Right-ear advantage drives the link between olivocochlear efferent 'antimasking' and speech-in-noise listening benefits

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The mammalian cochlea receives feedback from the brainstem medial olivocochlear (MOC) efferents, whose putative 'antimasking' function is to adjust cochlear amplification and enhance peripheral signal detection in adverse listening environments. Human studies have been inconsistent in demonstrating a clear connection between this corticofugal system and behavioral speech-in-noise (SIN) listening skills. To elucidate the role of brainstem efferent activity in SIN perception, we measured ear-specific contralateral suppression of transient-evoked otoacoustic emissions (OAEs), a proxy measure of MOC activation linked to auditory learning in noisy environments. We show that suppression of cochlear emissions is stronger with a more basal cochlear bias in the right ear compared with the left ear. Moreover, a strong negative correlation was observed between behavioral SIN performance and right-ear OAE suppression magnitudes, such that lower speech reception thresholds in noise were predicted by larger amounts of MOC-related activity. This brain-behavioral relation was not observed for left ear SIN perception. The rightward bias in contralateral MOC suppression of OAEs, coupled with the stronger association between physiological and perceptual measures, is consistent with left-hemisphere cerebral dominance for speech–language processing. We posit that corticofugal feedback from the left cerebral cortex through descending MOC projections sensitizes the right cochlea to signal-in-noise detection, facilitating figure-ground contrast and improving degraded speech analysis. Our findings demonstrate that SIN listening is at least partly driven by subcortical brain mechanisms; primitive stages of cochlear processing and brainstem MOC modulation of (right) inner ear mechanics play a critical role in dictating SIN understanding. *NeuroReport* **26:483–487**

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Introduction

Auditory perceptual and physiological studies in humans have established a functional bias between the right and left ears, with a right-ear advantage exhibited in a wide variety of listening tasks [1]. Dichotically presented speech materials are more accurately perceived when delivered to the right compared to the left ear [2]. Right-ear dominance in perceptual tasks, particularly those recruiting verbal processing, is thought to reflect the contralateral bias of the auditory system and the (leftward) hemispheric lateralization for speech–language function [2].

Physiological responses from the human cochlea similarly exhibit functional asymmetries, with larger transient-evoked otoacoustic emissions (OAEs) measured in the right ear compared with the left ear [3,4]. OAEs are bioacoustic sound emissions measured in the ear canal that reflect cochlear health and peripheral auditory processing. OAEs are thought to originate from sound-evoked oscillations of the cochlear outer hair cells (OHCs), which amplify basilar membrane motion and increase hearing sensitivity for low-level stimuli. OHCs are innervated by crossed medial olivocochlear (MOC) efferent neurons originating in the caudal brainstem. Activation of the MOC bundle dampens OHC responses through inhibition, resulting in suppression of OAEs [5]. MOC fibers are engaged in humans through contralateral acoustic stimulation (CAS), which acts to attenuate OAEs measured in the ipsilateral ear canal. Differences in cochlear emission levels between recordings made with and without CAS provide a non-invasive assay of MOC strength [5]. Indeed, a right-ear advantage in OAE suppression occurs when CAS noise is directed to the left ear and OAEs are recorded from the right ear [3]. These studies imply a functional asymmetry (and rightward laterality) in the earliest peripheral stages of auditory processing in responses generated from within the cochlea [4].

Real-world speech communication rarely occurs in quiet environments. When analyzing the auditory scene (e.g. classrooms, cocktail parties, restaurants), listeners are faced with extracting target information (e.g. speech) from a backdrop of acoustic interference. A putative role of the MOC efferents is to improve the detectability of signals in these types of noisy environments [5–7]. MOC

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activation in animal models enhances auditory nerve fiber responses in the presence of noise [7,8]. These findings suggest that MOC feedback may improve figure-ground contrast by providing an 'antimasking' function that improves signal-in-noise extraction [5,8]. In humans, MOC activation has been linked to performance on simple auditory tasks, for example, tone detection and intensity discrimination in noise [6].

Despite its presumed role in signal-in-noise enhancement, studies on whether MOC efferent activity is directly related to speech-in-noise (SIN) perceptual abilities have yielded contradictory findings. Some studies have concluded that speech detection in noise is 'not related' to MOC-mediated OAE suppression [9,10]. In contrast, other studies have shown that the degree of CAS suppression effects 'is related' to the amount of improvement in speech detection scores during SIN listening tasks [11,12]. The interpretation of these studies is complicated by the fact that different reports utilized different SIN tasks, different noise stimuli, and different assays to quantify the amount of CAS-induced suppression of OAEs [12]. Nevertheless, another factor not fully accounted for by previous research involves the comparison of right and left ear performance. Given the ubiquity of the right-ear advantage in audition, exploration of the relationship between speech detection in noise and CAS-induced suppression of transient evoked otoacoustic emissions (TEOAEs) would conceivably benefit by examining the role of the right-ear advantage in SIN tasks.

In the present study, we aimed to directly assess the connection between brainstem MOC efferent activity and SIN listening skills. We compared individuals' degree of contralateral OAE suppression (a proxy of MOC activation) with behavioral performance on measures of SIN perception. On the basis of the ubiquity of the right-ear advantage in audition and contralaterality of the brain's speech–language pathway, we hypothesized that listeners' noise-degraded speech understanding would be predicted by MOC efferent control to the right cochlea. A rightward asymmetry in cochlear feedback would bolster the notion that the hemispheric specialization for speech observed in the cerebral cortex is reflected subcortically as early as the inner ear [4]. Moreover, linking lateralized human MOC activity with SIN would affirm that noise-degraded speech perception is influenced by initial cochlear processing, but in an ear-specific manner.

Materials and methods

Participants

Fifteen English-speaking young adults without musical training (age: 25.5 ± 2.4 years) participated in the experiment. All were right-handed and had normal hearing bilaterally (threshold ≤ 10 dB HL from 250–8000 Hz; see Supplementary Methods, Supplemental digital content 1, *http:///links.lww.com/WNR/A321*). Participants gave written informed consent, in compliance with a protocol approved by the University of Memphis Institutional Review Board.

Otoacoustic emission recording protocol and response analysis

Bilateral OAEs were recorded from each participant separately for each ear (Otodynamics 296). Stimuli were 80 μs clicks (rate = 50/s) presented at 60 dB peak equivalent sound pressure level (SPL) (see Supplementary Methods, Supplemental digital content 1, *http:///links.lww.com/WNR/A321*). Waveform averaging was terminated after obtaining 260 low-noise sweeps. OAE recordings were interleaved in two conditions, with (CAS+) and without (CAS−) concurrent contralateral broadband noise. Critically, CAS presentation levels did not exceed middle-ear reflex thresholds for any of the participants, ruling out myogenic activity as a potential confound.

A poststimulus analysis window was imposed on emission waveforms from 8 to 18 ms. We calculated the amount of OAE root mean squared suppression (in dB) for each participant as the average difference between CAS− and CAS+ waveforms (Echomaster Software; Kresge, Troy, Michigan, USA). In addition, we measured the amount of OAE suppression in nine, 2 ms time intervals between 2 and 20 ms to examine time-varying changes in MOC activity. Analysis of time-varying OAE suppression typically provides larger estimates of CAS-induced MOC activation than averaging across the entire recording epoch window [13].

Behavioral speech-in-noise task

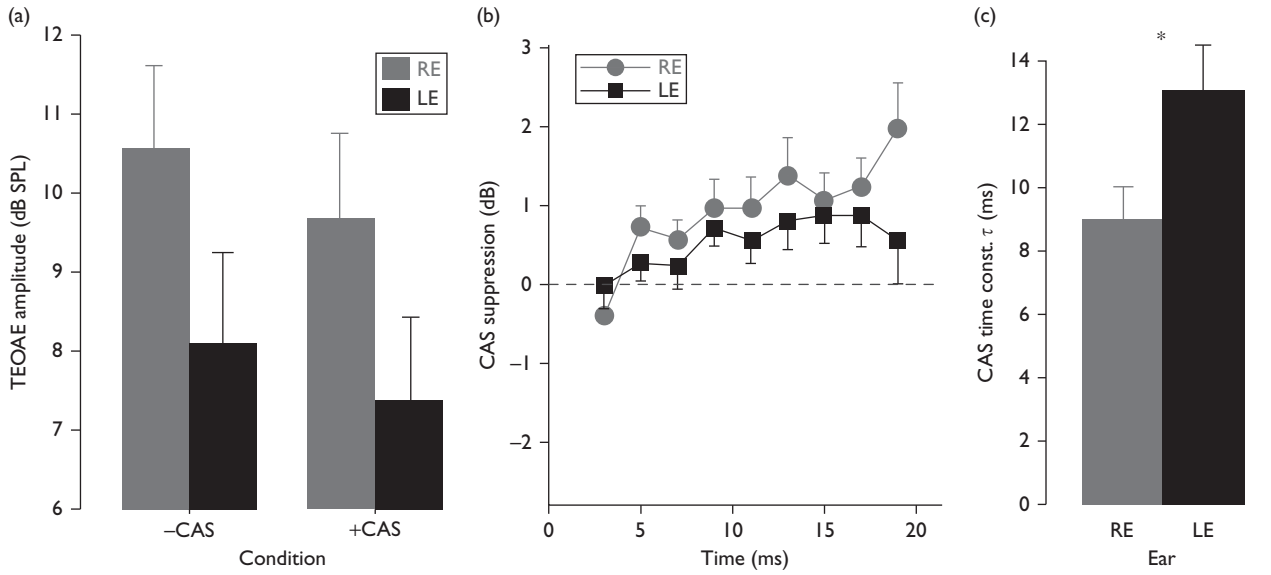
We measured listeners' speech reception threshold in noise using the QuickSIN test [14]. Participants were presented with two lists (normed for equivalence) of six sentences with five keywords per sentence embedded in four-talker babble noise. Sentences were presented at a combined amplitude of 70 dB SPL, using prerecorded signal-to-noise ratios (SNRs) that decreased in 5 dB steps from 25 dB (very easy) to 0 dB (very difficult). Participants were required to repeat each sentence after auditory presentation. 'SNR loss' (in dB) was determined by subtracting the total number of correctly identified words from 25.5. This index represents the SNR required to correctly identify 50% of the target keywords [14]. Left and right ears were tested separately. Different lists were used within and between ears to avoid familiarization.

Results

Contralateral suppression effects on ear-specific otoacoustic emissions

OAE amplitudes with (+CAS) and without (−CAS) the presence of contralateral noise are shown for each ear in Fig. 1a. A repeated measures analysis of variance with two within-subject factors (stimulation mode: −CAS, +CAS; ear: left ear, right ear) revealed a significant main effect of stimulation mode ($F_{1,14} = 14.66$, $P = 0.0018$) and ear ($F_{1,14} = 7.66$, $P = 0.015$) on OAE amplitudes. The main effect of stimulation mode indicates that emissions were reduced in the presence of CAS stimulation across the board, whereas the main effect of ear indicates higher

Fig. 1



TEOAEs are suppressed with CAS. (a) Ear-specific OAE amplitudes recorded with (+CAS) and without (−CAS) contralateral noise. Little change is observed in the left ear (LE); prominent suppression is observed in the right ear (RE). (b) Time-course of CAS-induced OAE suppression between ears. Positive values denote a reduction (i.e. suppression) in ipsilaterally recorded OAE with contralateral noise; negative values = response facilitation. CAS suppression grows as OAEs unfold over time. (c) Time-constant (τ_{CAS}) for CAS-induced OAE suppression defined as the time at which CAS suppression time courses [i.e. (b)] reached 50% of their final magnitude. Efferent-induced suppression occurs faster in the right compared with the left ear. Error bars = ± 1 SEM. CAS, contralateral acoustic stimulation; SPL, sound pressure level; TEOAEs, transient evoked otoacoustic emissions. *$P < 0.05$.

emission levels in the right compared with the left ear, both with and without CAS.

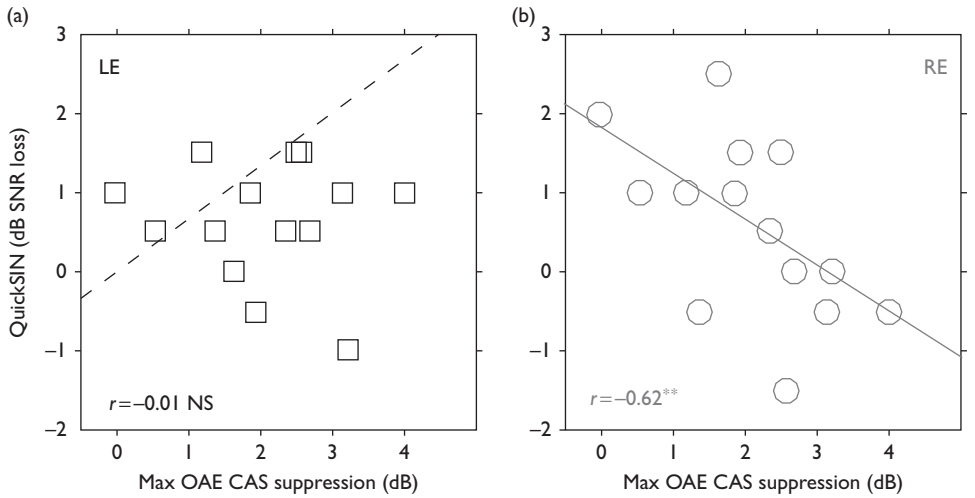
Temporal dynamics of the CAS suppression effect are shown in Fig. 1b. CAS magnitudes showed a monotonic increase over the first 20 ms of the response ($F_{8,112} = 6.19$, $P < 0.0001$). This linear effect was strongly present in the right ($F_{1,133} = 16.03$, $P = 0.0001$) and only marginally present in the left ear ($F_{1,133} = 4.07$, $P = 0.045$). To further characterize CAS time courses per ear, we computed the time-constant of CAS growth (τ_{CAS}), calculated as the time point at which OAE suppression (Fig. 1b) reached 50% of its final magnitude (see Fig. 1b; 20 ms time point). It is important to note that this measure does not reflect the time-constant for the onset of the MOC reflex itself, which is in the order of 100–200 ms [15]. Rather, τ_{CAS} can be interpreted in terms of MOC suppression as a function of cochlear location; early τ_{CAS} reflects efferent suppression occurring in more basal cochlear regions (because of the shorter traveling wave and reflection times), whereas later τ_{CAS} can be interpreted as suppression effects occurring in low-frequency, apical cochlear regions. We found that suppression time-constants (τ_{CAS}) were smaller in the right ear compared with the left ear ($t_{14} = -2.48$, $P = 0.026$; Fig. 1c). Collectively, these results indicate an ear dominance in contralateral efferent control that is both stronger and occurs in more basal (i.e. high-frequency) cochlear regions in the right compared with the left ear.

Brain–behavior relations between peripheral 'antimasking' and behavioral speech-in-noise

Behaviorally, QuickSIN scores did not differ between the right and left ears ($t_{14} = 0.18$, $P = 0.85$), consistent with test–retest reliability of this measure [14]. To assess correspondences between peripheral cochlear processing and behavioral SIN abilities, we carried out ear-specific correlational analyses. For each ear, participants' maximal CAS OAE suppression (extracted from CAS time courses; Fig. 1b) was regressed against their individual QuickSIN score for the same ear. Analyses by ear allowed us to evaluate whether or not the connection between MOC-mediated efferent suppression (i.e. 'antimasking') and SIN perception showed a functional laterality between ears.

Separate brain–behavior correlations per ear are shown in Fig. 2. No correspondence was observed between QuickSIN and OAE suppression in the left ear (Spearman's rank correlation: $r_s = -0.01$, $P = 0.96$). In stark contrast, we found a strong negative association between MOC-induced suppression in the right ear (contralateral noise in the left ear) and listeners' QuickSIN performance ($r_s = -0.62$, $P = 0.014$). This correspondence between physiological OAE and behavioral SIN measures was stronger in the right ear relative to the left ear (Fisher r-to-z transform: $z = 1.79$, $P = 0.037$). The negative association between OAE suppression and SIN abilities indicates that stronger peripheral cochlear processing – that is, stronger MOC feedback or

Fig. 2



Brain–behavior correspondence between SIN performance and MOC-mediated OAE suppression. Correspondence between CAS cochlear suppression magnitude and behavioral SIN listening skills for the (a) left and (b) right ears. Robust correlations are observed between peripheral OAE measures and SIN recognition for the RE; larger CAS suppression (i.e. more 'antimasking') predicts better QuickSIN performance. No correlation is observed between OAE measures and SIN performance for LE presentation. Solid line = significant relationship; dotted line = NS. $^{**}P < 0.01$. CAS, contralateral acoustic stimulation; LE, left ear; MOC, medial olivocochlear; OAE, otoacoustic emission; RE, right ear; SIN, speech-in-noise; SNR, signal-to-noise ratio.

'antimasking' – predicts better speech recognition at less favorable SNRs. The fact that this association exists primarily in one ear suggests a laterality in SIN listening skills that is dominated by a right-ear advantage in cochlear efferent control.

Discussion

Previous studies have provided equivocal findings with regard to the relationship between MOC activity and behavioral SIN skills [9,10–12], the presumed functional role of the brainstem efferents. Our data provide evidence that degraded speech listening skills depend on lateralized, 'top–down' modulatory feedback from the MOC subsystem. Indeed, we found (i) stronger contralateral suppression of cochlear emissions in the right compared with the left ear, which occurred with a basal (high-frequency) cochlear bias, and (ii) a robust link between OAE suppression (i.e. 'antimasking') and SIN recognition performance for right but not left ear stimulation. Our findings bolster the notion that noise-degraded speech perception in humans is influenced by initial cochlear processing but in an ear-specific manner.

Hearing sensitivity is often more acute and OAEs are larger in the right compared with the left ear; it is speculated that these ear asymmetries might be a contributing factor to the development of cerebral laterality and left-hemisphere specialization for speech and language processing [4]. Neurophysiological studies have shown that OAE responses and MOC-induced cochlear suppression are larger in the right compared with the left ear, even in neonates [16]. Conceivably, establishment of the right-ear advantage in cochlear output and MOC efferent feedback control early in life could sensitize the left hemisphere of the brain to process speech differently from the right hemisphere [4] through corticofugal pathways including corticocollicular and collicular–cochlear fiber tracts (for review, see [17]). Indeed, resection of the human superior temporal gyrus produces stronger changes in peripheral MOC activity on the contralateral side [18]. Hence, speech – arguably the most salient acoustic feature of an infants' environment – would presumably be transduced more efficiently in the right ear, leading to enhanced neural representation of speech in the left hemisphere. Experience-dependent neural plasticity could potentiate corticofugal feedback control from the left hemisphere through the crossed/uncrossed brainstem MOC efferent pathways to the right cochlea [17]. A reduction in the transmission of spectral energy related to environmental noises could then benefit the detection of noise-degraded speech by providing MOC-mediated 'antimasking' of the target signal [5,7,8].

Our results are consistent with the emerging notion that central auditory processing plays a critical role in mediating robust speech recognition abilities [19–22]. Previous studies have demonstrated that perceptual abilities are predicted on the basis of neurophysiological encoding of speech at both subcortical [19–21,23] and cortical levels of auditory processing [19,21,22]. That is, more salient neural representations for acoustic features of speech (i.e. larger 'neural SNR') allow a listener to better exploit those cues behaviorally [23]. This suggests that an individual's success with speech comprehension in degraded listening environments might be governed by early physiological processing along the auditory

pathway, well before conscious awareness of the auditory stimulus.

Our findings advance previous results by demonstrating that even the earliest forms of auditory processing (i.e. gain modulation of cochlear responses) contribute to the much later perceptual operations governing SIN behaviors. They also confirm the putative 'antimasking' role of the MOC efferent pathway [5,7,8] in humans by establishing its connection with superior SIN abilities. We found that modulation of peripheral cochlear processing, as assessed through contralateral suppression of OAEs, was stronger in the right ear, particularly for high-frequency cochlear regions. More critically, efferent modulation of OAEs predicted listeners' behavioral SIN performance. These findings corroborate the aforementioned neuroimaging data that reveal the importance of central physiological brain mechanisms in governing degraded speech perception. The right-ear bias in MOC suppression of cochlear emissions and the stronger association between these variables for right-ear stimulation further suggest a rightward asymmetry in SIN processing.

A rightward laterality in cochlear response is reminiscent of other well-known asymmetries observed throughout the auditory pathway. Functional biases have been observed – for example, in auditory processing in the human cerebral cortex [24], the brainstem [25], and the cochlea [4]. These studies provide evidence for lateralized neurophysiological activity dependent on spectrotemporal features and the behavioral relevance of the auditory input, whereby ecologically relevant stimuli (e.g. speech) are right-lateralized compared with less relevant sounds (e.g. nonspeech) [24,25]. We posit that the observed right-ear laterality in cochlear feedback and its correspondence with SIN perception might be an early precursor to the left-hemispheric bias for language processing found in the cerebral cortex. In this regard, our data help affirm that important auditory scene analysis skills reflect a hierarchy of neurocomputations from the cochlea to the cortex [22,26] and highlight the interplay between central and peripheral mechanisms in successful reception of degraded communication signals.

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Conflicts of interest

There are no conflicts of interest.

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