Stability of Eye Movement-Related Eardrum Oscillations to acoustic and gravitational manipulations

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Abstract

Recent studies describe Eye Movement-related Eardrum Oscillations (EMREOs), low-frequency signals recorded in the ear canal that arise from the tympanic membrane and are triggered by saccadic eye movements. Because EMREOs are thought to arise from motor elements in the peripheral auditory system, we examined how two known modulators of these elements affect the EMREO time course. First, the activity of outer hair cells (OHC) can be suppressed by the medial olivocochlear reflex (MOCR). If OHCs contribute to the generation of EMREOs, activation of this reflex should reduce EMREO amplitude. To test this, we compared EMREO amplitudes elicited by saccades performed in silence and in the presence of contralateral noise. Second, gravitational cues linked to head orientation may influence EMREOs via oculomotor control circuits that possibly modulate middle ear muscles. To test this, we recorded EMREOs while participants made saccades with their head upright (0° azimuth) and with their head tilted 30° in either direction. Across both experiments our data reveal no clear modulation of the EMREO time course by these experimental manipulations. Together with other recent studies these findings advocate for a stability of the EMREO time course towards multiple experimental modulations and fuel speculations that the signal may serve as a temporal reference frame when combining signals across the senses.

1. Introduction

Eye movement-related eardrum oscillations (EMREOs) are low-frequency signals recorded from the tympanic membrane following saccadic eye movements (Gruters et al., 2018). Recent studies describe that EMREOs last for up to 100 ms after saccade onset and exhibit deflections of opposing sign and distinct timing for saccades in different directions along the horizontal and vertical dimensions (Sotero Silva et al., 2025; Bröhl and Kayser, 2023; King et al., 2023; Lovich et al., 2023a). In particular, the EMREO induced by horizontal saccades is a reliable signal that carries information about saccade direction and possibly also amplitude (King et al., 2023; Lovich et al., 2023a). However, the precise origin of the EMREO and the neural pathways and structures giving rise to this phenomenon remain unclear. The EMREOs are likely generated by motor components in the middle ear and the cochlea, promoting the middle ear muscles (MEMs) and the outer hair cells (OHCs) as key candidates (Gruters et al., 2018; Gallagher, Diop and Olson, 2021; Lovich et al., 2023a). The MEMs and OHCs play a role in actively adjusting sound transduction in response to sudden loud sounds. However, the underlying reflexes and feedback pathways also receive information about other motor-related signals, such as self-vocalization, eye and head movements associated with shifts in attention, or body posture (Mukerji et al., 2010), which are visible as contextual or cross-modal influences on auditory reflexes (Prendergast et al., 2024; Tasko et al., 2022; Soi et al., 2012). These feedback signals entering the pathways to the OHCs and MEMs likely induce the EMREO in a saccade-specific manner. However, they may also shape the EMREO by additional sensory or body-related information that is not directly tied to the execution of a saccade (Kocabay et al., 2025; Schroeer et al., 2023; Delano et al., 2007). We here probed for such non-saccade contextual effects on EMREOs by testing how changes in acoustic context - the presence of a contralateral noise - and non-acoustic context - tilting the head - shape the EMREO time course in the human ear.

The OHCs help protecting the cochlea from external noise, improve speech-in-noise perception, and facilitate spatial hearing (Çelikgün and Derinsu, 2022; Lauer et al., 2022; Ciuman, 2010). Previous studies suggest that the OHCs may also receive information about oculomotor behavior, possibly as descending information from the thalamus and/or superior colliculus via the superior olivary complex (Abbassi et al., 2025; Lovich et al., 2023a). These oculomotor signals possibly contribute to the generation of the EMREO. However, one could expect that experimental manipulations interfering with normal OHCs function may also affect the EMREO, in particular if a contribution to the EMREO signal arises from OHCs. One way by which one can interfere with OHCs function is the medial olivocochlear reflex (MOCR; Sliwinska-Kowalska and Kotylo, 2002, Khalfa et al., 2001). This can be triggered by a suppression noise, which when presented to one ear induces a hyperpolarization of the OHCs in the opposing ear (Lauer et al., 2022; Guinan Jr., 2018; Giraud et al., 1995). The effect of this suppression can be seen in the reduction of transient evoked otoacoustic emissions (TEOAEs; Silva et al., 2025; Ciuman, 2010; Kemp, 2002). These are transient sounds generated by the OHCs in response to brief acoustic stimuli, which can be routinely recorded using in-ear microphones and are used in clinical screening (Jedrzejczak et al., 2020). We here tested whether inducing the MOCR, as confirmed by a suppression of contralateral TEOAEs, alters the time course of the EMREO induced by horizontal saccades in the opposing ear.

The MEMs, i.e., the stapedius and tensor tympani, are connected to the tympanic-ossicular system and adjust sound transmission in loud environments via the acoustic reflex (Cho et al., 2023; Lovich et al., 2023b; Edmonson et al., 2022; Tasko et al., 2022). Importantly, the pathways mediating the acoustic reflex involve structures that receive multisensory and motor-related signals, whose anatomical origin remains partly unknown (Mukerji et al., 2010; Lee et al., 2008; Borg et al., 1984; Møller, 1984). Again, these pathways offer a possible route for oculomotor signals to shape middle ear function and may contribute to the EMREO. In fact, non-oculomotor signals have been shown to activate the MEMs, thus reducing the response from the auditory system to body sounds (self-voice, heartbeats, joints creaking; Schneider and Mooney, 2019). Since oculomotor control in everyday situations requires the combination of eye, head and body-related spatial information (Fetsch and Noppeney, 2023; Morimoto et al., 2011; Proudlock and Gottlob, 2007; Paloski et al., 2006), one could assume that the pathways providing motor-related information to the MEMs also carry information related to the orientation of the head in space to the middle ear. For example, the extraocular muscles receive feedback from the vestibular system that is taken into account when coordinating eyes and head during gaze control and this information may also be relayed to the MEMs. In addition, changes in body posture have been shown to induce subtle changes in hearing thresholds and otoacoustic emissions, induced by changes in cochlear fluid pressure and by triggering MEMs contractions

(Soi et al., 2012; Büki et al., 1996). We tested for the presence of such head-posture-related information in the pathways giving rise to the EMREO. For this we compared EMREOs between conditions that differ in their vestibular context by having participants tilt their head to the left or right.

Collectively, the present study tested whether two distinct contextual factors, the presence of contralateral suppression noise and changes in head-tilt, shape the EMREO time course. Our primary goal was to determine whether these factors have an influence on the EMREO time course in humans, information that helps constrain our understanding of its putative function and the neural pathways giving rise to this phenomenon. Our goal was not to determine directly whether or how strongly the OHC or MEMs in isolation contribute to the EMREO, and quantifying their individual contribution would require experiments with additional and more invasive manipulations. For our study we recorded EMREO signals in human participants in two experiments that required them to perform visually guided saccades (Fig. 1). In one experiment, participants performed horizontal saccades while we measured EMREOs in the presence and absence of a contralateral suppression noise that successfully reduced TEOAEs in the ear under study. In the second experiment, the same participants performed saccades along horizontal, vertical and diagonal directions with their head straight, or tilted to the left or right. Overall, our results demonstrate a stability of the EMREO properties and time course across the tested conditions. This suggests that the EMREO constitutes a phenomenon that is tied to the execution of a saccade but is otherwise robust to various contextual manipulations.

2. Materials and Methods

Participants

A total of 47 participants of both sexes were recruited through a dedicated online platform among the university students and community members (31 female, 16 male, mean ± SD age = 30,19 ± 9,75). The sample size was planned based on previous studies studying the properties of EMREOS (Bröhl and Kayser, 2023; Lovich et al., 2023b; Sotero Silva et al., 2025; Sotero Silva et al., 2026). The study was approved by the Bielefeld University Ethics Review Board (#2024-037). All participants provided written informed consent, reported no history of hearing or neurological disorders and were compensated with 15 Euros per hour. Participants first underwent hearing screening, consisting of a visual inspection of the ear canal, Pure Tone Audiometry (PTA), tympanometry and testing of acoustic reflexes, as described previously in detail (Sotero Silva et al., 2025). Participants with hearing loss (PTA average of 500, 1000, 2000 and 4000Hz above 20 dB) or middle ear impairments (as ear canal obstructions, membrane curves type B or C) in at least one ear were excluded from the study. We also tested participants' visual acuity, and accepted participants with uncorrected impairment of < ± 2 diopters. Participants were given the option to perform the experiment with or without glasses or contact lenses.

Experimental setup

Participants were recruited and the experiments were conducted between April and July 2025. The experiments were carried out in a soundproofed, dark and electrically shielded booth. Participants were seated 100 cm away from a sound-permeable screen (Screen International Modigliani, 2 × 1 m) with their head on a chinrest aligned to the center of the screen. In-ear microphone recordings were performed using two Etymotic ER-10C (Etymotic Research) systems, via probes that served both for sound presentation (to induce TEOAEs) and in-ear recordings (TEOAEs and EMREOs). Acoustic stimuli for TEOAEs (clicks) and noise for contralateral suppression were created using a Sound Blaster X3 Soundcard (Creative Technology Ltd., sampling rate 48’000 Hz) and amplified with a HeadAMP 4 (ARTcessories) amplifier. Click stimuli were presented via the ER-10C probes and the noise was delivered via a unilateral headphone (Radio Ear DD45C headphones, model HB3045). The recorded microphone signals were pre-amplified using the ER-10C

DPOAE amplifiers (Etymotic Research) with gain set to +20 dB. Signals were digitized through an ActiveTwo AD-box (BioSemi) at a sampling rate of 16’388 Hz. The intensity of the acoustic stimuli was measured with a Hand-held Sound Level Meter (Model 2250, Bruel & Kjær, Denmark) using Instantaneous Peak Sound Level parameters (LCpeak, 1s). Visual stimuli were projected (Acer Predator Z650, Acer; 60 Hz refresh rate) onto the screen. Stimulus presentation was controlled using the Psychophysics toolbox (Brainard, 1997) for MATLAB (The MathWorks, 2022), which was synchronized to the recording system using transistor-transistor logic (TTL) pulses.

Eye movements were recorded at 1000 Hz from the left eye using a desktop mounted infrared-based EyeLink 1000 Plus Eye Tracker (SR Research Ltd., 2015) running Host Software vs 5.15. Eye tracking calibration and validation was performed at the beginning of each block using a 5-point grid. The parameters for saccade detection in the EyeLink system were a velocity threshold of 30°/s and an acceleration threshold of 8000°/s (“cognitive” setting). Eye position was recorded as horizontal and vertical position coordinates in degrees. In all experiments the eye tracker camera was aligned with the chinrest and participants’ head. Fig 1 presents schematic representation of the experimental setup and paradigms for Experiment 1 (Fig.1 A) and Experiment 2 (Fig.1 B, C).

We performed control measurements for the in-ear microphones to ensure system calibration prior to each session. These recordings included an empty-room measurement consisting of 15 seconds of silence and the presentation of 20 tone stimuli (10 stimuli at 100 Hz, 10 stimuli at 200 Hz, duration 400 ms) presented from the speakers behind the screen. For this empty-room measurement, the in-ear probes were attached to the chinrest to simulate their typical (in-ear) position related to participants’ heads. The same measurement was repeated with the in-ear probes inserted into the participants' ear canals. The baseline noise spectrum and the signal amplitudes in response to these tones were used to adjust the ear-probe insertion and to calibrate the signal levels between ears, as in our previous studies (Sotero Silva et al., 2025).

Measurement and suppression of TEOAEs

To induce and measure TEOAEs we followed established procedures (Probst et al., 1991). The paradigm presented a series of 600 binaural clicks (rectangular monopolar signals of 0.1 ms duration, delivered at 83 ± 2 dB) presented with inter-click intervals of 380 to 420 ms (uniform, random). Every fourth click had an inverted polarity and three times the amplitude of the standard clicks. Participants were instructed to sit and listen as quietly as possible and to not move their head.

To induce the suppression of TEOAEs, we presented the same clicks to one ear while presenting a suppression noise to the other ear. The suppression noise consisted of a white noise (sampled at 48’000 Hz, delivered at 71 ± 2 dB) presented continuously for the presentation of 8 clicks followed by a silent interval of the same duration. The intensities for the click and noise were chosen based on established procedures (Demir et al., 2024; Aksoy et al., 2019; Santos et al., 2023). For each participant TEOAEs were first measured without suppression, then with unilateral suppression. For the latter, during the second and third blocks we substituted one of the in-ear probes with the unilateral headphone over which we presented the same suppression noise (Fig 1A). The order of which ear was suppressed first was counterbalanced across participants.

Measurement and suppression of EMREOs

We collected EMREOs during visually-guided horizontal saccades, similar to our previous studies (Bröhl and Kayser, 2023; Sotero Silva et al., 2025). As in the TEOAEs paradigm, we first measured baseline EMREOs, then EMREOs in one ear while the other ear was presented to the same noise as used to suppress TEOAEs (Fig 1A). The visual saccade task comprised horizontal saccades either from a central fixation position to a left (-12°) or right (12°) target, or back from these eccentric targets to the central position. In each trial, the fixation dot (0.2° radius, white on the gray background) was presented steady for 650 ms at the respective start location before it jumped either to one of the two eccentric targets or back to the central position. The dot remained on the screen continuously. Each eccentric position was presented 40 times, the central position 80 times per block, resulting in 160 saccades per block. Intertrial intervals lasted between 750 and 1050 ms (uniform). Participants were instructed to fixate their gaze on the dot and to follow this as quickly as possible. For data analysis, we separated trials by saccade direction (left, right), for which we obtained 80 trials each. During the second and third blocks one ear was suppressed in the same way as during the TEOAE paradigm.

Measurements of EMREOs during head tilts

To test the influence of head-tilt on EMREOs, we collected EMREOs during visually-guided saccades along horizontal, vertical and diagonal dimensions. The paradigm was similar as in Experiment 1, but here the fixation target jumped from the central position to one of eight eccentric positions spaced at 45° from each other (at 8° distance from the center). In alternating trials, the fixation dot either jumped to an eccentric target (in a pseudo-random sequence) or back to the center. Each eccentric position was presented 15 times per block, the central position 120 times, resulting in a total of 240 saccades.

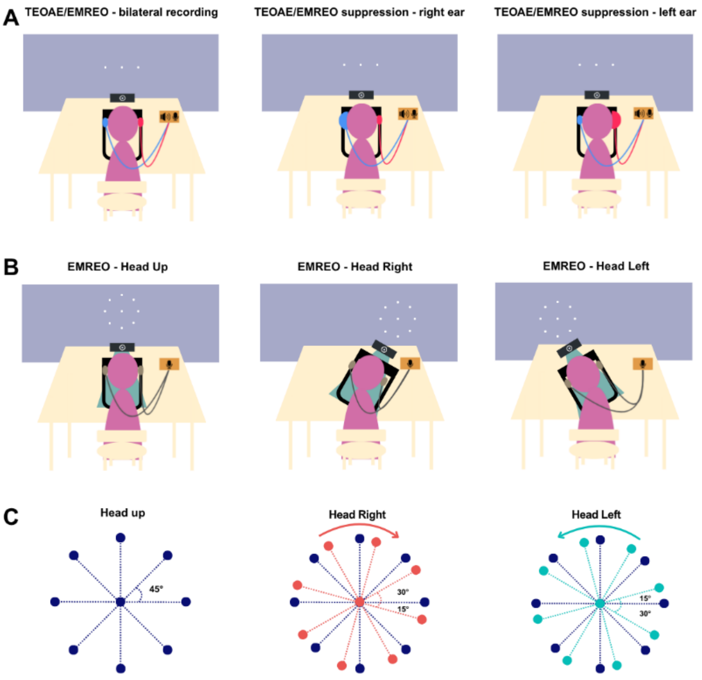
A
TEOAE/EMREO - bilateral recording
TEOAE/EMREO suppression - right ear
TEOAE/EMREO suppression - left ear
B
EMREO - Head Up
EMREO - Head Right
EMREO - Head Left
C
Head up
45°
Head Right
30°
15°
Head Left
15°
30°

Fig 1. - Schematic representation of the experimental paradigms. (A) The setup used in experiment 1 for recording TEOAEs and EMREOs for horizontal saccades. Participants sat in front of a screen onto which saccade targets were projected while we recorded eye movements and in-ear signals. From left to right: in different blocks we either recorded bilateral TEOAEs or EMREOs, or recorded these signals in one ear (smaller ear probe) while the other ear was suppressed using noise (larger headphone). (B) The setup used in experiment 2 for recording EMREOs during head-tilts for saccades along cardinal and oblique axes. From left to right: we recorded EMREOs while participants had their head upright or tilted to the right or left. For this, the chinrest and the eye tracker were mounted on a tiltable platform. (C) Schematic of saccade target positions in experiment 2 for the different conditions. Saccade targets

were presented along the horizontal, vertical and oblique dimensions on the screen (dark blue). In the Head Right and Head Left conditions participants' heads were rotated by 30° to the right and left respectively, inducing a relative rotation of head and screen coordinates. Arrows indicate the direction of the head tilt.

The main rationale of this experiment was to test whether tilting the head would influence the EMREO time course. For this experiment we mounted the chinrest and the eye tracker onto a platform that could be tilted and secured in three different positions: in the first block the platform was kept at 0° (head upright). For the second and third blocks, the platform was tilted 30° to the right or the left (order counterbalanced across participants). Participants were instructed to keep the body as straight as possible and only tilt their neck to adjust the head position. For the head-tilted conditions, the stimulus projection was adjusted on the screen to ensure that the center fixation was at the same level to participants' eyes in each block (see Fig. 1 B). Since in the tilted blocks the axis of the head and the calibration grid on the screen were rotated relative to each other, we transformed all eye positions into head-centered coordinates for data analysis. Note that although the degree of head tilt (30°) was not the same as the spacing of saccade directions (45°), this difference does not constrain the interpretation of the results (see below, also Fig. 1C). The head tilt implements an experimental condition that misaligned world and head axes and induces differences in vestibular and body-related signals. During data analysis we accounted for this as explained below.

Analysis of TEOAEs

The microphone signals were converted to mPa sound pressure based on the amplifier settings and the specifications of the in-ear probes provided by the manufacturer. The signals were high-pass filtered at 600 Hz and epoched around the individual clicks in windows of -25 to 30 ms. Epochs whose standard deviation exceeded 1.7 the standard deviation of the collective data across all epochs were discarded. To obtain an estimate of the noise level in the signal, we extracted the same number of epochs from randomly selected periods in between clicks (termed ‘baseline epochs’), which were devoid of any acoustic stimulus or response of the auditory system (ensuring a distance of >50 ms from each click). We then analyzed the TEOAE and baseline epochs in the frequency domain. For this we calculated average signal power between 600 to 5000 Hz in steps of 66Hz across epochs (FFT with Hanning taper, zero-padded to the next power of two). For each participant we then computed the difference in signal power between clicks and baseline, to obtain an estimate of the effective TEOAE in the frequency domain. This TEOAE spectrum was obtained separately for each block (considering only the non-noise ears). For each ear, we then compared the group-level spectra between blocks without and with suppression (see below). To summarize the TEOAE signal amplitude, we integrated the difference between signal and baseline spectra between 576 Hz and 1856 Hz for each channel and participant (shown in Fig. 2B; insets).

Analysis of saccade characteristics

To ensure that the saccades driving the EMREOs in the different experimental conditions are comparable in their characteristics, we extracted saccade duration and amplitude from the eye tracking data. We averaged these characteristics across trials within each participant, separately for each EMREO condition, and compared the resulting averages between conditions across participants (Fig. 5).

Analysis of EMREOs

For each participant we computed the epoch-averaged EMREO as in previous work (Sotero Silva, Kayser and Bröhl, 2025; Bröhl and Kayser, 2023). The microphone data were aligned to the detected onsets of the largest saccade observed in a 2 second period following the jump of the fixation dot. To avoid artifacts, we only included saccades whose amplitude was within the range 2 to 16° degrees, for which the initial fixation prior to the saccade was stable and for which the entire horizontal and vertical traces of the eye position were contained in an 18 x 18 degree window around the central fixation point. The resulting data epochs were z-scored and screened for extreme values: epochs for which the maximal z-score of the EMREO signal at any point in time exceeded 4.5 SDs of the overall signal were discarded. For each ear, we averaged the epochs separately for saccades to the left or right (Experiment 1) or for saccades in each of the four cardinal directions in head coordinates (Experiment 2). We then visually inspected the resulting epoch-averaged EMREO time courses and excluded participants with noisy or flat EMREOs from subsequent analysis. Based on these criteria we retained data from 31 participants for each task.

For the suppression experiment, we asked whether the EMREO time course at any point differs significantly with the presence or absence of the contralateral suppression noise. We performed this comparison separately for the EMREOs induced by saccades to the left and right, given the known difference in EMREO time course for saccades in different directions, and separately for each ear. For this we calculated for each block the epoch-averaged EMREO for all saccades oriented to the left or right, regardless of the starting point of the saccade (center or one of the eccentric positions). This analysis was based on an average of 373 ± 16.6 (mean, s.e.m.) epochs per participant (reflecting about 80% on average of the recorded data epochs). The statistical analysis was based on a within-participant comparison of conditions using randomization statistics (see below). To summarize the EMREO data, we extracted the average EMREO amplitude around the first main peak (5 to 15 ms) for each participant, ear and saccade direction (Fig. 3, insets). To correlate the suppression effect in the EMREO amplitudes with that in the TEOAEs we further averaged these amplitudes for each participant and ear across saccade directions, adjusting for the difference in EMREO sign for saccades to ipsi- and contralateral directions.

The data from the head-tilt experiment were analyzed in two ways. First, we focused on the EMREOs induced by saccades along the four cardinal axes of the head (left, right, up, down in head coordinates) and tested whether these are affected by changes in head tilt (Fig. 4). For this we computed the epoch-averaged EMREOs for saccades aligned with the cardinal directions along the head by selecting, for each direction and participant, all saccades whose direction was aligned with the respective cardinal direction in an angular window of ± 10°. This was the case for a subset of the saccades and this analysis was based on 503.6 ± 11.9 (mean, s.e.m.) data epochs per participant (reflecting about 70% on average of the recorded data epochs). We then contrasted these EMREOs between the different head tilts. Since the experiment comprised three conditions (no tilt, head-tilt to the left and right) this amounts to a large number of statistical contrasts (2 ears x 4 saccade directions x number of statistical comparisons between conditions x number of time points to be compared). To simplify this, we visualize and describe the data from all three conditions but based the statistical analysis on the comparison of the two head-tilts only. We hence effectively asked, for each ear and saccade direction, whether the EMREO time course differs between tilting the head to the left or right. This statistical analysis was based on a within-participant comparison of conditions using randomization statistics (see below).

In a second analysis we used a regression model to capture the influence of saccade direction and amplitude on the EMREOs, similar to previous work (Abbassi et al., 2025; Bröhl and Kayser. 2023; Lovich et al., 2023a, 2023b; King et al., 2023; Gruters et al., 2018). In those studies, it was shown that the EMREO deflection for any saccade can be predicted based on the vertical and horizontal amplitudes and directions of a saccade. Implementing such a regression model allowed us to include all data epochs in the analysis, regardless of the precise saccade direction, and allowed capturing the combined influence of both horizontal and vertical saccade properties and of the tilt manipulation on the EMREO time course in the same analysis. This analysis was based on 527.7 ± 14.1 (mean, s.e.m.) data epochs per participant.

We implemented this regression model based on the saccade properties encoded in head-directions, using the following formula, where Sx and Sy reflect the horizontal and vertical saccade amplitude (including its sign) and tilt the experimental block (coded as -1, 0, +1) and t denotes the time point during the EMREO:

$$\text{EMREO}(t) \sim Sx + Sy + Sx*tilt + Sy*tilt + tilt \qquad \text{(e.q.1)}$$

We fit this model separately for each participant, including the data epochs from all three blocks. We then extracted the slopes of each predictor, the overall explained variance (R2) of the model, and the model Akaike Information Criterion (AIC). The group-level slopes and associated errors are shown in Figure 6. To quantify the relevance of individual predictors, and to test whether head tilt adds explanatory power to the model, we also computed reduced models that omitted each particular predictor of interest (i.e. Sx, Sy or tilt). From these we derived the unique variance explained by each predictor, defined as the difference in the variance explained by the full and the respective reduced model (Abbassi et al., 2025; Bröhl and Kayser. 2023; Lovich et al., 2023a, 2023b; King et al., 2023; Gruters et al., 2018). We also computed the participant-summed AIC values for each model to compare the model-predictive power of each predictor.

Statistical testing

Group-level inference on the EMREO time courses, or the TEOAE spectra, was based on within-participant contrasts and cluster-based permutation tests controlling for multiple comparisons along the dimensions of interest (e.g. frequency for TEOAE spectra or time for EMREOs). First-level contrasts were based on paired t-tests (onetailed for the TEOAEs; two-tailed for EMREOs). The outcome of these first-level tests was thresholded at $p<0.05$ and the test statistic was aggregated across neighboring significant bins (computing the max-sum as cluster-forming statistics and requiring a minimal cluster size of 8 bins)(Nichols and Holmes, 2002). The resulting clusters in the actual data were compared to potential clusters in 10’000 sets of surrogate data, obtained after randomly flipping the effect-sign for each participant. Clusters with a second-level $p < 0.01$ were deemed significant. To report a measure of effect size, we report the associated effect size of the underlying within participants t-test (Cohen’s D).

Group-level inference on the EMREO regression analysis was based on the model evidence (AIC values) and the slopes of the individual predictors. To test whether head tilt provides explanatory power on the EMREOs, we contrasted the AIC values between the full model and the model excluding tilt and its interactions with saccades. We converted the difference in AIC values into Akaike model weights, which reflected the conditional probability of each model given the data (Wagenmakers and Farrell, 2004). To test whether individual factors were significant predictors, we relied on cluster-based permutation tests to test the slope of each factor against zero, correcting for multiple tests along time. Saccade characteristics were compared based on paired t-tests (for amplitude and duration).

When interpreting Cohen’s D effect size, we label effects around $d=0.2$ as small, effects around $d=0.5$ as medium and $d>0.8$ as large. When interpreting Bayes factors we follow the nomenclature of Raftery (1995): we consider BF below 3 as weak evidence, BF between 3 and 20 as positive, BF between 20-150 as strong, and BF above 150 as very strong evidence. Bayes factors larger than 1 indicate evidence that a given predictor adds predictive power, while values smaller than 1 indicate evidence against this hypothesis (Wagenmakers, 2007).

3. Results

TEOAE suppression

We analyzed TEOAEs and their suppression by a contralateral noise in the frequency domain. Fig. 2A shows the group-average TEOAE spectra obtained in silence for each ear. This reveals characteristic power above baseline between about 500Hz and 2 kHz, in line with known properties of TEOAEs (Francis and Guinan Jr, 2010; Morlet et al., 1999). Importantly, this TEOAE signal was significantly reduced during presentation of a contralateral noise (Fig 2B). For the left ear, the suppression was significant between 640 and 1536 Hz (n=31 participants; permutation test, controlling for multiple comparisons along frequency bins; p=0.0001) with a large effect size (Cohen's d=0.82); for the right ear it was significant between 576 and 2048 Hz (p=0.0001) with medium to large effect size (Cohen's d=0.60). The insets in Fig 2B show the participant-wise frequency-averaged suppression values (group-level mean ± SD: right ear 1.22 ± 2.28; left ear 0.9 ± 1.22), showing that some individuals showed suppression of up to 5 dB.

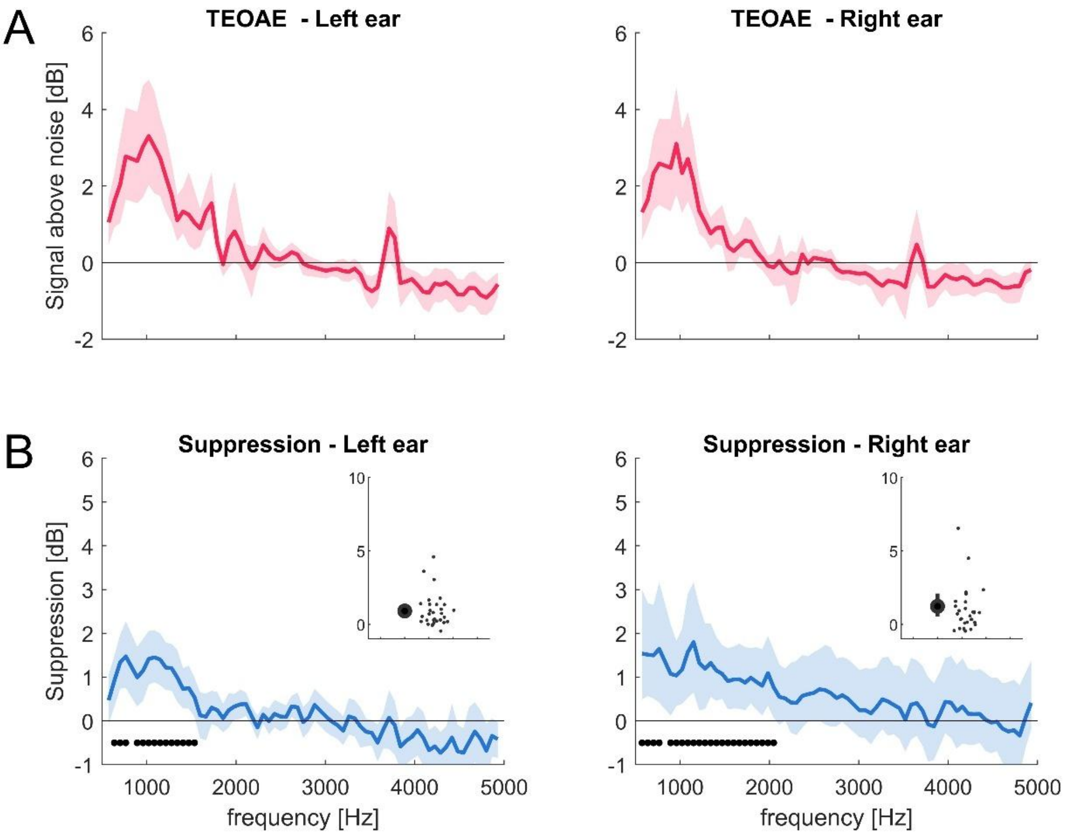

Fig 2. Suppression of TEOAEs. (A) Average TEOAEs spectra above noise for both ears as a function of frequency (pink). Lines indicate group-mean and 95th percentile bootstrap confidence interval (n=31). (B) Average TEOAE suppression for both ears (blue). Black dots indicate statistically significant suppression (cluster-based permutation test; p<0.01). Insets indicate the frequency-averaged suppression values, showing the group mean and s.e.m. and the data for individual participants (dots).

No effect of suppression noise on EMREOs

In experiment 1 we recorded EMREOs for horizontal saccades to the left and right. The EMREO time course followed the previously described pattern, with opposing deflections in the same ear for saccades to opposing directions and lasting about 80 ms (Fig 3A,B; ‘Silence’). We then tested whether the EMREO time course is altered by the presence of a contralateral noise (Fig 3A,B, ‘Noise’). A statistical comparison revealed no significant differences for either ear or saccade direction (n=31 participants; at p<0.05; corrected for multiple tests along time). To interpret the observed condition-differences, the lower panels in Figs 3A,B show the associated effect sizes (Cohen’s d) for the within participant comparison of the two conditions. These effect sizes were below 0.5, reflecting small effects. The Bayes factors associated with underlying paired t-tests, at the time points of largest effect size, were also small and indecisive (left ear BF= 1.47 and 1.01; right ear: 0.65 and 1.22). We interpret this as the suppression having at best a small influence on the EMREO time course.

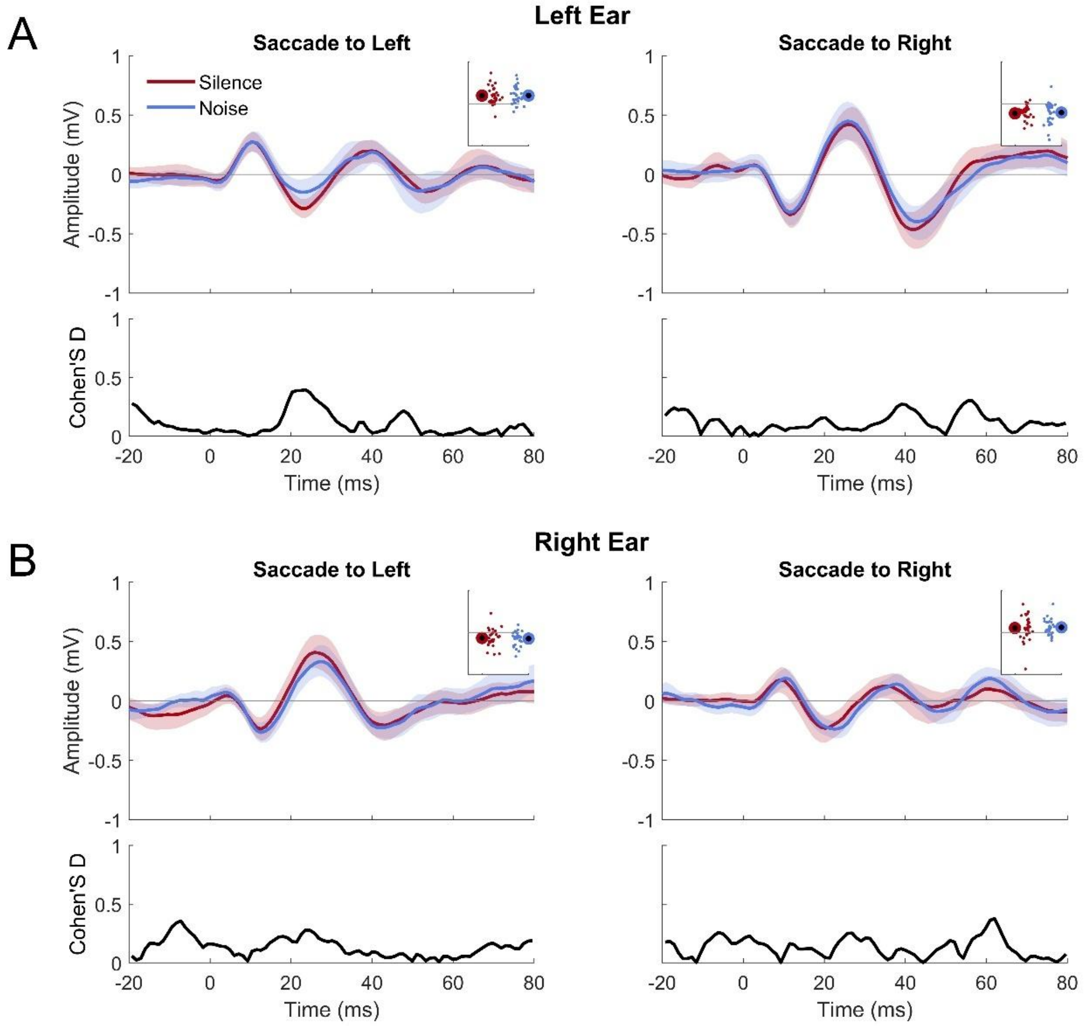

Fig 3. EMREOs for horizontal saccades in silence and with contralateral suppression. The upper panels show the group-average EMREO for the left (A) and right ear (B), split by saccade direction and conditions: saccades in silence (pink) and with contralateral suppression noise (blue). Lines indicate the group-average (n=31), shaded areas the 95th percentile bootstrap confidence interval. Insets indicate the EMREO amplitudes, showing the group mean and s.e.m. and the data for individual participants (dots). The lower panels show Cohen's d effect size (black) for the within participant comparison across conditions.

We also tested for an association between the suppression effect seen in the TEOAE and the difference in the EMREO amplitudes. For this we extracted the EMREO amplitude around the initial peak and computed the condition-difference for each ear (mean ± SD: right ear 0.045±0.123; left ear -0.002±0.161). Across ears (n=62) the correlation between the TEOAE and EMREO condition differences were not significant (rho=0.04, p=0.74).

Analysis of saccade properties

Since the EMREOs are shaped by the duration and the amplitude of the inducing saccade we analyzed the saccade properties for the different experiments and conditions. This was to ensure that there are no differences in saccade parameters that may confound the main comparisons of EMREOs. Fig 4A shows the saccade amplitudes and durations characteristics for the two conditions in the suppression paradigm and Figs 4B, C for the Head tilt experiment.

For the suppression paradigm the statistical tests (ANOVA) revealed no significant effects of condition on either the saccade amplitude (n=31 participants; F(60)=0.102, p=0.750) or duration (F=0.144, p=0.705). For the head tilt experiment this revealed no effect of saccade direction (n=31 participants; F(113)=3.40, p=0.067) and no effect of condition on saccade amplitude (F=3.62, p=0.06). Saccade durations did differ between saccade directions (F=8.99, p=0.003) but not between conditions (F=1.155 p=0.21). Hence, overall saccades did not differ between the two tilt conditions. Fig 4D shows the average saccade landing points in the head tilt experiment for each participant and condition. This reveals a rotation of the end points with the orientation of the head, as expected given the experimental manipulation. However, as observed in a previous study, the resulting distribution of end points does not completely follow the head rotation and reveals larger variability and a compression along the vertical direction (Reeves et al., 2022).

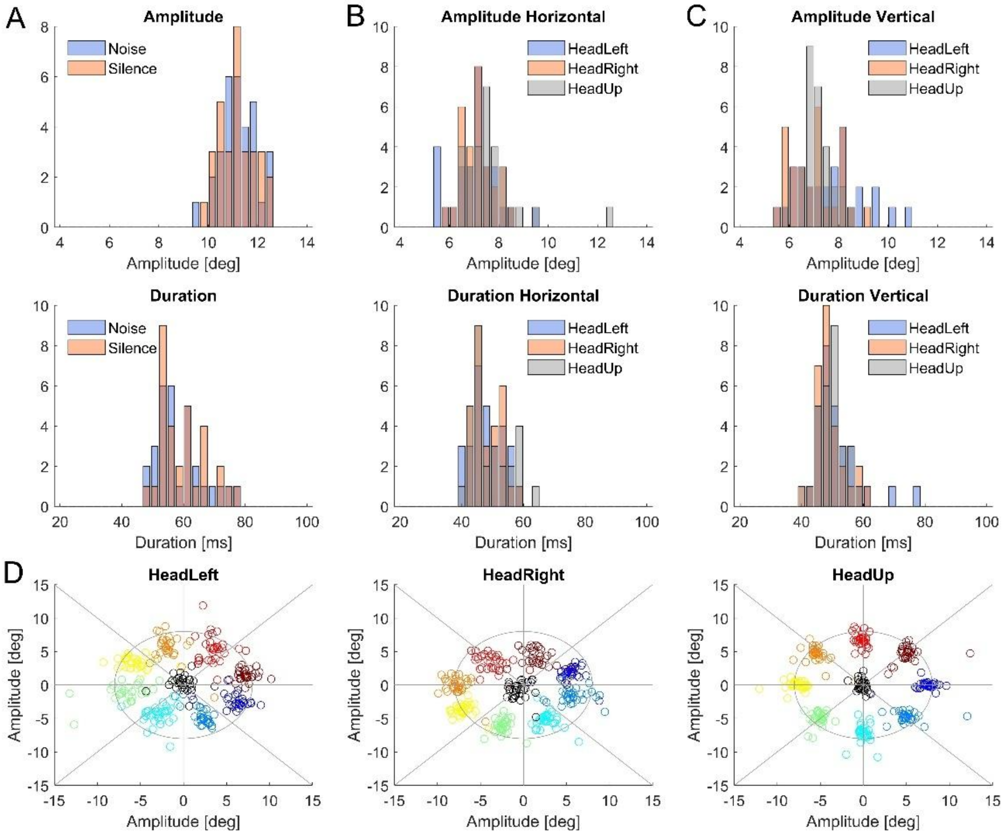

Fig 4. Saccade properties. Participant-wise saccade amplitudes and durations in the different conditions for each paradigm. Panel (A) shows the noise (blue) and silence (orange) conditions for the suppression paradigm. Panels (B) and (C) show the head left (blue), head right (orange) and head up (gray) conditions for in the head-tilt paradigm. Panel (D) shows average saccade end points in head coordinates in the head tilt paradigm (n=31).

EMREOs are not affected by head tilt

For the head tilt task, we analyzed the EMREOS for saccades along the cardinal directions of the head (left, right, up and down) across three conditions (Head Up, Head Left and Head Right). Fig 5 shows the group-level EMREOs for each saccade direction, condition and ear. The time courses for the two horizontal directions reflect the opposing EMREO deflections seen in the suppression paradigm above. The EMREOs for the two vertical directions revealed also consistent modulations but with smaller deflections in line with previous studies (Bröhl and Kayser, 2023; King et al., 2023; Lovich et al., 2023).

To test for an influence of head tilt on EMREOs, we contrasted these time courses between the two tilt conditions (tilt left vs. tilt right), separately for each ear and saccade direction. This revealed no significant differences (n=31 participants; at p<0.05, corrected for multiple comparisons along time points). Similar as for the suppression paradigm, the associated effect sizes (Cohen's D) were generally small and reached medium effect size only for a few time points (Fig. 5, lower panels). To further illustrate this influence of head tilt on EMREOs, Fig. 5 insets show the participant-wise EMREOs amplitude for each condition, ear and saccade direction.

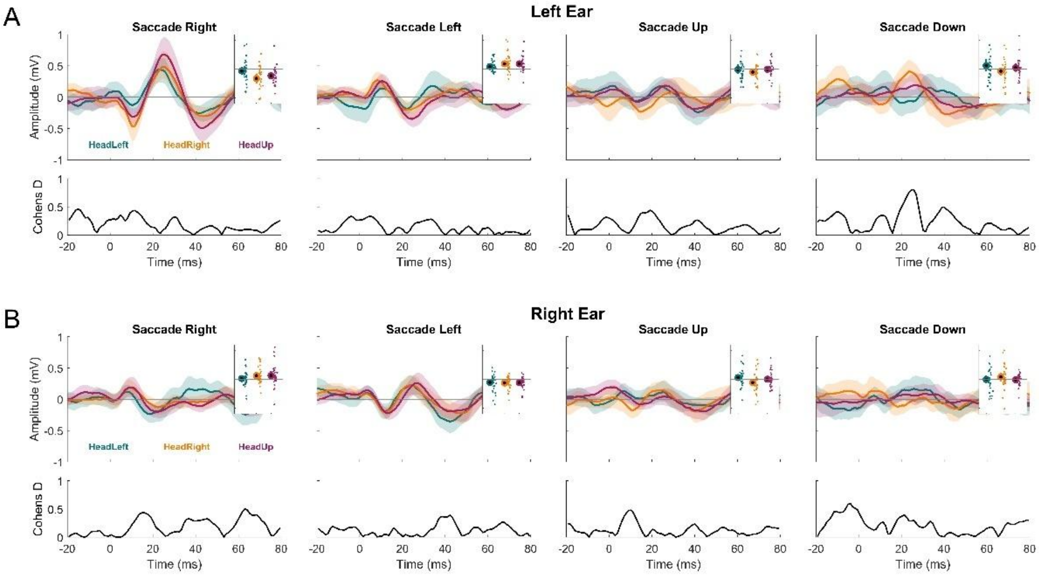

Fig 5. EMREOs in the head-tilt task. The upper panels show the group-average EMREO for the left (A) and right ear (B), split by saccade direction and conditions: head left (green), head right (orange) and head up (red). Lines indicate the group-average (n=31), shaded areas the 95th percentile bootstrap confidence interval. Insets indicate the EMREO amplitudes, showing the group mean and s.e.m. and the data for individual participants (dots). The lower panels show Cohen's d effect size (black) for the within participant comparison across conditions.

In a second analysis, we used regression models to predict the EMREO time course based on the horizontal and vertical saccade amplitude and the head-tilt condition. Fig 6A shows the explained variance of the full regression model. This explained considerable variance, in particular around the major deflections in the EMREO between about 5 and 50 ms as shown previously (Bröhl and Kayser. 2023;

Lovich et al., 2023a, 2023b; King et al., 2023). To determine the specific contribution of each model predictor, we computed the unique variance explained by these. This revealed that the horizontal saccade component explained by far the most unique variance, and much less variance was explained by the vertical component (Fig.6A): averaged across ears and the first 50ms following a saccade, the unique variance explained by the horizontal component was 0.0117±0.0019 (mean ± s.e.m.), that of the vertical component only 0.0014±0.0004.

Importantly, also the tilt condition and its interactions with the saccade components explained very little variance (tilt x horizontal: 0.0016±0.0003 tilt x vertical: 0.001±0.0003; tilt 0.0007±0.0006). For statistical analysis we tested the significance of each model predictor. This revealed multiple clusters of significant time points for the horizontal component (Fig. 6B; all $p<0.001$) but no significant effects for the vertical component, the tilt or the interactions of tilt and saccade properties (Fig. 6B,C; at $p<0.05$). Last, we used a model comparison to probe whether knowledge about the tilt condition allowed better predicting the EMREO. This revealed overwhelming evidence that the regression model without tilt explained the EMREO better than a model including tilt (difference in AIC scores: 171.1, Akaike weight of model without tilt ~ 1). All in all, this provides converging evidence that the EMREOs were not affected by the manipulation of head tilt.

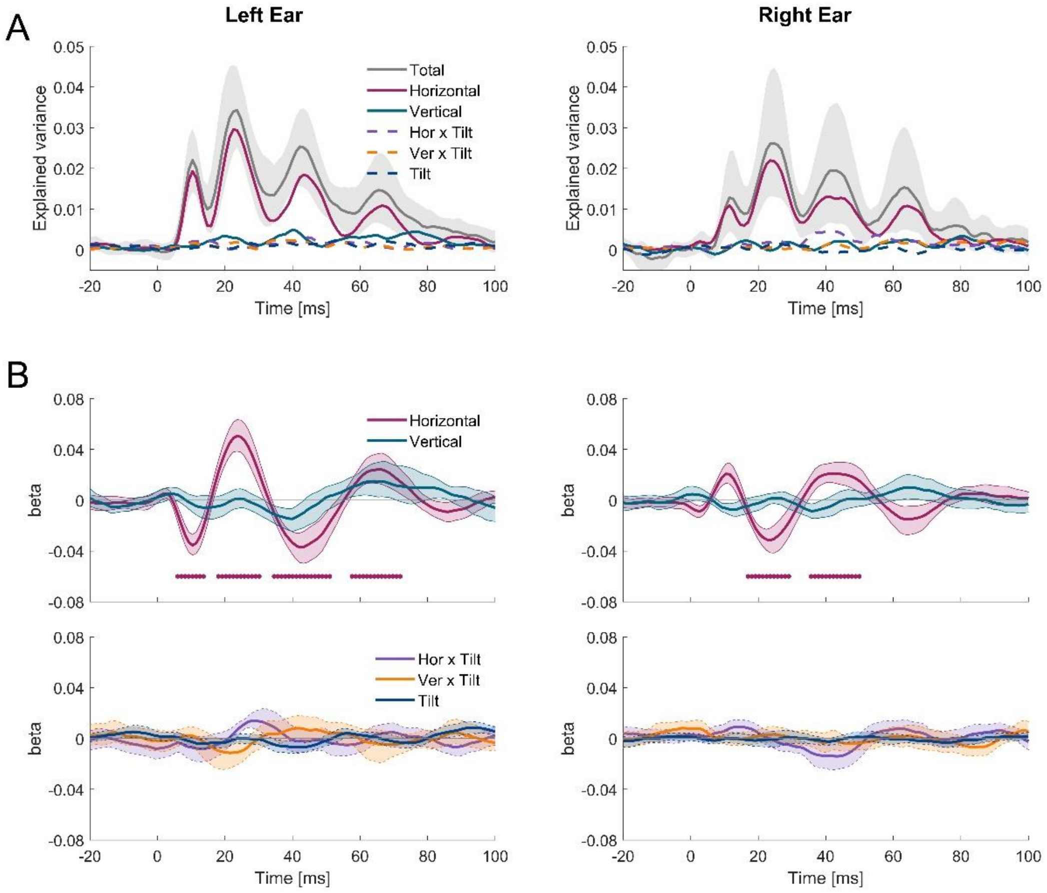

Fig 6. Regression analysis of EMREOs for the Head tilt task. (A) Total variance explained by the full regression model (black) and unique variance explained by individual predictors for ERMEOs in each ear (n=31). (B) Upper panels show the slopes for the predictors of horizontal (red) and vertical (blue) saccade components. Lower panels show the slopes for tilt condition (green) and its interactions with either the horizontal (yellow) and vertical (purple) saccade components. Black bars indicate statistically significant suppression (cluster-based permutation test; p<0.01). Lines indicate the group-average time course is and shaded areas the 95th percentile bootstrap confidence interval.

4. Discussion

While EMREOs have been reported in a number of studies, their properties and the underlying neural pathways giving rise to this phenomenon remain unclear. We here tested for an effect of two experimental manipulations that are known to either influence cochlear activity or which are likely to alter body- and oculomotor-related feedback signals to the ear, and hence could possibly influence the EMREO phenomenon. However, neither the presentation of a contralateral suppression noise, which reduced TEOAEs, nor tilting the head by a significant amount, induced clear and significant changes in the EMREO time course. All in all, this suggests that the EMREO signal reflects a robust and temporally stable signal.

Known properties of EMREOs

The first systematic description of the EMREO phenomenon was made based on recording in humans and monkeys in silence in 2018 (Gruters et al., 2018). Since then, several studies have corroborated this phenomenon and have described a number of properties of the EMREO signal recorded in the ear canal that we summarize in the following.

EMREOs emerge for saccades in all directions (i.e., for the horizontal, vertical and diagonal dimensions; Gruters et al., 2023; Lovich et al., 2023b; King et al., 2023) but the EMREO signal is more reliable and more strongly modulated for horizontal compared to vertical saccades (King et al., 2023; Lovich et al., 2023b). The amplitude and the time course of vertical EMREOs shows higher inter-individual variability, and shows no reliable pattern of phase opposition compared to horizontal saccades (King et al., 2023). Our data corroborate this observation as they reveal a stronger EMREO amplitude and a more pronounced temporal structure for horizontal compared to vertical saccades (c.f. Fig. 5). The interpretation of this difference in EMREO properties for horizontal and vertical saccades remains unclear, and requires further investigation.

The EMREO for horizontal saccades is more time-locked to saccade onset than to offset (Gruters et al., 2018; Lovich et al., 2023b; King et al., 2023) and generally comparable in the left and right ears (Gruters et al., 2018, Sotero Silva et al., 2025). However, within each ear, the EMREO time course differs for saccades to targets ipsi- and contralateral to the ear under study, and the signal starts with deflections of opposing signs for the two saccade directions. Although this results in a pattern of apparent phase-opposition between saccade directions, the eardrums in the two ears don’t move in strict antiphase for a given saccade: accounting for the difference in EMREO sign between saccades to ipsi- and contralateral targets still leaves a significant difference in the signal time course between saccade directions (Sotero Silva et al., 2025). Hence, for any given horizontal saccade, the underlying movements of the tympanic membranes in the left and right ears differ, resulting in a net-difference between the state of the two eardrums over time.

Still, across all saccade directions the EMREO signal can be modelled based on knowledge of the saccade target (King et al., 2023; Lovich et al., 2023a; Lovich et al., 2023b). Our regression analysis directly corroborates this, but also suggests that the horizontal saccade amplitude is a more reliable predictor of the EMREO amplitude compared to the vertical saccade amplitude. The observation of this relation between saccade properties and EMREO led to the suggestion that the EMREO signal may reflect some form of spatial coordinate transform between eye and ear centered maps, possibly playing a role in coordinating the encoding of multisensory signals (King et al., 2023; Lovich et al., 2023a; Gruters et al., 2018). However, the accuracy of such a coordinate transformation remains unclear, given that the scaling of EMREO amplitude with saccade eccentricity does not seem to be linear (King et al., 2023).

While many studies recorded EMREOs during visually-guided saccades, EMREOs also emerge during free-viewing (Lovich et al., 2023b), auditory-guided saccades (Sotero Silva et al, 2025), in darkness (Leon et al., 2026; Abbasi et al., 2025) and with the eyes closed (Leon et al., 2026). The EMREO time course appears very similar during free-viewing and auditory induced saccades compared to visually-guided saccades (Lovich et al., 2023b, Sotero Silva et al., 2025), suggesting that the EMREO phenomenon is tied to the execution of a saccade and not the specific sensory signal or goal driving the motor command. This is also supported by a study reporting that a visual cuing signal prior to a saccade was successful in increasing perceptual sensitivity, but not changing the EMREOs (Bröhl and Kayser, 2023), and by studies showing that the EMREO signal is not affected by concurrent acoustic stimuli that are not serving as saccade targets (Gruters et al., 2018; Bröhl and Kayser, 2023).

Given that the eardrums in the left and right ears move largely in opposite directions but not in strict antiphase, studies have asked whether this relative movement of the two eardrums has a consequence for auditory perception. One study tested this for a task requiring participants to detect a faint click presented before, during or after the saccade. However, this found no impact of the sound-to-EMREO relation on detection performance (Bröhl and Kayser, 2023). A second study tested participants' ability to judge the relative horizontal position of two tones, one of which was presented at different time points during the EMREO. However, also in this task, which required participants to exploit spatial acoustic information, there was no significant influence of the timing of the sounds relative to the EMREO time course on behavioral performance (Sotero Silva et al, 2026). Hence while the emergence of EMREOs is a very robust phenomenon, its relation to hearing or perception in general remains elusive.

Similar to the potential impact of EMREOs on perception, also their origin remains unclear. Prominent candidates include the outer hair cells and the middle ear muscles. However, their specific contribution to the EMREO signal remains to be elucidated. The motivation of the present study was that interfering with their normal function, or otherwise stimulating the pathways activating these, should also modulate the EMREO signal. However, as discussed in the following this was not the case.

EMREOs and outer hair cells

In the first experiment, we tested whether inducing the medial olivocochlear reflex (MOCR) would affect the EMREO signal. During the MOCR, the contralateral presentation of a noise reduces OHC activity in the opposite ear and this reduces the amplitude of transient otoacoustic emissions (TEOAEs). In our data, this suppression was prominent between about 550 and 2048 Hz in the frequency domain. This is consistent with previous studies showing that the MOCR is most prominent at the low frequency end of the human hearing spectrum (Francis and Guinan Jr, 2010; Morlet et al., 1999). The average TEOAE suppression was between 0.9 dB (left ear) to 1.22 dB (right ear), values that are comparable to reports in the literature (Lauer et al., 2022; Jedrzejczak et al., 2021, Veuillet et al., 1999; Berlin et al., 1993). Interestingly, our data also reflect a slight asymmetry between ears, with higher suppression in the right compared to the left ear, again consistent with previous work (Urnau and Tochetto, 2012; Mor and Azevedo, 2005; Morlet et al., 1999; Khalfa et al., 1997).

The suppression of OAEs by contralateral noise seems robust to changes in task context, such as during performance of an additional visual task (Jedrzejczak et al., 2020, 2017). However, large changes in gaze direction were reported to modulate the degree of contralateral suppression of TEOAEs (Soi et al., 2012). This points to an influence of oculomotor related signals on the medial olivocochlear system mediating the suppression. Thus, if the EMREOs were generated by the same pathways giving rise to the suppression of OAEs by contralateral noise, one could speculate that the same suppression should also affect the eye movement-related signals emanating from the ear, such as EMREOs. However, our data do not support this.

In fact, the same noise that consistently reduced TEOAEs did not significantly affect the EMREO time course. One interpretation is that this directly speaks against the OHC as the central effector producing the EMREO phenomenon. However, dissociating the influences of OHCs and MEMs is inherently difficult. Some studies suggest that also the product of OAEs as measured in the ear canal may reflect contributions from both the cochlea and the middle ear (Goodman et al., 2013; Goodman and Keefe, 2006). Data from patients shows that the stapedius reflex does not interfere with the contralateral suppression of TEOAEs, but cannot rule out contributions of the tensor tympani to this (Giraud et al., 1995). Hence while the data from the suppression paradigm support the notion that the EMREO signal is shaped to a strong part by the middle ear and not the OHCs, dissociating the contribution of different elements in the ear remains a challenge.

EMREOs and head-tilts

The oculomotor, auditory and vestibular systems are intricately connected and information about our head position profoundly contributes to the execution of saccades (Hikosaka and Maeda, 1973; Kobayashi et al., 1986). This includes the vestibulo-ocular reflex (VOR), which activates the eye muscles contingent on the head position (Higgins et al., 2023; Morimoto et al., 2011) and which can induce rotations of the eyes that compensate opposite movements of the head (Rucker, 2010). Vestibular information related to head, neck and body movements contributes to stability of gaze during movements (Reeves et al., 2022; Morimoto et al., 2011; Paloski et al., 2006). This information also reaches the auditory pathways (Carmel and Starr, 1964; Mukerji et al., 2010), where it presumably stimulates the MEMs motor neurons, shaping the acoustic reflex (Schneider and Mooney, 2018; Mukerji et al., 2010) and possibly modulating the EMREO. However, whether vestibular signals related to change in head tilt modulate the EMREO has not been studied before.

Our data support that EMREOs are robust to such a vestibular influence despite vestibular-ocular reflexes likely operating during the head tilt. While this finding does constrain our understanding of how OHCs or MEMs contribute to the EMREO, it raises questions about how the underlying processes could help in coordinating visual and auditory signals during natural free viewing.

5. Conclusion

The processes underlying the EMREO signal have been implicated in contributing to the coordination of spatial information between the visual and auditory senses (Lovich et al., 2023a). However, such a role seems only partially plausible given that the EMREO signal is shaped mostly by the direction of a saccade (ipsi- or contralateral to the ear under study) and not the precise amplitude (King et al., 2023), given that vertical EMREOs seem less reliable than horizontal ones and given that the position of the head is not factored in. A recent study now offers an alternative idea, speculating that the processes underlying the EMREO may serve more the temporal coordination of multisensory signals than the spatial coordination of these (King et al., 2026). In fact, it has long been known that both eye movements and visual stimuli shape rhythmic activity along the auditory pathways and temporally adjust the excitability of thalamic and cortical auditory regions (O'Connell et al., 2020; Kayser et al., 2008 Fu et al., 2004). One physiological mechanism underlying this form of temporal multisensory interaction is a phase reset of ongoing rhythmic activity, which supposedly serves to coordinate the temporal encoding of sensory signals between different senses (Obleser and Kayser, 2019; Schroeder et al., 2008). Intriguingly, rhythmic activity not only prevails in auditory cortical circuits but has recently been revealed in the ear itself (Gehmacher et al., 2022; Köhler et al., 2021) and exhibits similar attention-related multisensory effects as seen in cortical activity (Donoso-San Martín et al., 2024; Köhler and Weisz, 2023; Dragicevic et al., 2019). Hence one possibility is that the EMREO signal is reflecting neural processes that serve the temporal coordination of the encoding of multisensory signals. However, as other speculations about the EMREO phenomenon, this requires careful future work.

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Author contributions

NSS and CK Conceived and Designed research. NSS Performed experiments. NSS and CK Analyzed data, Interpreted results of experiments, Prepared figures, Drafted and Edited the manuscript. CK Revised and Approved final version of the manuscript.

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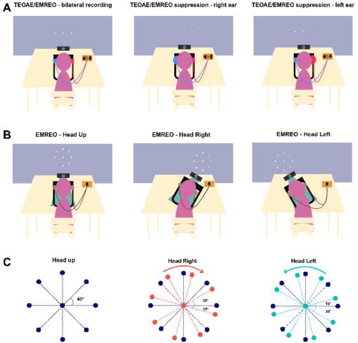
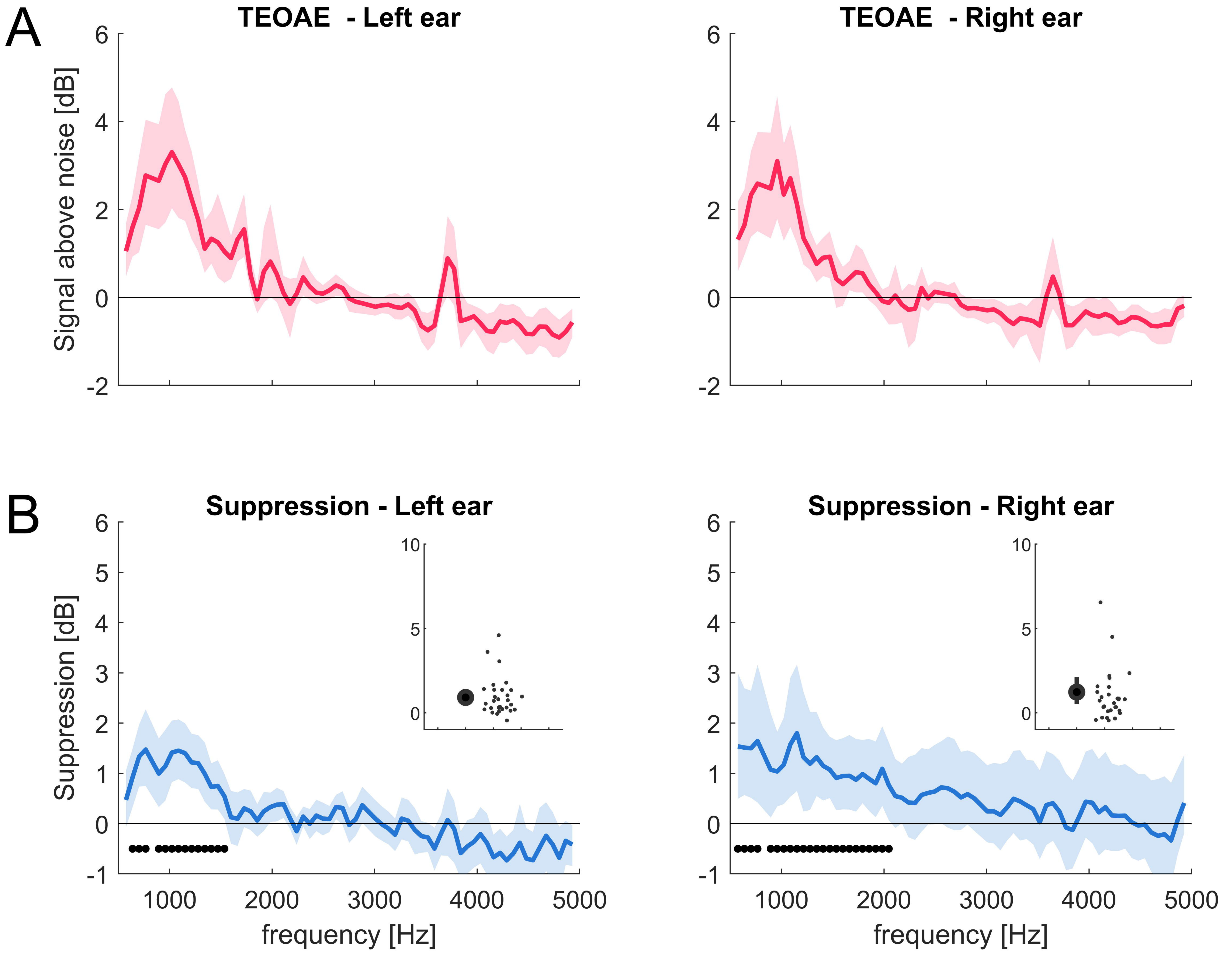
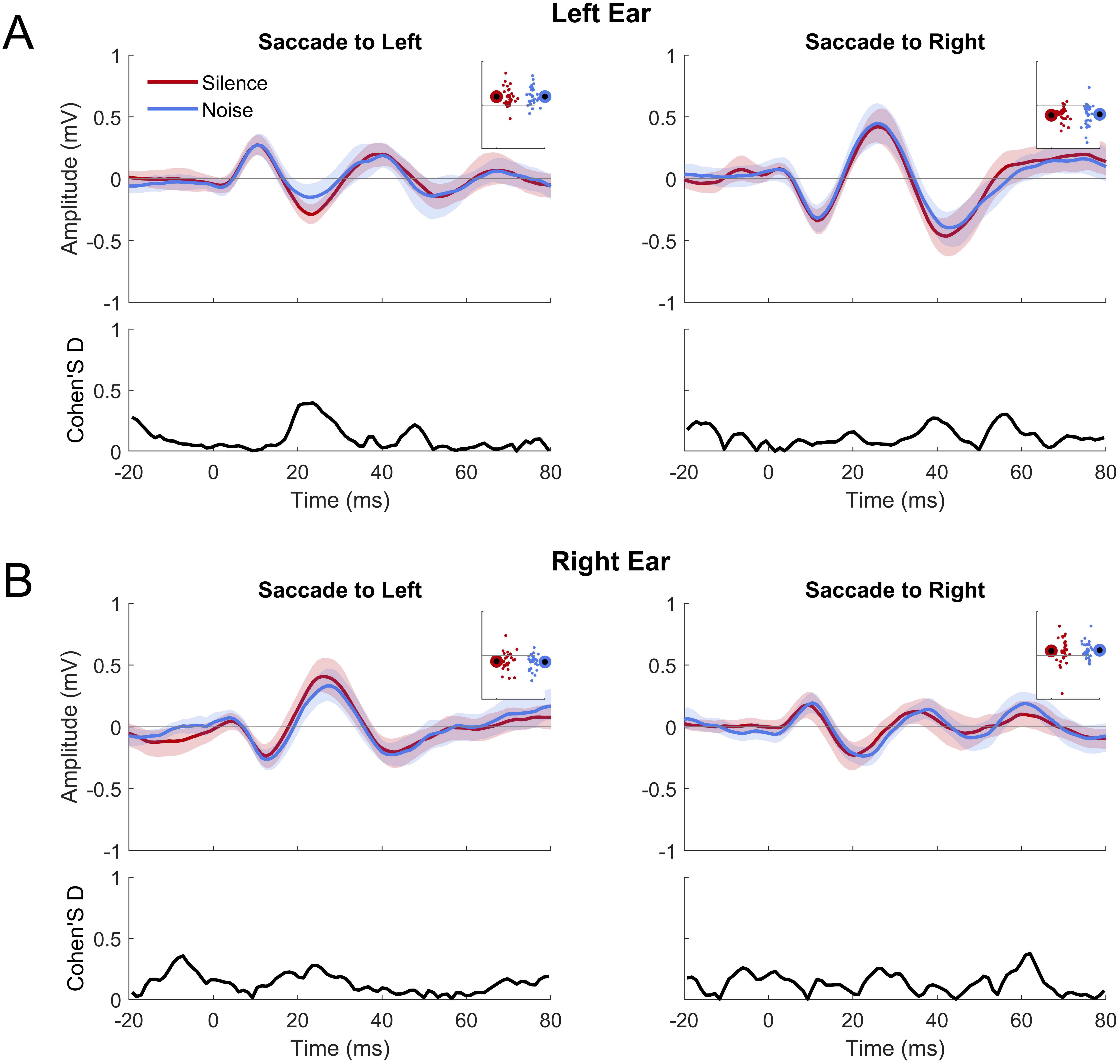
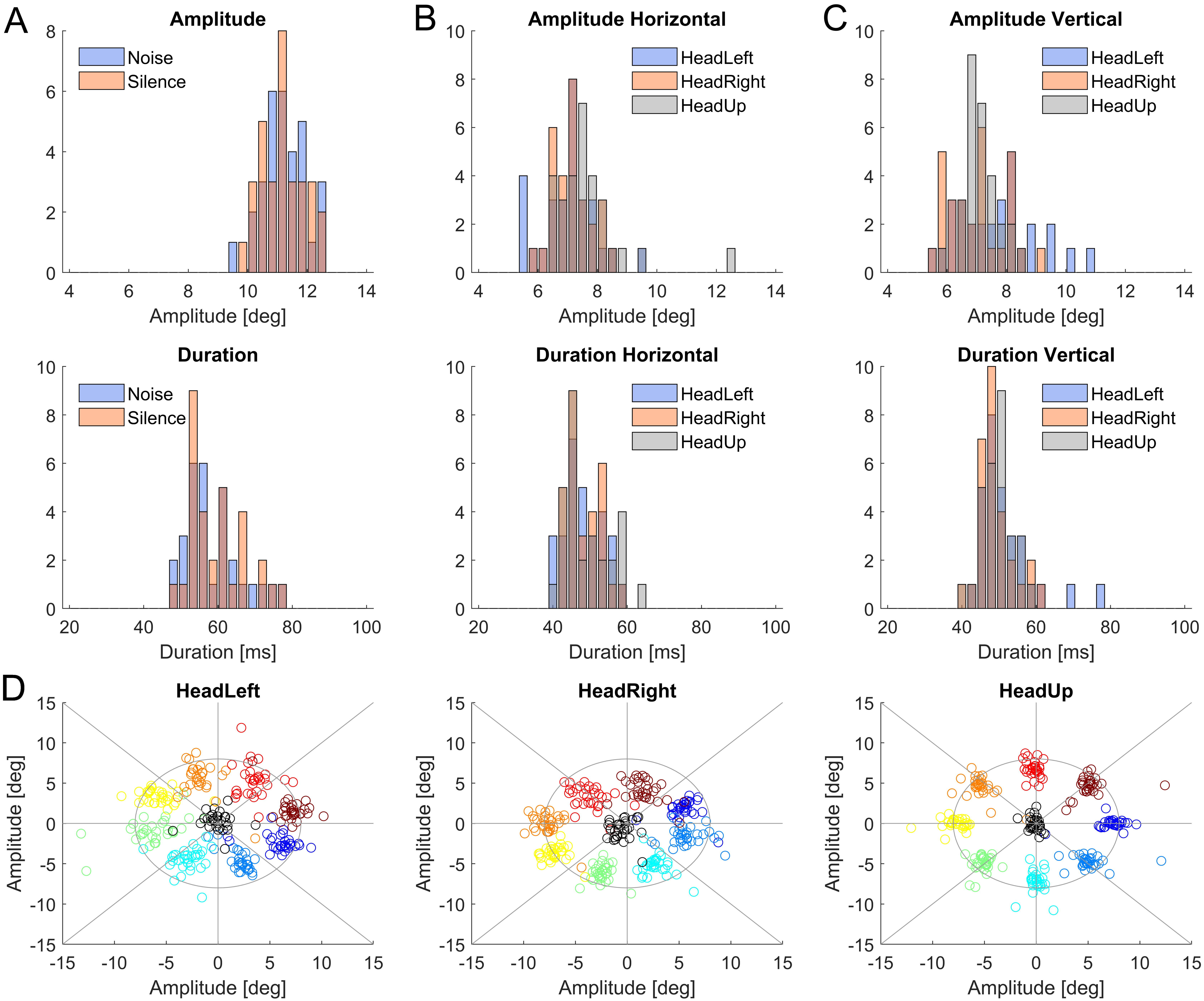
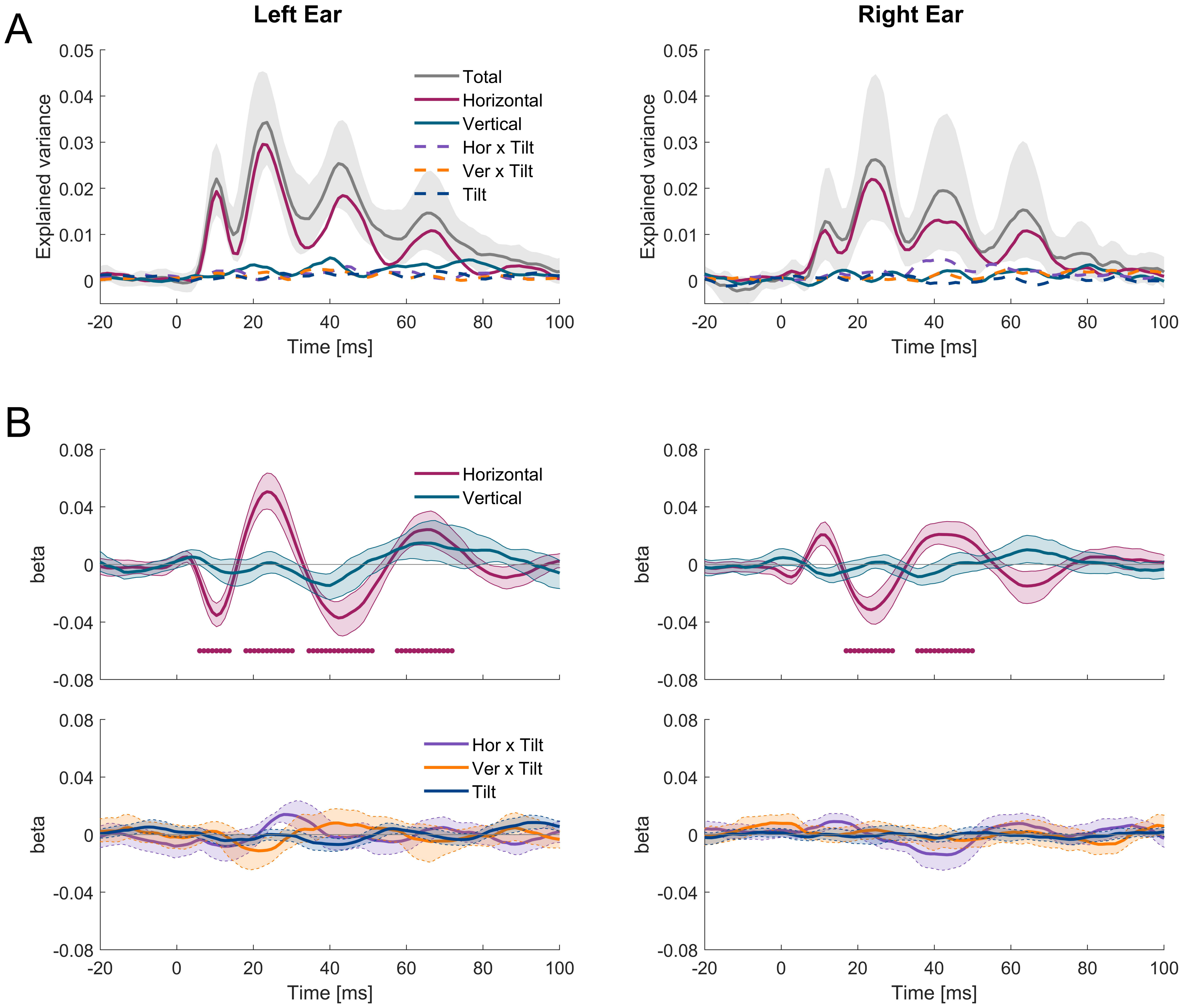

A
TEOAE/EMREO - bilateral recording
TEOAE/EMREO suppression - right ear
TEOAE/EMREO suppression - left ear
B
EMREO - Head Up
EMREO - Head Right
EMREO - Head Left
C
Head up
45°
Head Right
30°
15°
Head Left
15°
30°


A
TEOAE - Left ear
TEOAE - Right ear
Signal above noise [dB]
6
4
2
0
-2
B
Suppression - Left ear
Suppression - Right ear
Suppression [dB]
6
5
4
3
2
1
0
-1
10
5
0
1000
2000
3000
4000
5000
frequency [Hz]


A
Left Ear
Saccade to Left
Saccade to Right
Silence
Noise
Amplitude (mV)
1
0.5
0
-0.5
-1
Cohen'S D
Time (ms)
-20
0
20
40
60
80
B
Right Ear
Saccade to Left
Saccade to Right


A
Amplitude
Noise
Silence
Amplitude [deg]
B
Amplitude Horizontal
HeadLeft
HeadRight
HeadUp
Amplitude [deg]
C
Amplitude Vertical
HeadLeft
HeadRight
HeadUp
Amplitude [deg]
Duration
Noise
Silence
Duration [ms]
Duration Horizontal
HeadLeft
HeadRight
HeadUp
Duration [ms]
Duration Vertical
HeadLeft
HeadRight
HeadUp
Duration [ms]
D
HeadLeft
HeadRight
HeadUp
Amplitude [deg]
Amplitude [deg]

A
Left Ear
Saccade Right
Saccade Left
Saccade Up
Saccade Down
Amplitude (mV)
1
0.5
0
-0.5
-1
HeadLeft
HeadRight
HeadUp
Cohens D
1
0.5
0
-20
0
20
40
60
80
Time (ms)
B
Right Ear
Saccade Right
Saccade Left
Saccade Up
Saccade Down
Amplitude (mV)
1
0.5
0
-0.5
-1
HeadLeft
HeadRight
HeadUp
Cohens D
1
0.5
0
-20
0
20
40
60
80
Time (ms)


A
Left Ear
Right Ear
Explained variance
0.05
0.04
0.03
0.02
0.01
0
Total
Horizontal
Vertical
Hor x Tilt
Ver x Tilt
Tilt
-20
0
20
40
60
80
100
Time [ms]
B
beta
0.08
0.04
0
-0.04
-0.08
Horizontal
Vertical
Hor x Tilt
Ver x Tilt
Tilt
Time [ms]