), masker enhancement (Viemeister & Bacon, 1982), and vowel spectrum enhancement (Summerfield et al., 1984; Summerfield et al., 1987). There is converging psychophysical (Byrne et al., 2011) and neurophysiological evidence (Nelson & Young, 2010) to suggest that this enhancement is due to adaptation of inhibition. If inhibition adapts over the course of a precursor, the ensuing target (or masker) is released from inhibition that would otherwise be present if the target onset were coincident with the precursors onset. Although there are no psychophysical studies designed to test enhancement of AM detection, there is neurophysiological evidence showing that the presence of off-frequency spectral components enhances AM coding in neurons in the cochlear nucleus (Moller, 1975).

A notable difference between the current study and previous enhancement studies is the difference in level between off-frequency and probe-frequency components. The notched noise used to restrict off-frequency listening in the current experiment was 50 dB/Hz below the spectrum level of the carrier, while in previous studies components of off-frequency maskers are usually above the level of the probe when enhancement is observed (Byrne et al., 2011; Viemeister & Bacon, 1982; Viemeister et al., 2013). Moreover, effects of suppression and inhibition weaken as the probe level increases relative to a constant-level, notched-noise suppressor/inhibitor (Rhode & Greenberg, 1994). This suggests that enhancement effects (if present) were relatively weaker in the current study compared to previous studies. Future studies are needed to fully determine to what extent the notched noise used to restrict off-frequency listening may have facilitated enhancement.

2.6 Experiment II: AM detection with and without a precursor as a function of modulation frequency

Results from Experiment I show that a notched-noise precursor presented before a high-frequency carrier improves AM detection at moderate-to-high carrier levels for low (fm = 20 Hz) modulation frequencies. Experiment II assessed whether these improvements apply to other modulation frequencies by measuring TMTFs for short carriers with and without a precursor.

2.6.1 Methods

2.6.1.1 Subjects

Five young, normal-hearing listeners (S1, S2, S3, S4, and S5) from Experiment I also participated in this experiment.

2.6.1.2 Stimuli

The precursor, off-frequency listening noise, and short carrier were the same as in Experiment I. Thresholds for long carriers were not tested. The 65 dB SPL carrier was modulated at fm = 20, 40, 60, 80, 100, or 500 Hz, resulting in 12 total conditions (6 modulation frequencies * 2 precursor conditions). Conditions were randomized by modulation frequency. For a given modulation frequency, AM thresholds were obtained for the no-precursor condition, followed by the precursor condition.

2.7 Results and discussion

2.7.1 50-ms carrier without a precursor

Temporal modulation transfer functions measured with the 50-ms carrier in the absence of a precursor are displayed as open circles in Figure 2.4. AM detection thresholds improved with increasing modulation frequency up to 80-100 Hz, where the average improvement between thresholds for 20 Hz and 100 Hz modulation frequencies was 5.5 dB. For fm=500 Hz, AM thresholds were worse (except S5) by 3-5 dB (S1, S2), or 1-2 dB (S3, S4) compared to fm=100 Hz.

2.7.2 50-ms carrier with a precursor

Filled circles in Figure 2.4 display TMTFs for the 50-ms carrier with a precursor. AM thresholds for fm $\leq$80 Hz are roughly constant (S1, S3), or improve slightly with increasing modulation frequency (S2, S4, S5). On average, this improvement was 2.1 dB, which is smaller than that observed for the 50-ms carrier without a precursor. A two-way rmANOVA was conducted with condition (precursor, no precursor) and modulation frequency (20, 40, 60, 80, 100, 500 Hz) as repeated measures. The main effects of condition [$F(1,4)=69.63$, $p<0.005$] and modulation frequency [$F(5,20)=19.21$, $p<0.005$] were significant, as was the condition * modulation frequency interaction [$F(5,20)=11.30$, $p<0.01$]. Consistent with this interaction, post-hoc tests revealed that the precursor-no precursor difference was significantly larger when averaged across fm$\leq$60 Hz than fm$\geq$80 Hz [$t(4)=-3.85$, $p=0.018$], suggesting that the effect of the precursor is largest at low modulation frequencies.

The larger precursor-no precursor difference at low compared to high modulation frequencies is similar to better AM thresholds for continuous than gated carriers reported in

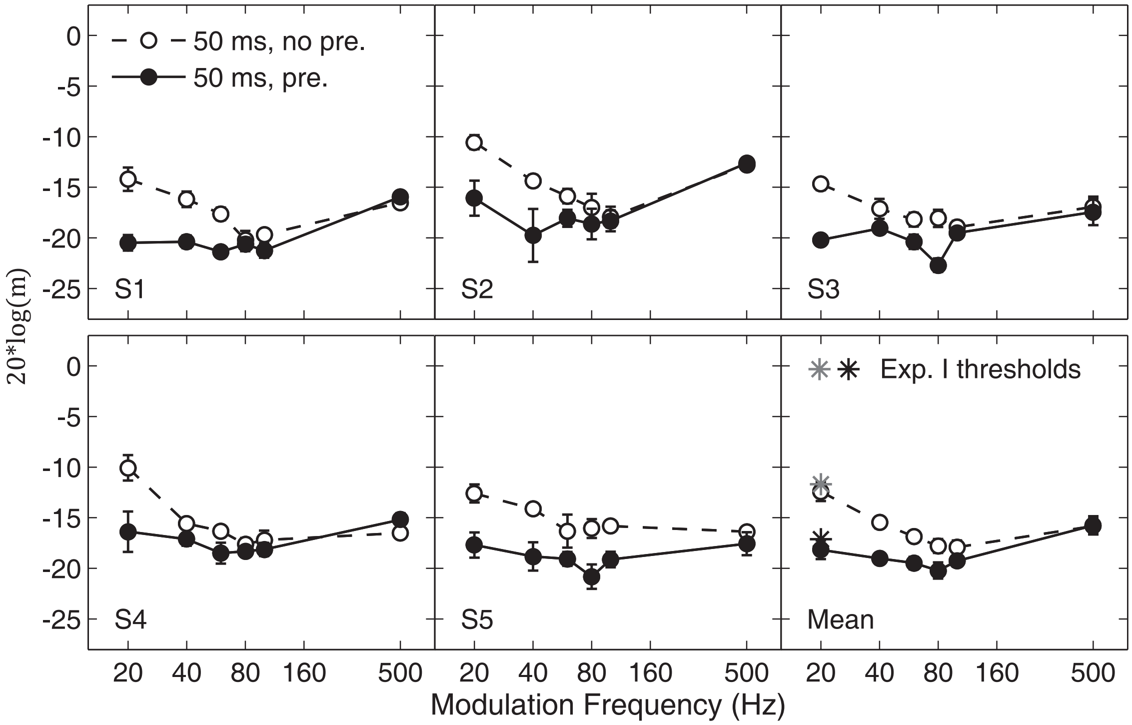

Figure 2.4. Modulation depth at threshold as a function of modulation frequency for 65 dB SPL carriers preceded by silence (open circles) or by a notched-noise precursor (closed circles). Panels are results for individual subjects except the lower right panel, which displays the mean data. Mean data from Experiment I (black and gray asterisks), where fm = 20 Hz, are replotted in the lower right panel to show consistency between measurements. Error bars are the standard error of the mean. The smallest error bars may be covered by data markers.

previous studies (Sheft & Yost, 1990; Viemeister, 1979). Adaptation is a common explanation for poorer thresholds with gated than with continuous carriers (Klump & Okanoya, 1991; Moody, 1994; Sheft & Yost, 1990; Viemeister, 1979). This explanation posits that, with gated carriers, cycles of modulation occurring during the onset response of auditory nerve fibers are less informative than cycles occurring during the steady-state response. Presumably this “onset insufficiency” (Sheft & Yost, 1990) influences the detection of low-frequency AM more than high-frequency AM for gated carriers because more cycles of modulation occur after the onset response for high- than for low-frequency AM, thus increasing the opportunity for multiple looks (Viemeister, 1979; however, see Yost & Sheft, 1997). Consistent with this theory, the neural synchrony of auditory nerve fibers in starling is more disrupted at the onset of gated AM stimuli for low- than for high-frequency AM (Gleich & Klump, 1995). Although adaptation and onset insufficiency hypotheses may partly explain why the precursor-no precursor differences are smaller at higher than at lower modulation frequencies, it is not clear how this hypothesis accounts for the level dependence of the precursor-no precursor difference reported in Experiment I. For example, it is not clear how onset insufficiency predicts precursor effects to be largest at mid carrier levels, smaller at high carrier levels, and absent at low carrier levels. However, these level effects are accounted for by the theoretical framework in Figure 2.1 based on a reduction in cochlear gain over the course of the precursor.

AM detection thresholds in the no precursor condition were generally poorer for lower than higher modulation frequencies. When the modulation index at threshold is expressed as ΔI in dB (Long & Cullen, 1985), average thresholds improve from 4.25 dB to 2.25 dB as modulation frequency increases from 20 to 100 Hz. This improvement is roughly consistent with the 1.3 dB improvement expected from multiple looks (Eq. 2.3) and a 4-cycle critical duration for AM detection (Lee & Bacon, 1997). Studies on forward masking suggest that growth of masking is not influenced by the slope of the cochlear I/O function unless masker and probe levels at threshold fall on parts of the cochlear I/O function with different slopes (Oxenham & Plack, 1997; Oxenham & Plack, 2000). In the context of AM detection, the valleys and peaks of the AM stimulus are analogous to the masker and probe in masking, respectively. Thus, decompression of the I/O function as a result of a reduction in cochlear gain from the precursor may only produce a substantial change in AM thresholds when thresholds without a precursor are relatively large (i.e., fm$\leq$40 Hz). At higher modulation frequencies (fm from 60-100 Hz), thresholds without a precursor are relatively small (i.e., the acoustic peaks and valleys of the AM signal are processed similarly by the cochlear I/O function), thus a reduction in gain is expected to only mildly improve effective modulation depth at high modulation frequencies[3].

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[3] Currently it is unclear why the precursor-no precursor difference is absent for fm = 500 Hz despite the moderately higher thresholds at this frequency than at moderate modulation frequencies (60-100 Hz)

2.8 Summary and conclusions

Amplitude modulation detection thresholds for a short narrow-band noise carrier centered on 5000 Hz are better with than without a low-level, notched-noise precursor for moderate-to-high carrier levels, and low ($\leq$100 Hz) modulation frequencies. Improved thresholds with compared to without a precursor are consistent with a reduction in cochlear gain. A potential candidate for this reduction is the MOC reflex, which when stimulated by sound reduces outer hair cell gain with a time constant of roughly 70 ms (Backus & Guinan, 2006). The advantage of this interpretation is the ability to account for the level dependence of the precursor-no precursor difference, although off-frequency listening may complicate this interpretation at the highest carrier levels. From an ecological perspective, these results suggest that the auditory system may improve the effective modulation depth of modulated stimuli over the first several-hundred milliseconds of acoustic stimulation. This improvement may lead to robust neural coding of the amplitude envelope of speech and ultimately lead to robust speech perception in quiet and in background noise.

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CHAPTER 3

EFFECTS OF INTENSITY ON AMPLITUDE MODULATION DETECTION USING HIGH- AND LOW-FLUCTUATING NOISES

3.1 Abstract

Amplitude modulation (AM) detection was measured with short (50 ms) and long (500 ms) narrow-band noise carriers as a function of carrier level. The carrier was either high- or low-fluctuating noise. The purpose of this experiment was to test the hypothesis that the inherent fluctuations of narrow-band noise carriers are influenced by cochlear compression. Specifically, the inherent fluctuations of short carriers may be reduced as the carrier level is increased from low to moderate levels where cochlear responses are more compressive. A long carrier was included due to evidence that cochlear response may be different for short and long durations. For 50-ms, low-fluctuating carriers, AM detection thresholds were poorer for moderate-level carriers compared to lower- or higher-level carriers, resulting in a "mid-level hump". For 500-ms, low-fluctuating carriers, AM detection thresholds were better compared to 50 ms carriers, primarily for moderate-to-high level carriers; thus, eliminating this mid-level hump. For high-fluctuating carriers (50 and 500 ms), AM detection thresholds are relatively constant across carrier levels. The mid-level hump observed for 50-ms, low-fluctuating carriers is consistent with a reduction in post-cochlear modulation depth as a result of cochlear compression. The absence of the mid-level hump for long, low-fluctuating carriers is consistent with the combined effects of cochlear compression and multiple looks and/or a reduction in cochlear gain during the forward fringe of the long carrier, leading to improved thresholds at the moderate levels. For high-fluctuating carriers, low level linear and moderate level compressive cochlear response growth may have resulted in constant envelope signal-to-noise ratios, due to cochlear response growth equally affecting

target modulation and inherent carrier fluctuations. Thus, AM detection for high-fluctuating carriers is constant as a function of carrier level.

3.2 Introduction

The ability of listeners to detect amplitude modulation (AM) depends on several factors including carrier duration (Sheft & Yost, 1990; Viemeister, 1979; Yost & Sheft, 1997), carrier level (Kohlrausch et al., 2000; Millman & Bacon, 2008; Moore & Glasberg, 2001), and inherent fluctuations of noise carriers (Dau et al., 1999). The effects of these factors are dependent on the type of the carrier (sinusoidal or noise) and carrier spectrum (wide-band or narrow-band) for noise carriers. For example, the effects of carrier level on AM detection are pronounced for sinusoidal carriers (Kohlrausch et al., 2000; Millman & Bacon, 2008; Moore & Glasberg, 2001) and low-fluctuating narrow-band noise carriers (Chapter 2 of the current manuscript), but relatively nonexistent for wide-band noise carriers above $\sim$10-20 dB spectrum level (Bacon & Viemeister, 1985; Viemeister, 1979). Furthermore, previous studies showed that AM detection is influenced by the inherent fluctuations of narrow-band noise carriers, where AM detection thresholds are poorer for high-fluctuating compared to low-fluctuating carriers (Dau et al., 1999). This is likely due to the increased possibility of modulation masking arising from the inherent fluctuations of high-fluctuating carriers. The concept of modulation filters was introduced by Dau et al. (1997a,b) to account for modulation masking. This model performs a decomposition of the AM envelope through a set of bandpass filters ("modulation filters"). For narrow-band noise carriers, the detectability of the target modulation is determined by the effective modulation depth of the target and the spectral density of the carrier's inherent fluctuations falling through the modulation filter centered on the target modulation frequency.

At the level of the cochlea, the target modulation depth is expected to be reduced by cochlear compression. For example, AM detection thresholds are poorer at moderate compared to low and high carrier levels for short, low-fluctuating narrow-band noise carriers, consistent with the predicted effects of the cochlear compressive input-output (I/O) function (Experiment I of Chapter 2). Given these level-dependent changes in AM detection, the current experiment tests the hypothesis that inherent fluctuations of narrow-band noise carriers are influenced by cochlear compression. Specifically, it was hypothesized that the effects of the inherent fluctuations in high-fluctuating carriers on AM detection are constant for all carrier levels. For low-fluctuating carriers, AM detection thresholds are expected to worsen with increasing carrier level due to cochlear compression. To examine these effects, AM detection thresholds were measured for low- and high-fluctuating carriers at low, moderate, and high carrier levels to encompass linear and compressive cochlear responses.

The interaction between the inherent fluctuations of narrow-band noise stimuli and cochlear compression has been demonstrated in gap detection studies, a topic closely related to AM detection (Galsberg & Moore, 1992; Horwitz et al., 2011; Moore et al., 2001). For example, Horwitz et al. (2011) measured gap detection for narrow-band noise markers as a function of marker level using markers with flat (1000 Hz wide) and fluctuating (50 Hz wide) envelopes. A background noise was also included to serve as the trough of the envelope and thus limit the envelope depth. For low-fluctuating markers, gap detection thresholds for normal-hearing listeners were poorer at moderate compared to low and high markers, consistent with a reduction in the effective envelope at moderate marker levels due to cochlear compression. For high-fluctuating markers, gap detection improved with increases in marker level. This is expected as cochlear compression leads to reduced depth of the marker fluctuations and thus reduces confusion between the inherent fluctuations and the imposed gap. Alternatively, increased compression with increasing marker level predicts poorer gap detection due to a reduction in the effective envelope (see Horwitz et al., 2011). Moreover, Horwitz et al. (2011) found a trend between gap detection thresholds for the low-fluctuating markers at 51 dB SPL and psychophysical estimates of cochlear compression. Specifically, gap detection thresholds from low-to-moderate marker levels worsened at a faster rate for subjects with the shallowest I/O function slopes (i.e., the most compression).

In AM detection, the expected effects of cochlear compression on the inherent fluctuations of narrow-band noise carriers can be illustrated by considering the output at the modulation filter centered at the target modulation filter. First, the input "acoustic" envelope signal-to-noise ratio (acoustic "SNR_{ENV}") is defined as the ratio of target modulation power to the power of the inherent fluctuations of the carrier. The acoustic SNR_{ENV} passing through the modulation filter is called the "effective SNR_{ENV}" at the output of the modulation filter centered at the target modulation frequency.

For high-fluctuating carriers, the effective SNR_{ENV} is expected to be constant at all carrier levels. Specifically, for high-fluctuating carriers, the envelope power of the carrier and the envelope power of the target modulation passing through the modulation filter are expected to be equally reduced (low effective SNR_{ENV}) by cochlear compression, resulting in a constant effective SNR_{ENV} and thus predicting constant AM thresholds as a function of level. To illustrate the effects of cochlear compression on the carrier-inherent fluctuations and the target modulation prior to passing through the modulation filter, the temporal envelopes of high-fluctuating carriers were passed through an I/O function for linear and compressive responses. Figure 3.1 demonstrates that a linear cochlear response equally maintains the inherent fluctuations and the target modulation (Figure 3.1, top panels), while a compressive cochlear response equally reduces the inherent fluctuations and the target modulation (Figure 3.1, bottom panels) at the output of the cochlea.

For low-fluctuating carriers, the envelope power of the carrier is less than the envelope needed to detect AM with a flat envelope (i.e., sinusoidal); thus, modulation masking does not occur for low-fluctuating carriers and detection is determined by sensitivity to the target effective modulation at the output of the modulation filter in the absence of envelope energy. To illustrate the effects of cochlear compression on the target effective modulation depth of a low-fluctuating carrier prior to filtering in the modulation domain, the temporal envelopes of low-fluctuating carriers were passed through an I/O function for linear and compressive responses. Consequently, a linear cochlear response at low carrier levels is expected to maintain the effective modulation depth of the target (Figure 3.2, top panels) allowing for better AM detection thresholds. At moderate carrier levels where the cochlear I/O function is compressive, the effective modulation depth of the target is expected to be reduced (Figure 3.2, bottom panels), leading to higher AM detection thresholds. When off-frequency listening is considered at high carrier levels, the input AM is detected through auditory filters where the cochlear response is more linear; thus, the effective modulation depth of the target is expected to be large and consequently improve AM thresholds. Thus, a mid-level hump is expected for short, low-fluctuating carriers.

The mid-level hump observed for short, low-fluctuating carriers is expected to be reduced as the carrier duration is substantially made longer (e.g., 500 ms). This prediction may be partly related to the combined effect of cochlear compression and multiple looks. When the carrier duration is lengthened, the modulation depth at threshold (i.e., criterion modulation

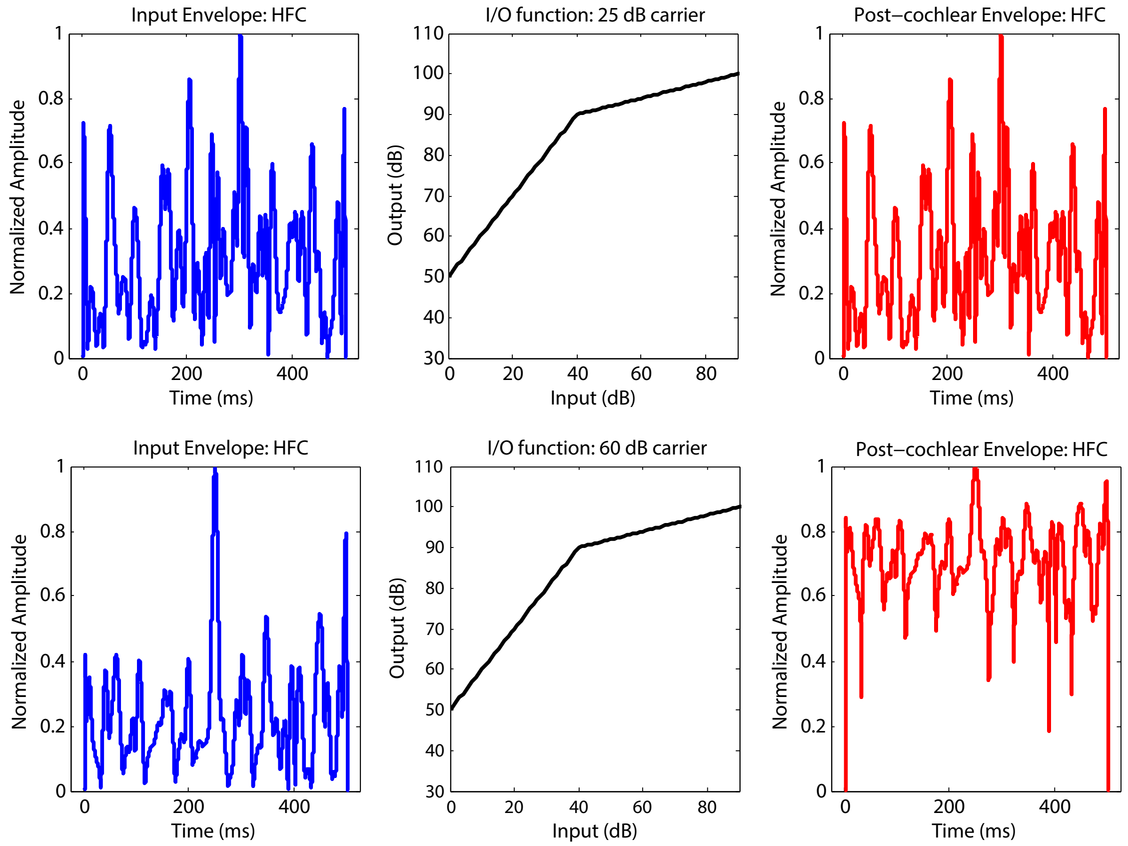

Figure 3.1. The temporal envelopes of 500 ms, high-fluctuating (HFC), narrow-band noise carriers modulated at 20 Hz illustrating the expected effects of cochlear compression on the inherent fluctuations and the target modulation. The left temporal envelopes represent the input temporal waveforms while the right panels represent the temporal waveforms at the output of the cochlea. The upper three panels illustrate the effects of cochlear linear responses on the carrier inherent fluctuations and the target modulation depth while the bottom three panels illustrate the effects of compressive cochlear responses on the carrier inherent fluctuations and the target modulation depth. The input temporal envelope was passed through an input-output (I/O) function and presented at 25 dB SPL for a linear response and at 60 dB SPL for a compressive response.

depth) is expected to be smaller due to multiple looks. At low carrier levels where the cochlear response growth is linear, the improvement in AM detection for longer carriers is also determined by multiple looks. At moderate carrier levels, the smaller criterion modulation depth is expected to improve AM detection for long compared to short carriers. In other words, the improvement in target modulation depth for long compared to short carriers is constant across level. However, to reach the criterion effective modulation depth, the acoustic modulation depth must be changed by a greater magnitude for moderate carrier

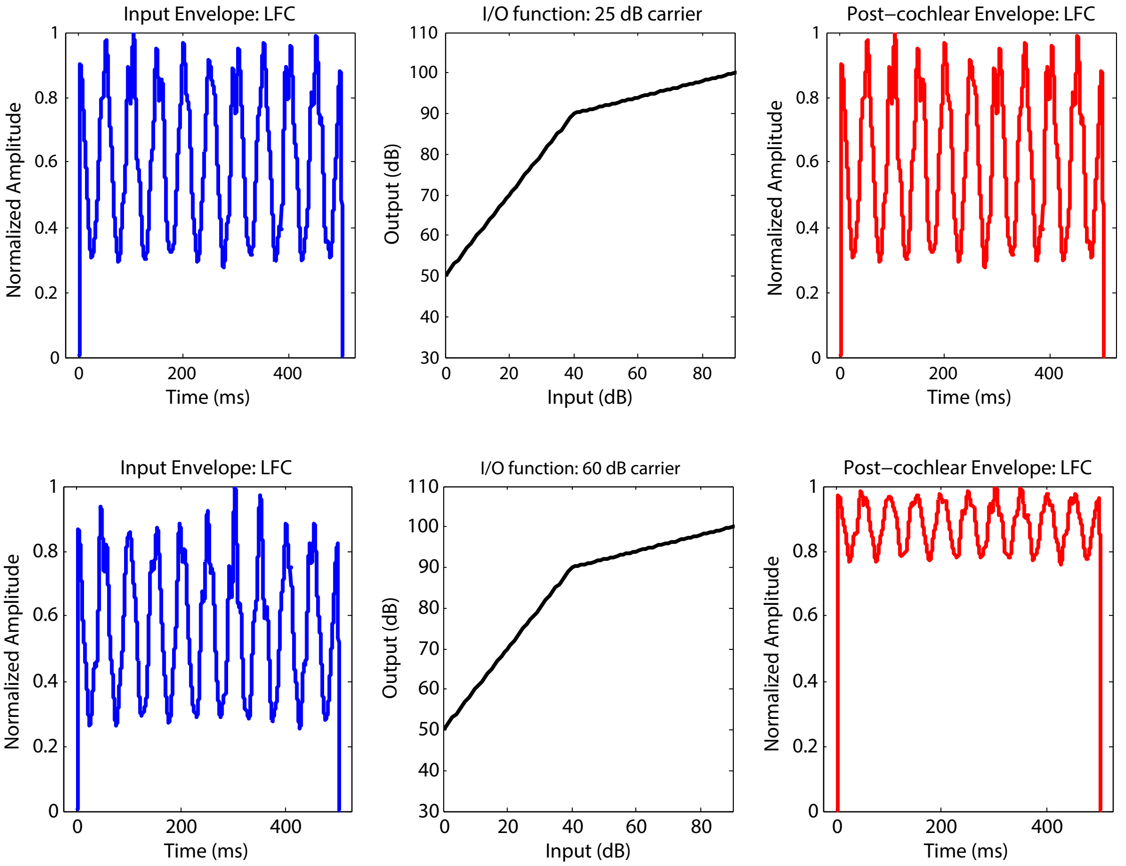

Figure 3.2. The temporal envelopes of 500 ms, low-fluctuating (LFC), narrow-band noise carriers (100-Hz wide) modulated at 20 Hz illustrating the expected effects of cochlear compression on the effective modulation depth. The left temporal envelopes represent the input modulation depth while the right temporal envelopes represent the effective modulation depth at the output of the cochlea. The upper three panels illustrate the effects of cochlear linear responses on the effective modulation depth while the bottom three panels illustrate the effects of compressive cochlear responses on the effective modulation depth. The carrier temporal envelope was passed through an input-output (I/O) function and presented at 25 dB SPL for a linear response and at 60 dB SPL for a compressive response.

levels undergoing compression, compared to lower carriers that are processed linearly.

Alternatively, for long carriers, the cochlear I/O is expected to be decompressed due to a reduction in cochlear gain over the course of the forward fringe of the carrier. A potential mechanism for this gain reduction is the medial olivocochlear (MOC) reflex. This reflex has an onset delay of 25 ms, followed by a growth and decay of approximately 70-100 ms (Backus & Guinan, 2006). This MOC-based explanation predicts that the improved AM detection thresholds for long compared to short carriers should be largest at moderate compared to low levels due to decompression of the I/O function.

The primary goal of the present study was to examine the effects of carrier level using short and long and high- and low-fluctuating narrow-band noise carriers to test the following hypotheses: (1) AM detection will be constant across carrier levels for high-fluctuating carriers due to cochlear compression equally affecting carrier envelope power and target envelope power, (2) AM detection thresholds for short, low-fluctuating carriers will worsen with increasing carrier level due to cochlear compression, consistent with the findings of Chapter 3, and (3) AM detection thresholds for long, low-fluctuating carriers will improve at moderate carrier levels due to decompression of the I/O function via a reduction in cochlear gain over the course of the forward fringe of the carrier and/or due to the combined effects of cochlear compression and multiple looks.

3.3 General methods

3.3.1 Subjects

Four normal-hearing subjects (aged 20 to 32 years, two males) participated in the experiments. Subjects had thresholds $\leq$20 dB HL at audiometric frequencies between 250 and 8000 Hz, and normal middle ear function based on tympanometry. The right ear of each subject was tested. Subjects were inexperienced with psychoacoustic tasks except subject 1 (S1), who was the first author. All subjects, except S1, were paid hourly for their participation.

3.3.2 Apparatus and stimuli

Stimuli were digitally generated using custom-built MATLAB software and output through a LynxTWO-B sound card (sampling rate, 44.1 kHz; 24-bit resolution) to the listener's right ear via ER-2 insert earphones driven by a headphone buffer (Tucker-Davis-Technologies [TDT], HB7). AM detection thresholds were measured using a narrow-band noise (bandwidth = 100 Hz) carrier whose spectrum was arithmetically centered on 5000 Hz (fc). The 20-Hz sinusoidal modulation (fm) occurred over the entire duration of the carrier starting in cosine phase. The durations of the carrier and the modulator were 50 or 500 ms (excluding 2 ms onset/offset ramps). Low- or high-fluctuating carriers were achieved by generating "low-noise noise" (Kohlrausch et al., 1997) or Gaussian noise carriers, respectively. Carrier levels were 45, 65, and 85 dB SPL. Off-frequency listening (Johnson-Davies &

Patterson, 1979; O'Loughlin & Moore, 1981) was restricted by gating an additional notched noise simultaneously with the carrier, where the noise level was 50 dB/Hz below the carrier spectrum level (Nelson et al., 2001). The spectral notch of the off-frequency listening noise extended from 0.9*fc to 1.2*fc (i.e., 4500-6000 Hz), similar to Oxenham and Plack (1997). The outer frequency cutoffs of the off-frequency listening noise were 1250 and 10000 Hz. Figure 3.3 shows the time waveform (left panels) and spectrogram (right panels) of the 50 and 500 ms high- and low-fluctuating carriers.

3.3.3 Procedure

Subjects participated in the experiment in a sound-attenuating booth. The dependent variable was AM threshold, expressed as modulation depth (m) in dB. AM detection thresholds were measured using an adaptive three-interval, three-alternative forced-choice (3AFC) task. During a trial, the carrier was presented in each interval separated by 500 ms and marked by lighted squares on a computer monitor. During a randomly chosen interval, the carrier was sinusoidally amplitude modulated. In order to eliminate level cues, the overall power of the carrier was the same in all observation intervals (Viemeister, 1979). The subject pressed a button on a keyboard to indicate the interval in which the modulation was perceived and visual feedback was provided to indicate a correct or incorrect response.

During an adaptive track, the modulation depth was adjusted using a two-down one-up rule, which measures the modulation depth necessary to achieve 70.7% correct on the psychometric function (Levitt, 1971). The initial 8 dB step size was decreased to 2 dB after the second reversal. Twelve reversals were obtained and the mean modulation depth of the last eight reversals was defined as the AM threshold for that adaptive track. Adaptive tracks with a standard deviation greater than 5 dB were discarded and then repeated. The need to obtain an additional threshold occurred a total of 8 times of the measured experimental thresholds.

Learning was measured for each condition by the change in threshold per repetition (i.e., slope) across these four adaptive tracks. If the slope was greater than 3 dB/repetition, an additional threshold was obtained and the slope was recalculated. This process was continued until the slope fell below 3 dB/repetition and performance was then assumed to have stabilized. None of the subjects exceeded the 3 dB/repetition criterion; therefore,

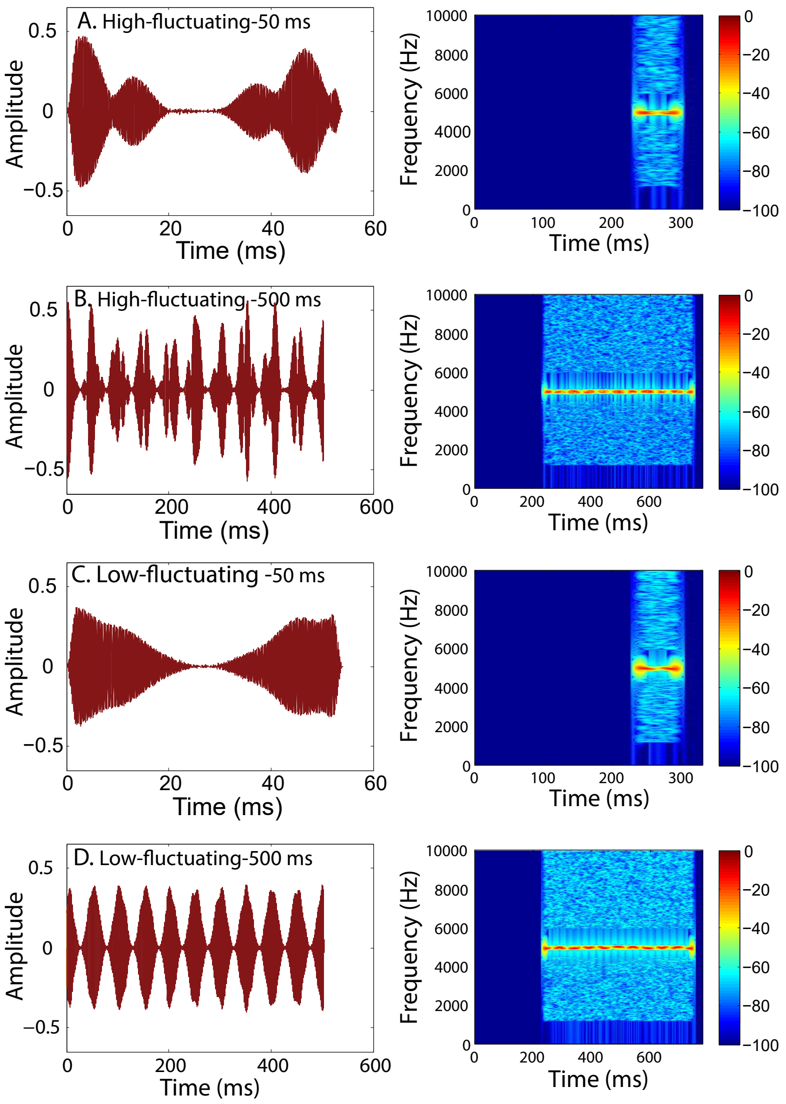

Figure 3.3. Time waveforms (left) and spectrograms (right) of high-fluctuating (top four panels) and low-fluctuating (bottom four panels) narrow-band, amplitude-modulated carriers. The carrier duration was either 50 or 500 ms (plus 2-ms rise/fall ramps). Off-frequency listening was limited by gating an additional notched noise with the carrier. For the spectrogram, dark colors represent relatively higher amplitudes.

only the initial four thresholds were averaged to compute the final threshold. Experimental sessions were limited to 1.5-2 hours. Total number of sessions was about 12/subject.

Prior to data collection, each subject was given at least 2 hours of training to minimize learning effects. Two consecutive AM thresholds were measured for 45, 65, and 85 dB SPL carriers per condition (2 conditions for carrier fluctuations [high- and low-fluctuating carriers] * 2 carrier durations [50 ms and 500 ms] * 2 [thresholds] = 24 thresholds). Thresholds measured during training were discarded. Conditions were blocked by carrier level and were counterbalanced between subjects. Within each block, high- and low-fluctuating noise carriers were randomized and thresholds were obtained for 500 ms first followed by 50 ms carriers for a given carrier fluctuation.

3.4 Results and discussion

Figure 3.4 shows individual and mean AM detection thresholds (20*log m) as a function of carrier level. The parameters are the carrier duration and the carrier fluctuation. Squares and circles represent thresholds for high- and low-fluctuating noise carriers, respectively; solid and dashed lines represent thresholds for 50- and 500-ms carrier durations, respectively. A three-way repeated-measures analysis of variance (rmANOVA) was performed, with carrier level (three levels), carrier fluctuation (two levels), and carrier duration (two levels) as repeated measures.

3.4.1 Low-fluctuating carriers

There are considerable differences in the shape of AM threshold as a function of carrier levels for short and long high- and low-fluctuating noise carriers, as revealed by the statistically significant carrier level*duration*fluctuation interaction [$F(2, 6)=7.853$, $p=0.02$]. For low-fluctuating, 50-ms carriers, AM detection thresholds worsened as carrier level increased from 45 to 65 dB SPL and then improved as carrier level increased from 65 to 85 dB SPL (Figure 3.4, closed red circles), reminiscent of the mid-level hump. Post hoc t-tests revealed a statistically significant difference between 45 and 65 dB SPL [t(3)=-4.015, $p=0.028$] and between 65 and 85 dB SPL [t(3)=29.341, $p=0.001$]. This finding is consistent with the findings of Chapter 3 and intensity discrimination studies (Carlyon & Moore, 1984; Nizami, 2006; Roverud & Strickland, 2015a). This mid-level hump is consistent with the expected effects of cochlear compression on the target effective modulation depth such that the cochlear I/O function is compressive at moderate levels. Therefore, the effective modulation depth is expected to be reduced, leading to higher AM detection thresholds (consistent with the findings of Chapter 3).

For low-fluctuating, 500-ms carriers, AM detection thresholds were lower (better) (Figure 3.4, open circles) compared to 50 ms carriers (Figure 3.4, closed circles). Moreover, the effects of carrier duration became bigger with increasing carrier level; with the largest

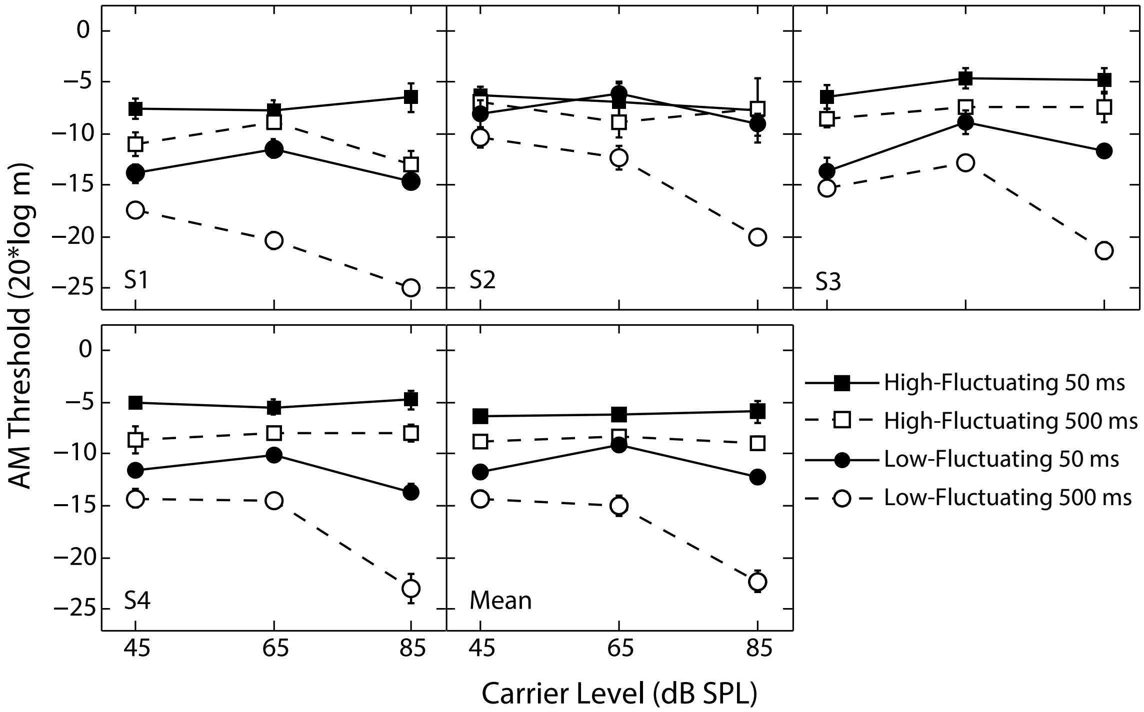

Figure 3.4. Modulation depth at threshold as a function of carrier level for short (closed symbols) and long (open symbols) carriers. High- and low-fluctuating narrow-band noise carriers (100-Hz wide centered at 5000 Hz) are represented by squares and circles, respectively. The modulation frequency was 20 Hz. Lower values represent better AM detection (i.e., lower modulation depth (m) at threshold). Panels are results for individual subjects except the lower right panel, which displays the mean data. Error bars are the standard error of the mean. The smallest error bars may be covered by data markers.

improvement occurring at 65 [t(3)=5.148, p=0.0139] and 85 dB SPL [t(3)=5.917, p=0.0096], but not 45 dB SPL [t(3)=0.264, p=0.808], which is reminiscent of the “near miss” to Weber law. The improvement in AM detection thresholds (averaged across subjects in terms of [20*log (m)]) for long compared to short carriers was 2.7, 5.8, and 10.1 dB for 45, 65, and 85 dB SPL carrier levels, respectively.

3.4.2 Interpretation of carrier duration effects

The nonmonotonic AM detection behavior observed for low-fluctuating carriers was eliminated in 3/4 subjects when the carrier duration was lengthened to 500 ms. The increasing size of the duration effect with increasing level may be related to the combined effects of cochlear compression and multiple looks. For short and long carriers presented at low levels and thus processed linearly, the modulation depth is maintained for both carriers, and the only factor determining differences between short and long carriers is the number of opportunities or "looks" available to detect modulation. This suggests that the improvement of AM detection for long compared to short carriers at low carrier levels is expected to be equal to what is predicted from multiple looks. This is consistent with the experimental data at 45 dB SPL. Lee and Bacon (1997) reported a critical duration of ∼4 cycles for AM detection using sinusoidal carriers modulated at 20 Hz, suggesting that despite the availability of 10 cycles for the 500-ms carrier, only 4 of these cycles contributed to improvements in thresholds compared to 50-ms carriers. Based on a 4-cycle critical duration for detection of 20-Hz AM, the predicted improvement in thresholds with long carriers relative to those with short carriers is 3.01 dB. This value is close to the value observed from the data for low-fluctuating carriers at 45 dB SPL carrier level (2.7 dB). Findings of Chapter 3 argue against multiple looks as the sole mechanism for the improved thresholds in the long carrier condition, because thresholds improved by a constant regardless of the carrier level for long carriers compared to short carriers with precursors. This suggests that stimulation prior to the carrier's onset is a primary factor determining improvements in thresholds for long compared to short carriers.

3.4.2.1 Explanation based on static nonlinearity

The improved AM thresholds at moderate and high levels for long compared to short, low-fluctuating carriers is larger than the expected value predicted by the 4-cycle critical duration. For short and long carriers presented at moderate-to-high carrier levels, the target modulation depth will undergo compression for both short and long carriers, but due to multiple looks, there are more "looks" to detect the modulation for long carriers, thus resulting in smaller criterion modulation depth of the target. This requires a corresponding decrease in the acoustic envelope modulation depth at threshold and thus improved AM detection for long compared to short carriers.

3.4.2.2 Explanation based on dynamic nonlinearity

The long carrier (500 ms) may have elicited the MOC reflex during the forward fringe of the carrier and thus decompressed part of the cochlear I/O function. This decompression predicts that improvements in AM detection thresholds for 500 ms compared to 50 ms carriers should be largest for moderate carrier levels, and smaller for low or high carrier levels (consistent with the findings of Experiment I in Chapter 2). The smaller 500 ms-50 ms difference at high carrier levels is expected because (1) detection is assumed to depend only on the auditory filter centered on the carrier frequency (Viemeister, 1983), (2) the forward fringe of the 500 ms carrier is assumed to produce a constant reduction in gain for all carrier levels (Warren & Liberman, 1989), and (3) cochlear gain is minimal at high levels (Robles & Ruggero, 2001). For low-fluctuating carriers, the 500 ms-50 ms difference was larger at 65 and 85 dB SPL compared to 45 dB SPL. Despite this, the difference is largest at 85 dB SPL, which is inconsistent with the theoretical framework. One reason to consider when interpreting the long carrier data obtained at high carrier levels is the finding that AM detection for short carriers improves with increasing carrier level above 65 dB SPL. This finding is consistent with the detection of AM in remote auditory filters via the upward spread of excitation (Florentine & Buus, 1981), which is a violation of the first assumption of the theoretical framework presented in Chapter 1 (i.e., AM detection depends only on the auditory filter centered on the carrier frequency). Experiment I in Chapter 3 showed that AM detection thresholds for 500 ms without precursors improved by a constant compared to 50 ms carrier with precursors, suggesting that this improvement can be in part explained by decompression of the I/O function.

3.4.3 High-fluctuating carriers

For high-fluctuating, 50-ms (Figure 3.4, closed squares), and 500-ms carriers (Figure 3.4, open squares), AM detection thresholds were roughly constant as a function of carrier level, with the exception of S1 who showed a small mid-level hump for the 500 ms carrier. Post hoc t-tests for AM thresholds obtained with 50 ms carriers did not reach significance between 45 and 65 dB SPL [t(3)=0.313, p=0.774] or between 65 and 85 dB SPL [t(3)=0.514, p=0.642]. Compared to 50 ms carriers, AM thresholds for high-fluctuating, 500-ms carriers improved by 2.65, 2.08, and 3.21 dB (averaged across subjects) for 45, 65, and 85 dB SPL, respectively, consistent with what is predicted based on the 4-cycles critical duration.

The absence of level-dependent changes in AM detection for high-fluctuating carrier can be explained by the magnitude of the effective SNR_{ENV} in the modulation filter centered at the target modulation frequency. For high-fluctuating carriers, the envelope power of the carrier and the envelope power of the target modulation passing through the modulation filter are expected to be equally reduced (low effective SNR_{ENV}) by cochlear compression, resulting in constant effective SNR_{ENV} at all carrier levels and predicting constant AM thresholds as a function of carrier level.

3.5 Summary and conclusion

This experiment investigated the extent to which changes in AM detection with level are consistent with expected changes in the target modulation depth of low-and high-fluctuating carriers due to level-dependent changes in cochlear compression. AM detection for low-fluctuating, 50-ms narrow-band noise carriers was poorer at moderate compared to low and high carrier levels reminiscent of the mid-level hump. Moreover, unlike low-fluctuating carriers, AM detection thresholds for high-fluctuating carriers were independent of carrier level. The main features of these results can be explained by the cochlear input-output function and by whether or not the acoustic SNR_{ENV} is maintained or reduced by linear and compressive cochlear responses, respectively. For high-fluctuating carriers, the envelope power of the carrier and the envelope power of the target modulation are expected to be equally reduced by cochlear compression; leading to low effective SNR_{ENV} at the output of the modulation filter centered at the target modulation frequency; thus predicting constant AM thresholds as a function of level. For low-fluctuating carriers, detection is mainly determined by the envelope power of the target modulation due to the envelope power of the carrier being lower than detection thresholds required to detect a carrier with a flat envelope such as sinusoidal carriers. This suggests that detection is determined primarily by sensitivity to the target modulation depth, which is reduced by cochlear compression at moderate carrier levels thus predicting a mid-level hump in AM detection.

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CHAPTER 4

GENERAL DISCUSSION

4.1 Summary and conclusions

The identity of a sound is defined by its temporal fluctuations (envelope) and how that envelope varies over time. There is evidence that an accurate representation of the envelope is essential for speech understanding in quiet(Shannon et al., 1995) and in noise (Heinz & Swaminathan, 2009; Houtgast & Steeneken, 1973). Indeed, Shannon et al. (1995) found that a minimum of three to four processing bands of noise vocoded speech, which has preserved temporal envelope and degraded spectral cues, are necessary to ensure near-perfect recognition of consonants, vowels, and sentences in quiet in normal-hearing listeners. AM stimuli are used to grossly approximate the peaks and valleys of the speech envelope. AM stimuli are more ecologically relevant than pure tones because sounds in everyday life fluctuate in amplitude over time. An understanding of how the auditory system encodes the temporal envelope of AM may reveal mechanisms responsible for robust speech understanding in quiet and in noise. A primary function of the peripheral auditory system is to ensure that the envelope is accurately represented when delivered to more central neural structures. Along the auditory pathway, the AM envelope undergoes a series of transformations. At the level of the cochlea, AM stimulus envelope is subject to compressive nonlinearity in the basilar membrane and the amplification provided from the cochlear OHCs. Furthermore, the efferent feedback to the OHCs via the MOC neurons may influence the representation of the AM envelope, as this reflex reduces the amplification provided by the OHCs when stimulated by sound. The primary goal of this dissertation was to test the influence of cochlear compression and the MOC reflex on AM detection.

Chapter 2 addressed the hypothesis that AM detection for short (50 ms) low-fluctuating carriers modulated at 20 Hz worsens with increasing carrier level due to cochlear compression and that acoustic stimulation using notched-noise precursors improves the AM effective modulation depth due to a reduction in cochlear gain via the MOC reflex. The experiments of this chapter have shown that AM thresholds for short carriers are poorer at moderate compared to low and high carrier levels, resulting in a mid-level hump. Poorer AM detection at moderate compared to low and high levels is consistent with relatively poorer effective modulation depth due to compression. When the short carrier was preceded by a long precursor (200 ms), AM detection thresholds at the mid-level hump improved. Although the sample size was small, the difference between the precursor and no-precursor conditions was statistically significant using both parametric (rmANOVA: $F(1,6)=64.5$, $p<0.001$) and nonparametric (Friedman test: $\chi^2(2)=150.957$, $p<0.0001$) tests. This improvement in AM thresholds with a precursor is consistent with a reduction in cochlear gain via the MOC reflex, whose effect is greatest at low to moderate levels and 70-100 ms after the onset of the eliciting stimulus. Furthermore, the improvements in AM detection thresholds with precursors are limited to low modulation frequencies (<100 Hz). The statistically significant difference between precursor and no precursor conditions as a function of modulation frequency was verified using the nonparametric Friedman test [$\chi^2(2) = 106.279$, $p<0.0001$]. From an ecological perspective, these results suggest that the auditory system may improve the effective modulation depth over the first several hundred milliseconds of acoustic stimulation. This improvement may lead to robust neural coding of the amplitude envelope of speech and ultimately lead to robust speech perception in quiet and in background noise.

Chapter 3 addressed the hypothesis that the inherent temporal fluctuations of narrowband noise carriers are influenced by cochlear compression. The results of this chapter revealed differences in AM detection with increasing carrier level between low- and high-fluctuating carriers. These differences also hold when the data were plotted for the median thresholds. For 50-ms, low-fluctuating noise carriers, AM detection thresholds worsened as carrier level increased from low to mid carrier levels and then improved with further increases in carrier level, reminiscent of the mid-level hump. These findings are similar to the findings of Chapter 2, and are consistent with greater cochlear compression at moderate levels. For high-fluctuating carriers, AM thresholds were roughly constant across carrier levels. For high-fluctuating carriers, AM detection is determined by the effective SNR_{ENV} at the output of the modulation filter centered at the target modulation frequency. Specifically, the envelope power of high-fluctuating carriers and the envelope power of the target modulation are expected to be equally reduced by cochlear compression, resulting in constant effective SNR_{ENV} across level at the output of the modulation filterbank. This predicts constant AM thresholds as a function of level.

4.2 Limitations and future directions

The experiments of this manuscript involve young normal hearing listeners; therefore, these data cannot be extrapolated to listeners with hearing loss or other age groups. In individuals with hearing loss, the OHCs may become damaged and limit the ability of the MOC reflex to adjust OHC amplification. This would prevent the expected improvements in AM detection when the MOC reflex is stimulated. Although not addressed in the current study, the following can be predicted for listeners with hearing loss based on the I/O function and MOC reflex framework. Reduced compression due to OHCs damage predicts better-than-normal AM detection compared to listeners with normal hearing. Furthermore, the presence of a precursor is expected to result in little or no change of cochlear gain and predicts no change in AM detection with compared to without a precursor.

Another limitation is that our studies could be strengthened by having an independent physiological measures of MOC reflex function. Despite the proposed benefits of the MOC reflex, perceptual studies have lagged behind physiologically inspired theories in confirming the role of the reflex in perception. Such a link can be strengthened by combining the perceptual AM detection experiments with electrophysiological measurements such as the envelope following responses (EFRs). EFRs are far-field responses to an AM stimuli and provide a convenient noninvasive measure of subcortical envelope coding. Bharadwaj et al. (2015) presented preliminary data suggesting that stimulation of the olivocochlear efferents of normal hearing listeners with a contralateral noise significantly enhances the amplitude of the EFR and thus enhances neural temporal coding. Future experiments may examine the effects of ipsilateral and contralateral precursors compared to conditions without precursors on EFRs measured in quiet and in background noise from age-matched groups of normal and impaired hearing listeners. Stimulation of the MOC reflex using precursors may lead to increased EFR amplitudes in normal hearing listeners and no changes in EFR amplitudes in listeners with hearing loss. This approach of combining perceptual and electrophysiological experiments is a powerful method for linking perception to the underlying physiological mechanisms. Such a link is essential for understanding why hearing-impaired listeners struggle to understand speech in noisy environments, even when wearing the best hearing devices.

4.3 References

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APPENDIX

PRELIMINARY EXPERIMENTS

A.1 Introduction

This section describes a number of preliminary experiments undertaken to examine if the effects of carrier level and precursors on AM detection are consistent with cochlear compression and the MOC reflex. Furthermore, these experiments were designed to examine how stimulus parameters influence AM detection, including duration of the carrier, carrier level, noise carrier fluctuations, and the effect of ipsilateral precursors. The goal was to choose an appropriate set of conditions to reliably measure carrier level and precursor effects on AM detection with short carriers.

A.2 General methods

A.2.1 Apparatus and stimuli

Stimuli were digitally generated using custom-built MATLAB (The MathWorks, Natick, MA) software (Bidelman et al., 2015) and output through a LynxTWO-B (Lynx Studio Technology, Costa Mesa, CA) sound card (sampling rate, 44.1 kHz; 24-bit resolution) to listeners' right ears via a ER-2 (Etymotic Research Inc., Elk Grove, IL) insert earphone driven by a headphone buffer (Tucker-Davis-Technologies [TDT], HB7, Alachua, FL). Several AM detection experiments were performed. In these experiments, high-frequency carriers ($\geq$ 4000) were used because cochlear amplifier gain is greatest in the base of the cochlea (Cooper & Rhode, 1995) and previous studies have shown the largest moderate level effects on AM detection at high carrier frequencies [(>4000-6000 Hz, (Long & Cullen, 1985)]. Low modulation frequencies (e.g., 20-40 Hz) were used based on previous experiments that showed better AM thresholds at low modulation frequencies for continuous compared to gated carriers (Sheft & Yost, 1990; Viemeister, 1979). Sinusoidal AM was applied in cosine phase. Carriers were scaled to the desired root-mean-square (rms) level after applying AM.

In Experiment I, AM detection was measured as a function of carrier level for 50 and 500 ms (2 ms onset/offset ramps) carriers.

In experiments examining the effects of precursors (Experiments II-IV), the carrier duration was 50 ms (2 ms onset/offset ramps). The precursor (if present) had a duration of 200 ms (5 ms onset/offset ramps) and was presented at 40 dB SPL (overall level). There was no delay between the offset of the precursor and the onset of the carrier. In experiments measuring the temporal modulation transfer function (Experiment IV), the carrier level was presented at 65 dB SPL for modulation frequencies of 20, 40, 60, 80, and 100 Hz. Off-frequency listening (Johnson-Davies & Patterson, 1979; O'Loughlin & Moore, 1981) was restricted by gating an additional notched noise simultaneously with the carrier, where the noise level was 50 dB/Hz below the carrier spectrum level (Nelson et al., 2001). The spectral notch of the off-frequency listening noise extended from 0.9*fc to 1.2*fc (i.e., 4500-6000 Hz), similar to Oxenham and Plack (1997). The outer frequency cutoffs of the off-frequency listening noise were 2000 and 8000 Hz.

For the notched-noise precursor experiments (Experiment III), the notched noise was created by generating two bands of noise, one above the carrier frequency (high-frequency noise band) and the other below the carrier frequency (low-frequency noise band). AM detection thresholds were measured as a function of precursor notch width. The notch width (Δf) specifies the spectral distance between the carrier center frequency and the upper and lower cutoff frequencies for the high- and low-frequency noise bands, respectively. The notch width was arithmetically symmetric in frequency around the carrier. The effects of the notch width on AM detection thresholds were examined in two ways. First, high- and low-frequency noise bands had a bandwidth of 3000 Hz. Second, the precursor outer edges were fixed at 2000 and 8000 Hz while the inner cutoffs were varied. Specifically, for both methods, AM thresholds were measured for Δf equal to 0.0, 0.1, 0.2, 0.4, and 0.6. It was hypothesized that 3000 Hz high- and low-band bandwidths may result in greater MOC effects with decreasing notch width due to the fact that the largest MOC effects are produced by wide-band stimuli and decrease with decreasing elicitor bandwidth (Lilaonitkul & Guinan, 2009).

A.2.2 Procedure

Subjects participated in the experiments in a sound-attenuating booth. The dependent variable was AM threshold, expressed as modulation depth (m) in dB. AM detection thresholds were measured using an adaptive three-interval, three-alternative forced-choice (3AFC) task. During a trial, the carrier was presented in each interval separated by 500 ms and marked by lighted squares on a computer monitor. In order to eliminate level cues, the power of the carrier was the same in all observation intervals (Viemeister, 1979). During a randomly chosen interval, the carrier was sinusoidally amplitude modulated. The subject pressed a button on a keyboard to indicate the interval in which the modulation was perceived. Visual feedback was provided to indicate a correct or incorrect response. During an adaptive track, the modulation depth was adjusted using a two-down, one-up rule, which measures the modulation depth necessary to achieve 70.7% correct on the psychometric function (Levitt, 1971). The initial 8-dB step size was decreased to 2 dB after the second reversal. Twelve reversals were obtained, and the mean modulation depth of the last eight reversals was defined as the AM threshold for that adaptive track. Thresholds from two runs were averaged to compute the final threshold of each condition.

A.3 Results and discussion

A.3.1 Experiment I: Effects of carrier level and duration

The purpose of this preliminary study was to investigate the following: (1) the effects of carrier level on AM detection to examine if AM detection for a short carrier worsens as the carrier level increases from low to moderate levels, an effect consistent with greater cochlear compression at moderate levels, (2) whether AM detection thresholds improve for longer compared to shorter carriers an effect consistent with a reduction in cochlear gain via the MOC reflex due to the forward fringe of the longer carriers and/or multiple looks, and (3) if the effects of carrier level and duration depend on the inherent fluctuations of narrow-band noise carriers. To test these predictions, AM detection thresholds from two subjects were obtained using 5000 Hz sinusoidal carriers, low-fluctuating narrow-band noise carriers and high-fluctuating narrow-band noise (30 Hz wide) carriers, whose spectrum was arithmetically centered on 5000 Hz. The carriers were modulated with 40 Hz (for sinusoidal carrier) or 20 Hz (for low- and high-fluctuating noise carriers) modulation frequency. AM detection thresholds were obtained as a function of carrier level (sinusoidal carriers: 40, 50, 60, 70, and 80 dB SPL; narrow-band noise carriers: 45, 65, and 85 dB SPL).

Figure A.1 shows the average AM detection thresholds and standard errors of the mean as a function of carrier level for sinusoidal (A), low-fluctuating noise (B), and high-fluctuating noise carriers (C). The parameter of the figure is carrier duration, 50 ms (closed black circles) and 500 ms (open red circles). The 500-ms carrier condition was not tested for sinusoidal carriers. For short, sinusoidal (Figure A.1A), and low-fluctuating (Figure A.1B, closed black circles) carriers, AM detection thresholds increased (worsened) as carrier level increased up to 60 dB SPL and then improved as level was increased from 60 dB SPL to higher carrier levels. In contrast, AM detection thresholds for short, high-fluctuating noise carriers (Figure A.1C, black closed circles) were roughly constant as level increased from 45 to 65 dB SPL and then slightly worsened as level increased to 85 dB SPL. For 500-ms, low-fluctuating (Figure A.1B, open red circles) and high-fluctuating noise (Figure A.1C, open red circles) carriers, AM thresholds were relatively constant at low and moderate levels and slightly improved at high carrier levels. Averaged AM detection thresholds were always better for low-fluctuating than high-fluctuating carriers, consistent with a previous study (Dau et al., 1999).

The poorer AM detection thresholds at moderate compared to low and high carrier levels is reminiscent of the mid-level hump observed in intensity discrimination (Carlyon & Moore, 1984; Nizami, 2006; Roverud & Strickland, 2015a,b) and consistent with cochlear compression as predicted by the cochlear I/O function framework in Section 1.4. This mid-level hump is reduced or eliminated when the carrier is 500 ms. This improvement for longer carriers at the moderate levels can be explained, in part, by the combined effect of multiple looks and cochlear compression (see Section 1.6) or by a reduction in cochlear gain during the forward fringe of the 500 ms carrier.

A.3.2 Experiment II: Effects of wide- and narrow-band noise precursors on AM detection

This preliminary experiment examined the effect of an ipsilateral noise precursor preceding a short carrier on AM detection. The precursor was hypothesized to activate the MOC reflex. Specifically, the effect of the precursor is assumed to follow the time-course of the MOC reflex described by Backus and Guinan (2006), who showed that the MOC reflex has

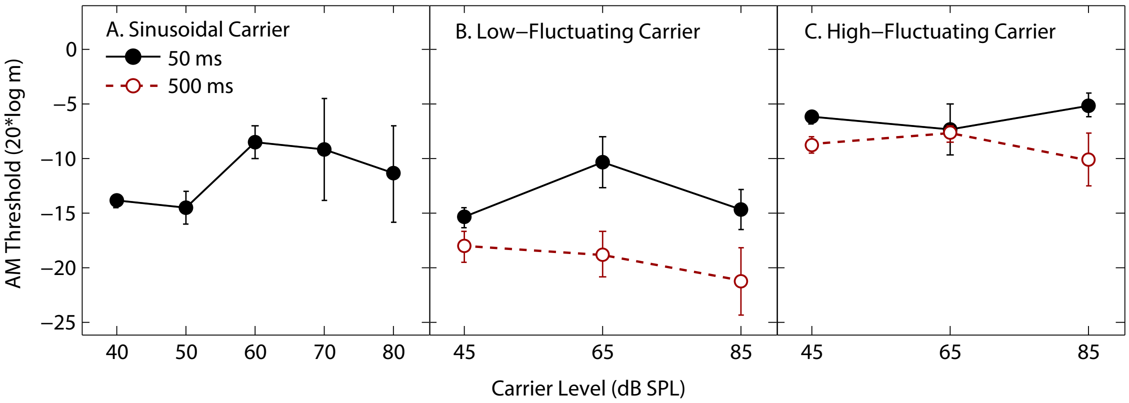

Figure A.1. Average AM thresholds as a function of carrier level for (A) sinusoidal (5000 Hz), (B) low-fluctuating narrow-band noise carriers, and (C) high-fluctuating narrow-band noise carriers centered at 5000 Hz. AM detection thresholds for 50 and 500 ms carriers are represented by the closed black circles and open red circles, respectively. The modulation frequency was 20 Hz for narrow-band noise carriers and 40 Hz for the sinusoidal carrier. Lower values represent better AM detection thresholds (i.e., lower modulation depth (m) at threshold). Error bars are the standard error of the mean.

an onset delay of 25 ms after the elicitor and has a time constant of 70-100 ms for response growth and decay effects. Eliciting the MOC reflex with the precursor is hypothesized to reduce the gain of the cochlear amplifier and thus the basilar membrane response at or near the CF. Based on the theoretical MOC framework (see Figure 1.7), MOC-mediated gain reduction decompresses a portion of the cochlear I/O function, and therefore, the effective modulation depth is expected to improve. To test this hypothesis, AM detection thresholds from two subjects were measured using low-fluctuating narrow-band noise carriers (100 Hz wide) centered at 5000 Hz. The precursor was a wide-band noise (100-8000 Hz) in Experiment IIa or narrow-band noise (200-Hz wide) in Experiment IIb.

A.3.3 Experiment IIa: Effects of wide-band precursor

Figure A.2 shows the average AM detection thresholds as a function of carrier level for the no-precursor (closed black circles) and precursor conditions (open red circles). For the no-precursor condition, AM detection thresholds slightly worsened as level increased from 45 to 65 dB SPL and then improved as level was increased to 85 dB SPL. For the precursor condition, AM detection thresholds were better compared to the no-precursor condition, except for the 45 dB SPL carrier. The difference in threshold between precursor

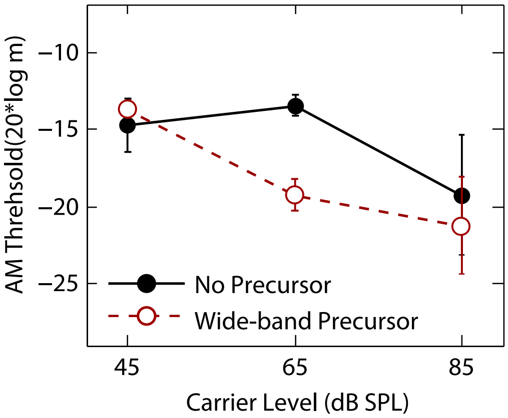

Figure A.2. Average AM detection thresholds as a function of carrier level for no-precursor (closed black circles) and precursor (open red circles) conditions. The carrier is a 100 Hz wide low-fluctuating carrier centered at 5000 Hz and modulated at 20 Hz. The carrier and the precursor durations were 50 and 200 ms, respectively. The precursor was a wide-band noise (100-8000 Hz).

and no-precursor conditions was 6 and 1 dB at 65 and 85 dB SPL, respectively. The improved AM detection thresholds for short carriers with compared to without a precursor is related to a reduction in cochlear gain during the course of the precursor. Based on the gain reduction framework (see Section 1.6), this MOC-mediated gain reduction is expected to decompress a portion of the cochlear I/O function (Cooper & Guinan, 2006; Jennings et al., 2009; Strickland, 2001), leading to a greater effective modulation depth. The slight worsening of AM thresholds at 45 dB SPL in the precursor condition compared to the no-precursor condition may reflect forward masking in the modulation domain and/or the audio-frequency domain. Forward masking of AM has been reported by Wojctzak and Viemeister (2005), who showed that sensitivity to amplitude modulation increases in the presence of a forward amplitude-modulated masker having the same modulation rate.

In the audio-frequency domain, the preceding stimulation of the wide-band precursor could fill in the valleys of the modulated carrier and thus reduce the effective modulation depth. Another possibility for the lack of precursor effects at low carrier levels may be related to near quiet threshold effects for both precursor and no-precursor conditions (Plack & Skeels,2007). Finally, the cochlear I/O function is linear at low levels regardless of the presence or absence of the precursor; therefore, a reduction in cochlear gain may not have improved the effective AM depth at low carrier levels.

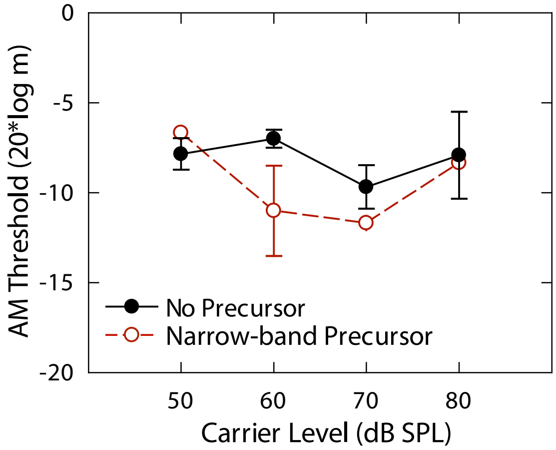

Figure A.3. Average AM detection thresholds as a function of carrier level for no-precursor (closed black circles) and precursor (open red circles) conditions. The carrier was a narrow-band, low-fluctuating noise centered at 4000 Hz (200 Hz wide) and modulated at 20 Hz. The precursor was a low-fluctuating narrow band (200 Hz wide) noise carrier. The carrier and the precursor durations were 50 and 200 ms, respectively.

A.3.4 Experiment IIb: Effects of narrow-band precursor

In this experiment, the carrier was a low-fluctuating, narrow-band noise (200-Hz wide) centered at 4000 Hz and modulated with 20-Hz modulation frequency. The precursor was a narrow-band, low-fluctuating (3900-4100 Hz) noise. Carrier levels were 50, 60, 70, and 80 dB SPL. AM detection thresholds from two subjects are shown in Figure A.3 as a function of carrier level for the no-precursor (closed black circles) and the precursor condition (open red circles). For the no-precursor condition, AM detection thresholds increased slightly from 50 to 60 dB SPL, decreased from 60 to 70 dB SPL, and slightly increased at 80 dB SPL. For the precursor condition, the average AM detection thresholds were better at moderate carrier levels compared to the no-precursor condition; however, this relation does not always hold for the individual results of the three subjects as revealed by the large variability in this condition (mostly at 60 dB SPL). A second experiment had identical stimulus parameters except a 4000 Hz sinusoidal carrier was used. AM detection thresholds from two subjects are shown in Figure A.4 where closed black circles represent the no-precursor condition and open red circles represent the precursor condition. AM detection thresholds were inconsistent among the two participants in this experiment. For S1, AM detection thresholds in both conditions worsen with increasing carrier level with greatest precursor effects at lowest carrier level. For S2, there was a clear mid-level hump in the no-precursor condition, which was eliminated in the presence of the precursor.

The greater precursor effect for the wide-band noise precursor (Figure A.2) compared to the narrow-band noise precursor (Figure A.4) may be related to the differences in the bandwidth of the precursor. Specifically, as the bandwidth of the precursor increases in the wide-band noise precursors, MOC effects increase (Lilaonkul & Guinan, 2009) leading to improved AM thresholds at moderate to high carrier levels compared to narrow-band noise precursors.

A.3.5 Experiment III: Effects of notched-noise precursors

The findings of the second preliminary experiment showed inconsistent effects of precursors on AM detection thresholds when precursors were wide-band or narrow-band noises. One potential way to reduce the modulation masking expected from wide-band or narrow-band noises is to introduce a noise precursor whose spectral energy does not fall in the critical band corresponding to the carrier center frequency. Notched noise, which has a spectral notch around the center frequency of the carrier, may be suitable for this purpose. In this preliminary experiment, a notched noise was used as the precursor. The notch of the precursor was varied systematically to investigate which notch widths produced the largest effects (see General Methods). The carrier was low-fluctuating, narrow-band noise (100-Hz wide) centered at 5000 Hz and modulated with 20-Hz modulation frequency. The carrier was presented at 65 dB SPL. Three subjects participated in this experiment.

Figure A.5 shows AM detection thresholds as a function of the precursor notch width when the high- and low-frequency bands are 3000 Hz wide (Figure A.5A) or when the outer edges of the precursor are fixed at 2000 and 8000 Hz (Figure A.5B). AM detection thresholds were in general better in the presence of the notched-noise precursor (Figure A.5, red circles) compared to the no-precursor condition (Figure A.5, black squares) for all the notch widths tested. In both manipulations, AM detection thresholds were less variable when the notch width was 0.2. In general, these data suggest that the effects with notched-noise precursors are most reliable for $\Delta f = 0.2$.

A supplementary experiment was undertaken to compare AM detection using wide-band and notched-noise precursors as a function of carrier level. Figure A.6 shows the average

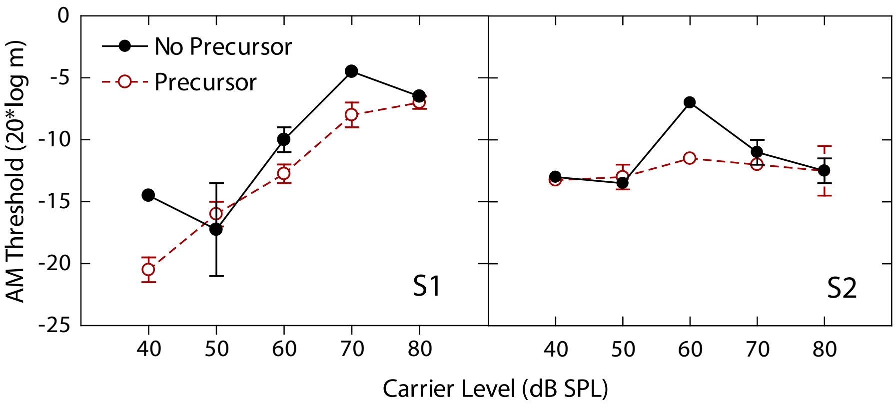

Figure A.4. AM detection thresholds for individual subjects as a function of carrier level for no-precursor (closed black circles) and precursor (open red circles) conditions. The 4000 Hz sinusoidal carrier was modulated at 20 Hz modulation frequency. The precursor was a low-fluctuating narrow-band (200 Hz wide) noise. The carrier and the precursor durations were 50 and 200 ms, respectively.

AM detection thresholds from two subjects as a function of carrier level for no precursor (closed circles), wide-band noise precursors (closed squares), and notched-noise precursors (Δf = 0.2., open squares). For the no-precursor condition, AM detection thresholds were worse at moderate levels compared to lower and higher carrier level. For wide-band noise precursors, AM thresholds were better with than without a precursor at moderate carrier levels, but were variable at lower and higher carrier levels. For notched-noise precursors, AM detection thresholds were better than without a precursor for all levels tested. Furthermore, the notched-noise precursors are more reliable compared to wide-band noise precursors.

A.3.6 Experiment IV: Effects of precursors on the temporal modulation transfer function

The previous experiments showed that precursors improve AM detection for a 20-Hz modulation frequency. This preliminary experiment examined whether the effects of a precursor hold for other modulation frequencies. AM detection thresholds measured as a function of modulation frequency results in a function referred to as temporal modulation transfer function (TMTF). For this experiment, low-fluctuating narrow-band noise carriers (200 Hz wide) centered at 4000 Hz or sinusoidal (4000 Hz) were used. The carrier was presented at 65 dB SPL. Precursors were either sinusoidal (4000 Hz) or wide-band noise (2000-8000 Hz). Two subjects participated in this experiment.

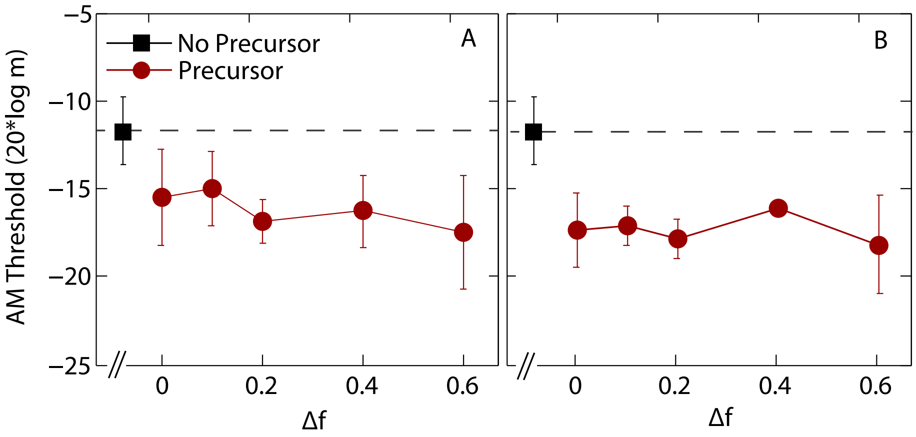

Figure A.5. Average AM detection thresholds as a function of the notch width of the precursor. Panel A: precursors formed from 3000 Hz high- and low-frequency bands. Panel B: precursors with fixed outer spectral edges, where lower and outer edges were fixed at 2000 and 8000 Hz, respectively. AM detection thresholds in the no-precursor condition are presented in the left of the panels as black squares and marked for reference with dashed horizontal lines.

Figure A.7 shows the TMTFs for no-precursor (closed black circles) and precursor (open red circles) conditions for each carrier type. The TMTFs for sinusoidal carriers are shown in the left panel, while TMTFs for wide-band noise carriers are shown in the right panel. For the no-precursor condition, AM detection thresholds improved with increasing modulation frequency. For both precursor types, AM detection thresholds with a precursor were better compared to no-precursor for low modulation frequencies.

A.4 Summary and conclusion

The results of the preliminary experiments are consistent with the expected effects of cochlear compression and the MOC reflex on AM detection as shown in previous experiments using simple tones. For short carriers, AM detection thresholds are poorer at moderate levels, reminiscent of the mid-level hump seen in intensity discrimination studies. There is evidence that the mid-level hump is related to cochlear compression (Heinz et al., 2001; Roverud & Strickland, 2015a). This mid-level hump is abolished in the presence of the precursor or for longer carriers. The precursor and the forward fringe of the carrier are hypothesized to stimulate the MOC reflex. Stimulation of the MOC reflex decompresses the cochlear I/O function and thus results in improved AM detection thresholds at the mid-level hump.

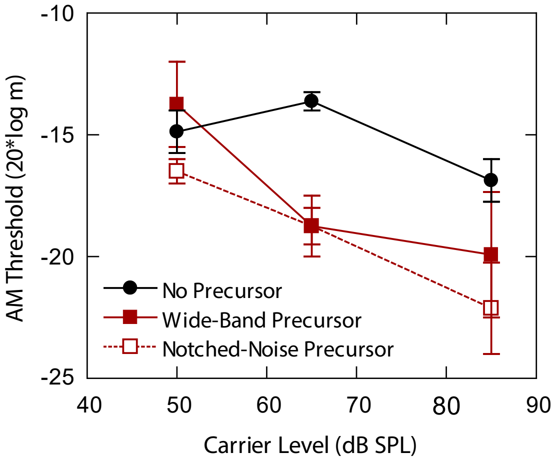

Figure A.6. Average AM detection thresholds as a function of carrier level for no-precursor (closed black circles), wide-band noise precursor (closed red circles), and notched-noise precursor (open red circles). The carrier was low-fluctuating narrow-band noise (100 Hz wide) centered at 5000 Hz and modulated at 20 Hz. The precursor was either wide-band noise (2000-8000 Hz) or notched-noise ($\Delta f = 0.2$). The carrier and the precursor durations were 50 and 200 ms, respectively.

The target sample size for the main experiment was estimated using preliminary data from pilot Experiment III comparing notched-noise precursor vs. no-precursor conditions to estimate the parameters needed for sample size determination and power estimation such as variance and eta-squared (η^2). Pilot data were subjected to a two-way repeated-measures ANOVA. The analysis indicated a large effect size ($\eta^2 = 0.759$). The power analysis was carried out using GPower program (Faul et al., 2007) while considering the condition*carrier level interaction in the two-way repeated-measures ANOVA. Power analysis indicated that 6-7 subjects are needed to have 80% power for detecting a medium sized effect when employing $\alpha = 0.05$ criterion of statistical significance.

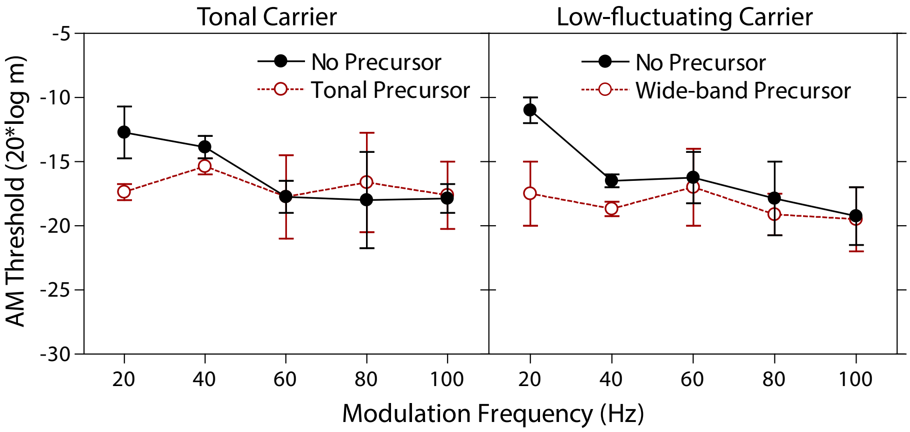

Figure A.7. Average AM detection thresholds as a function of modulation frequency for no-precursor (closed black circles) and precursor (open red circles) conditions. The carrier was either: 1) a 4000-Hz sinusoid, 2) narrow-band low-fluctuating noise centered at 4000 Hz (200 Hz wide). The carrier level was 65 dB SPL. The carrier and the precursor durations were 50 and 200 ms, respectively.

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