Developmental Conductive Hearing Loss Reduces Modulation Masking Release

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Abstract

Hearing-impaired individuals experience difficulties in detecting or understanding speech, especially in background sounds within the same frequency range. However, normally hearing (NH) human listeners experience less difficulty detecting a target tone in background noise when the envelope of that noise is temporally gated (modulated) than when that envelope is flat across time (unmodulated). This perceptual benefit is called modulation masking release (MMR). When flanking masker energy is added well outside the frequency band of the target, and comodulated with the original modulated masker, detection thresholds improve further (MMR+). In contrast, if the flanking masker is antimodulated with the original masker, thresholds worsen (MMR−). These interactions across disparate frequency ranges are thought to require central nervous system (CNS) processing. Therefore, we explored the effect of developmental conductive hearing loss (CHL) in gerbils on MMR characteristics, as a test for putative CNS mechanisms. The detection thresholds of NH gerbils were lower in modulated noise, when compared with unmodulated noise. The addition of a comodulated flanker further improved performance, whereas an antimodulated flanker worsened performance. However, for CHL-reared gerbils, all three forms of masking release were reduced when compared with NH animals. These results suggest that developmental CHL impairs both within- and across-frequency processing and provide behavioral evidence that CNS mechanisms are affected by a peripheral hearing impairment.

Introduction

Most hearing-impaired listeners can detect and identify sound cues in a quiet setting but struggle to hear these cues in the presence of background sounds. This outcome can often be attributed to cochlear processing pathologies (e.g., Moore, 2007). However, human behavioral evidence points to additional performance limitations that implicate central auditory processing deficits (Bharadwaj, Verhulst, Shaheen, Liberman, & Shinn-Cunningham, 2014; Eisenberg, Dirks, & Bell, 1995; Hind et al., 2011; Humes, 2005; Humes & Dubno, 2010; Ruggles, Bharadwaj, & Shinn-Cunningham, 2011). Furthermore, transient periods of developmental hearing loss that accompany *otitis media* are associated with reduced behavioral sensitivity that can persist long after audiometric thresholds return to normal (Aarhus, Tambs, Kvestad, & Engdahl, 2014; Caras & Sanes, 2015; Gay, Voytenko, Galazyuk, & Rosen, 2014; Hall & Grose, 1994; Whitton & Polley, 2011). Consistent with

these behavioral data, experimentally induced developmental hearing loss in nonhumans causes significant changes to central nervous system (CNS) membrane and synaptic properties (reviewed in Sanes, 2013), and sensory encoding (Chambers et al., 2016; Knudsen, Esterly, & Olsen, 1994; Moore et al., 1999; Rosen, Sarro, Kelly, & Sanes, 2012). Thus, the CNS deficits

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that arise from early sound deprivation could plausibly lead to perceptual difficulties, especially in challenging acoustic environments. The goal of this study was to assess this idea at the behavioral level.

Auditory sensitivity declines in noisy environments, through masking, but can improve when the noise level fluctuates, a phenomenon referred to as masking release (Verhey, Pressnitzer, & Winter, 2003). A common assay of masking release presents a target tone in the presence of a narrowband noise that is centered at the target frequency. Tone detection thresholds are then obtained when the noise envelope is either unmodulated or modulated, as illustrated in Figure 1. Compared with performance in unmodulated noise (Figure 1(a)), tone detection thresholds improve in modulated noise (Figure 1(c)), a benefit known as modulation masking release (MMR). In classical masking experiments, only masker energy that falls within the critical band of the target tone raises detection thresholds, an effect called energetic masking (Fletcher, 1940) that is thought to occur within the cochlea. When masker energy is added outside of the critical band of the target (i.e., Figure 1(b)), there is no change in detection thresholds. In contrast, under MMR conditions, tone detection performance in modulated background noise can be further enhanced by adding a second band of noise (a *flanker*), even when all of that flanker's energy falls outside the critical band of the target tone, but only when the envelope of that flanker is comodulated with the on-target masker band (Figure 1(d); cf. Carlyon, Buus, & Florentine, 1989; Hall, Haggard, & Fernandes, 1984). When the envelopes of the two modulated noise bands are in phase, the difference in performance between modulated and unmodulated conditions is referred to as comodulation masking release (MMR+). Listeners can receive a benefit of a modulated flanker band even when it is added out of phase with the target-band noise (MMR−, Figure 1(e)). However, the MMR− benefit is smaller than MMR+.

Both MMR and MMR+ are strongly reduced in hearing-impaired individuals and cochlear-implant users (Bacon, Opie, & Montoya, 1998; Ihlefeld, Shinn-Cunningham, & Carlyon, 2012; Léger, Reed, Desloge, Swaminathan, & Braida, 2015; Nelson, Jin, Carney, & Nelson, 2003; Oxenham & Kreft, 2014; Pierzycki & Seeber, 2014; Zirn, Hempel, Schuster, & Hemmert, 2013). Although peripheral dysfunction can explain much of this impairment, MMR is thought to arise from a combination of peripheral and CNS mechanisms (Christiansen & Oxenham, 2014; Dau, Ewert, & Oxenham, 2009; Dau, Piechowiak, & Ewert, 2013). The premise of several successful MMR models is that temporal correlation between masker bands at different frequencies makes it easier for listeners to detect a tone in the energetic dips of a fluctuating masker (Dau et al.,

2013; Pressnitzer, Meddis, Delahaye, & Winter, 2001), a computation that cannot be performed in the cochlea. These models predict that degraded sensitivity to amplitude modulation depth should impair MMR at any neural processing stage (e.g., Joris, Schreiner, & Rees, 2004; Las, Stern, & Nelken, 2005; Nelken, Rotman, & Yosef, 1999; Xie & Manis, 2013). Indeed, animals reared with conductive hearing loss (CHL) display decreased behavioral sensitivity to amplitude modulation cues (Caras & Sanes, 2015; Rosen et al., 2012). This raises the possibility that peripheral hearing loss leads to impairment of a central MMR mechanism.

Although MMR was first characterized in humans, it is also observed in many other species (Branstetter & Finneran, 2008; Goense & Feng, 2012; Hofer & Klump, 2003; Langemann & Klump, 2007; Las et al., 2005; Nieder & Klump, 2001). For example, Mongolian gerbils (*Meriones unguiculatus*) can benefit from MMR (Gleich, Kittel, Klump, & Strutz, 2007; Wagner, 2002) and are a suitable model for studying the effect of hearing loss.

Therefore, using a Go/NoGo procedure, we tested NH and CHL-reared adult gerbils on tonal target detection in the presence of five different background masking noises. Maskers parallel those used in both NH (Carlyon et al., 1989) and cochlear-implant human listeners (Ihlefeld et al., 2012). The specific hypothesis was that CHL rearing impairs central processing mechanisms, thereby diminishing MMR+ and MMR−.

Methods

All experimental procedures, including training and testing, were approved by the Institutional Animal Care and Use Committee at New York University.

Procedures

Animals were placed on controlled water access and were trained and tested on a target detection task using a Go/NoGo paradigm, as described previously (Buran et al., 2014). In this paradigm, the animal initiated each trial by interrupting the infrared beam on a nose poke detector. After a mandatory, fixed holding time of 300 ms, during which the animal had to maintain its position at the nose poke detector, a target stimulus either was or was not presented (Go or NoGo trial). During a subsequent response window, the animal indicated its response by obtaining a water reward from a lick spout, by repoking the nose poke, or by withholding. When the animal licked the water spout, this was interpreted as a *target present* response. The other two behaviors (repoking the nose poke or withholding) were interpreted as *target absent* responses. On Go trials, a target present response was scored as a *hit*, and a target absent response as a
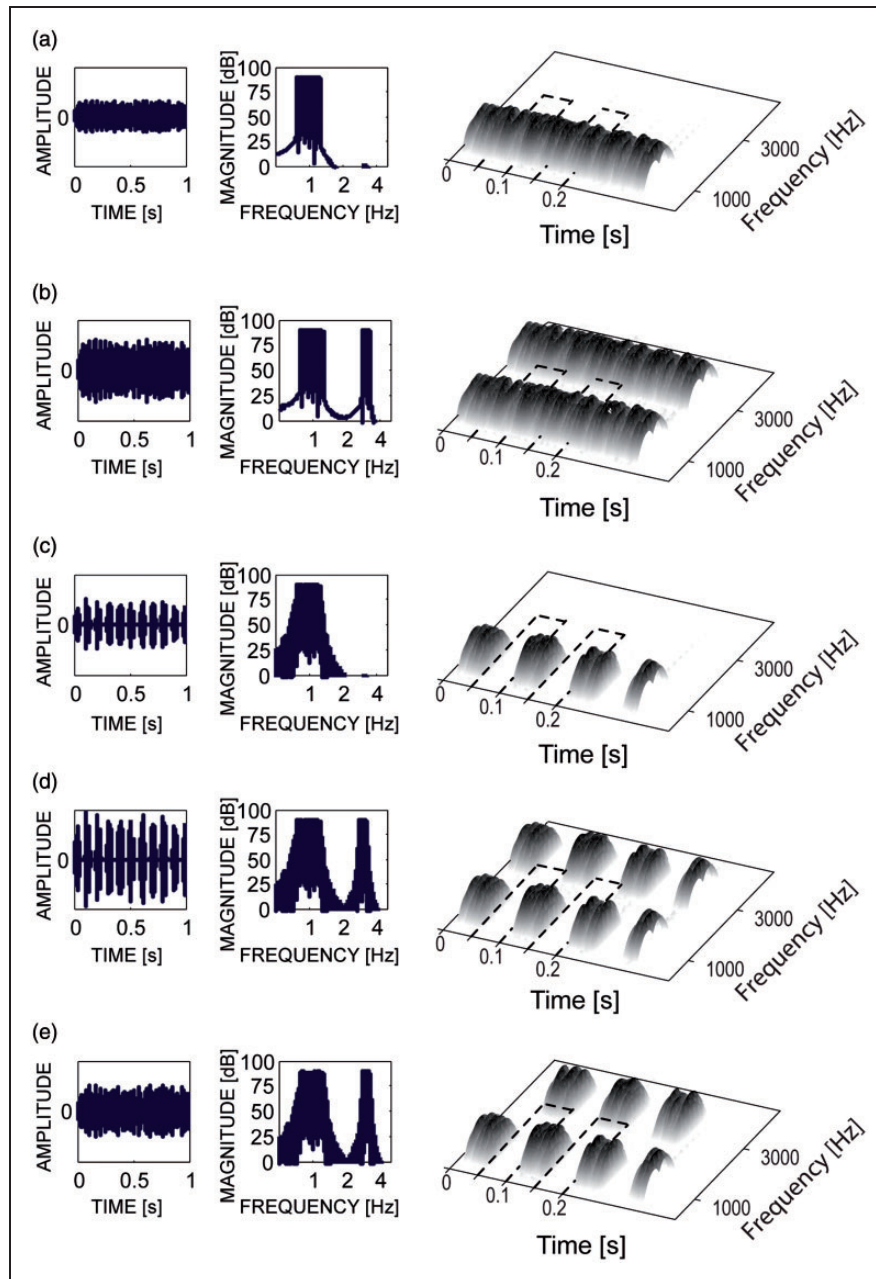
Figure 1. Stimulus design. (a) Unmodulated on-target noise, from left to right: waveform amplitude as a function of time, long-term spectrum and short-term spectrum. Dashed lines are fiduciary markers, positioned similarly across all short-term spectra in this figure, to emphasize the temporal relationship between on-target and flanking maskers. (b) Unmodulated flanker noise. (c) Modulated on-target noise. (d) Comodulated flanker noise. (e) Antimodulated flanker noise.

miss. On NoGo trials, a target present response was scored as a *false alarm*, and a target absent response as a *correct reject*. All animals were initially trained in quiet and then trained and tested in five different types of background sound (see *Stimuli* section). Masker type varied randomly from session to session but remained fixed throughout each session. Animals generally completed at least three sessions per masker type. At the conclusion of masked threshold assessment in Experiments 2 and 3, animals were additionally assessed in quiet to obtain pure-tone detection thresholds at the target frequency without background sound.

Stimuli. Throughout the study, each target on a Go trial consisted of a 1-kHz tone of 1-s duration, including 5-ms onset and offset cosine-squared ramps. On NoGo trials, no target stimulus was presented. One of the five types of frozen noise maskers was continuously presented as

background sound throughout each session. Figure 1 illustrates the acoustic properties of each masker type. The noise envelopes were either unmodulated (Figure 1(a) and (b)) or modulated (Figure 1(c)–(e)) with a 10-Hz rectangular waveform (5 ms cosine squared ramps, 50% duty cycle). Each of the five maskers had an on-target component, consisting of 100 tones with random phases of 60-s duration. The tones were spaced randomly over a 2/3-octave range centered at 1 kHz, constrained such that they were at least 2 Hz apart. As a result, all five frozen tokens of noise were periodic and could be played seamlessly in a loop (from the buffer of the TDT RZ-6) without audible transitions. Moreover, the power spectrum of the envelopes of the noise tokens was flat across envelope modulation frequency. The 2/3-octave spectral range was conservatively chosen to cover one critical band around the center frequency of the target (Kittel, Wagner, & Klump, 2002).

Two of the five maskers consisted of on-target bands only, either unmodulated (Figure 1(a)) or modulated (Figure 1(c)). The three other maskers had an additional flanker component, centered at 3 kHz. Flankers were constructed with identical frequency spacing and phases as the corresponding on-target masker. Thus, the slowly fluctuating envelope of the unmodulated flanker was identical to the envelope of its corresponding unmodulated on-target masker (Figure 1(b)). However, for modulated maskers and comodulated flankers, the two envelopes could either be in phase (*comodulated*, Figure 1(d)), or antiphasic (*antimodulated*, Figure 1(e)). Specifically, the five masker types were: (a) Unmodulated on-target noise, (b) Unmodulated on-target noise with unmodulated flanker (*unmodulated flanker noise*), (c) Modulated on-target noise, (d) Modulated on-target noise and comodulated flanker noise (*comodulated flanker noise*) (e) Modulated on-target noise and antimodulated flanker noise (*antimodulated flanker noise*).

The rationale for using the three different types of modulated noise was that MMR is generally thought to depend both on within- and across-channel processing (e.g., Schooneveldt & Moore, 1987). A modulated flanker band may enhance a listener's detection threshold but only if it is added in phase to the on-target band. Conversely, when added out-of-phase to the on-target band, central processing should reduce performance (e.g., Pierzycki & Seeber, 2010). Furthermore, to assess the possibility that an added flanker may increase energetic masking in the on-target band, thus reducing performance in the antimodulated conditions, two unmodulated masker conditions with and without flanker were tested. Should performance differ between the two unmodulated noise tokens, then this would be evidence that the flanker energetically masks the target.

Each noise was played at a fixed level throughout the entire session. In the on-target configurations, the total

broadband level of the noise equaled 43 dB SPL (Experiment 1), 23 dB SPL (Experiment 2), and 63 dB SPL (Experiment 3). In the flanker configurations, the total broadband level of the noise equaled 46 dB SPL (Experiment 1), 26 dB SPL (Experiment 2), and 66 dB SPL (Experiment 3). Because the long-term energy was identical for modulated and unmodulated noise tokens, the amplitudes of the modulated noise tokens were 3 dB higher than of the unmodulated noise tokens.

Using the method of constant stimuli, tone level was parametrically varied in 5 dB steps over a 25 dB range. Correct performance at the three highest tone levels was rewarded with 20 μl water per correct trial, whereas performance at the two lowest target levels was always unrewarded to discourage the animal from giving false alarm responses (Buran et al., 2014). Within each session, when the animal had performed at least four out of five Go trials correctly at the second-to-lowest level, the 25 dB range of levels was lowered by 5 dB overall and the formerly unrewarded sound intensity was now also rewarded. Each session started with relatively high target intensities that had previously been at least 20 dB above tone detection threshold in the noise condition for that session, to build up the animal's confidence in the task, and then lowered the target intensities gradually throughout the session.

All target intensities were interleaved randomly from trial to trial, with a 50% probability of Go versus NoGo trials, constrained by the limitation that there could be no more than five consecutive NoGo trials. However, when an animal scored a false alarm, repeat NoGo trials were presented until the animal no longer false alarmed. The number of repeat NoGo trials was not limited in those cases.

Apparatus

Stimuli were generated digitally in Python 2.7 with a sampling frequency of 48828 Hz and 32 bit resolution, D/A converted with Tucker-Davis Technologies TDT RZ-6 processor, and amplified with a Crown D75A amplifier. An overhead speaker (Vifa DX25TG05-04) delivered the stimuli to the animal performing in a cage underneath (see Figure 2 for experimental setup). Sound calibration measurements with a ¼ inch free-field condenser recording microphone (Brüel & Kjær) placed in the center of the cage verified proper function of the custom-written stimulation software. Moreover, at the beginning of each testing day, microphone readings confirmed proper function of the testing equipment.

Data Analysis

Percent correct scores were fit by logistic psychometric functions using Bayesian inference from the toolbox
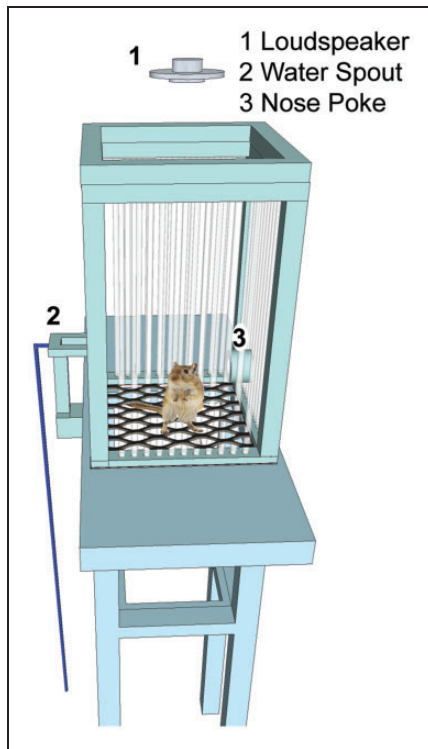
Figure 2. Experimental setup. A speaker (1) was mounted above the cage. To start a trial, gerbils were trained to break an infrared beam on the nose poke (2). A water spout (3) only delivered water when the gerbil responded correctly during Go trials.

psignifit v3.0 such that the lower asymptote of each fitted function matched the false alarm rate for that animal and session, whereas the upper asymptote (ceiling) was constrained to match the lower of the two values: best hit rate for that animal and session or 95% correct (Fründ, Haenel, & Wichmann, 2011). Percent correct scores were then converted to d' scores, by calculating the difference in z-scores of hit rate versus false alarm rate, to correct for bias (Klein, 2001). For each fitted psychometric function, threshold and slope were extracted at $d' = 1$. Overall threshold per animal and masker was calculated as the across-session average of the three sessions with best thresholds, excluding (a) outlier sessions with thresholds more than 10 dB different from the median threshold across all sessions and (b) all sessions where the best d' was below 2. In four instances in Experiment 1, this meant that only one or two sessions were included in the final threshold estimate for that experiment, animal and masker. Data were analyzed with repeated measures analyses of variance (rANOVAs) using SPSS version 24.

Listeners

Experiments 1 and 2 tested NH gerbils. Experiment 3 tested animals reared with CHL. To induce CHL, bilateral malleus removal surgery was performed before ear

canal opening (P10) through a perforation in the tympanic membrane (Buran et al., 2014; Rosen et al., 2012; Tucci, Cant, & Durham, 1999). During the procedure, animals were briefly anesthetized with methoxyflurane.

Results

Experiment 1

Experiment 1 tested six NH gerbils in background noise. Figure 3(a) shows the across-NH-animal average psychometric functions for the five maskers as a function of the energy ratio between the target and the on-target masker band (target-to-masker ratio [TMR], the difference between the dB SPL level of the target minus the dB SPL level of the on-target masker). Each line denotes a different masker type, with solid lines illustrating performance in unmodulated noise and dashed lines illustrating performance in modulated noise. Here and elsewhere, shaded curves show the standard error of the mean across animals after partialing out the between-animal variance (Loftus & Masson, 1994). Thresholds in units of dB TMR and slopes in units of 1/dB TMR of the fitted curves, averaged across animals, are listed in Table 1. Colors denote whether a flanking band was present in the masker, with red lines illustrating performance in on-band masker background. The blue lines depict performance when a comodulated flanker band was added. The yellow line shows performance in antimodulated noise. TMR detection thresholds, where $d' = 1$, are shown in Figure 3(b). Animals display better performance in modulated than in unmodulated noise. The average MMR, defined here as the on-target modulated−unmodulated difference in thresholds, equaled 14.3 dB (Figure 3(c)). The size of the MMR depended on the presence of flankers. The addition of a comodulated flanker further increased the average MMR to 19.8 dB (MMR+, the difference in thresholds between on-target modulated noise with comodulated flanker noise minus on-target unmodulated noise with unmodulated flanker noise). The antimodulated flanker, however, reduced the average MMR to 8.8 dB (MMR−, the difference in thresholds between on-target modulated noise with antimodulated flanker noise minus on-target unmodulated noise with unmodulated flanker noise). A paired two-tailed t-test found a significant difference between MMR+ ($M = 19.8$, $SD = 6.2$) and MMR− ($M = 8.8$, $SD = 4.0$), $t(5) = 6.4$, $p = .001$.

To determine whether energetic masking from the flanker band reduced target detection, it is instructive to compare the two unmodulated masker conditions with the modulated on-target condition and the comodulated masker condition. Thresholds for these masker conditions were analyzed with rANOVA, with main
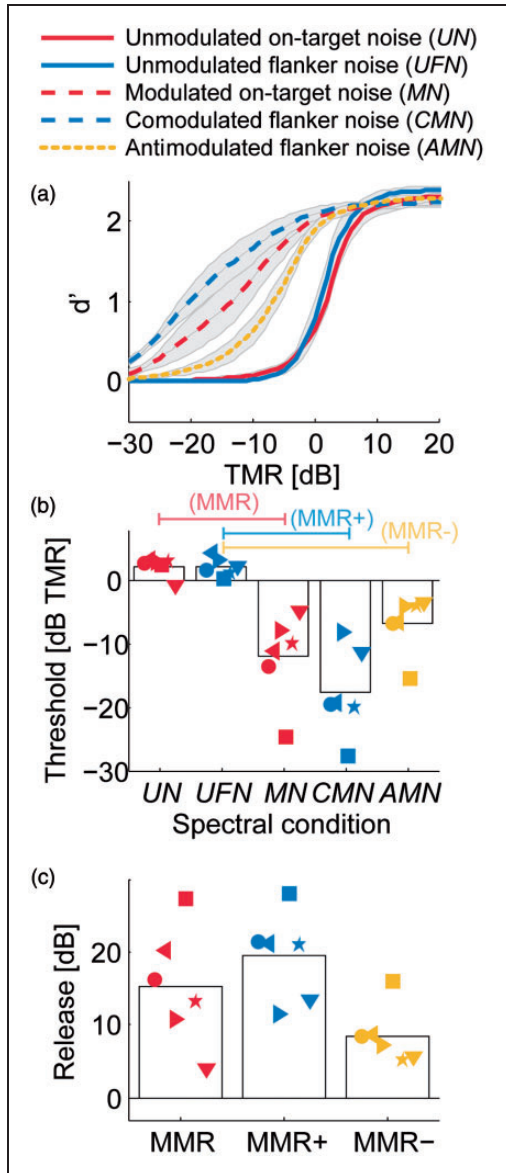
Figure 3. Performance for NH animals at approximately 40 dB SL (Experiment 1). (a) Fitted psychometric curves. Each masker type is shown by a different line, with solid lines illustrating performance in unmodulated noise and dashed lines in modulated noise. Shaded curves show one standard error of the mean across animals after partialing out the between-animal variance (Loftus & Masson, 1994). (b) Thresholds for each of the five masker conditions, where $d' = 1$. Different symbols denote individual animals. Colored horizontal lines illustrate how spectral conditions were contrasted to obtain the different MMRs. (c) MMR, MMR+, and MMR− for all animals, as derived from the thresholds in Panel B. Performance was better in modulated versus unmodulated noise. The MMR was larger in the comodulated (MMR+) than in the antimodulated flanker condition (MMR−). *Note.* NH = normal hearing; SL = sensation level; MMR = modulation masking release.

Table 1. Across-Animal Averages of the Intercepts and Slopes of the Psychometric Function Fits Relating d'-Scores to Target Tone Intensity.

Experiment 1. Threshold (dB)	
Unmodulated on-target noise	2.8 [2.6, 3.0]
Unmodulated flanker noise	2.4 [1.0, 3.8]
Modulated on-target noise	−14.3 [−21.3, −9.4]
Comodulated flanker noise	−18.7 [−25.5, −11.1]
Antimodulated flanker noise	−8.2 [−13.2, −4.7]
Experiment 1. Slope (1/dB)	
Unmodulated on-target noise	0.31 [0.19, 0.47]
Unmodulated flanker noise	0.28 [0.21, 0.35]
Modulated on-target noise	0.18 [0.14, 0.22]
Comodulated flanker noise	0.16 [0.11, 0.20]
Antimodulated flanker noise	0.16 [0.11, 0.21]
Experiment 2. Threshold (dB)	
Quiet	6.4 [5.4, 7.6]
Unmodulated on-target noise	4.5 [3.2, 5.2]
Unmodulated flanker noise	1.8 [1.8, 1.9]
Modulated on-target noise	−16.8 [−20.1, −13.4]
Comodulated flanker noise	−15.2 [−17.1, −12.7]
Antimodulated flanker noise[a]	−9.6 [−11.6, −7.6]
Experiment 2. Slope (1/dB)	
Quiet	0.24 [0.23, 0.26]
Unmodulated on-target noise	0.24 [0.18, 0.28]
Unmodulated flanker noise	0.40 [0.34, 0.44]
Modulated on-target noise	0.14 [0.8, 0.20]
Comodulated flanker noise	0.17 [0.10, 0.25]
Antimodulated flanker noise[a]	0.23 [0.16, 0.31]
Experiment 3. Threshold (dB)	
Quiet	36.2 [30.7, 40.3]
Unmodulated on-target noise	4.6 [4.0, 5.4]
Unmodulated flanker noise	3.8 [2.1, 5.5]
Modulated on-target noise	−2.0 [−4.0, −0.06]
Comodulated flanker noise	0.11 [−4.76, 4.30]
Antimodulated flanker noise	1.28 [−2.78, 5.35]
Experiment 3. Slope (1/dB)	
Quiet	0.24 [0.23, 0.26]
Unmodulated on-target noise	0.18 [0.15, 0.22]
Unmodulated flanker noise	0.18 [0.14, 0.21]
Modulated on-target noise	0.17 [0.12, 0.21]
Comodulated flanker noise	0.18 [0.14, 0.23]
Antimodulated flanker noise	0.15 [0.13, 0.23]

Note. Note that quiet thresholds are reported in dB SPL and that the noise-masked thresholds are reported in terms of dB TMR. Lower and upper 95% confidence intervals, as obtained through simple bootstrapping with 1,000 samples, are listed in square brackets.
[a]Only measured in four of the five animals tested in this experiment.

factors of masker envelope and flanker presence. The analysis found significant main effects of whether the envelope was modulated, $F(1, 5) = 39.3$, $p = .002$, and whether a flanker was present, $F(1, 5) = 12.2$, $p = .017$. There was a significant interaction between envelope and flanker, $F(1, 5) = 11.0$, $p = .021$, confirming the finding that the MMR was bigger when flankers were present (MMR+) as compared to absent (MMR). A separate rANOVA analyzed the slopes of the psychometric functions and found a significant effect of envelope, $F(1, 5) = 19.9$, $p = .007$, reflecting the fact that slopes were steeper in the unmodulated when compared with modulated conditions. The main effect of flanker was not significant, $F(1, 5) = 0.2$, $p = .677$. Tone detection in unmodulated on-target noise did not statistically differ from tone detection in unmodulated flanker noise, rANOVA, $F(1, 5) = 0.0$, $p = .859$, consistent with the interpretation that the added flanker did not increase energetic masking in the critical band surrounding the target tone.

Experiment 2

We sought to test CHL animals at sound intensities that were high enough for the animals to perform the task but that also simulated aspects of everyday listening. Background talkers in a noisy cocktail party realistically can fall in the range of 65 dB SPL, corresponding to roughly 20 dB sensation level (SL), for gerbils with comparable CHL as in the current study (Buran et al., 2014; Rosen et al., 2012). In human listeners, MMR decreases with decreasing masker level (Bernstein & Grant, 2009; Moore & Shailer, 1991). Moreover, at low SLs, floor effects are possible, where MMR cannot further improve with added flanker energy because the signal intensity is too close to absolute threshold. Experiment 1 tested gerbils at 43 dB SPL (~40 dB SL, as calculated from Ryan, 1976, where the average tone detection threshold at 1 kHz equaled 6 dB SPL). To control for the effect of overall level, we therefore tested five NH gerbils with the same stimuli as in Experiment 1, except that the masker sounds were now presented at approximately 20 dB SL. Two of those gerbils had previously performed Experiment 1 and three were newly trained and tested.

Experiment 2 tested five NH animals in low-intensity background sound (NH$_{soft}$). One of these five NH animals often performed fewer than 50 Go trials per session, not enough to obtain full psychometric functions, and was therefore only tested in four of the five maskers, leaving out the antimodulated masker condition. Quiet thresholds were assessed post testing and equaled on
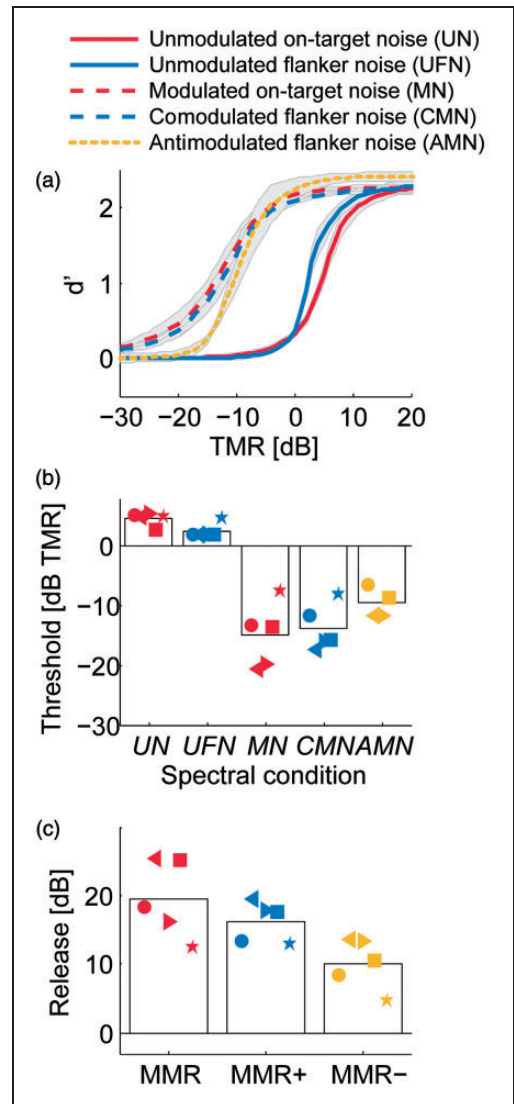

Figure 4. Performance for NH animals at approximately 20 dB SL (Experiment 2), plotted similarly to Figure 3. Performance was better in modulated than in unmodulated noise, and MMR− was smaller than MMR+. Note. NH = normal hearing; SL = sensation level; MMR = modulation masking release.

average 6.4 dB SPL (standard error of the mean across animals [SEM] = 0.6, see also Table 1), consistent with previous results (Ryan, 1976). Figure 4(a) shows the across-animal average psychometric functions for the five maskers, similar to Figure 3. Animals showed better performance in modulated than in unmodulated noise. Thresholds and masking release are displayed in Figure 4(b) and (c), respectively. A paired two-tailed *t*-test revealed a significant difference between

MMR+ ($M = 16.2$, $SD = 2.9$) and MMR− ($M = 10.1$, $SD = 3.7$), $t(3) = 9.1$, $p = .003$.

To check whether the flanker band energetically masked the target tone, detection thresholds were analyzed with rANOVA, with main factors of masker envelope and flanker presence. The analysis found a significant main effect of envelope modulation, $F(1, 4) = 95.7$, $p = .001$, but no significant effect of flanker presence or absence, $F(1, 4) = 2.9$, $p = .163$. A separate rANOVA analyzed the slopes of the psychometric functions and found a significant effect of envelope, $F(1, 4) = 12.5$, $p = .024$, but not of flanker, $F(1, 4) = 6.7$, $p = .061$. Moreover, tone detection in unmodulated on-target noise was not statistically different from tone detection in unmodulated flanker noise, paired t-test, $t(4) = 3.1$, $p = .072$ for unmodulated on-target versus unmodulated flanker noise thresholds, with Bonferroni correction. This supports the idea that the flanker band did not energetically mask the target.

Experiment 2 showed within-band MMR in the on-target conditions, similar to Experiment 1. Performance was worse in the antimodulated as opposed to the comodulated on-target condition (MMR− was significantly smaller than MMR+). In addition, performance did not differ significantly between the unmodulated on-target and unmodulated flanker conditions. A caveat, in the antiphasic modulation condition, where the on-target band was absent when the flanking band was present, it is possible that animals were interpreting the acoustic information over many small time windows that were shorter than the period of the modulating envelope of the noise. In that case, a local measurement of effective target and masker levels would be different for the antimodulated versus the unmodulated conditions, potentially reducing MMR−. However, here, the center frequency of the flanker band is 1.5 octaves higher than the target center frequency. It is unlikely that downward spread of masking from the flanker would strongly affect performance in the antimodulated conditions. On balance, our results suggest that energetic masking from the flanker did not limit performance in the antimodulated versus modulated on-target condition. Thus, the results from Experiment 2 are similar to those of Experiment 1 in that the reduction of MMR− relative to MMR is consistent with a central component of MMR.

Experiment 3

Experiments 1 and 2 showed that NH gerbils can benefit substantially from MMR when listening for a target tone in background sound. Experiment 3 asked whether CHL-reared animals displayed degraded MMR, MMR+, and MMR−. Five gerbils with juvenile-onset CHL were tested on the same stimuli as the NH animals
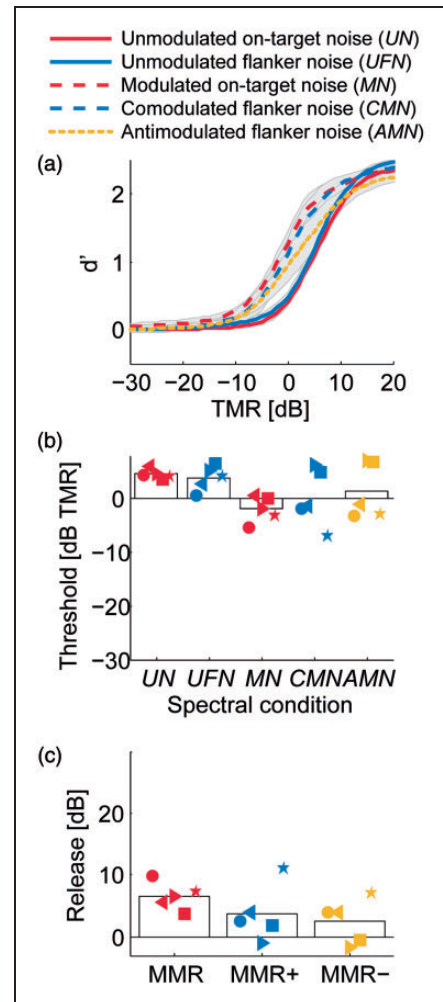

Figure 5. Performance for CHL animals at approximately 25 dB SL (Experiment 3), plotted similarly to Figure 4. Performance was better in modulated than in unmodulated noise, but MMR− and MMR+ did not differ appreciably. *Note.* CHL = conductive hearing loss; SL = sensation level; MMR = modulation masking release.

except that the masker level equaled 63 dB SPL. Quiet thresholds equaled on average 36.2 dB SPL (SEM = 2.5, see also Table 1), resulting in an average on-target band masker level of approximately 25 dB SL. In other words, CHL animals have approximately 30 dB hearing loss when compared with NH controls. Figure 5(a) shows the across-animal average psychometric functions for the five maskers. Each line shows performance for a different masker type, identical to Figures 3 and 4. Animals showed better performance in modulated than in unmodulated noise. Detection thresholds and masking release are shown in Figure 5(b) and (c). Paired two-tailed t-tests found no significant difference between MMR+ ($M = 3.7$, $SD = 2.0$) and MMR− ($M = 2.5$, $SD = 1.6$), $t(4) = 1.4$, $p = .245$.

To test whether potentially broader critical bands in CHL gerbils may have caused energetic masking of the
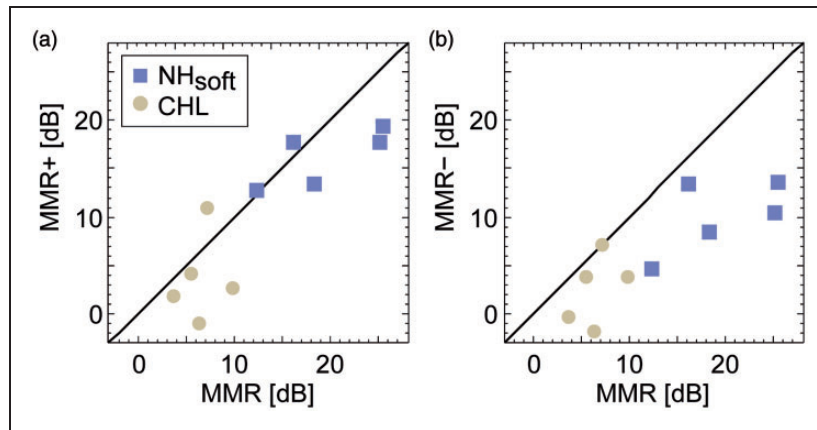
Figure 6. MMR comparison across NH$_{soft}$ and CHL animals (Experiments 2 and 3), listening at comparable sensation levels. MMR, MMR+, and MMR− are smaller for CHL than for NH$_{soft}$ animals. *Note.* CHL = conductive hearing loss; MMR = modulation masking release; NH$_{soft}$ = normal-hearing animals in low-intensity background sound.

target tone by the flankers, detection thresholds were analyzed with rANOVA, with main factors of masker envelope and flanker presence. The analysis found a significant main effect of envelope modulation, $F(1,4) = 18.1$, $p = .013$, but not whether a flanker was present, $F(1, 4) = 0.2$, $p = .661$. A separate rANOVA analyzed the slopes of the psychometric functions and found no significant effects of envelope or flanker, $F(1, 4) = 0.1$, $p = .826$ for envelope and $F(1, 4) = 0.6$, $p = .496$ for flanker.

In Figure 6, Panels A and B directly compare MMR versus MMR+ and MMR versus MMR− across NH$_{soft}$ and CHL animals. Squares show performance for NH gerbils in low-intensity background sound (Experiment 2) and circles for CHL (Experiment 3). To the extent that central processing affects performance, results should fall above the diagonal in Figure 6(a) and below the diagonal in Figure 6(b). This was observed for all animals with the antimodulated masker (symbols fall below diagonal in Figure 6(b)). However, for comodulated noise, both groups of animals failed to reach statistical significance in the *t*-test analysis for comodulated versus modulated noise (squares and circles do not fall consistently above diagonal in Figure 6(a)). Furthermore, because sizable MMR+ was observed for the NH animals in Experiment 1, and not for the NH animals in Experiment 2, it is likely that the NH$_{soft}$ and CHL animals were tested at sound levels that were too low to reveal full MMR+ due to floor effects.

Comparing between NH$_{soft}$ and CHL group, a univariate ANOVA found that indeed, MMR was significantly reduced in the CHL group when compared with NH$_{soft}$, $F(1, 8) = 21.9$, $p = .002$. MMR+, $F(1, 8) = 27.5$, $p = .001$, and MMR−, $F(1, 7) = 17.6$, $p = .004$, were both significantly smaller for CHL than for NH$_{soft}$.

A mixed ANOVA comparing the slopes of the psychometric functions for the unmodulated noise conditions between NH$_{soft}$ and CHL group revealed that the CHL animals had significantly shallower slopes when compared with NH$_{soft}$, $F(1, 8) = 23.0$, $p = .002$, with Bonferroni correction. This is consistent with the interpretation that CHL animals had increased variability in their underlying decision process when compared with NH controls.

Discussion

Background sound is challenging for hearing-impaired listeners and this could be due to peripheral deficits alone or a combination of peripheral and central deficits. MMR offers a behavioral paradigm that can assess both peripheral and central mechanisms through signal detection in the presence of modulated noise. An extensive literature demonstrates that for comodulation masking release to occur, sound information needs to be combined across a wide range of frequencies (e.g., Dau et al., 2013; Pressnitzer et al., 2001) and predicts that this phenomenon cannot solely originate from the cochlear processing stage.

NH gerbils displayed robust MMR at two different SLs. Keeping the across-time-average on-target masker energy fixed, performance improved when the envelope of the on-target noise was modulated as compared to unmodulated (Figures 3(a) and 4(a)), as found previously for humans (Carlyon et al., 1989; Hall et al., 1990; Verhey & Ernst, 2009). At the higher SL, thresholds improved even further when a comodulated flanker band was added (compare blue vs. red dashed lines in Figures 3(a)) and at both SLs, they decreased when an antimodulated flanker band was added (see yellow vs. blue lines Figures 3(a) and 4(a)), again paralleling human studies (Pierzycki & Seeber, 2010). These data are consistent with previous findings that gerbils can benefit from MMR and MMR+ (Gleich et al., 2007;

Wagner, 2002) and extend those results by demonstrating that gerbils, like humans (Pierzycki & Seeber, 2010; Schooneveldt & Moore, 1987), can experience MMR− interference from antimodulated flankers. However, MMR, MMR+, and MMR− were much reduced in animals reared with bilateral CHL (Figure 6).

Within- and Across-Frequency Contributions to MMR

To assess within- and across-frequency contributions to MMR, the current experiments compared performance in modulated to unmodulated noise with and without flanking bands that were either comodulated or antimodulated. The flanking band configuration assessed energetic masking effects. Specifically, if performance was limited by within-critical-band listening with critical bands that are wide enough to include the flanker, then performance in unmodulated noise with flanker should have been worse than performance in unmodulated noise without flanker, due to the additional masker energy in the flanking condition. However, if across-frequency factors affected performance in this task then added flanker energy should cause differential performance changes for unmodulated versus modulated maskers. Specifically, added flankers should not affect performance in the unmodulated conditions but worsen or improve performance in the modulated conditions.

One caveat is that, the flanker in the antimodulated conditions could *fill in* energetic masking during the dips of the modulated on-target masker. In contrast, the masking noise was consistently *on* in the unmodulated masker condition with flanker, leaving little room for a flanker to affect detection thresholds. Therefore, a conservative interpretation of the current results is that in the antimodulated conditions, the flanker may have caused additional on-frequency masking during those time epochs when the on-target band was low in level. This additional off-frequency masking due to downward spread of masking from the flanker would not have occurred in the unmodulated case. If this interpretation is correct, then the masking release that was observed for the comodulated conditions would have been enhanced by across-channel MMR processing and decreased by within-channel masking. In addition, the masking release observed for the antimodulated conditions would then have been worsened through both impaired across-channel modulation release and within-channel masking.

However, at least in humans, downward spread of masking is typically restricted to a narrow range of frequencies. For instance, when detecting a pure tone at around 1 kHz in the presence of a higher frequency narrowband masker, thresholds are not appreciably affected by the masker for target frequencies that are half an octave below the center frequency of the masker or smaller (Scharf, 1971; Wegel & Lane, 1924). At the target

frequency of 1 kHz, the critical band in gerbil is approximately two thirds of an octave wide or about twice as wide as in humans (Glasberg & Moore, 1990; Kittel et al., 2002). Thus, one could reasonably expect to see an effect of downward spread of masking at up to about one octave of separation between target frequency and center frequency of the flanker. However, here, the center frequency of the flanker was one and a half octaves above the target. Thus, we deem it unlikely that downward spread of masking from the flanker differentially affected thresholds in the unmodulated versus antimodulated conditions.

Here, for NH gerbils, tone detection in unmodulated on-target noise was not statistically different from tone detection in unmodulated flanker noise, confirming that indeed, the flanker band fell outside of the critical band surrounding the target signal (cf., Kittel et al., 2002; Lingner, Wiegrebe, & Grothe, 2012). Moreover, depending on the phase of the envelope, adding a modulated flanker band decreased or increased the observed masking release. Thus, our behavioral observations on MMR are consistent with both peripheral and central components. Together, these results support the idea that the CNS could plausibly contribute to MMR in gerbil, by allowing gerbils to selectively listen in the dips of the masker.

The MMR measures observed here are comparable in magnitude to those observed by Wagner (2002) but larger than those observed by Gleich et al. (2007). To understand the difference in reported thresholds with the latter study, it is instructive to compare the designs of both studies. Gleich et al. tested gerbils on detection of 2-kHz tones in two types of background noise of medium intensity (59 dBA): random Gaussian noise and unintelligible babble noise with speech-like spectro-temporal fluctuations. Thresholds were estimated at $d' = 1.8$. They tested young and old normal-hearing and old hearing-impaired animals. When collapsed across all animals, Gleich et al. reported 2 dB of masking release. They found that a modulated masker resulted in psychometric functions with slopes that were shallower than the slopes resulting from an unmodulated masker. Relative to the modulated noise used by Gleich et al., the modulated noise in the current study was much more steeply modulated (100% here as compared to 25%– 75%). The modulation spectrum here was flat except for a periodic envelope with rectangular gating at 10 Hz and 50% duty cycle, as opposed to the faster and more irregularly fluctuating speech-shaped modulation spectrum in the previous work. In humans, MMR is largest at around 10 Hz modulation frequency (e.g., Carlyon et al., 1989), increases with increasing duty cycle (e.g., Nelson & Jin, 2004), and is generally larger for regular than for irregular masker envelopes (e.g., Buss, Hall, & Grose, 2012; Verhey & Ernst, 2009). Furthermore, the center frequency of the target tone in

the study by Gleich et al. was higher than in the current study and MMR in humans decreases with increasing target center frequency (e.g., Schooneveldt & Moore, 1987). Moreover, applying a lower threshold criterion, comparable to the current study, would increase the observed MMR in the study by Gleich et al. Together, these methodological differences contribute to the larger observed masking release in the current study.

Across-Listener Differences

Across all NH gerbils in the current study, MMR− was generally smaller than MMR+. However, NH gerbils differed in their ability to benefit from MMR. Previous work on MMR in gerbils typically did not report individual thresholds. Here, individual differences across animals were much more strongly pronounced in the modulated than in the unmodulated masking conditions. Many studies report shallower slopes in modulated when compared with unmodulated masking conditions (e.g., Bernstein & Grant, 2009). One possibility is that when trying to detect a target in a temporally fluctuating masker, the animals may have been more uncertain about when to listen as compared with unmodulated masker conditions. This should have increased response variability, therefore reducing the slope of the resulting psychometric function. Although it is impossible to confirm this possibility with the current data, it is worth noting that in humans, even in studies with relatively few listeners, 10–15 dB differences in MMR+ across NH individuals have been reported (e.g., Carlyon et al., 1989; Fantini, Moore, & Schooneveldt, 1993; Goldman, Baer, & Moore, 2012). Nevertheless, given the methodological differences between animal and human experiments, which differ dramatically in the number of trials that can be collected per training and testing session and how motivated a listener may be, a direct comparison between the two species should be undertaken with caution.

Effect of Juvenile Sound Deprivation on MMR

Animals reared with CHL displayed MMR, but the magnitude of release was much reduced, when compared with NH$_{soft}$ animals, even after controlling for SL.

The CHL animal performance in the modulated on-target condition suggests poor usage of dips in the masking envelope. The fact that MMR− was smaller in CHL when compared with NH$_{soft}$ animals listening in soft background sound demonstrates that when juvenile animals experience CHL, this can reduce their sensitivity to across-frequency cues. The MMR+ results indicate that the usage of envelope dip information remains poor even when across-channel envelope information is added. The poor performance in both the on-target and flanking band

conditions are consistent with impaired central processing. Specifically, the finding that MMR+ was also reduced in CHL versus NH$_{soft}$ is consistent with the interpretation that juvenile-onset CHL impairs central processing of modulated background sound. However, because overall level was low, floor effects in the comodulated condition may have further reduced MMR+ for CHL and NH.

Studies on CI users suggest that a comodulated flanker can interfere with target identification, presumably because CI users form an obligatory grouping of target and flanker (Kwon & Turner, 2001; Nelson et al., 2003; Oxenham & Dau, 2001). Here, we did not see evidence of increased obligatory fusion in CHL versus NH. Indeed, the antimodulated flanker did not dramatically worsen performance for CHL gerbils, when compared with the modulated on-target band alone. Instead, the CHL animals were overall less affected by the flanker band when compared with NH gerbils, displaying reduced MMR− in addition to reduced MMR.

Plausible Mechanisms

In humans, the MMR task bears clinical relevance. Hearing-impaired human listeners often show little or no MMR, and this is thought to contribute to their perceptual deficits when listening in background sound. Reduced MMR in hearing-impaired listeners has multiple causes, including lower audibility (Bernstein & Grant, 2009), diminished peripheral compression (Schooneveldt & Moore, 1987), reduced fine structure information (Lorenzi, Gilbert, Carn, Garnier, & Moore, 2006; but see also Freyman, Griffin, & Oxenham, 2012), and more forward masking (Dubno, Horwitz, & Ahlstrom, 2002). However, across many studies in humans, 25% to 30% of the variance for suprathreshold deficits remains unaccounted for (e.g., Grant & Walden, 2013). While the impact of peripheral dysfunction is well established, the current results suggest that additional CNS factors could play a role in the neural processing that limits sensitivity in hearing-impaired listeners.

Evidence supporting this idea stems from clinical findings that a transient period of childhood sound deprivation, produced by *otitis media* with effusion, diminishes behavioral MMR, even though audiometric thresholds have returned to normal at the time of testing (Hall & Grose, 1994). Moreover, CI users do not benefit from MMR+ to better identify closed-set speech in modulated noise, even though NH listeners can utilize the highly degraded cues of CI speech for this purpose (Ihlefeld et al., 2012). Further support for the idea that impaired CNS mechanisms plays a role in MMR, the duration of hearing loss preimplantation correlates with the amount of MMR experienced by CI listeners (Zirn et al., 2013). An extensive literature demonstrates that sound deprivation through hearing loss induces long-lasting changes

in the CNS along the entire auditory neuraxis (e.g., Chambers et al., 2016; Knudsen et al., 1994; Moore et al., 1999; Rosen et al., 2012; Sanes & Bao, 2009). Indeed, even short bouts of transient hearing loss can directly alter sensory processing in the CNS of gerbils (Caras & Sanes, 2015).

In addition, CHL could impair the central efferent input to the periphery, thereby changing temporal processing at the cochlea and reducing MMR. There is controversy in the literature as to whether, in addition to attenuating sound, CHL may alter the tuning of cochlear filters. There is evidence that CHL through malleus removal does not lead to sensorineural hearing loss (Tucci et al., 1999). However, a recent study investigated the vulnerability of cochlear innervation following CHL through *otitis media* in mice (Liberman, Liberman, & Maison, 2015). Oval window removal can cause loss of inner hair cell afferent innervation, but this effect is only pronounced for cochleotopic positions above 5 kHz (Liberman et al., 2015). In contrast, the current study was conducted in the low frequency region (<4 kHz), In conclusion, chronic sound deprivation due to juvenile CHL alters CNS anatomy and physiology. Impaired CNS function is a plausible mechanism by which MMR could be reduced in animals reared with CHL.

Summary

These results support the conclusion that juvenile sound deprivation adversely affects the ability to combat background sound. These adverse effects are especially severe for modulated background sound where sound deprivation can reduce the ability to listen in the dips of a fluctuating masker. Results raise the possibility that hearing loss-induced changes to the CNS could contribute to perceptual deficits when listening in situations with background sound.

Declaration of Conflicting Interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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