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1 Direct cochlear recordings in humans show a theta 2 rhythmic modulation of auditory nerve activity by 3 selective attention

4 Attentional modulations of the human auditory nerve

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30 **Abstract**

31 The architecture of the efferent auditory system enables prioritization of strongly overlapping
32 spatiotemporal cochlear activation patterns elicited by relevant and irrelevant inputs. So far,
33 attempts at finding such attentional modulations of cochlear activity delivered indirect insights in
34 humans or required direct recordings in animals. The extent to which spiral ganglion cells
35 forming the human auditory nerve are sensitive to selective attention remains largely unknown.
36 We investigated this question by testing the effects of attending to either the auditory or visual
37 modality in human cochlear implant (CI) users (3 female, 13 male). Auditory nerve activity was
38 directly recorded with standard CIs during a silent (anticipatory) cue-target interval. When
39 attending the upcoming auditory input, ongoing auditory nerve activity within the theta range (5-
40 8 Hz) was enhanced. Crucially, using the broadband signal (4-25 Hz), a classifier was even able
41 to decode the attended modality from single-trial data. Follow-up analysis showed that the effect
42 was not driven by a narrow frequency in particular. Using direct cochlear recordings from deaf
43 individuals, our findings suggest that cochlear spiral ganglion cells are sensitive to top-down
44 attentional modulations. Given the putatively broad hair-cell degeneration of these individuals,
45 the effects are likely mediated by alternative efferent pathways as compared to previous studies
46 using otoacoustic emissions. Successful classification of single-trial data could additionally have
47 a significant impact on future closed-loop CI developments that incorporate real-time
48 optimization of CI parameters based on the current mental state of the user.

49 *Keywords:* auditory, auditory nerve, cochlear implants, lateral olivocochlear complex, LOC,
50 selective attention, top-down

51 **Significance Statement**

52 The efferent auditory system in principle allows top-down modulation of auditory nerve activity,
53 however evidence for this is lacking in humans. Using cochlear recordings in participants
54 performing an audiovisual attention task, we show that ongoing auditory nerve activity in the
55 silent cue-target period is directly modulated by selective attention. Specifically, ongoing
56 auditory nerve activity is enhanced within the theta range when attending upcoming auditory
57 input. Furthermore, over a broader frequency range, the attended modality can be decoded
58 from single-trial data. Demonstrating this direct top-down influence on auditory nerve activity
59 substantially extends previous works that focus on outer hair cell activity. Generally, our work
60 could promote the use of standard cochlear implant electrodes to study cognitive neuroscientific
61 questions.

62 Introduction

63 Attention describes a process by which sensory information can be prioritized. For all sensory
64 modalities common spatiotemporal cortical activity patterns have been reported, suggesting
65 modality-independent mechanisms to select or ignore features by alterations of oscillatory
66 activity in the alpha (Frey et al., 2014; Mazaheri et al., 2014; Weise et al., 2016) and beta band
67 (Buschman and Miller, 2007; Iversen et al., 2009; Lee et al., 2013). As the auditory system
68 comprises a unique complex subcortical network (Terrerros and Delano, 2015; Elgueda and
69 Delano, 2020), cochlear activity can in principle be altered by top-down signals from the auditory
70 cortex via only one extra relay through the superior olivary complex (SOC). However, studying
71 peripheral attentional mechanisms requires special recording and analysis techniques (Elgueda
72 and Delano, 2020) and has therefore been rarely investigated.

73 Noninvasively, evidence in humans comes from studies on otoacoustic emissions (OAEs),
74 sounds that are generated by outer hair cell (OHC) activity in the cochlea. OHCs are modulated
75 by a pathway from the medial olivocochlear (MOC) system that itself originates in the superior
76 olivary complex (SOC). Spiral ganglion cells making up the auditory-nerve fibers are mainly
77 innervated by connections of the lateral olivocochlear complex (LOC) respectively (Warr and
78 Guinan, 1979; Elgueda and Delano, 2020). Attentional modulations of OAEs can thus be seen
79 as a proxy for subcortical attentional modulations via MOC synapses and have been connected
80 with low-frequency (<10 Hz) oscillatory mechanisms at the cochlear level during alternating
81 selective attention (Dragicevic et al., 2019), with increases in the theta band (~6 Hz) when
82 attending to upcoming auditory input during a silent cue-target interval (Köhler et al., 2021).

83 Further evidence for attention modulations of cochlear activity stems from direct recordings in
84 animals with chronically implanted round-window electrodes, showing decreased auditory nerve
85 action potentials to task-irrelevant click sounds during alternate states of visual attention in cats

86 (Oatman, 1971) and during selective attention in chinchillas (Delano et al., 2007). However,
87 whether *human* auditory nerve activity can be directly modulated via selective attention remains
88 unknown.

89 While direct recordings are normally not feasible in humans, cochlear implants (CI) provide a
90 unique opportunity for recording auditory nerve activity. Besides stimulating nerve fibers inside
91 the cochlea, conventional CI electrodes are used to measure short responses (~0.2-0.8 ms) to
92 biphasic pulses, so called electrically evoked compound action potentials (ECAPs), to assure
93 auditory nerve and device functioning during and after surgery (Miller et al., 2008; Ramekers et
94 al., 2014). However, the aforementioned effects of selective attention were reflected in slow
95 oscillatory activity <30 Hz, which cannot be measured with standard short-latency ECAPs.
96 Assuming as a working hypothesis that selective attention modulates human auditory nerve
97 activity in a similar frequency range, our approach appended short recording windows in a silent
98 cue-target period. This technique allows for discrete sampling of that period within a single trial
99 that can later be processed like standard electroencephalographic (EEG) recordings.
100 Interestingly, CI recipients lack the efferent MOC reflex that leads to cochlear dynamic
101 compression in normal hearing (Wilson et al., 2003; Lopez-Poveda et al., 2016; Marrufo-Pérez
102 et al., 2019). As they additionally show substantial degeneration of OHCs which are further
103 damaged during surgical implant insertion, proposed CI recordings during selective attention
104 should mostly reflect modulations of spiral ganglion cell activity via LOC connections (Lopez-
105 Poveda, 2018) rather than modulations of scattered OHC populations by residual MOC
106 efferents. This argument is strengthened by Liberman and Liberman (2019), who quantified
107 cochlear innervation density by MOC and LOC efferents, highlighting a general paucity of MOC
108 projections that dramatically increases with age whilst LOC populations remain unaffected by
109 this aging-effect.

Using an audiovisual crossmodal attention task adapted from Hartmann and Weisz (2019, see **Figure 1A**), we show that ongoing auditory nerve activity in a silent cue-target interval is modulated by focused attention using standard MED-EL CIs as recording devices (see **Figure 1B**). In addition to this average condition-level effect, we show that a classifier is even able to decode attended modality on a single-trial basis, which could have important implications for the use of conventional CIs in a closed-loop system.

Figure 1. Schematic illustration of the crossmodal attention task and CI recordings. (A) Each trial started with a fixation cross, followed by a cue indicating either to attend the visual or auditory domain. A second fixation cross appeared and an auditory and visual stimulus were presented afterwards. When the stimulus in the attended modality was deviant (visual: gabor patch tilt, auditory: oddball sound), participants had to respond by pressing the spacebar. The additional response time accounted for trials

122 where the gabor patch tilted towards the end of the stimulation. At the end of each trial, feedback was
 123 given in the form of a smiley face. The red line denotes the time window where auditory nerve activity was
 124 recorded via the CI. (B) Left: Participants were seated in front of a computer screen and were asked to
 125 remove their CI processor and coil to replace it with a coil connected to one of the ports of the MAX
 126 Programming Interface. Middle: Each recording window was 1.7 ms long, followed by a 13.68 ms reset
 127 period (three recordings of an exemplary participant are shown). Due to filter artifacts, the first 100
 128 samples from every recording window were discarded (shaded grey area in the recordings). Each
 129 recording was averaged and treated as one sample point. By concatenating these single samples, a
 130 recording length of 1 second with a sampling frequency (f_s) of 65 Hz was reached in every trial. Right:
 131 Single trials were averaged and spectral analysis was performed separately for the two conditions.

132 **Materials and Methods**

133 *Participants*

134 21 right-handed CI users (4 females, $M_{\text{age}} = 57.5$, $SD_{\text{age}} = 11.9$) participated in the study, all with
 135 a minimum CI experience of six months. Participants were recruited via the ear-nose-throat
 136 (ENT) departments of the hospitals in Salzburg ($n = 10$) and Wels-Grieskirchen ($n = 11$). Three
 137 participants were excluded because of a too weak contact between transmitting CI coil and
 138 receiver that was required for the study. One participant showed no N1 in recorded ECAPs,
 139 which could indicate a measurement problem and was therefore excluded. One participant quit
 140 during the session due to concentration problems. This led to a final sample size of 16
 141 participants (3 females, $M_{\text{age}} = 53.8$, $SD_{\text{age}} = 12.0$). All participants reported no previous
 142 neurological or psychiatric disorders, and reported normal or corrected-to-normal vision. All
 143 participants signed an informed consent and were reimbursed with 10 Euro per hour. The
 144 experimental protocol was approved by the ethics committee of the University of Salzburg and
 145 was carried out in accordance with the Declaration of Helsinki.

146 *Stimuli and experimental design*

147 The experimental procedure was implemented in MATLAB 8.6 (The MathWorks Inc., Natick,
 148 Massachusetts, USA) using custom scripts. Presentation of visual stimuli and response
 149 collection was achieved with a previous version (th_ptb; https://gitlab.com/thht/th_ptb) of the
 150 Objective Psychophysics Toolbox (o_ptb; Hartmann and Weisz, 2020), which adds an additional
 151 class-based abstraction layer in addition to the Psychophysics Toolbox (Version 3.0.14;
 152 Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). Cochlear stimulation as well as recording was
 153 performed via the MAX Programming Interface, a device which is part of the clinical standard
 154 setup that enables control of the implant, together with the Research Interface Box 2 Dynamic-
 155 link library (RIB2 DLL provided by the University of Innsbruck, Innsbruck, AT; Litovsky et al.,
 156 2017). To ensure accurate stimulus presentation and triggering, timings were measured with the
 157 Black Box ToolKit v2 (The Black Box ToolKit Ltd., Sheffield, UK).

158 Participants were seated in front of a computer screen and were asked to remove their CI
 159 processor and coil to replace it with a coil connected to the MAX Programming Interface. For
 160 bilateral CI users, the side with the better subjective hearing performance and/or longer
 161 implantation date was used. Primarily the CI coil model MAX Coil was used, but if the magnet
 162 was too weak to ensure a stable connection, the CI coil model MAX Coil S was used. As a first
 163 step, the individual electrical hearing threshold was determined with a standard tone with a
 164 stimulation frequency of 100 Hz and a duration of 300 ms. To ensure that the auditory
 165 stimulation was at a comfortable level during the experiment, the individual maximum loudness
 166 was determined, for the standard and an oddball tone respectively. An oddball tone with the
 167 maximum possible stimulation frequency of 9990 Hz (based on the used phase duration of 30
 168 μ s per phase for sequential biphasic pulses) and a duration of 300 ms was used. The described
 169 routines were implemented using custom scripts and the Palamedes Toolbox (Prins and
 170 Kingdom, 2018).

171 Afterwards, as a functionality check of the measurement setup, ECAPs were recorded (Bahmer
 172 et al., 2010). ECAPs were biphasic pulses (anodal polarity of the first pulse phase) with a 40 μ s
 173 phase duration and a 147 μ s interpulse interval. In each participant, the first (i.e. most apical)
 174 electrode was used for stimulation and the second for recording. Phase amplitudes and amount
 175 of ECAPs measured in each participant were defined between the minimum amplitude given by
 176 the electrical hearing threshold and the maximum amplitude given by the maximum loudness of
 177 the standard tone (phase amplitude: in steps of 9.45 current units (CU); amount: in steps of
 178 one).

179 For the crossmodal attentional task described later, it was necessary that two stimulation
 180 frequencies could be distinguished. Because of interindividual differences when hearing with a
 181 CI, it was necessary to adjust these stimulation frequencies for every participant. Participants
 182 were asked, after hearing a standard and oddball tone, if the first or the second tone had a
 183 higher stimulation frequency. The standard tone had a stimulation frequency of 100 Hz and a
 184 duration of 300 ms. The initial stimulation frequency of the oddball tone (also with a duration of
 185 300 ms) was determined by the results of the aforementioned maximum loudness procedure.
 186 This procedure was carried out using a Bayesian active sampling protocol to estimate the model
 187 parameters of the psychometric function (Kontsevich and Tyler, 1999; Sanchez et al., 2016) and
 188 was implemented with the VBA Toolbox (Daunizeau et al., 2014). To define the individual
 189 oddball stimulation frequency for the subsequent crossmodal attention task, the algorithm
 190 searched for the optimal difference in logarithmic steps from 1 to 9890 Hz and this value was
 191 subsequently added to the standard stimulation frequency. Six participants heard no clear
 192 difference and it was necessary to adjust the oddball stimulation frequency manually, with
 193 values between 114 and 600 Hz.

194 The actual experiment was carried out as a crossmodal attention task (see **Figure 1A**; similar to
 195 Hartmann and Weisz, 2019) in six blocks, with 85 trials per block. Each trial started with a 500

196 ms fixation cross, followed by a cue that indicated either to attend the auditory or the visual
 197 modality. Every block had 43 auditory and 42 visual cues. The cue was a picture of an eye or
 198 ear, presented for 500 ms. A second fixation cross appeared for 1000 ms and the audiovisual
 199 stimulation started afterwards. The auditory stimulation consisted of a 300 ms tone with a
 200 stimulation frequency of 100 Hz and was directly presented via the CI coil. The visual
 201 stimulation was a vertically oriented gabor patch (spatial frequency: 0.01 cycles/pixel, sigma: 60
 202 pixels, phase: 90°), presented for 1300 ms in the center of the screen. In every block, 8 trials
 203 were randomly chosen as visual oddball trials. Independently, another 8 trials were chosen to
 204 be auditory oddball trials. Therefore, it was possible that a trial was a visual and auditory oddball
 205 trial simultaneously. In visual oddball trials, the gabor patch tilted 10° to the left, with a random
 206 onset. In auditory oddball trials, a 300 ms tone with the individual oddball stimulation frequency
 207 was presented. Participants had to press the spacebar if the current trial had an oddball in the
 208 cued domain. To account for trials where the visual oddball onset was towards the end of the
 209 stimulation, an additional response time of 300 ms was provided. After each trial, feedback in
 210 the form of a smiley face displayed for 1000 ms, indicated if the response was correct or not. To
 211 ensure that participants understood the task and responded appropriately, they completed one
 212 block as a practice run before the actual experiment. The total duration of the experiment was
 213 about 90 minutes including breaks and preparation.

214 *Recording of auditory nerve activity*

215 We exploit the ability of CIs to record electrical activity from the cochlea in short time windows,
 216 but in contrast to previous approaches (Mc Laughlin et al., 2012; Abbas et al., 2017), in a silent
 217 cue-target period. Using a custom developed MATLAB toolbox to abstract MAX Programming
 218 Interface commands, we recorded auditory nerve activity via the CI electrode. In every
 219 participant, the first (i.e. most apical) electrode was used for the recordings. Each recording
 220 window was 1.7 ms long, followed by a 13.68 ms reset period resulting in a sampling frequency

of 65 Hz (see **Figure 1B**; 1.7 ms recording + 13.68 ms reset time). The sampling rate of each 1.7 ms recording window was 1.2 Mhz (i.e. 2048 sample points in each recording window). The technical specifics of the measurement system added a random offset to each of the recordings (Gaussian noise, $SD = 0.4$ mV). Because of the USB connection between the computer and the MAX Programming Interface, the start of the first recording window had a jitter of 27 ms, but the system sent a highly precise trigger when it started. Due to technical limitations, it was not possible to record and stimulate simultaneously. We performed recordings in the 1000 ms prestimulus window (see red line in **Figure 1A**).

Data preprocessing

The raw data was analyzed in MATLAB 9.8 (The MathWorks, Natick, Massachusetts, USA). Due to filter artifacts (using the standard filter from the used RIB2 package), the first 100 samples (= 0.083 ms) from every recording window were discarded. Afterwards, the recording was averaged and treated as one sample point. By repeating these steps for every window and concatenating the single samples, a recording length of 1 second with a sampling frequency of 65 Hz was reached. The data was further preprocessed with the FieldTrip toolbox (revision ea6897bb7; Oostenveld et al., 2010) and a bandpass filter between 4 and 25 Hz was applied (hamming-windowed sinc FIR filter, onepass-zerophase, order: 424, transition width: 0.5 Hz). For one participant, 15 trials had to be rejected because the CI coil fell off during the last trials of one block. Only trials with a correct response were analyzed, which were on average 488 trials ($SD = 15.8$). The number of correct trials was not significantly different between the two conditions (see Behavioral results).

Frequency analysis

Next, data was demeaned, detrended and power spectral density (PSD) from 4 to 25 Hz was computed on the whole 1000 ms prestimulus window ('mtmfft' implementation in FieldTrip with a

245 Hann window) separately for the two conditions. For **Figure 2A**, no bandpass filter was applied,
 246 condition-specific power spectra were smoothed (five-point moving average), grand-averaged,
 247 and corrected error bars for within-subjects designs were calculated (O'Brien and Cousineau,
 248 2014).

249 We defined two frequency bands of interest (FOI), theta (5-8 Hz) and alpha (9-13 Hz). Theta
 250 was selected because of previous work on OAEs that showed attentional modulations in this
 251 FOI (Dragicevic et al., 2019; Köhler et al., 2021). On a cortical level, previous work showed that
 252 auditory alpha activity reflects attentional processes (Weisz et al., 2011, 2014; Müller and
 253 Weisz, 2012; Frey et al., 2014; Mazaheri et al., 2014; Weise et al., 2016). Therefore, we
 254 decided to analyze this FOI at the cochlear level.

255 *Decoding analysis*

256 For decoding of attended modality on a single-trial basis, we performed k-nearest neighbors
 257 (kNN) classification of single-trial power spectra using scikit-learn (Version 0.23.1 running on
 258 Python 3.7.7; Pedregosa et al., 2011) separately for a broadband signal (4-25 Hz) followed by
 259 standard frequency bands associated with selective attention (theta: 5-8 Hz, alpha: 9-13 Hz,
 260 beta: 14-24 Hz). We decided to use the kNN classification approach as data was recorded from
 261 a single CI channel over a one second period resulting in low numbers of features (i.e.
 262 frequency points per band), a classification problem usually solved better by a kNN approach
 263 (Eisa et al., 2018).

264 At first, a subject's data was standardized to unit variance and zero mean. For the classification
 265 process of each subject, the best number of neighbors was determined by searching the hyper-
 266 parameter space for the best cross-validation (CV) score of a kNN model using the
 267 implemented *GridSearchCV* function with a 2-fold CV on shuffled class samples
 268 (*StratifiedKfold(shuffle=True)*) that was fit to the data for every FOI. Our decision for a 2-fold CV

269 was based on recommendations in case of low sample/effect size data (Jamalabadi et al.,
 270 2016). The numbers of neighbors to use during the gridsearch were defined as ranging from
 271 one to 10% of trials in the dataset in odd numbers (1, trials/10, stepsize=2) to avoid the conflict
 272 of even neighbors in a two-class problem (attend auditory vs. visual).

273 *Statistical analysis*

274 *Cluster-based permutation statistics of the power spectra*

275 To test the hypothesis that power was higher when the auditory domain was attended, statistical
 276 testing of PSD was performed with a cluster-based permutation test (dependent samples t-test,
 277 10000 randomizations, one-tailed; Maris and Oostenveld, 2007). We averaged the theta and
 278 alpha FOI and tested them separately.

279 *Decoding analysis statistics*

280 Given the novel approach, we could not exclude that the classifier would pick up on a few
 281 outlying data points. In order to address this issue explicitly, the classifier was tested on the
 282 same noisy data, albeit with randomly shuffled condition labels. Samples were thus classified
 283 and tested for significance with the best scoring number of neighbors in a 1000 random
 284 permutation test and the aforementioned 2-fold CV procedure. The resulting *Observed* and
 285 *Chance* accuracy values (where chance level was calculated as the mean accuracy of the 1000
 286 random permutation scores) for every FOI were then statistically tested using pingouin (Version
 287 0.3.8 running on Python 3.7.7; Vallat, 2018). In a first step, to test whether auditory nerve
 288 modulation was generally reflected within classification results, broadband values (*Observed* vs.
 289 *Chance*) were compared using a one-sided t-test. Then, classification results of all four FOI
 290 were compared in a two-factor repeated measures ANOVA with the factors FOI (broadband,
 291 theta, alpha, beta) and Type (*Observed* vs. *Chance*) to check whether the attention effect was
 292 driven by one of the predefined FOI. Finally, theta, alpha, and beta bands were also tested for

293 significant differences during focused attention computing three one-sided t-tests with
 294 respective values (*Observed* vs. *Chance*).

295 *Code Accessibility*

296 The data and code necessary for statistical analysis and generating the figures are available at
 297 the corresponding author's GitLab repository (<https://gitlab.com/qubitron>).

298 **Results**

299 Sixteen CI users performed a crossmodal attention task (similar to Hartmann and Weisz, 2019)
 300 where attention had to be focused on an upcoming auditory or visual stimulus (see **Figure 1A**).
 301 Auditory nerve activity was recorded directly via their first (i.e. most apical) CI electrode in the
 302 silent cue-target interval. We calculated the power spectral density of the signal and compared
 303 the two conditions (attend auditory vs. visual) in the theta and alpha band. Afterwards, a
 304 classifier was utilized to decode the attended modality on a single-trial basis using the
 305 broadband signal and frequency bands typically associated with selective attention (theta,
 306 alpha, beta).

307 *Behavioral results*

308 Participants gave a correct response in 96% ($SD = 2.7\%$) of all trials. The number of correct
 309 trials did not differ significantly between the two conditions, according to a dependent sample t-
 310 test (auditory: $M = 245$ ($SD = 9.8$); visual: $M = 242$ ($SD = 8.8$); $t(15) = 1.32$, $p = 0.21$, $d = 0.33$).
 311 When there was an oddball in the cued domain, a correct response was given in 75% ($SD =$
 312 19.0%) of the trials. In the auditory condition, the percentage of correct oddball trials was 72%
 313 ($SD = 30.8\%$) and in the visual condition 78% ($SD = 14.2\%$). Overall, the behavioral findings
 314 suggested that participants performed the task in a compliant manner.

315 *Human auditory nerve activity is modulated by selective attention*

316 In a first analysis step, we calculated the broadband PSD from 4-25 Hz, separately for each
 317 condition (attend auditory/attend visual). The resulting power spectra (see **Figure 2A**) by
 318 themselves showed no clear peaks, however the grand average condition contrast spectrum
 319 indicates differences that are mainly centered in distinct frequency ranges. Based on previous
 320 OAE and M/EEG work (Mazaheri et al., 2014; Köhler et al., 2021), we statistically compared the
 321 two conditions in the theta (averaged between 5-8 Hz) and alpha frequency band (averaged
 322 between 9-13 Hz; **Figure 2B**). A cluster-based permutation test in the theta frequency band
 323 showed that prestimulus power is higher when attending the auditory domain ($p = 10.00e^{-05}$, $d =$
 324 0.49). No cluster was found in the alpha frequency band ($p = 1.00$, $d = 0.20$). Given the
 325 distribution of the individual average power in both FOI, a rather high interindividual variability
 326 can be seen. In addition, we also tested the beta frequency band (averaged between 14-24 Hz),
 327 where no cluster was found ($p = 1.00$, $d = -0.16$).

328 We further wanted to investigate whether the effect in the theta band was related to behavioral
 329 performance. Correlating individual average theta power in each condition with behavioral
 330 performance showed a very small and non-significant relationship (auditory: $r = 0.019$, $p =$
 331 0.944; visual: $r = 0.096$, $p = 0.723$). A potential explanation could be the rare occurrence of
 332 oddball trials (see Materials and Methods), resulting in a very high overall behavioral
 333 performance (auditory: $M = 96\%$, $SD = 3.1\%$; visual: $M = 95\%$, $SD = 3.6\%$).

334 The results so far showed that selective attention modulates directly recorded cochlear activity,
 335 with the effect being in particular pronounced in the theta frequency range: attending to an
 336 upcoming auditory stimulus resulted in higher power recorded from the CI electrode.

337

338 **Figure 2.** Prestimulus power modulations and decoding of selective attention. (A) Grand average
 339 prestimulus power spectra from 4-25 Hz when attending the auditory or visual domain. The top panel
 340 indicates the relative change between the auditory and visual domain. The shaded areas in the bottom
 341 panel represent the standard error of the mean for within-subjects designs (O'Brien and Cousineau,
 342 2014). (B) Average prestimulus power in the theta and alpha band, separated by the two conditions.
 343 Black dots indicate the group mean for the respective condition. A cluster-based permutation test in the

344 averaged theta FOI resulted in a statistically significant difference when testing the hypothesis that
 345 performance is higher when attending the auditory domain ($p = 10.00e^{-05}$, $d = 0.49$). No cluster was found
 346 in the alpha band ($p = 1.00$, $d = 0.20$). The asterisks indicate a statistically significant difference (n.s. = not
 347 significant). (C) A kNN-Classifer was used to decode attended modality from single-trial prestimulus
 348 power spectra. Resulting *Observed* accuracies were contrasted with respective *Chance* levels of a
 349 random permutation test for all FOI. Contrasts revealed significant ($p < 0.001$) decoding performance
 350 throughout spectra with fairly similar effects (broadband: $t(15) = 5.60$, $p = 2.60e^{-05}$, $d = 1.96$; theta: $t(15) =$
 351 5.83 , $p = 1.70e^{-05}$, $d = 2.11$; alpha: $t(15) = 6.78$, $p = 3.00e^{-06}$, $d = 2.34$; beta: $t(15) = 6.40$, $p = 6.00e^{-06}$, $d =$
 352 2.33) on a group level (represented by black dots; error bars = 95% CI). However, on a single-subject
 353 level, the attention effect was most pronounced for individually specific FOI, resulting in significant above
 354 chance decoding for 12 out of 16 subjects. As indicated in the top right of the broadband column (S1:
 355 purple, S16: yellow), each subject is represented by the same color in all four FOI columns.

356 *Auditory nerve as origin of the signal*

357 Our results so far suggest a theta rhythmic modulation of human auditory nerve **activity** by
 358 selective attention, with increased theta activity when attending an upcoming auditory stimulus.
 359 However, one concern of the recording approach was the origin of the recorded signal being
 360 actually any cortical source instead of auditory nerve activity. Even though electrode
 361 configurations with close (extracochlear) reference on the implant housing should already pick
 362 up quite local sources, an empirical approach was needed to exclude possible effects of volume
 363 conduction. To show that our effects truly resemble auditory nerve modulations, we exploited an
 364 additional EEG dataset that was simultaneously recorded to the CI signal for one of the
 365 participants. Addressing this issue, we cross-correlated the CI signal with the EEG signals of 55
 366 electrodes (9 had to be excluded due to their location directly above the subject's implant). If
 367 signals at the CI were due to volume conduction, this should go along with strong cross-
 368 correlations at zero-lag. To test the absence of this instantaneous volume conduction effect, we

369 calculated the average Bayesian Pearson correlation between CI and EEG signals for 510 trials
 370 using the 'bayesFactor' package for Matlab (see <https://klabhub.github.io/bayesFactor>). The
 371 implemented correlation function uses the Jeffreys-Zellner-Siow (JZS) prior as proposed for
 372 Bayesian hypothesis test for correlational analysis by Wetzels & Wagenmakers (2012). We
 373 report ln-transformed Bayes factors, $\ln(\text{BF}_{10})$, where values > 1.1 would mean substantial
 374 evidence for volume conduction and values > 2.3 would mean strong evidence for volume
 375 conduction (Jeffreys, 1998). Results of this analysis show no evidence for volume conduction
 376 according to $\ln(\text{BF}_{10})$: $M = -0.98$ ($SD = 0.40$), with values ranging from -1.60 to 0.20 between all
 377 electrodes. Respective r-values show a mean of $r = 3.46e^{-04}$ ($SD = 0.0074$), ranging between -
 378 0.016 and 0.011 over all channels. The analysis substantially strengthens our argument that the
 379 attentional effects are genuinely recorded from the auditory nerve.

380 *Attended modality can be decoded from single-trial CI recordings*

381 We used prestimulus power spectra for a kNN-Classfier to show that attention modulation of
 382 ongoing auditory nerve activity in humans is even reflected in single-trial CI recordings. To
 383 ensure that the classifier was able to differentiate auditory nerve activity when attending the
 384 auditory compared to the visual domain in general, we calculated a t-test between *Observed*
 385 classification accuracies and respective *Chance* levels of broadband power spectra, showing
 386 that this attention effect was decodable significantly above chance ($t(15) = 5.60$, $p = 2.60e^{-05}$, d
 387 $= 1.96$; **Figure 2C**). Given the significant difference over a broad frequency range, we were
 388 further interested in whether this attention effect was driven by one of the FOI usually connected
 389 with selective attention in OAE and M/EEG studies. We therefore calculated a two-factor
 390 repeated measures ANOVA to compare the effect of selective attention on kNN-Classification
 391 accuracy for different FOI (broadband, theta, alpha, beta) and Types (*Observed*, *Chance*).
 392 Results show no significant effect of FOI ($F(3, 45) = 0.37$, $p = 0.78$, $\eta_p^2 = 0.02$), yet show a
 393 significant effect for *Observed* vs. *Chance* accuracies ($F(1, 15) = 136.55$, $p = 6.21e^{-09}$, $\eta_p^2 =$

0.90), with higher accuracies for *Observed* ($M = 0.53$) than *Chance* ($M = 0.50$) levels. No FOI x Type interaction on decoding results was found ($F(3, 45) = 0.36$, $p = 0.78$, $\eta_p^2 = 0.02$). As a main effect of Type and no interaction of FOI x Type indicated that selective attention can be decoded from all FOI separately, in addition we computed three t-tests for theta, alpha, and beta bands contrasting respective *Observed* and *Chance* levels. For all three FOI a significant difference was found for selective attention decoding (theta: $t(15) = 5.83$, $p = 1.70e^{-05}$, $d = 2.11$; alpha: $t(15) = 6.78$, $p = 3.00e^{-06}$, $d = 2.34$; beta: $t(15) = 6.40$, $p = 6.00e^{-06}$, $d = 2.33$; **Figure 2C**). Additionally, random permutation tests of kNN classification within all four different FOI gave insights into single-subject decoding performance across the different frequency spectra. Independent of FOI, an overall number of 12 subjects (i.e. 75% of the sample) showed significant ($p < 0.05$) above chance decoding of focused attention during the silent cue-target interval.

Discussion

The efferent auditory system comprises a complex arrangement of subcortical pathways, which can alter cochlear activity by top-down signals (Terrerros and Delano, 2015; Elgueda and Delano, 2020). Profound evidence supports the notion of altered oscillatory neural activity by selective attention on a cortical level within the alpha (Frey et al., 2014; Mazaheri et al., 2014; Weise et al., 2016) and beta band (Buschman and Miller, 2007; Iversen et al., 2009; Lee et al., 2013). Much less is known for subcortical structures along the efferent pathway, especially when it comes to the *human* cochlea as special recording and analysis techniques are required (Elgueda and Delano, 2020). So far, investigating attentional modulation of cochlear activity in humans had to rely on indirect recordings of OAEs, a noninvasive approach for measuring OHC activity. Recent evidence suggests slow modulations (<10 Hz) of cochlear activity (Dragicevic et al., 2019) that is even enhanced during a silent cue-target period when attending the auditory

418 modality (Köhler et al., 2021). However, studying OAEs cannot address direct modulation of
 419 auditory nerve activity since spiral ganglion cells are efferently innervated by a separate, lateral
 420 pathway. In contrast to the MOC, most LOC fibers project to the ipsilateral cochlea (Robertson,
 421 1985) and are evenly distributed from the apical to the basal end (Guinan, 1996). In humans,
 422 little is known about their function in sound processing since its unmyelinated axons are difficult
 423 to electrically stimulate and record from (Guinan, 2018), while measured responses are
 424 inconclusive about MOC or LOC origin. To our knowledge, attentional modulation via the LOC
 425 remains completely unknown, as direct recordings of auditory nerve activity are normally not
 426 feasible in humans. Given the absence of the efferent MOC reflex in CI recipients (Wilson et al.,
 427 2003; Lopez-Poveda et al., 2016; Marrufo-Pérez et al., 2019) in addition to substantial OHC
 428 degeneration, as well as the overall scarcity of efferent MOC projections (Liberman and
 429 Liberman, 2019), potential alterations of respective auditory nerve activity in a selective
 430 attention paradigm should largely reflect top-down signals from the LOC (Lopez-Poveda, 2018).
 431 Crucially, LOC innervation density peaks at the apical end of the cochlea, whereas MOC
 432 projections peak in mid-cochlear regions (Liberman and Liberman, 2019). As we exclusively
 433 recorded from the most apical electrode, the reported effects should most definitely reflect
 434 modulations of apical LOC innervations. Our results show that ongoing auditory nerve activity is
 435 top-down modulated, hereby putatively suggesting a role of the LOC pathway in selective
 436 attention. Future applications that are able to simultaneously record from multiple CI electrodes
 437 could exploit the different electrode positions along the cochlea and draw conclusions about
 438 frequency specific terminal distributions of LOC efferents. Setups with bilateral CI recordings
 439 could even address the LOC's role in analysis of interaural differences in frequency and
 440 intensity, as assumed by Ciuman (2010).

441 Importantly, we ruled out any cortical source to drive the demonstrated effects as Somers et al.
 442 (2021) recently showed that tailored CIs can be used to intentionally obtain evoked potentials

443 from the auditory cortex with a recording setup that is fairly comparable with only small
 444 differences to the one used in this study. Whilst Somers et al. used reference electrodes located
 445 on the temporal muscle, MED-EL implants have reference and ground electrodes in the actual
 446 implant housing. It was therefore important to rule out any cortical origin with additional analysis.
 447 Cross-correlation of simultaneously recorded CI and EEG electrodes for one participant clearly
 448 showed the absence of any instantaneous correlations which would be caused by volume
 449 conduction.

450 While cortical and OAE-based measures suggest attention-related effects in distinct frequency
 451 bands (Mazaheri et al., 2014; Köhler et al., 2021), our results are mixed in this respect. The
 452 broadband frequency analysis of the prestimulus interval showed no clear peaks (**Figure 2A**).
 453 This, however, may also be the result of low signal-to-noise ratios (SNRs), as commercial CIs
 454 are so far not optimized to do these kinds of continuous electrophysiological recordings. Indeed,
 455 a grand average of the condition differences points to maximal effects in a frequency range
 456 overlapping with the one reported by Köhler et al. (2021), resulting in enhanced theta power
 457 while attending to the auditory modality (**Figure 2B**). This result corroborates our previous
 458 finding using a similar paradigm, where ongoing OAEs in the theta band (~6 Hz) were enhanced
 459 while attending an upcoming auditory stimulus (Köhler et al., 2021). We found no selective
 460 attention effect in the alpha nor in the beta band in concordance with aforementioned studies of
 461 otoacoustic activity. It is therefore possible that these frequency bands do not play a central role
 462 in selective attention at the peripheral level. A caveat of the present study concerns a possible
 463 involvement of the delta band that cannot be ruled out by the analyzed frequency range of 4-25
 464 Hz due to the restricted 1000 ms recording periods. Further studies with an optimized recording
 465 setup will be necessary to address this issue. However, the dominance of theta rhythmic
 466 modulations in the auditory periphery across the reported studies are striking. Arguably, feature
 467 selection on a cochlear level shares top-down mechanisms with working memory (WM)

468 prioritization processes reflected within the theta band (Riddle et al., 2020). In this context,
 469 selective attention could support WM processes in its ability to exclude irrelevant information,
 470 i.e. WM filtering efficiency (Arnell and Stubitz, 2010) or expectation-driven WM benefits
 471 (Bollinger et al., 2010). This could explain our results with regards to predominance of theta
 472 oscillations. However, we think that condition-related increases in the theta band in the current
 473 study mainly reflect processes of selective attention rather than visual WM since the cues were
 474 fairly similar and the task not demanding in terms of WM capacity. This idea should be further
 475 explored in future studies that additionally manipulate memory load and assess WM
 476 performance outcomes and how this is affected by individual theta in-/decreases already at a
 477 cochlear level. This becomes especially relevant as Marcenaro et al. (2021) just recently
 478 established a link between visual WM and acoustic suppression of distortion product OAEs,
 479 suggesting top-down modulations of cochlear responses via MOC efferents during visual WM
 480 periods.

481 Building upon conventional analyses of condition-level fast Fourier transform (FFT) averages,
 482 we decided to use single-trial frequency spectra to classify anticipatory attentional focus during
 483 the silent cue-target period. With this approach we aimed to get more detailed insight into fine-
 484 grained differences between attentional states coded within modulations of direct cochlear
 485 recordings that could be missed by condition-level averaging approaches and indirect OAE
 486 measurements. Strikingly, classification of the broadband signal (4-25 Hz) revealed significantly
 487 improved differentiation of attended modality compared to the average condition-level effect of
 488 the FFT results (**Figure 2C**). Follow-up analysis showed that the performance was not driven by
 489 one of three FOI (theta, alpha, beta) usually associated with selective attention, but instead it
 490 revealed that the contribution of each of these frequency bands to broadband classification was
 491 fairly similar. However, the decoding approach allowed for additional insight into single-subject
 492 classification performance and showed high interindividual variability in terms of an optimal

493 spectral frequency band. It remains to be determined whether this effect is driven by local
494 idiosyncrasies at the peripheral level (e.g. synaptic connections between LOC and spiral
495 ganglion cells) or even involves particular activity patterns at higher hierarchical levels.
496 Independent of the precise origins of our effects observed at the auditory nerve, the decoding
497 results open up avenues to future developments towards closed-loop CIs that incorporate
498 mental states of the recipient into adaptive stimulation in real time. As we show, a classifier
499 could use the frequency information of this signal to anticipate the attentional state of the
500 recipient. Future research will need to address which cognitive states can be decoded directly at
501 the auditory nerve and how this information could be exploited in a closed-loop CI setup. In this
502 regard, overall classification results might seem rather small with accuracies ranging between
503 50% - 60%, yet they are comparable to many others in the field of cognitive neuroscience (see
504 Varoquaux et al., 2017, for a review on decoding in neuroimaging). Considering that the results
505 are based on simplistic decoding of noisy single-channel data, the reported accuracies are
506 highly valuable and most importantly interpretable. Future approaches with improved recording
507 setups would most probably allow for higher decoding accuracies as they were necessary for
508 functional closed-loop systems. Additionally, albeit substantial interindividual variability, the
509 classifier yielded accuracies at a quite consistent above chance level. It remains an open
510 question to what extent interindividual differences are functionally relevant. In the current study,
511 we did not observe any relation to behavioral performance, however this may be due to the
512 simplistic task leading to a ceiling effect obscuring associations.

513 In summary, this study shows that individuals with a CI form a model population to deepen our
514 understanding of how cognition can leverage the efferent auditory system to modulate auditory
515 input at the earliest stages of processing. To the best of our knowledge, our study is the first to
516 investigate attentional effects on activity recorded directly from the auditory nerve in humans.
517 We confirm and extend previous indirect measurements, suggesting attentional modulations in

the theta frequency range. Importantly, we also show that selective attention can be decoded above chance at a single-trial and even individual level. Previous reports on attentional modulations of cochlear activity relied on OAEs, which are driven by the MOC pathway. Our results strongly suggest that the LOC pathway can also be exploited in a top-down fashion to affect spiral ganglion cells directly.

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