

1 **Title:** Effect of digital noise-reduction processing on subcortical speech encoding and  
2 relationship to behavioral outcomes

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12

13 **Abstract (150 words or fewer)**

14 Perceptual benefits from digital noise reduction (NR) vary among individuals with different  
15 noise tolerance and sensitivity to distortions introduced in NR-processed speech; however, the  
16 physiological bases of the variance are understudied. Here, we developed objective measures  
17 of speech encoding in the ascending pathway as candidate measures of individual noise  
18 tolerance and sensitivity to NR-processed speech using the brainstem responses to speech  
19 syllable /da/. The speech-evoked brainstem response was found to be sensitive to the addition  
20 of noise and NR processing. The NR effects on the consonant and vowel portion of the  
21 responses were robustly quantified using response-to-response correlation metrics and spectral  
22 amplitude ratios, respectively. Further, the f0 amplitude ratios between conditions correlated  
23 with behavioral accuracy with NR. These findings suggest that investigating the NR effects on  
24 bottom-up speech encoding using brainstem measures is feasible and that individual  
25 subcortical encoding of NR-processed speech may relate to individual behavioral outcomes  
26 with NR.

27

## 28 1. Introduction

29 Modern hearing aids utilize noise-reduction (NR) algorithms to attenuate the noise level  
30 to help people with hearing impairment in challenging listening environments [e.g., Bentler and  
31 Chiou (2006); Bentler et al. (2008)]. Unfortunately, the NR processing typically used in hearing  
32 aids often introduces speech distortion whenever there is spectral overlap between target  
33 speech and the background noise [e.g., Arehart et al. (2013); Kates (2008)]. This drawback has  
34 been a significant concern for individuals who might perceive speech distortions more  
35 sensitively and prefer not to use NR, whereas other users find the benefit of attenuated noise  
36 outweighs such distortions and prefer to use NR (Brons, Dreschler, et al., 2014; Brons, Houben,  
37 et al., 2014; Neher, 2014; Neher et al., 2014; Neher & Wagener, 2016; Neher et al., 2016).  
38 However, little is known about the physiological mechanisms underlying this individual  
39 variability. The current study focused on *subcortical* speech encoding in the presence of noise  
40 and investigated the effect of NR in the ascending auditory pathway.

41 Subcortical auditory processing varies even among individuals with normal hearing  
42 (Bharadwaj et al., 2022; Bharadwaj et al., 2019; Bharadwaj et al., 2015; Moore, 2008; Picton,  
43 2013; Plack et al., 2014; Ruggles et al., 2011). As a measure of subcortical auditory function, the  
44 scalp-recorded auditory brainstem response (ABR) provides non-invasive insights into the  
45 ascending auditory system's ability to encode and process sounds (Felix et al., 2018; Hall, 1992;  
46 Krishnan, 2023). Several studies have shown that speech-evoked ABR using brief syllables such  
47 as /da/, or ABR to complex sounds (cABR), can be a sensitive tool to probe the fidelity with  
48 which an individual's ascending auditory system encodes the spectrotemporal features of  
49 speech sounds (BinKhamis, Léger, et al., 2019; Easwar et al., 2020; Kraus & Nicol, 2005; Nuttall

50 et al., 2015; Skoe & Kraus, 2010), with strong correlations observed between characteristics of  
51 speech-evoked ABRs and behavioral outcomes in noise (Anderson & Kraus, 2010; Anderson et  
52 al., 2013; Bidelman & Momtaz, 2021; Hornickel et al., 2009; Parbery-Clark et al., 2009). Further,  
53 speech-evoked ABR has significant potential as an objective aided outcome measure (Anderson  
54 & Kraus, 2013; Easwar et al., 2023; Easwar et al., 2015; Jenkins et al., 2018; Karawani et al.,  
55 2018).

56 Few studies have utilized speech-evoked ABR to evaluate an individual's physiological  
57 reaction to signal processing schemes employed in hearing aids, such as NR. The literature has  
58 documented that the effects of background noise on the subcortical processing of speech  
59 sounds significantly differ among individuals [e.g., Parbery-Clark et al. (2009); Song et al. (2011);  
60 Wong et al. (2007)]. Nevertheless, in investigating the physiological reaction to NR-processed  
61 speech, an additional layer of complexity arises because of potential spectral distortions  
62 induced by NR, in addition to attenuated noise levels (Kim et al., 2024; Kim, Schwalje, et al.,  
63 2021; Kim et al., 2022). Recent studies investigated these mixed effects of NR on *cortical*  
64 representations of target speech in the presence of noise (Alickovic et al., 2020; Alickovic et al.,  
65 2021; Kim et al., 2022). However, ABR measures have the advantage of evaluating the  
66 physiological processing of speech sounds in the early sensory portion of the auditory pathway  
67 while being relatively unaffected by top-down processes such as attentional modulation  
68 (Figarola et al., 2023; Varghese et al., 2015), and thus more readily applicable in the audiology  
69 clinic (BinKhamis, Léger, et al., 2019; Jafari et al., 2015; Rocha-Muniz et al., 2014).

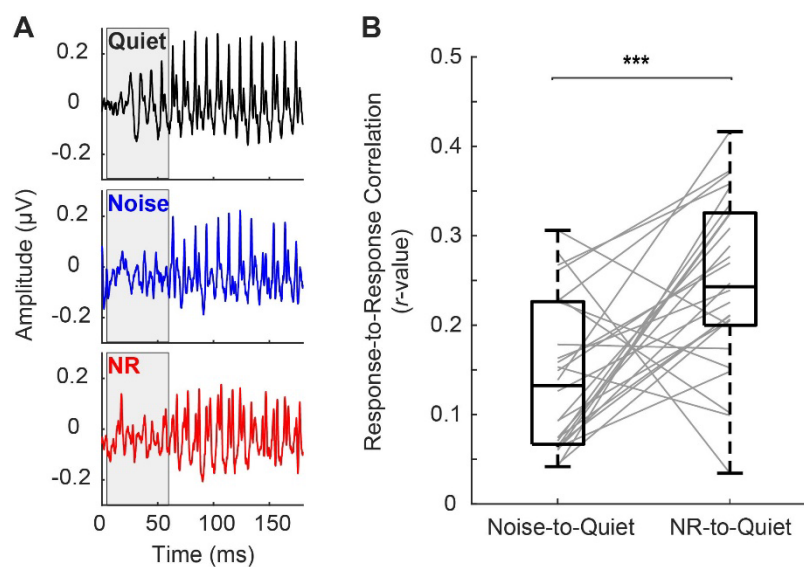
70 The current study utilized brainstem responses to speech syllable /da/ to investigate the  
71 effect of NR on speech encoding in the ascending auditory pathway and relationship to

72 behavioral outcomes. We hypothesized that temporal and spectral characteristics of speech-  
73 evoked ABR are sensitive to the addition of noise and NR processing and that such subcortical  
74 index relates to behavioral outcomes with NR.

## 75 2. Results

### 76 2.1 Response-to-response Correlations

77 Correlation coefficients calculated from the consonant portions of brainstem responses  
78 (5-60 ms) were compared (**Figure 1A**) across different stimulus conditions. Paired *t*-tests  
79 showed that a greater degree of similarity was revealed between brainstem responses in the  
80 NR condition compared with quiet than the responses in the noise condition compared with  
81 quiet ( $t(25) = -3.93$ ,  $p < 0.001$ ; noise-to-quiet: mean = 0.14, SD = 0.083; NR-to-quiet: mean =  
82 0.25, SD = 0.096) (**Figure 1B**). This result suggests that the effect of NR on the brainstem  
83 response can be robustly quantified using response-to-response correlation metrics and that  
84 NR reduces the degradative effect of noise on the responses.



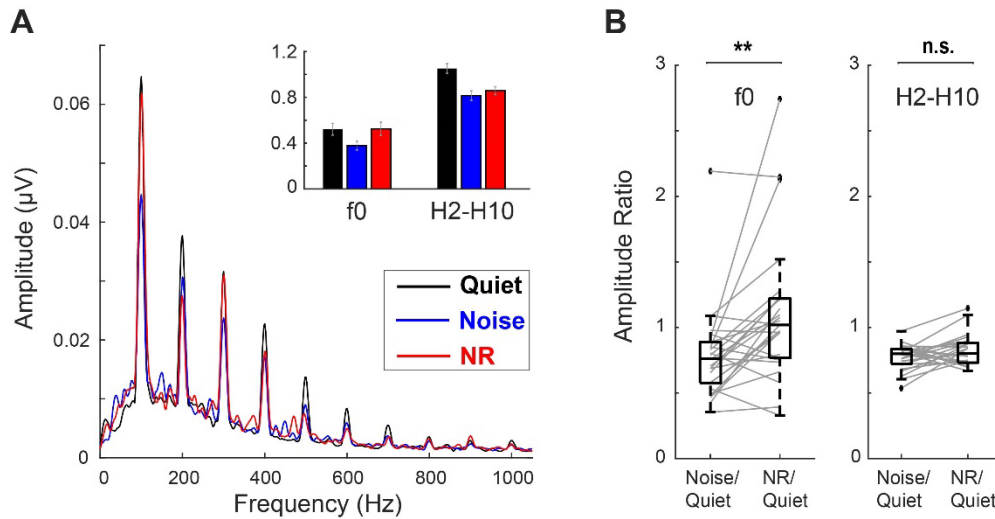
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86 **Figure 1. A.** Auditory brainstem response waveforms in three conditions with shaded regions  
87 indicating the consonant portion of the response (5-60 ms). **B.** The noise reduction (NR)-to-  
88 quiet correlation was significantly greater than the noise-to-quiet correlation ( $t(25) = -3.93$ ,  $p <$   
89  $0.001$ ), suggesting the role of NR in limiting the degradative effect of noise. \*\*\*: significant at  $p$   
90  $< 0.001$ .

91

## 92 2.2 Spectral Encoding

93 The amplitude spectrums resulting from the fast Fourier transform performed on the  
94 vowel portions of the response (60-180 ms) were compared (**Figure 2A**) across different  
95 conditions. For  $f_0$ , paired  $t$ -test results showed that spectral amplitude in the NR condition  
96 compared with quiet was significantly greater than the amplitude in the noise condition  
97 compared with quiet ( $t(25) = -3.57$ ,  $p = 0.0015$ ; noise-to-quiet ratio: mean = 0.78, SD = 0.35; NR-  
98 to-quiet ratio: mean = 1.11, SD = 0.54) (**Figure 2B** left panel). For upper harmonics (H2-H10), no  
99 significant difference was revealed between the NR-to-quiet and noise-to-quiet amplitude  
100 ratios ( $t(25) = -1.84$ ,  $p = 0.078$ ; noise-to-quiet ratio: mean = 0.77, SD = 0.095; NR-to-quiet ratio:  
101 mean = 0.82, SD = 0.12) (**Figure 2B** right panel). This result suggests that spectral amplitude  
102 ratios of brainstem responses between conditions are sensitive to NR effects (especially  $f_0$   
103 amplitude) and that NR processing can lead to enhanced spectral encoding in noise.



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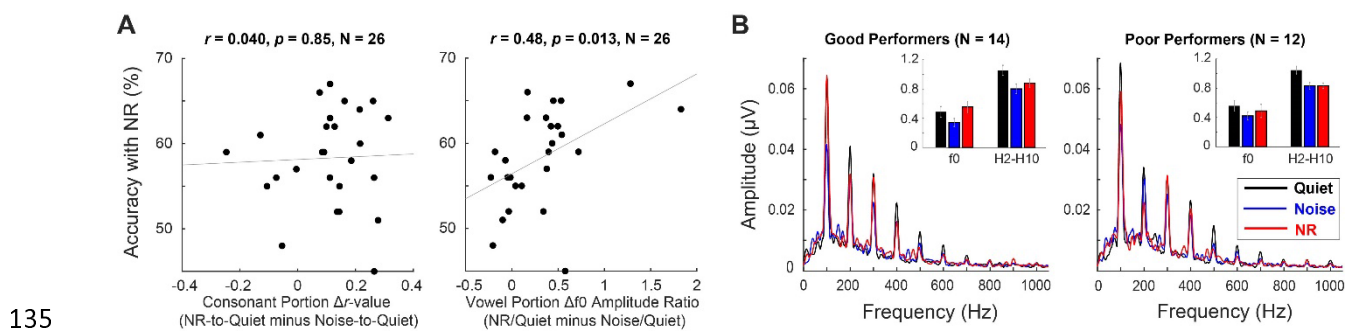
105 **Figure 2. A.** Fast Fourier transform of the vowel portions of the response (60-180 ms) with the  
106 bar graphs indicating resulting spectral amplitudes in three conditions for  $f_0$  and upper  
107 harmonics (H2-H10), respectively. **B.** The noise reduction (NR)-to-quiet amplitude ratio for  $f_0$   
108 was significantly greater than the noise-to-quiet ratio ( $t(25) = -3.57, p = 0.0015$ ), indicating that  
109 NR processing may enhance encoding of  $f_0$  in noise. \*\*: significant at  $p < 0.01$ , n.s.: not  
110 significant.

111

### 112 2.3 Relationship between Brainstem Measures and Behavioral Outcomes

113 At the individualized SNR level (-6 to -11 dB, median: -8 dB) measured through an  
114 adaptive test, behavioral accuracy was obtained in the noise condition (mean = 58.58%, SD =  
115 7.67%). The SNR levels provided to the individual listeners were deemed adequate for targeting  
116 the midpoint (62.5%) of the psychometric function relating to SNR and accuracy, with the  
117 chance level at 25%. The mean accuracy in the NR condition was 58.31% (SD = 5.64%), which  
118 indicated that NR processing did not improve speech-in-noise performance (paired  $t$ -test:  $t(25)$   
119 = 0.24,  $p = 0.81$ ), consistent with the literature [e.g., Alcántara et al. (2003); Bentler et al.  
120 (2008); Ricketts and Hornsby (2005)].

121 Pearson correlation analyses were used to investigate whether the effects of noise and  
122 NR processing on brainstem responses predicted behavioral accuracy. A change in  $r$ -value from  
123 correlations between responses to the consonant (i.e., NR-to-quiet minus noise-to-quiet  
124 correlations) was not related to behavioral accuracy in the NR condition ( $r = 0.040$ ,  $p = 0.85$ )  
125 (**Figure 3A** left panel) and in the noise condition ( $r = 0.17$ ,  $p = 0.41$ ). A change in spectral  
126 amplitude ratios for  $f_0$  (i.e., NR-to-quiet minus noise-to-quiet ratio) significantly correlated with  
127 accuracy in the NR condition ( $r = 0.48$ ,  $p = 0.013$ ) (**Figure 3A** right panel), whereas upper  
128 harmonics (H2-H10) did not ( $r = 0.21$ ,  $p = 0.31$ ). Neither the encoding of  $f_0$  ( $r = 0.36$ ,  $p = 0.069$ )  
129 nor the upper harmonics ( $r = 0.073$ ,  $p = 0.72$ ) correlated with accuracy in the noise condition. A  
130 post hoc two-sample  $t$ -test showed that NR benefits in  $f_0$  encoding (i.e., NR-to-quiet minus  
131 noise-to-quiet ratio) were more salient in the better performance group (i.e., a group with  
132 accuracy in the NR condition greater than the mean: 58.31%) than the other ( $t(19.77) =$   
133  $3.23$ ,  $p = 0.0042$ ) (**Figure 3B**). These results suggest that better encoding in  $f_0$  with NR captured  
134 by brainstem measures is associated with better behavioral outcomes with NR.



136 **Figure 3. A.** A comparison between brainstem measures and behavioral outcomes shows that  
137 the  $f_0$  amplitude ratio predicts behavioral accuracy with noise reduction (NR). **B.** Illustration of  
138 differences in spectral encoding revealed in the fast Fourier transform results between two  
139 performance groups divided based on accuracy with NR.

140



141 *3. Discussion*

142           The temporal and spectral metrics derived in the current study from the speech ABR  
143 were effective in capturing NR effects on subcortical speech encoding, indicating their  
144 sensitivity and feasibility. The significant correlation between the f0 amplitude ratios and  
145 behavioral accuracy with NR suggests that the individual subcortical encoding of NR-processed  
146 speech sounds influences individual behavioral outcomes related to NR processing. Our findings  
147 align well with evidence emphasizing the role of subcortical sources in accounting for individual  
148 variability in speech-in-noise perception (Bidelman & Momtaz, 2021; Gorina-Careta et al., 2021;  
149 White-Schwoch et al., 2022) and illustrating potential applications of speech-evoked ABR or  
150 envelope following response (EFR) as an objective aided outcome measure (Anderson & Kraus,  
151 2013; Easwar et al., 2023; Easwar et al., 2015; Jenkins et al., 2018; Karawani et al., 2018).  
152 Indeed, the speech-evoked has been tested in clinical applications in recent studies with adult  
153 hearing aid users, although they did not report NR effects on brainstem responses and found no  
154 correlation between speech-evoked ABR characteristics (e.g., f0 amplitude) and behavioral  
155 outcomes (BinKhamis, Elia Forte, et al., 2019; Perugia et al., 2021; Seol et al., 2020). The current  
156 study suggests that our ABR paradigm has the potential to be an objective measure of  
157 individual noise tolerance and sensitivity to NR-processed speech and a reliable predictor of  
158 behavioral outcomes with NR.

159           Our findings show that individual variations in peripheral and/or subcortical physiology  
160 contribute to individual differences in preferences related to NR processing. Indeed, individual  
161 variations in the peripheral encoding of complex sounds can arise from a range of overt and  
162 hidden forms of sensorineural hearing loss (Hauser et al., 2024). For instance, in people with

163 mild-to-moderate hearing loss who are typical candidates for hearing aid use, individual  
164 variability and suprathreshold hearing deficits may stem from reduced cochlear sensitivity and  
165 reduced frequency selectivity (Henry & Heinz, 2012; Horst, 1987; Liberman & Dodds, 1984;  
166 Moore, 2007) as well as cochlear deafferentation (Bharadwaj et al., 2014; Kujawa & Liberman,  
167 2009), potentially leading to significant differences in subcortical encoding fidelity among  
168 individuals. Further, emerging evidence indicates that peripheral hearing damage also induces  
169 distorted cochlear tonotopy, where hypersensitive cochlear tuning curve tails allow low-  
170 frequency sounds to commandeer the temporal response of the basal half of the cochlea  
171 (Bharadwaj et al., 2024; Henry et al., 2016; Henry et al., 2019; Parida & Heinz, 2022). Lastly,  
172 although the scalp-recorded brainstem response to speech stimuli is generally assumed to be  
173 unaffected by cortical generators [see a review from Chandrasekaran and Kraus (2010)], given  
174 that NR effects in the current study were observed at 100 Hz ( $f_0$ ), some contribution from  
175 cortical and non-sensory cognitive variables is also possible (Forte et al., 2017; Hoormann et al.,  
176 2004; Lehmann & Schönwiesner, 2014). Future work should explore how variations in  
177 subcortical encoding interact with individual differences in cognitive processes, such as auditory  
178 selective attention (Kim, Emory, et al., 2021; Shim et al., 2023), in ultimately determining  
179 behavioral outcomes.

## 180 4. Methods

### 181 4.1 Participants

182 Twenty-six adults (3 male, 12%) with normal hearing participated in the experiments. All  
183 participants were native speakers of American English, with air-conduction thresholds no  
184 greater than 20 dB HL at any frequencies, tested in octaves from 250 up to 8000 Hz, and their  
185 ages ranged from 19 to 41 years (mean = 24.54 years, SD = 5.01 years). All study procedures  
186 were conducted at Purdue University and were reviewed and approved by the Purdue  
187 University Institutional Review Board. All work was carried out following the Code of Ethics of  
188 the World Medical Association (Declaration of Helsinki), and written informed consent was  
189 obtained for everyone.

### 190 4.2 Stimuli and Procedures

#### 191 4.2.1 Speech-evoked ABR Test

192 The current study followed well-established procedures of Parbery-Clark et al. (2009)  
193 unless otherwise noted. We used the speech syllable /da/ constructed using the KlattGrid  
194 speech synthesizer (Klatt, 1980). The speech syllable was 170 ms long with 5 ms onset and  
195 offset ramps and had an average fundamental frequency ( $f_0$ ) of 101 Hz (100 to 106 Hz). During  
196 the first 50 ms formant transition period, the first, second, and third formants changed from  
197 482 to 765 Hz, 2046 to 1131 Hz, and 2695 to 2483 Hz, respectively, but stabilized for the  
198 following 120 ms steady-state (vowel) portion of the stimulus. The fourth, fifth, and sixth  
199 formants remained constant at 3626, 4060, and 5249 Hz, respectively. The acoustical  
200 characteristics described above were estimated by Praat (Boersma, 2001). Speech-shaped noise

201 generated using a 512-order finite impulse response filter was added to the speech syllable for  
202 the noise and NR conditions.

203 The speech syllable was presented at 90 dB SPL monaurally to the better ear, chosen  
204 based on pure-tone air conduction threshold averaged across 0.5, 1, 2, and 4 kHz, through  
205 insert ER-2 earphones (Etymotic Research, Elk Grove, IL). In the noise and the NR conditions,  
206 the speech syllable was presented at a +3 dB SNR over speech-shaped noise that started 40 ms  
207 before the syllable onset and continued until 40 ms after the syllable offset. Thus, the overall  
208 250 ms long stimulus was presented in alternating polarities with an interstimulus interval of 40  
209 ms. Speech-evoked ABR was recorded at a 16 kHz sampling rate using the BioSemi ActiveTwo  
210 32-channel system (BioSemi B.V., Amsterdam, the Netherlands) in the international 10-20  
211 layouts over 3000 sweeps for each of three experimental conditions (i.e., quiet, noise, and NR  
212 conditions). The magnitude of offset voltages was adjusted to be less than  $\pm 30$  mV at each  
213 electrode before the beginning of data collection. Participants watched muted, captioned  
214 videos during the tests conducted in a single-walled, sound-treated booth (IAC Acoustics,  
215 Naperville, IL) through a computer monitor placed at zero-degree azimuth a half-meter distance  
216 from their eye level. The recordings spanned around 45 minutes and were controlled by custom  
217 scripts implemented in MATLAB (R2016b, the MathWorks, Natick, MA).

218 All EEG recordings were re-referenced to two earlobe electrodes and bandpass filtered  
219 from 70 to 2000 Hz (12 dB/octave with zero-phase shift). Trials with activity greater than  $\pm 35$   
220  $\mu\text{V}$  were considered artifacts and removed from the analysis. Epochs were generated from -10  
221 to 190 ms relative to the onset of the speech syllable /da/ and baseline-corrected relative to

222 mean activity in the pre-syllable period. In the current study, only single-channel analyses were  
223 conducted using the Cz electrode at the vertex.

#### 224 4.2.2 *Speech-in-noise Test*

225 The Iowa Test of Consonant Perception was administered to assess the perception of  
226 consonant-vowel-consonant monosyllabic English words embedded in speech-shaped noise  
227 (Geller et al., 2020). Participants were tested in the same environment described above (i.e.,  
228 participants tested in a sound booth, stimuli presented monaurally through an insert ER-2  
229 earphones, and tasks controlled in MATLAB).

230 Each trial started with the screen indicating a trial number in silence for 0.5 seconds,  
231 then switched to the screen with a fixation cross ('+') in the center to fix eye gaze during stimuli  
232 presentation to minimize eye-movement artifacts. Half a second after the cross symbol  
233 occurred on the screen, background noise started and continued for 1.5 seconds. The target  
234 word was presented 0.5 seconds after the noise onset. The composite stimulus was presented  
235 at 80 dB SPL. After the stimuli presentation, the participants were required to select one  
236 answer out of four choices shown on the screen using a keypad. For instance, for the target  
237 word *sat*, four answer options were provided: *sat*, *pat*, *fat*, and *that*. No feedback was provided  
238 during the experiment.

239 The current study targeted the threshold level for closed-set tests (i.e., 62.5% accuracy,  
240 halfway between the chance level of 25% and 100%). Kim et al. (2022) used an adaptive test  
241 with the two-down, one-up staircase procedure to find the SNR level targeting 70% accuracy  
242 (i.e., speech reception threshold, SRT-70) in the first 50 trials and reported that in listeners with

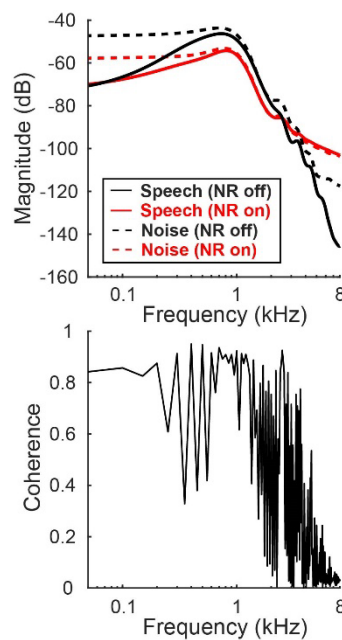
243 normal hearing, the SNR level 3-dB lower than the SRT-70 led to mean accuracy of 62.4%. The  
244 present study followed the procedures from Kim et al. (2022); for the first 50 trials, the  
245 adaptive test was used to find the SRT-70 for individual listeners, and then the SNR level 3-dB  
246 lower than the SRT-70 was given to them in the following two experimental conditions: the  
247 noise and NR conditions. One hundred ten words were presented in each condition using word  
248 sets balanced across speaker gender and initial phonemes and randomly assigned to each  
249 condition.

#### 250 *4.3 NR Algorithm*

251 In the NR conditions for both the speech-evoked ABR test and speech-in-noise test, the  
252 current study used the Ephraim-Malah NR algorithm, a modified spectral-subtraction NR that  
253 applies different gain across frequency channels in each short-time frame based on SNR  
254 estimation using a minimum mean-square error estimator (Ephraim & Malah, 1984). The  
255 Ephraim-Malah NR algorithm has relatively low computational complexity and thus has been  
256 implemented in modern digital hearing aids [e.g., Sarampalis et al. (2009); Stelmachowicz et al.  
257 (2010)].

258 **Figure 4** upper panel illustrates spectra of speech and noise stimuli from the speech-  
259 evoked ABR tests extracted using the phase-inversion technique (Hagerman & Olofsson, 2004):  
260 inverting the noise phase before processing two noisy signals through NR. The NR algorithm in  
261 the present study improved the SNR by approximately 2.5 dB based on the long-term RMS level  
262 of those extracted speech and noise stimuli. **Figure 4** lower panel shows magnitude-squared  
263 coherence up to 8 kHz for two speech stimuli (i.e., unprocessed vs. NR-processed speech stimuli

264 extracted from the phase-inversion technique) where coherence value zero indicates that input  
265 and output power spectra are not identical at all, whereas value one means they are entirely  
266 identical (Kay, 1988). The coherence value averaged across 8 kHz was at around 0.3 between  
267 speech stimuli from the speech-evoked ABR tests. For monosyllabic words used for speech-in-  
268 noise tests in the present study, approximately 3.5-dB benefit in SNR and average coherence at  
269 around 0.6 were reported by Kim et al. (2022).



270

271 **Figure 4.** The upper panel shows spectra of speech and noise stimuli for the speech-evoked  
272 auditory brainstem response (ABR) tests. Noise reduction (NR)-processed stimuli were  
273 extracted using the phase-inversion technique. The lower panel illustrates the magnitude-  
274 squared coherence across frequencies between unprocessed and NR-processed speech stimuli  
275 for the ABR tests.

276

#### 277 4.4 Statistical Analysis

##### 278 *Response-to-response Correlations*

279 Cross-correlation analyses were conducted to examine the effects of noise and NR on  
280 the consonant portion of brainstem responses (5-60 ms). Specifically, brainstem responses in  
281 both NR and noise conditions were compared to the responses in quiet, respectively. Given that  
282 adding noise or NR may delay the responses relative to the responses in quiet, the response  
283 waveforms in noise and NR conditions were shifted in time by up to 2 ms until reaching the  
284 maximum correlation coefficient (a Pearson's  $r$  value) (Parbery-Clark et al., 2009). A pair of  
285 correlation coefficients were compared: noise-to-quiet vs. NR-to-quiet.

### 286 *Spectral Encoding*

287 Fast Fourier transform analysis was conducted on the vowel portions of the response  
288 (60-180 ms) in the same manner as described by Parbery-Clark et al. (2009) to assess the effect  
289 of noise on spectral encoding to the vowel portions of the speech syllable and to examine if NR  
290 processing enhances spectral encoding in noise. The strength of harmonic representation (100-  
291 1000 Hz) with the first harmonic corresponding to the stimulus  $f_0$  (100 Hz) was quantified by  
292 summing spectral amplitudes across frequency bins that are 20-Hz wide and centered on each  
293 of the ten harmonics. Aside from calculating the  $f_0$  spectral amplitude, spectral amplitudes for  
294 the 2nd to 10th harmonics were combined to represent the strength of overall spectral  
295 encoding to the subsequent harmonics. NR-to-quiet and noise-to-quiet amplitude ratios were  
296 calculated and compared for  $f_0$  and upper harmonics, respectively.

### 297 *Relationship between Brainstem Measures and Behavioral Outcomes*

298 The relationship between the brainstem measures described above, correlations  
299 between responses to the consonant and spectral amplitude ratios for the vowel portion of the



300 response, and behavioral outcomes were assessed using Pearson correlation analysis.  
301 Specifically, the correlation analyses investigated if a change in  $r$ -value from response-to-  
302 response metrics and a change in spectral amplitude ratios correlate with behavioral accuracy,  
303 respectively. A post hoc two-sample  $t$ -test was conducted to compare NR benefits (or lack  
304 thereof) in f0 encoding between two participant groups divided based on accuracy with NR:  
305 one group with accuracy greater than the mean vs. the other group with accuracy less than the  
306 mean.  
307

308 **Data Availability**

309 All data is openly accessible and publicly available at <https://dx.doi.org/>

310 10.17632/5jgbmk6p42.1.

311 **Code Availability**

312 The code to reproduce the figures in this work is publicly available at <https://dx.doi.org/>

313 10.17632/5jgbmk6p42.1.

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318 **Author Contributions**

319 S.K. and H.M.B. designed the experiments and analyzed the data. S.K. and M.S. ran the

320 experiments. All authors wrote the manuscript.

321 **Competing Interests**

322 The authors declare no competing interests.

323

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