Improved tactile speech perception using

² audio-to-tactile sensory substitution with

³ formant frequency focusing

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11 Abstract

12 Haptic hearing aids, which provide speech information through tactile stimulation, could 13 substantially improve outcomes for both cochlear implant users and for those unable to 14 access cochlear implants. Recent advances in wide-band haptic actuator technology have 15 made new audio-to-tactile conversion strategies viable for wearable devices. One such 16 strategy filters the audio into eight frequency bands, which are evenly distributed across the 17 speech frequency range. The amplitude envelopes from the eight bands modulate the 18 amplitudes of eight low-frequency tones, which are delivered through vibration to a single 19 site on the wrist. This tactile vocoder strategy effectively transfers some phonemic 20 information, but vowels and obstruent consonants are poorly portrayed. In 20 participants 21 with normal touch perception, we tested (1) whether focusing the audio filters of the tactile 22 vocoder more densely around the first and second formant frequencies improved tactile 23 vowel discrimination, and (2) whether focusing filters at mid-to-high frequencies improved 24 obstruent consonant discrimination. The obstruent-focused approach was found to be 25 ineffective. However, the formant-focused approach improved vowel discrimination by 8%, 26 without changing overall consonant discrimination. The formant-focused tactile vocoder 27 strategy, which can readily be implemented in real time on a compact device, could 28 substantially improve speech perception for haptic hearing aid users.

29 Introduction

30 Sensory substitution devices that converted audio into tactile stimulation were used in the 31 1980s and early 1990s to support speech perception in people with a severe or profound 32 hearing loss. These haptic hearing aids (also called "tactile aids") allowed users to learn a large vocabulary of words through tactile stimulation alone¹ and could substantially improve 33 word recognition with lip reading²⁻⁴. However, by the mid-to-late 1990s, these haptic hearing 34 35 aids were rarely used clinically because of large improvements in the effectiveness of cochlear implants (CIs)⁵ and critical limitations in the haptic technology available^{5,6}. While 36 Cls have been life-changing for hundreds of thousands of people, millions in low-resource 37 38 settings still cannot access them because of their high cost and the need for advanced 39 healthcare infrastructure⁷. Even in high-resource settings, many are unable to access CIs because of barriers in complex care pathways⁸ and because of disorders that prevent 40 41 implantation (such as cochlear ossification). Furthermore, while CIs often effectively restore 42 speech recognition in quiet listening environments, users typically have substantial difficulties understanding speech in background noise^{9,10} and locating sounds¹¹. A new 43 44 generation of haptic hearing aids that exploit the huge recent advances in compact haptic

45 actuator, battery, and microprocessor technology might now be able to offer a viable low-

- 46 cost, non-invasive, and highly accessible alternative or complement to the CI.
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48 Previously, many haptic hearing aids have transferred audio frequency information by 49 mapping different frequencies to different locations of tactile stimulation on the skin¹²⁻¹⁶. Now, cutting-edge wide-band haptic actuator technology allows new audio-to-tactile conversion 50 51 strategies, with a frequency-to-frequency mapping, to be deployed on wearable devices. One such strategy is the tactile vocoder^{9-11,17-19}. In this approach, audio is first filtered into 52 53 different frequency bands. The amplitude envelope is extracted from each of these bands 54 and used to modulate the amplitude of low-frequency tones. The number of vibro-tactile 55 tones typically matches the number of frequency bands, with each band modulating a 56 different tone. This approach allows the frequency range of speech to be converted to the 57 frequency range where tactile sensitivity is high. The tactile tones are presented through 58 vibro-tactile stimulation at a single site.

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60 The frequency-to-frequency tactile vocoder strategy has been successfully used to improve speech-in-noise performance^{9,10,17,20} and sound localisation^{11,19} for CI users with 61 accompanying audio ("electro-haptic stimulation"⁹) and to transfer speech information 62 63 without accompanying audio¹⁸. However, while the latest iteration of the tactile vocoder 64 strategy can effectively transfer some important phonemic information, such as that used for 65 discrimination of voiced and voiceless consonants, it is poor at transferring phonemic cues for vowels and obstruent consonants¹⁸. Obstruent consonants are formed by obstructing 66 67 airflow and include plosives (such as p/), which are generated via closure followed by an abrupt release, and fricatives (such as /f/), which are generated via airflow through a narrow 68 opening in the vocal tract. 69

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71 The latest tactile vocoder strategy distributes audio frequency bands across the speech 72 frequency range using a rule that mimics the healthy auditory system (though with a much 73 lower resolution; see "Methods")^{9,17,18,20}. In the current study, we tested two alternatives to 74 this "wide focused" filtering approach. The first "formant focused" approach aimed to improve 75 vowel discrimination by focusing more bands around the first and second formant 76 frequencies (300 – 2,500 Hz). The second "obstruent focused" approach aimed to improve 77 obstruent consonant discrimination by more densely focusing bands at higher speech 78 frequencies (2,500 – 7,000 Hz). These new approaches exploit the fact that the tactile 79 system does not make assumptions about how speech will be distributed across frequency

80 (because speech is not usually received through vibration). In contrast, the auditory system

81 does have an expectation of how speech will be distributed across frequency, which can be

- 82 disrupted when frequency information is warped to focus on specific speech features 21,22 .
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86 87 Figure 1: Spectrograms for the vowel /u:/ (as in "bl<u>ue</u>") spoken by the female talker from the EHS Research Group Phoneme Corpus (see "Methods"). The left panel shows the input audio, and the central and right panels show the tactile envelopes extracted using

88 the wide-focused (baseline) and the newly developed formant-focused vocoder 89 strategies used in the current study. The frequency range shown focuses on the lower 90 frequencies around the first and second formants, which are marked for the input audio. 91 The audio spectrogram sample rate was 22.05 kHz, with a window size of 8 ms (Hann) 92 and a hop size of 1 sample. Each window was zero-padded to a length of 8192 samples. 93 The tactile spectrogram sample rate was 16 kHz (matching that used current study), with 94 no windowing applied. For the input audio, intensity is shown in decibels relative to the 95 maximum magnitude of the short-time Fourier transform. For the tactile envelopes, 96 intensity is shown in decibels relative to the maximum envelope amplitude. The 97 spectrograms were generated using the Librosa Python library (version 0.10.0).

Figure 1 shows an example of how the formant-focused approach can more effectively extract the first and second formants than the wide-focused approach, for the vowel /u:/.
With wide focusing (central panel), the two formants are not well distinguished, with a single broad lower-frequency peak in energy portrayed. In contrast, with formant focusing (right panel), the two formants are clearly distinguishable. Formants are critical to vowel perception and so this better formant representation was expected to improve vowel discrimination. 105 The effect of formant focusing on consonant perception was anticipated to be more complex. 106 as the importance of formants differs substantially across consonant types. Improved 107 discrimination would be expected for sonorant consonant pairs (approximants, such as /w/. 108 which are generated via formant resonances in a partially closed vocal tract, and nasals, 109 such as /n/, which are generated by transmission through the nasal cavity) that differ by 110 manner and place of articulation, as the frequency and amplitude of the second formant is 111 important in these distinctions. In contrast, the focusing of frequency bands towards lower 112 formant frequencies might worsen performance for consonants that rely on gross spectral 113 shape at higher frequencies (e.g., fricatives or plosives). Performance might also be reduced 114 for contrasts that rely on the distinction between voiced and voiceless cognates (phonemes 115 produced via the same manner and place of articulation and differing only by whether they 116 are voiced), because of the lack of a frequency band at the voicing bar (around the 117 fundamental frequency of a talker's voice). However, note that previous work in hearing has 118 shown that voicing perception can be tolerant to the removal of lower frequency audio 119 information^{23,24}. Because of the hypothesised both positive and negative impacts of formant 120 focusing, it was anticipated that overall performance with consonants would be unaltered. 121



123 Figure 2: The frequency spectrum for the consonant /s/ (spoken by the male talker), with 124 wide focusing (left) and obstruent focusing (right). The plot shows the audio spectrum (black 125 line) and the average envelope amplitude in each frequency band (with the band limits 126 highlighted with dashed lines). Spectrums were generated by calculating the power spectral 127 density (PSD) of the original audio, using a window length of 256 samples and an overlap of 128 128 samples. The windows were zero-padded to a length of 8192 samples. The envelope 129 amplitudes were extracted using the wide and obstruent focused approaches used in the 130 current study (see "Methods"). The envelopes were normalised by subtracting the difference 131 between the average envelope amplitude, weighted by the width of each frequency band. 132 and the average amplitude of the PSD.

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134 The aim of obstruent focusing was to better represent mid-to-high frequency noise 135 components (bursts and frication noise) and thereby improve discriminability of obstruent 136 consonants. An example of this can be seen in Figure 2, which shows the spectral 137 representation for the consonant /s/, with wide and obstruent focusing. Obstruent focusing 138 dedicates more bands to the upwards spectral tilt at mid-to-high frequencies than wide 139 focusing, with the tilt coded by the highest six frequency bands for obstruent focusing and 140 only the highest three bands for wide focusing. Spectral characteristics such as tilt are important for obstruent phoneme perception²⁵. While obstruent focusing was expected to 141 improve performance for plosives and fricatives, it was anticipated to reduce performance for 142 143 voiced-voiceless contrasts as so few frequency bands were focused near the voicing bar. 144 Obstruent focusing was also expected to have a small negative effect on vowel 145 discrimination. While the first and second formants, which are critical to vowel perception, 146 are poorly represented with obstruent focusing, this was expected to be partially 147 compensated for by better representation of the higher-frequency third and fourth formants.

148 Results



150 Figure 3: Percentage of phoneme pairs discriminated for each focusing approach, with 151 either the different phoneme types (consonant or vowel: left panel) or different talkers 152 (male or female; right panel) shown separately (N=20). The horizontal line inside the box 153 shows the median, and the top and bottom edges of the box show the upper (0.75) and 154 lower (0.25) guartiles. Outliers (values of more than 1.5 times the interguartile range) are 155 shown as unfilled circles. The whiskers connect the upper and lower quartiles to the 156 maximum and minimum non-outlier values. Chance performance is marked by a dashed 157 grey line. 158

- 159 Figure 3 shows the percentage phonemes discriminated with the three focusing approaches,
- 160 for the 20 participants who took part in this study. Results are shown either for each
- 161 phoneme type (left panel) or each talker (right panel). A three-way repeated-measures
- analyses of variance (RM-ANOVA) was run with the factors: focusing approach (wide,
- 163 formant, or obstruent focused), phoneme type (consonants or vowels), and talker (male or
- 164 female). Main effects were found for the focusing approach (F(1,19) = 25.5, p < .001; partial
- 165 eta squared (η^2) = .573), phoneme type (*F*(1,19) = 150.1, *p* <.001; η^2 = .888), and talker
- 166 (F(1,19) = 39.8, p < .001; $\eta^2 = .677$). No interaction was found between talker and either
- 167 phoneme type (F(1,19) = 1.6, p = .223) or focusing approach (F(1,19) = 2.2, p = .129), or
- between talker, phoneme type, and focusing approach (F(1,19) = 0.5, p = .608). A significant
- 169 interaction was found between focusing approach and phoneme type (F(1,19) = 19.1, p
- 170 <.001; η² = .501).
- 171

172 Overall performance with wide focusing was 58.2% (standard deviation (SD): 6.4%), with

formant focusing was 62.2% (SD: 8.0%), and with obstruent focusing was 56.0% (SD:

174 7.8%). With wide focusing, performance was 15.9% higher for consonants than for vowels

- 175 (SD: 6.9%); with formant focusing, performance was 9.6% higher (SD: 4.3%); and, with
- obstruent focusing, performance was 5.8% higher (SD: 5.8%). Performance with the female
- talker was higher for wide focusing by 4.8% (SD: 4.4%), for formant focusing by 3.7% (SD:
- 178 4.9%), and for obstruent focusing by 5.9% (SD: 3.8%).
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- 180 Contrasts revealed a significant overall improvement in performance with formant focusing compared to the wide-focusing baseline (F(1,19) = 27.5, p < .001; $n^2 = .591$). Formant-181 182 focusing improved performance across all phonemes by 3.9% on average (ranging from -4.7 183 to 10.3%; SD: 4.5%). The size of this improvement was significantly larger for vowels than for consonants (F(1,19) = 13.2, p = .002; $n^2 = .409$). For vowels, performance with formant 184 185 focusing was 7.7% higher on average than with wide focusing (ranging from -4.9 to 18.8%; 186 SD: 7.0%) and, for consonants, was 1.4% higher on average (ranging from -4.6 to 7.9%; SD: 187 3.3%). The benefit of formant focusing compared to wide focusing was not found to depend 188 on the talker (F(1,19) = 1.0, p = .335).
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- 190 Contrasts showed no significant overall difference in performance with obstruent focusing
- 191 compared to wide focusing (F(1,19) = 1.6, p = .218). However, the effect of obstruent
- 192 focusing compared to wide focusing was found to significantly differ between consonants
- and vowels (F(1,19) = 38.9, p < .001; $\eta^2 = .672$). For consonants, performance with obstruent
- 194 focusing was 6.3% lower on average than with wide focusing (with reductions ranging from
- 195 0.0 to 13.4%; SD: 3.0%) and, for vowels, performance was 1.4% higher on average (ranging

- from -10.4 to 16.0%; SD: 7.3%). No dependence of the effect of obstruent focusing compared to wide focusing was found between talkers (F(1,19) = 1.3, p = .266).
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- 199 Planned post hoc t-tests (corrected for multiple comparisons; see "Methods") were run to
- 200 compare formant focusing to obstruent focusing. Across all phonemes, performance was
- 201 6.2% better with formant focusing (ranging from 0.0 to 11.1%; SD: 3.3; *t*(19) = 8.7, *p* <.001;
- 202 Cohen's *d* = 0.76). For consonants, formant focusing was 7.7% better (ranging from 0.9% to
- 203 14.4%; SD: 4.3%; *t*(19) = 8.0, *p* <.001; *d* = 0.94), and for vowels formant focusing was 3.9%
- better (ranging from -6.9% to 15.3%; SD: 5.3%; t(19) = 3.2, p = .004; d = 0.44).
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Figure 4: Percentage of phonemes discriminated for the different focusing approaches, grouped by phoneme contrast type (N=20). Box plots are shown as in Figure 3. Chance performance is marked with a dashed grey line.

210 Figure 4 shows phoneme discrimination for each phoneme subgroup. Further post hoc 211 analyses (corrected for multiple comparisons) revealed significant improvements in 212 phoneme discrimination in some subgroups for formant focusing compared to wide focusing. 213 For voiced fricatives and for sonorants that differed by place of articulation, performance 214 improved with formant focusing by 11.5% (SD: 10.5%; *t*(19) = 4.9, *p* = .002) and 13.8% (SD: 215 12.5%; t(19) = 4.9, p = .002), respectively. Improvement in performance for voiced plosives 216 differing by place of articulation was also close to significance (mean change in performance 217 of 8.3%; SD: 11.4%; t(19) = 3.3, p = .057). Performance decreased for phoneme pairs 218 differing by whether they were voiced or voiceless by 13.3% (SD: 11.0%; t(19) = 5.4, p

<.001). For vowels, formant focusing improved performance for monophthongs by 5.8% (SD:
7.1%; *t*(19) = 3.7, *p* = .026) and for diphthongs by 11.5% (SD: 13.4%; *t*(19) = 3.8, *p* = .020).

222 Changes in performance for phoneme sub-groups were also observed for obstruent focusing 223 compared to wide focusing. No significant improvement in performance with obstruent 224 focusing was observed for any consonant subgroup, although improvement for sonorants 225 that differ by place of articulation approached significance (mean change in performance of 226 8.5%; SD: 12.6%; t(19) = 3.0, p = .077). Performance worsened with obstruent focusing 227 compared to wide focusing by 34.8% for consonants differing by whether they were voiced 228 or voiceless (SD: 10.4%; t(19) = 14.9, p < .001), by 11.5% for voiceless plosives differing by 229 place of articulation (SD: 11.5%; t(19) = 4.4, p = .005), and by 6.9% for consonants differing 230 by both manner and place of articulation (SD: 7.6%; t(19) = 4.1, p = .012). Decreased performance was also close to significance for voiceless fricatives differing by place of 231 232 articulation (mean decrease of 7.9%; SD: 11.1%; t(19) = 3.2, p = .056) and for consonants 233 differing by both place of articulation and voicing (mean decrease of 10.6%; SD: 14.6%; t(19) = 3.3, p = .058). No significant change for vowel subgroups was observed, although 234 235 improvement in performance approached significance for monophthongs (mean 236 improvement of 5.2%; SD: 7.7%; t(19) = 3.0, p = .077).

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Additional exploratory analyses assessed whether there was a correlation between
phoneme discrimination (for wide, formant, or obstruent focusing approaches) and either age
or detection thresholds for a 125-Hz vibro-tactile tone (measured during screening). No
evidence of a correlation between phoneme discrimination and either age or detection
threshold was found.

243

244 Finally, to assess whether fatigue, training, or adaptation effects might have influenced the 245 outcomes, performance was assessed for each of the four measurements made of each 246 phoneme pair and focusing approach. Note that each of these four repeats was completed in 247 sequence so that, for example, all phoneme pairs and focusing approaches were measured 248 once before the any of the second repeat measurements were conducted. For each repeat, 249 the order of conditions was re-randomised. For the first repeat, the mean performance 250 across all pairs and methods was 59.4% (SD: 7.2%), for the second repeat was 59.6% (SD: 251 8.0%), for the third repeat was 57.9% (SD: 6.9%), and for the final repeat was 58.0% (SD: 252 8.2%).

253 Discussion

- 254 Previously, it has been shown that tactile phoneme discrimination with the latest wide-
- focused tactile vocoder strategy is good for consonants but poor for vowels¹⁸. The current
- study tested a new version of the strategy, which was designed to improve vowel
- 257 discrimination by better transferring formant information. As hypothesised, vowel
- discrimination was substantially improved with this new formant-focused approach, while
- 259 overall consonant discrimination remained unaffected. In addition to being critical for haptic
- 260 hearing aids that target those unable to access CIs, enhanced vowel perception could be
- crucial for augmenting CI listening, particularly for lower-performing users who tend to have
- poor vowel perception even in quiet listening conditions²⁶.
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264 While the formant-focused vocoder strategy did not affect overall consonant performance, it 265 improved discrimination for some consonant sub-groups and worsened discrimination for 266 others. Improved discrimination was observed for voiced sonorants. This may have been 267 due to better representation of the second formant, which is important for place contrasts 268 among nasals or approximants. Unexpectedly, an improvement in performance was also 269 observed for voiced fricatives that differed by place of articulation. Voiced fricatives have a 270 "dual spectrum", with a low-frequency component at the voicing bar generated by the vocal 271 folds, and a high-frequency noise component generated by turbulent airflow in the oral 272 cavity. Formant focusing might have increased separation of these components across the 273 vibro-tactile tones through the denser concentration of mid-frequency bands, making them 274 more salient. Additionally, the spectral tilt of the mid-to-high frequency portion of the noise 275 component may have been portrayed more effectively.

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Discrimination of pairs differing by manner and place of articulation did not improve with
formant focusing, contrary to our expectation. This may have been due to the second
formant being relatively weak and close in frequency to the first formant for these phonemes.
Even with formant focusing, there may not have been adequate frequency separation or

- 281 dynamic range available to sufficiently represent the second formant.
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Formant focusing worsened performance for contrasts between voiced and voiceless consonants. This was expected as the two frequency bands that were focused on the voicing bar with the wide-focused approach were reallocated to formant frequencies. A future iteration of the formant-focused approach might explore whether allocating one or more of the bands to the voicing bar can recover discrimination of consonants differing by voicing, without reducing the benefits of formant focusing. Voicing information is not
accessible through lip reading and so effectively transferring this information could be
particularly important for those who receive limited acoustic information through other means
(e.g., their Cl)²⁷. Indeed, improved voicing perception has already been identified as an
important benefit of bimodal stimulation, where Cl listening is supplemented by residual lowfrequency acoustic hearing through a hearing aid in the other, in the small percentage of Cl

- 294 users for whom this is possible²⁸.
- 295

296 In addition to the formant-focused approach, another new approach was tested that 297 concentrated frequency bands towards higher speech frequencies to improve obstruent 298 consonant discrimination. This approach was found to be ineffective. In fact, overall 299 discrimination of consonants was worse with obstruent focusing than with the original wide-300 focused approach. This may in part reflect the greater importance of representing lower 301 formants for sonorant (approximants and nasal) consonants. As expected, performance on 302 consonants differing only by voicing was substantially impaired with obstruent focusing. This 303 was likely because frequency bands focused on or close to the voicing bar were reallocated 304 to higher frequencies (no bands represented frequencies below 300 Hz and only one band 305 represented frequencies between 300 and 2,500 Hz). For vowels, the expected reduction in 306 performance with obstruent focusing compared to wide focusing was not observed. This was 307 likely due, at least in part, to the increased resolution at higher speech frequencies improving 308 the representation of the higher formants, which can be used for vowel discrimination²⁹. 309

310 Overall performance, across all focusing approaches, was found to be better for the female 311 than for the male talker. This may have been partly due to spectral factors, such as the wider frequency spacing of formants for the female talker and the good alignment of the formants 312 313 with the tactile vocoder filter bands (as shown in Figure 1). Differences in broadband amplitude modulation profiles between the talkers³⁰ may also have played an important role. 314 315 This is supported by a previous study of tactile phoneme discrimination with the same 316 talkers, which found better performance with the female talker when only broadband 317 amplitude envelope cues were presented, precluding the influence of spectral cues¹⁸. 318 319 In the current study, training was deemed unnecessary because of the simplicity of the

discrimination task used. It was shown that, despite performance feedback being given on each trial (which would aid learning), scores were highly stable across different time points in the testing session (which lasted approximately two hours in total). In addition to indicating that training effects were minimal, this suggests that factors such as fatigue and long-term adaptation (e.g., ³¹) also had little or no impact. The absence of a requirement for training presents a significant advantage, as it allows relatively rapid testing of alternative audio-to-tactile conversion strategies.

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328 The lack of a need for training also stems from limitations of the phoneme discrimination 329 task. In higher-level tasks involving words or sentences, significant improvements with 330 training have been observed for tactile-only speech in guiet¹, for tactile stimulation used to 331 support lip reading³², and for audio-tactile speech in noise with Cl users⁹ and with simulated 332 CI audio in normal-hearing listeners^{17,33}. The phoneme discrimination task concentrates on 333 spectral or spectral-temporal aspects of speech, and not on detection of the temporal 334 boundaries of words, syllables, or phonemes in running speech (segmentation), which is 335 important in higher-level tasks. Previous studies have shown evidence that important 336 segmentation cues can be effectively delivered by providing syllable timing cues using tactile pulses³⁴ or by using tactile stimulation derived from the broadband amplitude envelope³⁵. 337 338 The wide-focused tactile vocoder strategy has previously been shown to substantially 339 improve phoneme discrimination compared to the broadband amplitude envelope¹⁸, and the 340 formant-focused tactile vocoder has been shown in the current study to further improve 341 discrimination. This would be expected to facilitate better segmentation by making phoneme distinctions clearer³⁶. However, the relationship between tactile phoneme discrimination and 342 343 speech segmentation is not yet well understood. Future work is required to confirm that the 344 benefits of formant focusing shown in the current study translate to benefits in more realistic 345 speech testing conditions.

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347 Another limitation of the current study is that the participant demographic did not match the 348 target user group for haptic hearing aids. All participants were under 40 years of age, but a 349 substantial portion of people with hearing loss are older. No evidence of a correlation 350 between age (which spanned 13 years) and tactile phoneme discrimination ability was found 351 in the current study or in previous work using the tactile vocoder¹⁸. Previous studies showing 352 speech-in-noise performance for CI users can be improved with tactile stimulation have also found no evidence of a relationship between age and tactile benefit^{9,10,17,20}. While aging does 353 354 not appear to affect tactile intensity discrimination^{37,38} or temporal gap detection for vibrotactile tones³⁹, vibro-tactile detection thresholds^{40,41} and frequency discrimination⁴² are both 355 known to worsen with age. This reduced tactile dynamic range and frequency resolution 356 357 would be expected to decrease the amount of speech information transferred using the 358 tactile vocoder strategy. However, the current study and previous work found no relationship 359 between vibro-tactile detection threshold and either tactile phoneme discrimination performance¹⁸ or audio-tactile benefit^{9,10,17,20}. Nonetheless, in future work it will be important 360

to establish what speech information can be effectively extracted from tactile stimulation indifferent user groups.

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364 As well as not fully spanning the age range of the target user group, participants in the 365 current study reported having no hearing impairment. Several studies have found no differences in tactile speech performance between normal-hearing and hearing-impaired 366 367 individuals^{9,17,18,43,44}. For example, similar improvements in speech-in-noise performance with 368 tactile stimulation using the tactile vocoder strategy were observed for CI users and for normal-hearing individuals listening to CI simulated audio^{9,10,17}. However, there is evidence 369 of increased tactile sensitivity in congenitally deaf individuals⁴⁵, and the current study might 370 371 therefore underestimate performance for this group. Further work is required to conclusively 372 determine whether tactile speech perception differs between normal-hearing listeners and 373 those with hearing loss.

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375 Future studies should also explore whether additional sound information can be transferred 376 by extending the formant-focused tactile vocoder strategy to use multiple tactile stimulation 377 sites. Studies with arrays of actuators have shown that vibrations are localised more precisely around the wrist than along the forearm^{46,47} and that at least four actuators 378 379 distributed around the wrist can be accurately discriminated^{48,49}. However, this does not 380 consider practical challenges that would be faced when building a device for the real world. 381 For example, microchips, batteries, and buckle mechanisms limit where actuators can be 382 placed, and actuators at the palmar wrist can become audible and change their response 383 characteristics if the user couples them with a surface, as is common in everyday activities like cooking or typing at a keyboard⁵⁰. The use of additional stimulation sites might allow the 384 385 delivery of phoneme information that was not optimally transferred with formant focusing, such as low-frequency voicing or pitch cues (e.g., ¹²). It could also allow transfer of additional 386 387 high-frequency sound information, which is important for sound localisation with haptics¹⁹. In 388 previous haptic sound-localisation studies, spatial hearing cues have been effectively delivered through differences in stimulation across the wrists^{11,19,37,50}, which leaves open the 389 390 possibility of transferring additional information through more local changes in stimulation 391 around the wrists. Alternatively, multiple sites might be used to increase the tactile dynamic 392 range available by transferring additional intensity information through the perceived spread 393 of stimulation across nearby sites.

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Another important area for future work will be establishing and maximising the robustness of the formant-focused vocoder strategy to background noise. CI users often struggle to identify vowels in background noise⁵¹, and so a noise-robust version of this new strategy could yield 398 larger benefits of tactile stimulation to speech-in-noise performance than previous tactile 399 vocoder methods^{9,10,17}. Recent studies suggest that amplitude envelope expansion, which 400 exaggerates larger amplitude envelope fluctuations, improves the noise-robustness of the 401 tactile vocoder^{9,10,17} and that high-frequency sound information can be critical for separating 402 speech and noise sources coming from different locations¹⁰. Further investigation of the 403 importance of dedicating bands to higher frequencies and of envelope expansion methods 404 for improving noise robustness is required. In addition, the effectiveness of traditional noise-405 reduction methods, such as minimum mean-square error estimators⁵², and of more advanced techniques. like those exploiting neural networks⁵³, should be assessed for tactile 406 407 speech in noise.

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409 Whether the effectiveness of haptic hearing aids can be improved by adapting the 410 stimulation strategy to the individual user should also be explored. For example, the dynamic 411 range of the device could be adapted based on the user's detection thresholds, as is already 412 done in hearing aids and CIs. Another approach could be to adapt the frequency focusing of 413 the vocoder to complement the individual's hearing profile. For example, more bands might 414 be dedicated to higher frequencies for people with a high-frequency hearing loss. Another 415 interesting avenue of investigation might be the design of complementary CI and haptic 416 stimulation strategies. For example, to maximize sound-information transfer, haptic 417 stimulation could focus on providing only lower-frequency sound information and the CI on 418 providing only the higher-frequency information. As has been argued previously¹⁷, this might 419 reproduce some of the benefits, including those to speech perception, that have been shown 420 for participants who retain low-frequency residual hearing after receiving a Cl⁵⁴. 421

422 In addition to individualisation of devices and the previously discussed motor placement 423 constraints, there are several other important considerations when developing a device for 424 real-world use. Manufacturers will need to establish the optimal real-time implementation of the tactile vocoder to minimise processing time and power usage (borrowing from current 425 426 techniques in CIs, which deploy a similar strategy), as well as the utility of methods for 427 reducing the impact of challenges such as wind-noise^{6,55}. Other critical work will be required 428 to establish the optimal microphone placement and the ability to stream audio from remote 429 microphones, which has been highly effective for other hearing-assistive devices⁵⁶. As well 430 as these design considerations, it will be important to understand whether tactile speech 431 perception is altered by factors such as skin temperature, which effects tactile sensitivity⁵⁷ 432 and often changes markedly between real-world environments.

- 434 The current study showed that formant focusing with the tactile vocoder strategy
- 435 substantially improves vowel discrimination, without impairing overall consonant
- 436 discrimination. This strategy is computationally lightweight and can readily be implemented
- in real time on a compact wearable device to deliver real-world benefit. It could substantially
- 438 improve outcomes, both for haptic hearing aid users who are unable to access CI technology
- and for the substantial number of CI users who have impaired vowel perception even in quiet
- 440 listening conditions.

441 Methods

442 Participants

443 Table 1: Participant characteristics. For each participant, the table shows: vibro-tactile

- 444 detection thresholds measured during screening; wrist temperature measured before testing
- begun; wrist height, width, and circumference; dominant hand; age; and biological sex.
- 446

ID	31.5 Hz	125 Hz	Wrist	Wrist	Wrist	Dom.	Age	Sex
	thresh.	thresh.	temp.	height/	circum.	hand	(yrs.)	(M/F)
	(m/s^{-2})	(m/s ⁻²)	(°C)	width (mm)	(mm)	(L/R)		
1	0.021	0.079	31.1	39/58	166	R	36	М
2	0.029	0.101	27.1	34/47	135	R	28	F
3	0.040	0.104	27.2	31/48	139	R	27	F
4	0.026	0.064	32.0	32/47	136	R	25	F
5	0.024	0.181	30.1	36/50	158	R	36	F
6	0.035	0.024	29.5	42/65	186	R	25	М
7	0.045	0.088	31.5	31/44	142	R	31	F
8	0.114	0.240	29.9	40/50	161	R	26	F
9	0.033	0.069	31.0	36/48	149	L	28	F
10	0.039	0.085	29.2	39/49	149	R	30	F
11	0.056	0.088	30.5	39/50	154	R	23	М
12	0.080	0.104	28.4	48/61	188	R	31	М
13	0.031	0.034	32.3	36/43	142	R	25	F
14	0.045	0.048	29.2	36/50	153	R	30	F
15	0.062	0.057	32.1	45/60	190	R	31	М
16	0.049	0.023	31.2	37/49	169	R	27	F
17	0.049	0.091	28.3	35/54	152	R	29	F
18	0.022	0.038	30.3	42/53	170	L	28	М
19	0.082	0.151	29.2	35/46	144	R	23	F
20	0.029	0.075	29.3	39/50	150	R	24	F
Mean	0.046	0.087	30.0	38/51	157	-	28	-

447

Table 1 shows the characteristics of the 20 participants who took part in the study. There

449 were 6 males and 14 females, with an average age of 28 years (ranging from 23 to 36

450 years). All participants had normal touch perception, as assessed by a heath questionnaire

- 451 and vibro-tactile detection thresholds at the fingertip (see "Procedure"). All the participants
- 452 reported having no hearing impairment. An inconvenience allowance of £20 was paid to
- 453 each participant for taking part.

454 Stimuli

- 455 The vibro-tactile stimuli used in the experiment phase (after screening), were generated
- 456 using the EHS Research Group Phoneme Corpus¹⁸. This contains an English male and
- 457 female talker saying each of the 44 British English phonemes, with four recordings of each
- 458 phoneme per talker.
- 459 Table 2: Consonant and vowel pairs used in the experiment, grouped by the type of contrast.
- 460 *Examples of the British English phonemes (bold and underlined) being used in words are* 461 *also shown (note that these words are for illustration only and were not used in testing).*

Consonants		Contrast type	Vowels		Contrast type	
t & p	(<u>t</u> ea/ <u>p</u> en)	Place in voiceless plosives	1&a: (k <u>i</u> t/c <u>ar</u> t)		Monophthongs	
t & k	(<u>t</u> ea/ <u>k</u> ey)	Place in voiceless plosives	i: & æ	(s <u>ea</u> /b <u>a</u> d)	Monophthongs	
k & p	(<u>k</u> ey/ <u>p</u> en)	Place in voiceless plosives	JI & I	(l <u>aw</u> /k <u>i</u> t)	Monophthongs	
<i>f</i> &θ	(f at/pa <u>th</u>)	Place in voiceless fricatives	и & a:	(p <u>u</u> t/c <u>ar</u> t)	Monophthongs	
f & s	(f at/ <u>s</u> un)	Place in voiceless fricatives	и: & л	(bl <u>ue</u> /m <u>u</u> d)	Monophthongs	
∫& s	(<u>sh</u> e/ <u>s</u> un)	Place in voiceless fricatives	æ & e	(b <u>a</u> d/b <u>e</u> d)	Monophthongs	
d & b	(<u>d</u> ay/ <u>b</u> ay)	Place in voiced plosives	υ&ι (p <u>u</u> t/k <u>i</u> t)		Monophthongs	
g & d	(g et/ <u>d</u> ay)	Place in voiced plosives	æ&v (b <u>a</u> d/l <u>o</u> t)		Monophthongs	
g & b	(g et/ <u>b</u> ay)	Place in voiced plosives	i: & u:	(s <u>ea</u> /bl <u>ue</u>)	Monophthongs	
v & ð	(<u>v</u> et/ <u>th</u> is)	Place in voiced fricatives	л & æ	(m <u>u</u> d/b <u>a</u> d)	Monophthongs	
v & z	(<u>v</u> et/ <u>z</u> oo)	Place in voiced fricatives	u: & v	(bl <u>ue</u> /p <u>u</u> t)	Monophthongs	
ð & z	(<u>th</u> is/ <u>z</u> oo)	Place in voiced fricatives	i: & e	(s <u>ea</u> /b <u>e</u> d)	Monophthongs	
l&r	(<u>l</u> ot/ <u>r</u> un)	Place in sonorants	э <i>1 & е</i> і	(b oy /d <u>ay</u>)	Diphthongs	
j & l	(<u>y</u> et/ <u>l</u> ot)	Place in sonorants	э <i>1 & a</i> v	(b oy /n <u>ow</u>)	Diphthongs	
m & n	(<u>m</u> en/ <u>n</u> ot)	Place in sonorants	аи & еі	(n <u>ow</u> /d <u>ay)</u>	Diphthongs	
z & s	(<u>z</u> ero/ <u>s</u> un)	Voicing	iə & əu	(n <u>ear</u> /n <u>o</u>)	Diphthongs	
3&∫	(vi <u>s</u> ion/ <u>sh</u> e)	Voicing	uə & ei	(p <u>oor</u> /d <u>ay</u>)	Diphthongs	
θ&ð	(pa <u>th/th</u> is)	Voicing	еә & иә	(f <u>air</u> /p <u>oor</u>)	Diphthongs	
t & s	(<u>t</u> ea/ <u>s</u> un)	Manner				
b & w	(<u>b</u> ay/ <u>w</u> et)	Manner				
tſ&∫	(<u>ch</u> at/ <u>sh</u> e)	Manner				
ð & b	(<u>th</u> is/ <u>b</u> ay)	Manner & place (two-feature)				
k & s	(<u>k</u> ey/ <u>s</u> un)	Manner & place (two-feature)				
g & r	(g et/ <u>r</u> un)	Manner & place (two-feature)				
v & s	(<u>v</u> et/ <u>s</u> un)	Place & voicing (two-feature)				
θ&z	(pa <u>th/z</u> ero)	Place & voicing (two-feature)				
m & v	(<u>m</u> en/ <u>v</u> et)	Place & voicing (two-feature)				

- Table 2 shows the subset of 45 phoneme pairs that were used in the phoneme
- 464 discrimination task. These were selected to cover a wide range of contrasts while
- 465 maximizing the functional relevance for potential users of haptic hearing aids. This includes

- 466 pairs that would not be discriminable using either lip-reading alone or acoustic cues alone
- 467 with a substantial high-frequency hearing-loss (which is the typical sensorineural hearing-
- 468 loss profile). Pairs are also included with common vowel and consonant confusions for CI
- 469 users²⁶ and for users of a previous multi-channel tactile aid (the Tactaid-VII)⁴⁴.
- 470

471 The stimulus duration was matched for each phoneme pair by fading out both phonemes

472 with a 20-ms raised-cosine ramp, except for pairs containing a diphthong or containing /g/,

473 /d/, /l/, /r/, /v/, /w/, or /j/. For these exceptions, production in isolation (without an adjacent

- 474 vowel) is impossible or differs acoustically from production in running speech. Duration
- 475 matching was done to prevent discrimination by comparing the total durations of the stimuli.
- The start of the stimulus was defined as the first point from the beginning of the sample that
- the signal reached 1% of its maximum. The fade out reached its zero-amplitude point at the
- 478 end of the shortest stimulus, which was defined as the first point from the end of the stimulus
- 479 at which the signal amplitude dropped below 1% of its maximum. The stimuli used in the
- 480 experiment had a mean duration of 391 ms (ranging from 105 to 849 ms).
- Table 3: Lower and upper audio band-pass filter limits for the different tactile vocoder
 frequency-focusing approaches.

Channel no.	Wide (low/hi	focus gh in Hz)	Formant focus (low/high in Hz)		Obstruent focus (low/high in Hz)		
1	50	190	300	424	300	2,500	
2	190	400	424	577	2,500	2,908	
3	400	716	577	767	2,908	3,376	
4	716	1,191	767	1,000	3,376	3,914	
5	1,191	1,904	1,000	1,374	3,914	4,533	
6	1,904	2,975	1,374	1,863	4,533	5,244	
7	2,975	4,584	1,863	2,500	5,244	6,061	
8	4,584	7,000	2,500	7,000	6,061	7,000	

483

484 In each of the experimental conditions, the audio was converted to vibro-tactile stimulation 485 using a tactile vocoder strategy similar to that used in previous studies^{9-11,17-19}. The audio 486 signal intensity was first normalised following ITU P.56 method B⁵⁸. It was then down 487 sampled to a sampling frequency of 16,000 Hz (matching that available in many hearing aids 488 and other compact real-time audio devices). Following this, the signal was passed through a 489 512th-order FIR filter bank with eight bands. The frequency limits of these bands differed for 490 the wide, formant, and obstruent focused approaches (see Table 3). With the wide-focused 491 approach, the bands matched those used previously by Fletcher et al.¹⁸, with the filters 492 equally spaced between 50 and 7,000 Hz on the auditory equivalent-rectangular-bandwidth 493 (ERB) scale⁵⁹. With the formant-focused approach, four of the eight bands were spaced between 300 and 1,000 Hz (targeting formant 1), three bands were spaced between 1,000 494 495 and 2,500 Hz (targeting formant 2), and one was spaced between 2,500 and 7,000 Hz (to

retain frequency information critical to obstruent phoneme discrimination). With the
obstruent-focused approach, one of the eight bands was spaced between 300 and 2,500 Hz
and the remaining seven were spaced between 2,500 and 7,000 Hz. This focuses on highfrequency spectral shape information, which is critical to obstruent phoneme perception²⁵.

- 500 Within these frequency ranges, all bands were equally spaced on the ERB scale.
- 501

502 After the band-pass filtering stage, the amplitude envelope was extracted for each band 503 using a Hilbert transform and a zero-phase 6th-order low-pass Butterworth filter, with a 504 corner frequency of 23 Hz (following Fletcher, et al. ¹⁸). These amplitude envelopes were 505 then used to modulate the amplitudes of eight fixed-phase vibro-tactile tonal carriers. The tone frequencies were 94.5, 116.5, 141.5, 170, 202.5, 239, 280.5 and 327.5 Hz. The 506 507 frequencies were centred on 170 Hz, which is the frequency at which vibration output is 508 maximal for numerous compact haptic actuators. They were spaced based on frequency discrimination thresholds at the dorsal forearm⁶⁰ (as equivalent data is not available at the 509 510 wrist) and remain within the frequency range (~75-350 Hz) that can be reproduced by 511 current commercially available compact, low-powered motors that are suitable for a wrist-512 worn device.

513

514 A frequency-specific gain was applied to each vibro-tactile carrier tone to compensate for 515 differences in vibro-tactile sensitivity across frequency^{18,61}. The gains were 13.8, 12.1, 9.9, 516 6.4, 1.6, 0, 1.7, and 4 dB, respectively. The eight carrier tones were summed together and 517 delivered through vibro-tactile stimulation at a single contact point. The tactile stimuli were 518 scaled to have an equal amplitude in RMS, giving a nominal output level of 1.2 G (141.5 dB 519 ref. 10⁻⁶ m/s²). This intensity can be produced by a range of compact, low-powered haptic 520 actuators. The stimulus level was roved by 3 dB around this nominal level (with a uniform 521 distribution) so that phonemes could not be discriminated using absolute intensity cues. Pink noise was presented through headphones at 60 dBA to ensure audio cues could not be used 522 523 to discriminate the tactile stimuli.

524 Apparatus

525 Throughout the experiment, participants sat in a vibration isolated, temperature-controlled 526 room (with an average temperature of 23°C; SD of 0.45°C). The temperature of the room 527 and of the participant's skin were measured using a Digitron 2022T type K thermocouple 528 thermometer. The thermometer was calibrated following ISO 80601-2-56:2017⁶², using the 529 method previously described by Fletcher, et al. ¹⁸. Control of skin temperature is important 530 as temperature is known to alter vibro-tactile sensitivity⁵⁷. 531

532 During screening, vibro-tactile detection threshold measurements were made using a HVLab Vibro-tactile Perception Meter⁶³ with a circular probe that had a 6-mm diameter. The probe 533 534 gave a constant upward force of 1N and had a rigid surround. A downward force sensor was 535 built into the surround, and the force applied was displayed to the participant. This sensor 536 was calibrated using Adam Equipment OIML calibration weights. The output vibration 537 intensity was calibrated using the Vibro-tactile Perception Meter's built-in accelerometers 538 (Quartz Shear ICP, model number: 353B43) and a Brüel & Kjær (B&K) Type 4294 calibration 539 exciter. All stimuli had a total harmonic distortion of less than 0.1% and the system conformed to ISO-13091-1:2001⁶⁴. 540

541





543 Figure 5: 3D renders of the EHS Research Group haptic stimulation rig. The left image 544 shows the rig with the participant's arm not in place. The right image shows a zoomed in 545 view with the participant's arm resting on the blue foam cushion and the shaker probe 546 contacting the dorsal wrist. Image reproduced from Fletcher, et al. ¹⁸ with permission of the 547 authors.

548

542

549 In the experiment phase, the EHS Research Group haptic stimulation rig was used (see 550 Figure 5)¹⁸. This consisted of a Ling Dynamic Systems V101 shaker, with a custom-printed 551 circular probe that had a diameter of 10 mm and was made from Verbatim Polylactic Acid 552 (PLA) material. The shaker was driven using a MOTU UltralLite-mk5 sound card, RME 553 QuadMic II preamplifier, and HV Lab Tactile Vibrometer power amplifier. The shaker was suspended using an adjustable elastic cradle from an aluminium strut frame, with the shaker 554 555 probe pointing downwards (so that it could terminate on the dorsal wrist of the participant). 556 Below the shaker was a foam surface (with a thickness of 95 mm) for the participant's 557 palmar forearm to rest on. The probe applied a downward force of 1N, which was calibrated using a B&K UA-0247 spring balance. The vibration output was calibrated using a B&K 558 559 4533-B-001 accelerometer and a B&K type 4294 calibration exciter. All stimuli had a total 560 harmonic distortion of less than 0.1%.

- 562 Masking audio was played from the MOTU UltralLite-mk5 sound card through Sennheiser
- 563 HDA 300 sound-isolating headphones. The audio was calibrated using a B&K G4 sound
- level meter, with a B&K 4157 occluded ear coupler (Royston, Hertfordshire, UK). Sound
- 565 level meter calibration was checked using a B&K Type 4231 calibrator.

566 Procedure

- 567 For each participant, the experiment was completed in one session that lasted approximately 568 two hours. Participants gave informed consent to take part and completed a screening 569 questionnaire. This ensured that they (1) did not suffer from conditions that could affect their 570 sense of touch, (2) had not had any injury or surgery on their hands or arms, and (3) had not 571 been exposed to intense or prolonged hand or arm vibration in the previous 24 hours. The 572 participant's skin temperature was then measured on the index fingertip of the dominant 573 arm. Participants were only allowed to continue when their skin temperature was between 27 574 and 35°C.
- 575

576 Next, vibro-tactile detection thresholds were measured at the index fingertip following BS 577 ISO 13091-1:2001⁶⁴. During the threshold measurements, participants applied a downward 578 force of 2N (monitored using the HVLab Vibro-tactile Perception Meter display). Participants 579 were required to have touch perception thresholds in the normal range (<0.4 m/s⁻² RMS at 580 31.5 Hz and <0.7 m/s⁻² RMS at 125 Hz), conforming to BS ISO 13091-2:2021⁶⁵. The fingertip 581 was used because normative data was not available for the wrist. If participants passed the 582 screening phases, the dimensions of the wrist were measured at the point where the 583 participant would usually wear a wristwatch, and they then progressed to the experiment 584 phase.

585

In the experiment phase, participants sat in front of the EHS Research Group haptic
stimulation rig (Figure 5), with the forearm of their dominant arm resting on a foam surface.
The probe from the shaker was adjusted so that it contacted the centre of the dorsal wrist (at
the position where the participant would normally wear a wristwatch). The participant's skin
temperature was required to be between 27 and 35°C before testing began.

591

592 The experiment phase involved a previously developed three-interval, three-alternative

- 593 forced-choice phoneme discrimination task¹⁸. For each trial, one phoneme pair from either
- the male or female talker was used (see "Stimulus"). Two intervals contained one phoneme
- from the pair (randomly selected) and one interval contained the other phoneme from the
- 596 pair. The intervals were separated by a gap of 250 ms and the order of the intervals was

- 597 randomised. The participant's task was to select which of the three intervals contained the
- 598 oddball stimulus (i.e., the phoneme presented only once) via a key press. They were
- 599 instructed to ignore the overall intensity of the vibration in each interval (as the level roving
- 600 that was deployed to prevent the use of overall intensity for discrimination rendered this an
- 601 unreliable cue). Visual feedback, which indicated whether the response was correct or
- 602 incorrect, was displayed for 500 ms after each trial.
- 603
- The percentage of phonemes correctly discriminated was measured for three conditions,
- each with a different band-pass filter allocation (Table 3). For each condition, all the
- 606 phoneme pairs were tested (Table 2) with both the male and female talker. For each talker,
- 607 each phoneme pair was measured four times, with the phoneme sample randomly selected
- in each trial from the four samples available in the corpus. This meant that there were a total
- of 1080 trials for each participant. All phoneme pairs and conditions were measured for each
- 610 repeat in sequence, with the order of trials randomised each time.
- 611
- 612 The experimental protocol was approved by the University of Southampton Faculty of
- 613 Engineering and Physical Sciences Ethics Committee (ERGO ID: 68477). All research was
- 614 performed in accordance with the relevant guidelines and regulations.

615 Statistics

616 The percentage of correctly discriminated phonemes was calculated for each condition for 617 the male and female talker. Primary analysis consisted of a three-way RM-ANOVA, with the 618 factors 'Focusing approach' (wide, formant, or obstruent), 'Phoneme type' (consonant or 619 vowel), and 'Talker' (male or female). Contrasts were also run to compare performance for 620 the obstruent and formant focused approaches to the baseline wide-focused approach. Data 621 were determined to be normally distributed based on visual inspection, Kolmogorov-622 Smirnov, and Shapiro-Wilk tests. Mauchly's test indicated that the assumption of sphericity 623 had not been violated. The RM-ANOVA used an alpha level of 0.05.

- 624
- Planned *post-hoc* analyses were then conducted. These assessed whether the effect of
 formant and obstruent focusing (compared to the baseline wide focusing) differed across all
 phonemes or for consonants or vowels alone. A Bonferroni-Holm correction⁶⁶ for multiple
 comparisons applied was applied (3 comparisons in total).
- 629
- 630 A second set of unplanned two-tailed *t*-tests were also conducted. These assessed the 631 differences between the baseline (wide focusing) and either the formant focused or

- obstruent focused conditions for each phoneme subgroup (see Table 2). A Bonferroni-Holm
- 633 correction for multiple comparisons was applied (25 comparisons in total).
- 634
- 635 Finally, six Pearson's correlations were run between either participant age or detection
- 636 thresholds for a 125 Hz vibro-tactile tone (measured during screening) and the overall
- 637 phoneme discrimination scores with either the wide focused, formant focused, or obstruent
- 638 focused approach. These exploratory additional analyses were not corrected for multiple
- 639 comparisons, as it was hypothesised that no correlation would be found in any of these
- 640 conditions, following results from previous studies (e.g., ¹⁸).

641 Data Availability

- 642 The datasets generated and analysed during the current study are available in the University
- of Southampton's Research Data Management Repository at:
- 644 <u>https://doi.org/10.5258/SOTON/D2969</u>

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652 Author Contributions

- 653 M.D.F. and C.A.V. designed the experiment, M.D.F. implemented the experiment, and E.A.
- and S.W.P. collected the data. M.D.F. and S.W.P. generated the figures. M.D.F. performed
- 655 the data analysis and wrote the manuscript text. All authors reviewed the manuscript.

656 Competing Interests

657 The authors declare no competing interests.

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