

1 Title: Speech motor facilitation is not affected by ageing but is modulated by task demands during
2 speech perception

3

4 Abbreviated title: Effect of ageing on speech motor cortex

5

6 Helen E. Nuttall¹, Gwijde Maegherman², Joseph T. Devlin³, Patti Adank²

7

8 1. Department of Psychology, Lancaster University, Fylde College, Fylde Avenue, Lancaster, UK, LA1
9 4YF

10 2. Department of Speech, Hearing and Phonetic Sciences, University College London, Chandler
11 House, 2 Wakefield Street, London, UK, WC1N 1PF

12 3. Department of Experimental Psychology, University College London, 26 Bedford Way, London, UK,
13 WC1H 0AP

14

15 Corresponding author: Dr Helen Nuttall, Department of Psychology, Lancaster University, Fylde
16 College, Fylde Avenue, Lancaster, UK, LA1 4YF

17

18 Acknowledgements: We gratefully acknowledge Dan Kennedy-Higgins' contribution to data
19 collection and SRT material development, as well as the time and effort given by all the participants
20 who took part in this study. This work was funded by a Project Grant from The Leverhulme Trust,
21 RPG-2013-254.

22

23 Conflict of interest: Authors report no conflict of interest.

24

25

26

27

28

29

30

31

32

33

34

35 Abstract

36 Motor areas for speech production activate during speech perception. Such activation may
37 assist speech perception in challenging listening conditions. It is not known how ageing affects the
38 recruitment of articulatory motor cortex during active speech perception. This study aimed to
39 determine the effect of ageing on recruitment of speech motor cortex during speech perception.

40 Single-pulse Transcranial Magnetic Stimulation (TMS) was applied to the lip area of left
41 primary motor cortex (M1) to elicit lip Motor Evoked Potentials (MEPs). The M1 hand area was tested
42 as a control site. TMS was applied whilst participants perceived syllables presented with noise (-10, 0,
43 +10 dB SNRs) and without noise (clear). Participants detected and counted syllables throughout MEP
44 recording. Twenty younger adult subjects (aged 18-25) and twenty older adult subjects (aged 65-80)
45 participated in this study.

46 Results indicated a significant interaction between age and noise condition in the syllable
47 task. Specifically, older adults significantly misidentified syllables in the 0 dB SNR condition, and missed
48 the syllables in the -10 dB SNR condition, relative to the clear condition. There were no differences
49 between conditions for younger adults. There was a significant main effect of noise level on lip MEPs.
50 Lip MEPs were unexpectedly inhibited in the 0 dB SNR condition relative to clear condition. There was
51 no interaction between age group and noise condition. There was no main effect of noise or age group
52 on control hand MEPs. These data suggest that speech-induced facilitation in articulatory motor cortex
53 is abolished when performing a challenging secondary task, irrespective of age.

54 Keywords: speech perception; ageing; motor cortex; TMS; MEPs

55

56 1. Introduction

57 It is well-known that age-related auditory and cognitive decline lead to difficulty
58 understanding speech in social settings, particularly when background noise is present (Pichora-
59 Fuller, 2003; Pichora-Fuller et al., 2016). Difficulty communicating in noise leads to reduced social
60 interaction in noisy environments, increasing isolation and decreasing mental wellbeing. Indeed,
61 several studies have found a significant relation between age-related hearing loss and the incidence
62 of cognitive decline and dementia (Gurgel et al., 2014; Thomson, Auduong, Miller, & Gurgel, 2017).
63 The relation between age-related hearing loss and cognitive decline remains after controlling for
64 age, gender, race, education, diabetes, smoking history, and hypertension (Peelle & Wingfield,
65 2016). It is therefore essential to understand how the neurobiological network subserving speech
66 perception changes with age, so we can best support social communication throughout the ageing
67 process.

68 Results from past studies indicate that brain areas including and extending beyond primary
69 and association auditory cortices are important for successful speech perception. Cortical regions
70 including, but not limited to, ventral premotor cortex, inferior frontal gyrus, and supplementary and
71 primary motor areas have also been suggested to be involved in speech perception (Adank, Davis, &
72 Hagoort, 2012; Londei et al., 2010; Schwartz, Basirat, Ménard, & Sato, 2012; Skipper, Devlin, &
73 Lametti, 2017; Tremblay, Sato, & Small, 2012). Indeed, it is now largely accepted that articulatory
74 motor areas are active when we perceive speech (Bartoli et al., 2015; Pulvermüller & Fadiga, 2010;
75 Smalle, Rogers, & Möttönen, 2014). The extent of motor activation during speech perception varies
76 depending on the acoustic properties of the stimulus and listening conditions. Murakami et al.
77 (2011) demonstrated that lip motor evoked potentials (MEPs), elicited by transcranial magnetic
78 stimulation (TMS) to the lip area of primary motor cortex (M1) are enhanced when perceiving

79 speech in noise relative to perceiving speech without noise. This finding has been interpreted to
80 reflect increased excitability in the cortical motor representation of the lips when listening to
81 degraded speech. This effect has been replicated and extended using similar paradigms and different
82 types of stimuli containing internal and external distortions (Nuttall, Kennedy-Higgins, Devlin, &
83 Adank, 2018; Nuttall, Kennedy-Higgins, Hogan, Devlin, & Adank, 2016; Nuttall, Kennedy-Higgins,
84 Devlin, & Adank, 2017). Relatedly, if a listener perceives speech that they believe to be dissimilar to
85 the speech they themselves produce, i.e., due to a different accent, there is greater speech motor
86 activity during perception of these speech utterances (Bartoli et al., 2015). This result indicates that
87 motor recruitment during speech perception is proportional to the variability and unpredictability in
88 the auditory environment, as well as to listening difficulty.

89 Knowledge of the motor contribution to human speech perception, and of the
90 neurobiological network for human speech perception in general, has been largely derived through
91 studying speech processing in younger adults. It remains unclear if healthy ageing engages a similar
92 neurobiological network, with similar scalable activity across motor areas. It has been hypothesised,
93 however, that in response to age-related sensory decline, there is compensatory recruitment of
94 more general cognitive areas (Du, Buchsbaum, Grady, & Alain, 2016; Erb & Obleser, 2013). Indeed,
95 neuroimaging evidence indicates that prefrontal regions associated with cognitive control, attention,
96 and working memory show increased activation when older adults process speech under challenging
97 listening conditions (Erb & Obleser, 2013; Peelle, Troiani, Grossman, & Wingfield, 2011; Vaden,
98 Kuchinsky, Ahlstrom, Dubno, & Eckert, 2015). It remains unclear whether similar adaptive
99 recruitment also occurs within the neurobiological network for speech processing. The speech motor
100 system may be a particular candidate for such adaptive activity following sensory decline, given
101 speech motor activity scales relative to the variability and unpredictability in the auditory
102 environment, as well as to listening difficulty (Bartoli et al., 2015; Murakami et al., 2011; Nuttall et
103 al., 2017).

104 One recent study used functional magnetic resonance imaging (fMRI) to investigate such
105 neurobiological adaptations in ageing during speech perception (Du et al., 2016). Speech motor
106 areas showed phoneme-specific activation to different consonant-vowel syllable (/ba/, /ma/, /da/
107 and /ta/) when listening to speech in noise. However, bilateral auditory cortices showed phoneme-
108 specific activation only when the noise was absent or presented at a very low level. Importantly, a
109 positive correlation under noise masking between activity in speech motor regions and behavioural
110 accuracy was observed in older adults, which indicated a possible compensatory frontal
111 upregulation. Furthermore, this sensorimotor integration occurred at lower task demands in older
112 adults compared with young adults. This increased sensorimotor integration at lower task demands
113 could indicate that older adults engage more speech motor compensation during perception of
114 speech in noise, even at low levels of noise, compared to younger adults.

115 Relatedly, Panoullieres and colleagues (2018) investigated the excitability of tongue motor
116 cortex during passive speech perception in younger and older listeners, using TMS and tongue MEPs
117 as a real-time quantification of activity in the motor pathway to the tongue muscles. It was observed
118 that the excitability of the tongue motor pathway was similarly facilitated during perception of clear
119 speech in younger and older adults with normal hearing, whereas tongue excitability during
120 perception of speech was reduced in older adults with hearing loss. This study suggests that ageing
121 alone does not enhance speech motor facilitation during passive speech perception. However, the
122 finding that speech motor facilitation is not enhanced contrasts with the findings of Du and
123 colleagues (2016), who found that ageing resulted in enhanced motor activity during active speech
124 perception. One reason for these contrasting results may arise from methodological differences in

125 the two studies. Du et al. (2016) utilised an active speech perception task where participants had to
126 detect phonemes, whereas Panoullieres et al. (2018) tested passive speech perception. It therefore
127 seems likely that the task-demands imposed on the listener can modulate observed motor activity
128 and are relevant to understanding how neurobiological activity during speech processing changes
129 with ageing.

130 Our study aimed to determine how ageing influences speech motor excitability during active
131 speech perception using TMS to measure MEPs. Participants detected speech syllables under
132 different levels of background noise. With regards to ageing, we had two alternative hypotheses: 1)
133 If the motor compensation hypothesis is supported, then older adults will show greater lip
134 excitability compared to younger adults particularly when cognitive load is high, in line with fMRI
135 data from Du et al (2016). 2) If motor activation is maintained and does not adapt as we age, then
136 there will be no difference in lip excitability between younger and older adults, in line with MEP data
137 from Panoullieres et al (2018). We also measured a number of variables to ascertain if subjects
138 differed in cognitive or speech processing ability as a function of age, including memory, hearing,
139 cognitive ability, and speech reception threshold.

140

141 2. Methods

142 2.1 Subjects

143 Forty subjects took part in the study; 20 younger adults (8 males); average age: 20.5, (SD
144 0.4), and 20 older adults (9 males); average age: 69.2 (SD 2.3). All subjects were right-handed,
145 monolingual, native speakers of British English, with reportedly normal language function.
146 Handedness was established via self-report. All participants reported normal hearing. Pure-tone
147 audiometric hearing thresholds were established using a diagnostic audiometer (AD229b,
148 Interacoustic A/S, Denmark) in accordance with The British Society of Audiology Recommended
149 Procedure (The British Society of Audiology, 2011), across 0.25, 0.5, 1, 2, and 8 kHz bilaterally. All
150 younger subjects had clinically normal thresholds bilaterally across all frequencies of ≤ 20 dB Hearing
151 Level (HL). The older adult group had clinically normal thresholds from 250 Hz through to 1 kHz, mild
152 hearing impairment at 2 and 4 kHz, and moderate impairment at 8 kHz. Pure-tone average (PTA)
153 audiometric thresholds were computed across the major speech frequencies from 500 Hz to 4 kHz
154 averaged across both ears, and this value was used for subsequent analyses. Subjects presented no
155 TMS contraindications, and did not report any neurologic/psychiatric disease, or that they were
156 under the effect of neuroactive drugs. All subjects had a minimum high school-level education, with
157 the majority studying to University level. There was no significant difference in educational level
158 between the two groups ($p > 0.2$). Younger subjects were recruited via a university research
159 participation platform, and older subjects were recruited via local community groups. Experiments
160 were undertaken with the understanding and written consent of each subject, according to the
161 university's Research Ethics Board (UREC #0599/001).

162

163 2.2 Speech stimuli

164 Stimuli consisted of twenty vowel-consonant-vowel (VCV) syllables containing an equal
165 distribution of lip- (/apa/, /aba/) or tongue-articulated (/ata/, /ada/) syllables. All stimuli were
166 recorded in a sound-attenuated room and produced by a twenty-seven year old female British
167 English speaker with an average vocal pitch of 215 Hz. All stimuli were naturally produced to be of

168 approximately the same duration (mean 975 ms) but were not synthetically manipulated to be
169 precisely the same length. Stimuli varied by a standard deviation of 61 ms. All stimuli were produced
170 with natural falling intonation, with stress placed on the initial syllable. Audio digitizing was
171 performed at 44.1kHz with 16 bits. All syllables were amplitude root-mean-square normalized offline
172 using Praat (Boersma and Weenink, 2016), and then presented using Matlab (R2013a; The
173 Mathworks Inc., Natick, MA) through ultra-shielded insert earphones (ER-2; Intelligent Hearing
174 Systems, FL), at a comfortable level of around 65 dB SPL. The presentation level was consistent
175 across subjects. For each subject, a stimulus list containing five occurrences of /apa/, /aba/, /ata/
176 and /ada/ stimuli was randomly permuted, and stimuli were presented according to this order. This
177 was repeated twice without cessation for all conditions (40 stimuli presented in total for each
178 condition). The speech-shaped noise used in the speech-in-noise conditions was created in Matlab
179 using a custom-written script, and contained the same long-term average spectrum as speech, but
180 without amplitude modulation. It is a non-speech noise signal. The noise was presented at three
181 different signal-to-noise ratios, with the noise presented either 10 dB SPL less than the speech, at
182 the same dB SPL as the speech, or 10 dB SPL more than the speech. The experiment took place in a
183 non-Faraday caged, double-walled sound-attenuating booth.
184

185 2.3 Design

186 The experiment was designed to test how activity in lip M1 is differentially modulated in
187 older and younger adults when actively listening to speech presented at different signal-to-noise
188 ratios (SNRs). The noise levels were chosen to cover a range of SNRs from favourable to challenging
189 due to a paucity of data on how speech motor processing interacts with speech-in-noise. Subjects
190 were instructed to listen to the speech stimuli attentively and identify the consonant in the vowel-
191 consonant-vowel sounds presented. The order of experimental conditions was randomised. The
192 following four experimental conditions were tested in blocks:

- 193 1) Clear: speech only
- 194 2) At an SNR +10 dB SPL: speech stimuli were presented in speech-shaped noise that was
195 10 dB SPL less intense than the speech
- 196 3) At an SNR of 0 dB SPL, where speech and noise were at an equivalent intensity
- 197 4) At an SNR of -10 dB SPL: speech stimuli were presented in speech-shaped noise that was
198 10 dB SPL more intense than the speech

199

200 The order of conditions was randomised across participants and all MEP data were collected within a
201 single session. To ensure active engagement with the speech stimuli, subjects were asked to listen
202 carefully to the speech sounds and to identify the consonant in the middle of the sound as either a
203 'p', 'b', 't' or 'd'. At the start of each condition, subjects were instructed to count how many syllables
204 containing consonant 'x' were presented (where 'x' was either 'p', 'b', 't', or 'd'). Which consonant
205 they were asked to listen to and count was randomised across participants and conditions. Subjects
206 were asked to retain this information in memory until the end of the condition, when they could
207 report it verbally to the experimenter. Subjects were not given any aids, writing or otherwise, to
208 assist them with counting the number of stimuli, and were instructed not to overtly articulate any
209 information or use finger-counting. All TMS conditions took place in one session, which lasted
210 approximately two hours. Subjects returned for a second session lasting approximately 1 hour 30
211 minutes, where PTA, working memory, short-term memory, Montreal Cognitive Assessment
212 (MOCA), and speech reception thresholds (SRTs) were also measured. No aspect of the sessions

213 were video-recorded, and verbal responses were verified by the experimenter, who was present
214 with the participant throughout both sessions.

215 2.4 Transcranial magnetic stimulation

216 Monophasic single TMS pulses were generated by a Magstim 200 unit and delivered by a
217 70mm diameter figure-of-eight coil, connected through a BiStim2 module (Magstim Co Ltd,
218 Whitland, UK) set to simultaneous discharge mode (inter-pulse spacing of 1 ms). The coil was placed
219 tangential to the skull at a 45 degree angle from the midline such that the induced current flowed
220 from posterior to anterior under the junction of the two wings of the figure-of-eight coil. The lip area
221 of M1 was found by using the functional 'hot spot' localization method, whereby application of TMS
222 elicits an MEP from the contralateral muscle, which is under active contraction at approximately 20%
223 of a subject's maximal contraction. Here, the coil position is adjusted in millimetre movements to
224 ascertain the location on the scalp at which the most robust MEPs are elicited. This location was
225 then marked on a cap and active motor threshold (aMT) determined, which constitutes the intensity
226 at which TMS pulses elicited 5 out of 10 MEPs with an amplitude of at least 200 μ V (Möttönen,
227 Rogers, & Watkins, 2014). In this way, we first located the hand area by asking subjects to perform a
228 pinching action where the index finger was held against the thumb to activate the first dorsal
229 interosseous. Following this, participants were asked to purse their lips (see section 3.5
230 Electromyography for details) and the lip area 'hot spot' was identified by moving the coil ventrally
231 and slightly anterior until an MEP was observed in the contralateral lip muscle, and the aMT
232 identified – this method is well documented in MEP literature and is a valid way to localise M1 in the
233 absence of subject-specific MRI scans (Möttönen et al., 2014). In the younger group, the mean aMT
234 for lip was 50% (SD 5.4%), and 40% for the hand (SD 7%). For the older group, mean aMT for lip was
235 45% (SD 7.4%), and 37% (SD 6.5%) for the hand. A mixed ANOVA with 'muscle threshold' as the
236 within-subjects factor (lip, hand), and 'age group' as the between-subjects factor (older adults,
237 younger adults) indicated a significant difference between lip and hand motor thresholds ($F(1,38) =$
238 $40.70, p < 0.001$), which is to be expected as hand motor thresholds are known to be lower than
239 speech motor thresholds (Adank, Nuttall, & Kennedy-Higgins, 2016). There was no significant
240 interaction between age group and motor threshold ($F(1,38) = .62, p = .44$). The intensity of the
241 stimulator was set to 120% of individual participants' aMT for the stimulation applied during the
242 experiment in order to ensure individual TMS pulses elicited a measurable MEP.

243 After establishing TMS test intensity, all subjects then received four test blocks of single-
244 pulse TMS to the lip area of M1 in the left hemisphere, and four blocks of single-pulse TMS to the
245 hand area of M1 in the left hemisphere. The muscle order was randomised across subjects, and all
246 blocks of muscle data were collected consecutively. During the TMS test blocks, subjects were
247 presented with the speech stimuli, and were asked to listen and count syllabic information (see
248 Methods 2.3). During the presentation of each speech stimulus, Matlab (R2013a; The Mathworks
249 Inc., Natick, MA) was used to externally trigger the TMS system, such that a TMS pulse was
250 generated 100 ms after the onset of the consonant in each stimulus type. TMS timing was based on
251 previous MEP studies where excitability of the left articulatory motor cortex has been found to occur
252 from 100 ms during speech perception (Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Sato, Buccino,
253 Gentilucci, & Cattaneo, 2010). All speech stimuli were accompanied by a TMS pulse; therefore, all 40
254 stimuli in each block were presented with TMS. There was an inter-stimulation delay of between 4.5-
255 5 s. Participants were given short breaks in between TMS test conditions, during which time the coil
256 was changed to prevent over-heating.

257
258

259 2.5 Electromyography

260 Electromyographic (EMG) activity was recorded from the lip muscle orbicularis oris using
261 surface electrodes (Ag/AgCl; 10-mm diameter) in a non-Faraday caged, double-walled sound-
262 attenuating booth. Electrodes were attached to the orbicularis oris on the right side of the mouth in
263 a bipolar montage, with an electrode placed at the right temple serving as a common ground. To
264 stabilize background EMG activity, subjects were trained for approximately five minutes to produce
265 a constant level of contraction (approximately 20-30% of maximum voluntary contraction) of the lip
266 muscles by pursing, which was verified via visual feedback of the ongoing EMG signal, in accordance
267 with standard practice for lip aMT thresholding (Möttönen et al., 2014; Watkins, Strafella, & Paus,
268 2003). Contraction of the lip muscle also facilitates a lower motor threshold relative to when the
269 muscle is at rest, enabling the use of lower levels of stimulation during the experiment. The raw
270 EMG signal was amplified by a factor of 1000, band-pass filtered between 100–2000 Hz, and
271 sampled at 5000 Hz online using a 1902 amplifier (Cambridge Electronic Design, Cambridge, UK), and
272 analog-to-digital converted using a Micro1401-3 unit (Cambridge Electronic Design, Cambridge, UK).
273 Continuous data were acquired and recorded using Spike2 software (version 8, Cambridge Electronic
274 Design, Cambridge, UK).

275

276 2.6 Speech processing ability

277 Participants' ability to perceive speech in noise was assessed by comparing their
278 performance on the Speech Reception Threshold (SRT) task (Plomp & Mimpen 1979a, 1979b). In this
279 task, sentences are presented in speech-shaped noise with the signal-to-noise ratio (SNR) varying
280 adaptively depending on individual participant performance. The task is designed to determine the
281 threshold at which participants can recognise about 50% of keywords in a sentence, and is similar to
282 clinically available speech perception tests.

283 The first sentence was presented at a favourable SNR, for example +20 dB. Correct
284 repetition of three or more keywords resulted in a reduction of 10 dB on subsequent trials, until
285 participants were unable to correctly repeat more than two keywords. At this point the SNR
286 increased in steps of 6dB until another reversal occurred (i.e., participants' correct repetition of
287 three or more of the keywords) with all subsequent changes occurring in steps of 4 dB. A reversal
288 refers to the shift in direction of SNR change from one trial to the next, for example, if a participant
289 repeated more than three keywords for four sentences in a row, then the SNR will reduce after each
290 sentence making the subsequent sentence on each occasion harder to perceive. If on the fifth
291 sentence the participant was unable to repeat at least three of the keywords, the SNR will increase
292 making the subsequent sixth trial easier to understand. Such a change in direction from decreasing
293 to increasing (or vice versa) SNR represents a 'reversal'. Participants' SRTs were computed by taking
294 the mean SNR (dB) from all trials where a reversal occurred tracking at 50% (Plomp & Mimpen,
295 1979a, 1979b).

296 After presentation of each sentence, participants were asked to repeat verbatim what they
297 heard. Responses were scored online immediately after each trial using a graphical user interface
298 (GUI) on a standard computer screen that was not visible to participants. Each sentence contained
299 five keywords upon which scoring was based, for example: "The MEAL was COOKED BEFORE the
300 BELL RANG" (keywords in uppercase letters). Keywords were also judged to be correct if
301 participants changed the grammatical number of presented words e.g. 'Meals' (plural) instead of
302 'Meal' (singular). All other digressions variations were scored as incorrect with no feedback given.

303 Orders of sentence list were counterbalanced using a Latin-square technique. All sentences
304 were pseudo-randomly ordered such that the order of presentation was different between
305 participants, but each sentence was only presented once per participant.

306

307 2.7 Digit span tasks

308 To determine forward and working memory spans, participants were presented with
309 auditory strings of digits of increasing length, which they were asked to repeat. At the start of the
310 task, participants were made aware they would be asked to repeat strings of digits in the forward
311 order (the order in which they had heard the digits), and then strings of digits in the reverse order,
312 depending on experimenter instruction. An example was given using a digit string of two, e.g. "8, 3".
313 Digits were read by the experimenter in a neutral voice and tone and at a rate of approximately one
314 digit per second. Participants were told that the first 6 strings of digits should be repeated in the
315 forward order, while the second 6 strings of digits should be repeated in the reverse order – this
316 change from forward to reverse order was also indicated verbally by the experimenter each time
317 during the task. The starting string was two digits long. If participants recalled at least five out of six
318 digits correctly, the test continued by increasing the number of digits to three, and so on. If
319 participants recalled fewer than five out of six digits correctly, the test was concluded. If participants
320 recalled five out of six digits for the forward but not the backward repetition, the backward
321 repetition task was concluded but the forward repetition task continued, and vice versa.

322

323 2.8 Data analysis

324 The difference score regarding syllables presented relative to syllables detected (syllables
325 presented-syllables detected) was calculated for each individual in each condition as a measure of
326 their active listening score. A score of zero would indicate perfect performance. A score greater or
327 less than zero would indicate less accurate performance. For the TMS data, individual EMG sweeps
328 starting 40 ms before the TMS pulse and ending 40 ms post-stimulation were exported offline from
329 the recording software into Matlab, where average MEPs were calculated for each condition in each
330 participant. MEPs exhibit substantial variability for reasons that are not fully understood, but may
331 reflect biological variation associated with the phase in the Mu rhythm at the time the MEP was
332 elicited, differences in neural recruitment, and differences in circadian rhythms (e.g., Keil et al.,
333 2014; Wassermann, 2002). Individual averages were rectified and the integrated area under the
334 curve (AUC) of this rectified EMG signal of each individual mean MEP was calculated from 8-35 ms
335 post-stimulation, which captured the time at which lip MEPs are expected to occur (Devlin &
336 Watkins, 2007). Deriving the area under the curve from averages in this manner was useful to
337 determine the systematic structure of the time-locked MEP, which removed subjective bias
338 associated with identifying the MEP window for each individual trial. The area under the curve of the
339 MEP was then converted into standard scores within-subjects (not standardised to group mean), to
340 control for inter-subject variability. The standardized AUCs of MEPs were used in the statistical
341 analyses. We included all MEP trials in the analysis and did not selectively pick trials with MEPs
342 exceeding a certain criterion in order to avoid bias. Raw (non-standardised) Lip and Hand AUCs were
343 tested (two-tailed) for age-group differences in AUC means and standard deviations. No significant
344 differences were observed ($p > 0.1$).

345 Statistical analyses were carried out using SPSS (version 28.0, IBM). Separate two-tailed
346 independent t-tests were conducted for the dependent variables of PTA, MOCA, SRT score, and

347 short-term, and working memory, with age group as the grouping factor. Mixed-factor ANOVAs were
 348 separately conducted on standardised lip MEP area under the curve (AUC) data, hand MEP AUC
 349 data, and active listening score data as the dependent within-subjects variables (4 levels: Clear, +10
 350 dB SNR, 0 dB SNR, -10 dB SNR), with age group as the between-subjects variable. To test our
 351 hypotheses, we conducted planned contrasts comparing the control condition (clear) to the three
 352 different noise conditions, to investigate whether speech motor processing differed depending on if
 353 the noise level was high (-10 dB SNR condition), medium (0 dB SNR condition), or low (+10 dB
 354 condition).

355

356 3. Results

357 3.1 Participant characteristics

358 Several cognitive variables were measured in order to determine whether the older and
 359 younger adults demonstrated differences in cognitive and speech processing abilities. Older adults
 360 had slightly lower scores on the test measuring cognitive ability, i.e., the MOCA, relative to the
 361 younger adults, but this pattern did not reach significance ($F(1,38) = 3.95, p = 0.054$; see Table 1 for
 362 participant characteristic data). The younger adults' short-term memory, as measured using the
 363 forwards digit span, was found to be significantly greater in capacity than the older adults' short-
 364 term memory ($F(1,38) = 5.44, p = 0.025$). There was no significant difference between older and
 365 younger adults' working memory capacities, measured using the backwards digit span ($F(1,38) =$
 366 $.975, p = 0.33$).

367 The results of the pure-tone audiometry averaged across both ears for all the tested
 368 frequencies are plotted in Figure 1A. The younger adults had normal thresholds at all tested
 369 frequencies. For the older adults, pure-tone thresholds were in the normal range (≤ 20 dB HL) across
 370 frequencies ranging from 250 Hz-1 kHz but indicated mild hearing impairment at 2 and 4 kHz, and
 371 moderate hearing impairment at 8 kHz. As expected, the pure tone average (PTA) across major
 372 speech frequencies 500 Hz to 4 kHz differed significantly between older and younger adults ($F(1,38)$
 373 $= 37.84, p < 0.001$). Older adults had significantly less sensitive hearing than the younger adults
 374 (higher hearing thresholds), in line with expected age-related hearing loss that occurs as a natural
 375 part of healthy ageing. There was an inter-aural PTA difference of 1.5 dB HL for older adults and 0.4
 376 dB HL for younger adults, but the groups were not significantly different ($t(38) = -1.85, p = .34$)

377 Speech perception skills were also tested by measuring speech reception thresholds (SRTs;
 378 see Methods for details). The SRTs for the older adults were significantly higher than the younger
 379 adults, indicating that older adults were not able to tolerate as much noise as the younger adults
 380 and could not report words as accurately in more intense levels of noise ($F(1,38) = 6.47, p = 0.015$).

381

382 Table 1. Participant characteristics of older and younger subject groups. Mean values represent
 383 mean raw scores (plus standard error [SE] for demographic variables measured. P-values represent
 384 significance of two-tailed independent t-tests used to compare younger and older groups.

385

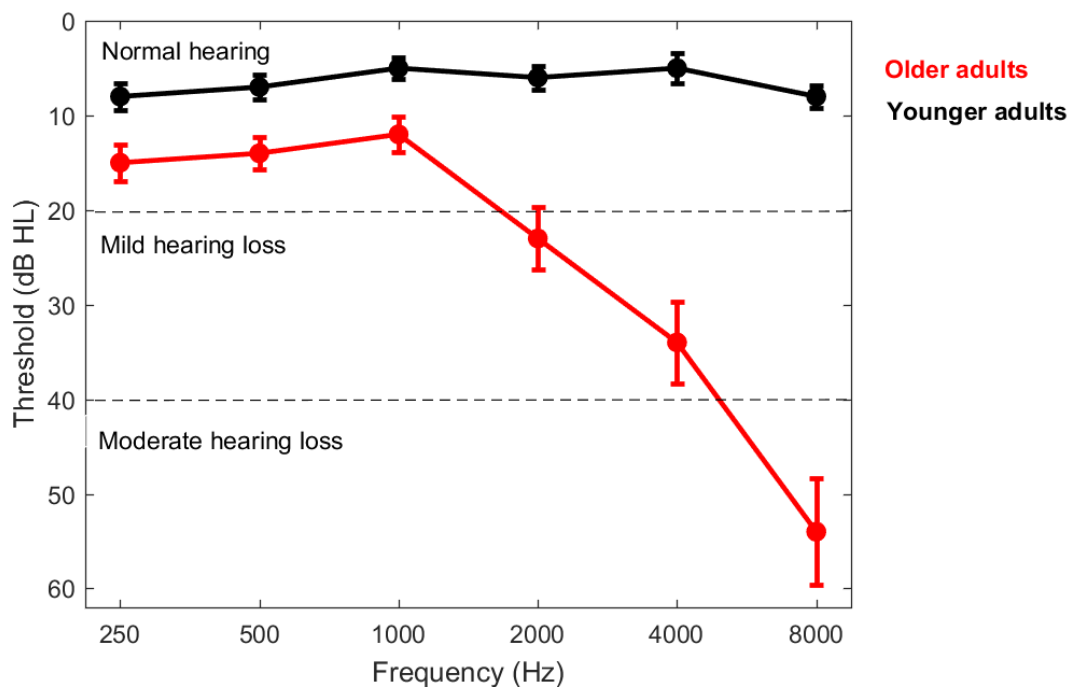
	Group	Mean (SE)	p-value
--	-------	-----------	---------

MOCA (cognitive ability)	Older	26.9 (0.3)	0.054
	Younger	27.8 (0.3)	
PTA (hearing sensitivity)	Older	20.7 (2.3)	<.001*
	Younger	5.8 (0.9)	
Digit span forwards (short-term memory)	Older	6.0 (0.2)	0.025*
	Younger	6.7 (0.2)	
Digit span backwards (working memory)	Older	4.9 (0.2)	0.33
	Younger	5.3 (0.3)	
SRT (speech reception threshold)	Older	-2.6 (0.5)	0.017*
	Younger	-4.1 (0.2)	

386

387

388



389

390

391 Figure 1. Bilateral audiometric threshold averages across all frequencies for older and younger
 392 populations. Error bars represent 1 SE.

393

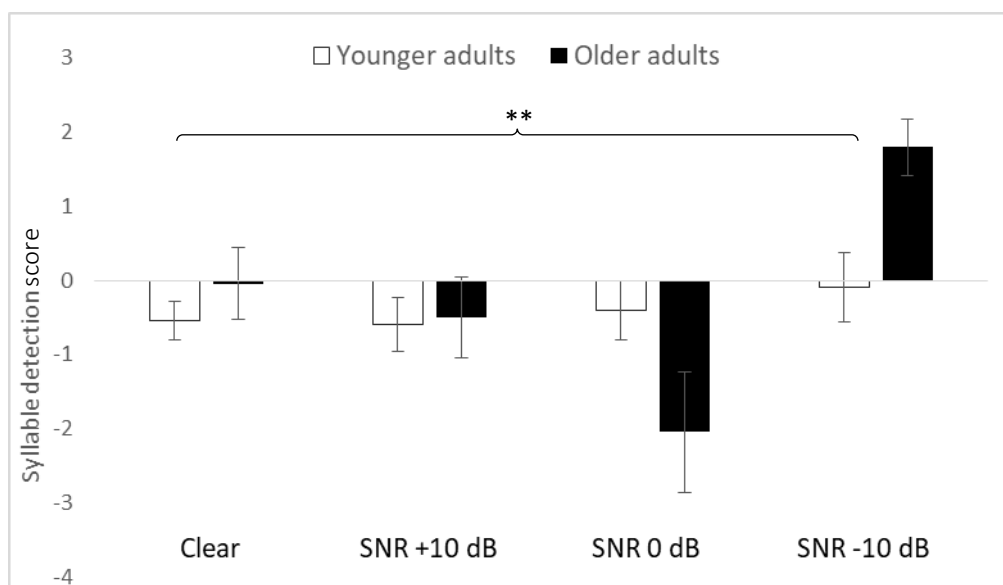
394 3.2 TMS behavioural data: Effect of age on active listening

395 During the TMS conditions, participants were asked to actively listen to the syllables and
 396 detect and count how many syllables of a certain type were presented, and to maintain this
 397 information in memory until the end of the condition. This was implemented to ensure participants

398 were engaging with the stimuli. At the end of each condition, we computed participants' active
 399 listening scores, by subtracting the number of syllables detected by the participant from the number
 400 of syllables actually presented in the condition. The active listening scores are shown in Figure 2 as a
 401 function of listening condition.

402 An active listening score of zero would indicate perfect performance (same number of
 403 syllables detected and counted as were presented). Any deviation from zero, therefore, represents
 404 an error in active listening. Specifically, a positive score would be indicative of stimuli being missed
 405 altogether (more stimuli presented than reported), whereas a negative score would be indicative of
 406 stimuli being misperceived (more stimuli reported than presented). Data in Figure 2 indicate that
 407 active listening ability varied as a function of listening condition in the older adults (black bars) but
 408 was reasonably consistent across listening conditions in the younger adults (white bars).

409



410

411

412 Figure 2. Mean active listening scores expressed as difference between syllables presented-syllables
 413 detected per condition, in both older adults (black bars) and younger adults (white bars). To achieve
 414 an active listening score of zero would indicate perfect performance (same number of syllables
 415 detected as presented). Any deviation from zero represents an error in syllable detection. Error bars
 416 represent 1 SE.

417

418 The mixed ANOVA confirmed a significant interaction between active listening scores and
 419 age group ($F(3,114) = 5.29, p = 0.002$). Planned contrasts indicated a significant difference in active
 420 listening scores in the Clear condition versus the 0 dB SPL condition ($F(1,38) = 4.7; p = 0.04$), and the
 421 Clear condition versus the -10 dB SNR condition ($F(1,38) = 11.4; p = 0.003$ [mean score Clear: -0.5 [SE
 422 0.4]; mean score 0 dB SNR: -2.1, [SE 0.6]; mean score SNR -10 dB SNR: 1.8 [SE 0.4]) in the older
 423 adults. There was no significant difference between Clear and +10 dB SNR in the older adults ($p >$
 424 0.5). There were no significant differences in any planned contrasts in the younger group (all $p > 0.4$).

425 In order to evaluate whether the significant interaction between age group and listening
 426 scores was driven by hearing acuity, we ran an exploratory analysis that including PTA (see Table 1)

427 as a covariate. The original study was powered for a 2 x 4 ANOVA, so it is likely that this exploratory
428 analysis may lack sufficient power. The ANCOVA with the PTA covariate added did not eliminate the
429 significant age group x listening score interaction ($p = 0.002$). It also did not impact the main effect of
430 listening condition ($p = 0.002$). There was also no significant interaction with the covariate ($p > 0.1$).
431 Based on these findings, the interaction between age group and listening score appears robust.

432 These findings indicate that the younger group made a similar (low) number of errors in
433 both the Clear condition and the noise conditions. The older group, however, made significantly
434 more errors in the SNR 0 dB and -10 dB conditions compared to the Clear condition. The poorer
435 performance of the older group in the SNR 0 dB condition suggests that they were more affected by
436 the background noise compared to the younger adults, such that they likely misperceived the stimuli
437 presented (more stimuli were reported than were presented). In the SNR -10 dB condition they were
438 also more adversely affected than the younger adults, and this resulted in stimuli being undetected
439 and thus missed entirely (relative to misperceived as in the SNR 0 dB condition).

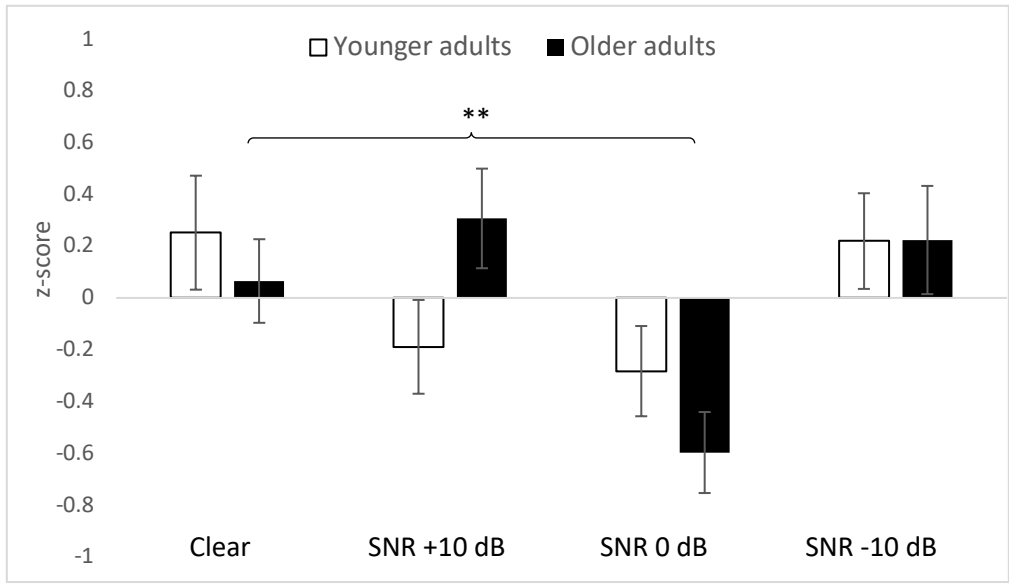
440 Taken together, these results indicate that the active listening task employed during the
441 TMS conditions did measure active listening ability in an age-sensitive manner. Specifically, active
442 listening was adversely affected at lower levels of noise in the older adult group, who first showed
443 decrements in the SNR 0 dB SPL condition.

444

445 3.3 TMS lip data: Effect of cognitive load but not ageing on lip MEPs

446 Figure 3 shows the effect of listening condition on lip MEP data, and indicates that MEPs
447 were inhibited in the 0 dB SNR condition relative to the other conditions. The mixed ANOVA
448 confirmed a significant effect of listening condition on MEP data ($F(3,114) = 3.92$; $p = 0.01$). Planned
449 contrasts indicated that there was a significant difference between MEPs in the Clear condition and
450 MEPs in the 0 dB SNR condition ($F(1,38) = 8.45$, $p = 0.006$). Z-scores indicate that MEPs were
451 inhibited (smaller) in the SNR 0 dB SPL condition relative to the Clear condition (SNR 0 dB SPL: -0.4
452 [SE 0.1]; Clear: 0.2 [SE 0.1]), suggesting that speech motor excitability was reduced in the SNR 0 dB
453 SPL condition compared to the Clear condition. There were no significant differences between the
454 Clear condition and the other noise conditions (SNR +10 dB SPL, $F(1,38) = 0.22$, $p = 0.64$; SNR -10 dB
455 SPL, $F(1,38) = 0.07$, $p = 0.79$). The interaction between listening condition and age group was not
456 significant ($F(3,114) = 1.37$, $p = 0.25$).

457



458

459

460

461

462

463

464

Figure 3. Mean lip MEP per condition in both older adults (black) and younger adults (white). MEP AUCs are expressed as z-scores, where a positive score indicates a larger response and a negative score indicates a smaller response, relative to the mean. Error bars represent 1 SE.

3.4 TMS hand data: No effect of cognitive load or ageing on hand MEPs

465

466

467

The control hand MEP data are shown in Figure 4. The mixed ANOVA confirmed that there was no significant effect of listening condition on hand MEP data ($F(3,114) = 0.89$; $p = 0.45$). The interaction between listening condition and age group was not significant ($F(3,114) = 0.57$, $p = 0.64$).

468

469

470

471

472

473

474

475

476

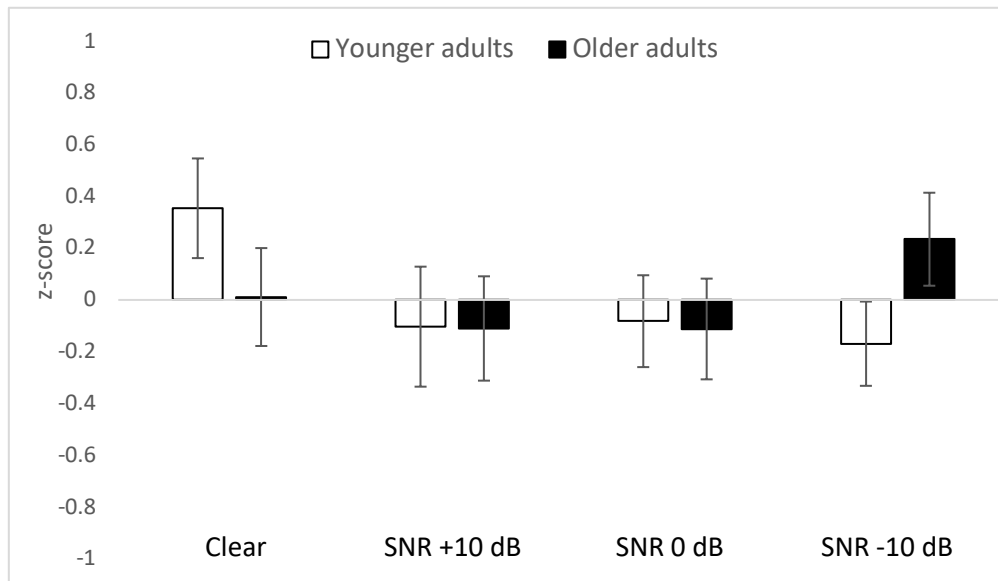
477

478

479

Taken together, these results indicate that excitability of the lip motor pathway during active speech perception was modulated by listening condition, and this modulation was not affected by age. Notably, the direction of this modulation was not as expected. Lip MEPs did not show evidence of the noise facilitation effect that others have found previously during passive speech perception (Nuttall et al., 2016; 2017). Instead, we found a novel observation that during active listening the noise facilitation effect is absent, and in the SNR 0 dB condition where stimuli were most frequently incorrectly misperceived according to the behavioural data (leading to a negative difference score), lip MEPs are instead inhibited. Importantly, this was not the case in the -10 SNR dB condition, where stimuli were most frequently missed altogether (leading to a positive difference score) and MEPs were not affected. Hand control data did not show evidence of any modulation, suggesting that this effect in the lip data does not represent a domain-general effect of active listening demands on the motor system, but is specific to lip motor cortex.

480



481

482

483 Figure 4. Mean hand MEP per condition in both older adults (black) and younger adults
 484 (white). MEP AUCs are expressed as z-scores, where a positive score indicates a larger response and
 485 a negative score indicates a smaller response, relative to the mean. Error bars represent 1 SE.

486

487 4. Discussion

488 The present study aimed to establish whether and how speech motor facilitation during speech
 489 perception is affected by age. We found that behavioural data from the active listening task
 490 involving syllable perception was significantly affected by age. Older adults made more errors in
 491 perception at medium noise levels, and missed many stimuli altogether at higher levels of noise,
 492 compared to younger adults who performed similarly across all noise levels. Interestingly, in
 493 contrast, we found no effect of age on the lip MEP data during perception of the stimuli. We also did
 494 not observe the expected noise facilitation effect in the MEP data. Instead, lip MEP data were
 495 suppressed in the medium noise condition (0 dB SNR) in both groups. We speculate that this novel
 496 and unexpected finding is a consequence of the active listening task that we used to ensure
 497 participants were actively engaging with the speech stimuli during MEP recording, as opposed to
 498 listening passively. One possibility it that engagement in this active listening task blocked the
 499 expected motor facilitation effect in the noise conditions. Furthermore, rather than totally abolish
 500 the motor facilitation effect, in the 0 dB condition the lip MEPs were indeed inhibited, showing
 501 evidence of a reversal of the predicted noise-facilitation effect.

502 Data from vision-based automatic imitation experiments shed important light on our finding
 503 of inhibited motor facilitation associated with the active listening task. Crucially, visuo-motor
 504 experiments find that attention plays a central role in the motor resonances that typically occur in
 505 the motor pathways involved in the execution of the action being visually perceived (Cracco et al.,
 506 2018; Heyes, 2011). Puglisi and colleagues (2018) note that adding a demanding perceptual
 507 secondary task, as we have done by asking participants to 1) selectively detect syllables and 2) count
 508 and maintain the total number detected in memory, can have a profound influence on the coding of
 509 the perceived action, resulting in the modification (Catmur, 2016) or even in the elimination (Bach,
 510 Peatfield, & Tipper, 2007; Chong, Cunnington, Williams, & Mattingley, 2009; Gowen, Bradshaw,

511 Galpin, Lawrence, & Poliakoff, 2010) of the resulting motor resonances. Our data seem to be
512 consistent with this explanation. The active listening requirement of our task, which was used to
513 ensure participants engaged with the stimuli, effectively added additional attentional demands
514 during speech perception that modulated speech motor resonances.

515 Relatedly, neuroimaging studies have shown that facilitation of motor cortex during action
516 observation is not an automatic event, but instead the effect scales relative to what attentional
517 resources are available to the observer at the time of perception (Bach et al., 2007; Chong et al.,
518 2009; Muthukumaraswamy & Singh, 2008; Perry & Bentin, 2010; Woodruff & Klein, 2013). This
519 highlights the possibility that motor resonances do not deploy in a binary fashion. Such a possibility
520 has been observed in facilitated (larger) speech MEPs during perception of speech in noise relative
521 to speech without noise, during passive speech perception. Whilst this may be the case during
522 passive speech perception, as has been repeatedly demonstrated, the elimination and suppression
523 of the motor facilitation effect during active speech processing underscores the complexity of the
524 motor resonance response. Indeed, data from the present study indicate that motor resonances can
525 be modulated by top-down influences associated with task demands. We did not include a non-
526 speech condition in our design, and therefore cannot verify the speech facilitation effect by
527 comparing speech data to non-speech data. However, the notion of speech motor facilitation is well-
528 documented in previous studies across several labs (Bartoli et al., 2015; Murakami, Kell, Restle,
529 Ugawa, & Ziemann, 2015; Nuttall et al., 2016; Nuttall, Kennedy-Higgins, Devlin, & Adank, 2018), and
530 thus the inclusion of a non-speech condition is not essential for the interpretation we are proposing
531 here.

532 One interpretation for these results is that attention modulates early auditory processing,
533 which affects subsequent later sensorimotor integration and resulted in the modulatory effect of the
534 present study's task demands on speech motor resonances during speech processing. Indeed,
535 electrophysiological evidence from auditory cortex has shown that selective attention decreased
536 neural responses to distractors relative to auditory targets (Schwartz & David, 2018). This
537 suppression enhanced neural target detection thresholds, suggesting that limited attention
538 resources serve to focally suppress responses to distractors that interfere with target detection. It
539 would therefore be interesting to know if the motor responses to the syllables that participants had
540 been told to selectively attend to were enhanced relative to the other distractor syllables. However,
541 as the present experiment was not designed to specifically test the effect of selective attention on
542 the speech motor system, this analysis is not possible as there are too few selectively attended trials
543 within each condition to perform any meaningful analysis. It is an important goal of our future work,
544 however, to explore this effect, and to test how it scales with background noise.

545 It is also interesting to note that the MEP inhibition effect is present specifically in the 0 dB
546 SNR condition, and not in the most acoustically adverse -10 dB SNR condition. The behavioural data
547 may offer some insight into this pattern in the results. Active listening scores in the 0 dB SNR
548 condition were less accurate and led to a negative score for older adults especially, indicating that a
549 greater number of syllables were reported as detected than were actually presented. This
550 performance was in contrast to the -10 dB SNR condition, where active listening scores were also
551 less accurate particularly for the older adults, but the scores were positive, indicating that a smaller
552 number of syllables were reported as detected than were actually presented. It is possible that the
553 noise level in the -10 dB SNR was simply too adverse for the older participants to perform the task.
554 Hence, the stimuli were not sufficiently detectable to show any evidence of the neurophysiological
555 response being modulated by the divided attentional demands of the task, as it is not clear that the
556 task was performed as intended, as many of the stimuli were missed on average. Our behavioural

557 results reflect previous findings of speech perception ability in adult listeners, who often perform at
558 floor when tested on speech recognition in -10 dB SNR (Holder, Levin, & Gifford, 2018).

559 With respect to the original hypotheses that this paper set out to address, however, we did
560 not find any differences in speech motor excitability between younger and older adults during active
561 speech perception. This is in contrast to findings from Du et al (2016) and Panouilleres et al. (2018).
562 However, absence of evidence does not imply evidence of absence, and it is possible that the
563 conditions we employed, such as divided attentional demands, obscure any ageing differences.
564 Hence, we cannot conclude from these data alone that there are no differences in speech motor
565 activity between younger and older adults whatsoever. Panouilleres et al's (2018) TMS paradigm did
566 not require participants to use any active listening strategies, and Du et al's (2016) fMRI study used
567 selective but not divided attention. Importantly, the lack of a neurophysiological ageing effect is not
568 due to a lack of task sensitivity, nor a lack of sensory decline in the ageing group: task performance
569 was affected by age as older adults' task performance was more negatively affected by less adverse
570 SNRs compared to younger adults. Additionally, older adults' hearing was less sensitive compared to
571 younger participants. The conflation of attentional resources required to perform the task here may
572 have reduced what compensatory motor resources were available to draw upon, ultimately
573 obscuring any group differences that may exist. Further studies that manipulate attentional load and
574 task difficulty are warranted to test this possibility. It should be acknowledged that it is a limitation
575 of the current study that we did not systematically investigate the role of hearing and its impact on
576 the experimental MEP manipulation. Future work should evaluate the contribution of hearing, along
577 with other factors known to be affected by ageing, on cognition or speech perception. This study
578 used a mixed ANOVA approach to investigate the effect of age group and listening condition on the
579 dependent variables. For demographic characterisation and transparency, we collected data on our
580 sample with regards to common variables that differ as a function of age. A larger study that
581 employs, for example, a linear mixed effects approach could model how these variables interact with
582 age and listening condition, which would build on the present findings and provide useful insights
583 into the relationships explored in the present study.

584 In summary, whilst we found evidence to indicate that ageing reduces cognitive and sensory
585 functioning, we did not find evidence to suggest that the speech motor cortex compensates for this
586 reduced function. Interestingly, however, we did observe the surprising and unexpected finding that
587 speech motor cortex is modulated by task demands, i.e., the active listening requirement of the task
588 used to control participants' engagement with stimuli. Speech perception often occurs in the
589 context of competing information, whereby the brain must strategically allocate resources to
590 multiple tasks simultaneously (Gennari, Millman, Hymers, & Mattys, 2018). How the neurobiological
591 network for speech perception controls resource allocation during difficult listening conditions is not
592 well-understood. Our data shed new light on this topic and indicate that auditory-motor modulation
593 adapts based on the attentional resources available. Future work should seek to clarify the
594 relationship between sensorimotor integration and attention and extend this to concurrent auditory
595 and visual processing to better understand the role of the speech motor system in resource
596 allocation during speech perception.

597

598 References

599 Adank, P., Davis, M. H., & Hagoort, P. (2012). Neural dissociation in processing noise and accent in
600 spoken language comprehension. *Neuropsychologia*, *50*(1), 77–84.
601 <https://doi.org/10.1016/j.neuropsychologia.2011.10.024>

- 602 Adank, P., Nuttall, H. E., & Kennedy-Higgins, D. (2016). Transcranial magnetic stimulation and motor
603 evoked potentials in speech perception research. *Language, Cognition and Neuroscience*, 1–10.
604 <https://doi.org/10.1080/23273798.2016.1257816>
- 605 Bach, P., Peatfield, N. A., & Tipper, S. P. (2007). Focusing on body sites: the role of spatial attention
606 in action perception. *Experimental Brain Research*, 178(4), 509–517.
607 <https://doi.org/10.1007/s00221-006-0756-4>
- 608 Bartoli, E., D’Ausilio, A., Berry, J., Badino, L., Bever, T., & Fadiga, L. (2015). Listener-Speaker Perceived
609 Distance Predicts the Degree of Motor Contribution to Speech Perception. *Cerebral Cortex*,
610 25(2), 281–288. <https://doi.org/10.1093/cercor/bht257>
- 611 Catmur, C. (2016). Automatic imitation? Imitative compatibility affects responses at high perceptual
612 load. *Journal of Experimental Psychology. Human Perception and Performance*, 42(4), 530–539.
613 <https://doi.org/10.1037/xhp0000166>
- 614 Chong, T. T.-J., Cunnington, R., Williams, M. A., & Mattingley, J. B. (2009). The role of selective
615 attention in matching observed and executed actions. *Neuropsychologia*, 47(3), 786–795.
616 <https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2008.12.008>
- 617 Cracco, E., Bardi, L., Desmet, C., Genschow, O., Rigoni, D., De Coster, L., ... Brass, M. (2018).
618 Automatic imitation: A meta-analysis. *Psychological Bulletin*, 144(5), 453–500.
619 <https://doi.org/10.1037/bul0000143>
- 620 Devlin, J. T., & Watkins, K. E. (2007). Stimulating language: insights from TMS. *Brain : A Journal of*
621 *Neurology*, 130(Pt 3), 610–622. <https://doi.org/10.1093/brain/awl331>
- 622 Du, Y., Buchsbaum, B. R., Grady, C. L., & Alain, C. (2016). Increased activity in frontal motor cortex
623 compensates impaired speech perception in older adults. *Nature Communications*, 7(1), 12241.
624 <https://doi.org/10.1038/ncomms12241>
- 625 Erb, J., & Obleser, J. (2013). Upregulation of cognitive control networks in older adults’ speech
626 comprehension. *Frontiers in Systems Neuroscience*, 7, 116.
627 <https://doi.org/10.3389/fnsys.2013.00116>
- 628 Fadiga, L., Craighero, L., Buccino, G., & Rizzolatti, G. (2002). Speech listening specifically modulates
629 the excitability of tongue muscles: A TMS study. *European Journal of Neuroscience*, 15(2), 399–
630 402.
- 631 Gennari, S. P., Millman, R. E., Hymers, M., & Mattys, S. L. (2018). Anterior paracingulate and
632 cingulate cortex mediates the effects of cognitive load on speech sound discrimination.
633 *NeuroImage*, 178, 735–743. <https://doi.org/10.1016/J.NEUROIMAGE.2018.06.035>
- 634 Gowen, E., Bradshaw, C., Galpin, A., Lawrence, A., & Poliakoff, E. (2010). Exploring visuomotor
635 priming following biological and non-biological stimuli. *Brain and Cognition*, 74(3), 288–297.
636 <https://doi.org/10.1016/J.BANDC.2010.08.010>
- 637 Gurgel, R. K., Ward, P. D., Schwartz, S., Norton, M. C., Foster, N. L., & Tschanz, J. T. (2014).
638 Relationship of Hearing Loss and Dementia. *Otology & Neurotology*, 35(5), 775–781.
639 <https://doi.org/10.1097/MAO.0000000000000313>
- 640 Halm, D. S. (2015). The Impact of Engagement on Student Learning. *International Journal of*
641 *Education and Social Science Wwww.Ijessnet.Com*, 2(2). Retrieved from
642 <http://www.ijessnet.com/wp-content/uploads/2015/02/3.pdf>
- 643 Heyes, C. (2011). Automatic imitation. *Psychological Bulletin*, 137(3), 463–483.
644 <https://doi.org/10.1037/a0022288>

- 645 Holder, J. T., Levin, L. M., & Gifford, R. H. (2018). Speech recognition in noise for adults with normal
646 hearing: Age-normative performance for AzBio, BKB-SIN, and QuickSIN. *Otology and*
647 *Neurotology*, *39*(10), e972–e978. <https://doi.org/10.1097/MAO.0000000000002003>
- 648 Keil, J., Timm, J., Sanmiguel, I., Schulz, H., Obleser, J., & Schönwiesner, M. (2014). Cortical brain
649 states and corticospinal synchronization influence TMS-evoked motor potentials. *Journal of*
650 *Neurophysiology*, *111*(3), 513–519. <https://doi.org/10.1152/jn.00387.2013>
- 651 Londei, A., D'Ausilio, A., Basso, D., Sestieri, C., Gratta, C. Del, Romani, G.-L., & Belardinelli, M. O.
652 (2010). Sensory-motor brain network connectivity for speech comprehension. *Human Brain*
653 *Mapping*, *31*(4), 567–580. <https://doi.org/10.1002/hbm.20888>
- 654 Möttönen, R., Rogers, J., & Watkins, K. E. (2014). Stimulating the lip motor cortex with transcranial
655 magnetic stimulation. *Journal of Visualized Experiments : JoVE*, (88).
656 <https://doi.org/10.3791/51665>
- 657 Murakami, T., Kell, C. A., Restle, J., Ugawa, Y., & Ziemann, U. (2015). Left Dorsal Speech Stream
658 Components and Their Contribution to Phonological Processing. *Journal of Neuroscience*, *35*(4),
659 1411–1422. <https://doi.org/10.1523/JNEUROSCI.0246-14.2015>
- 660 Murakami, T., Restle, J., & Ziemann, U. (2011). Observation-execution matching and action inhibition
661 in human primary motor cortex during viewing of speech-related lip movements or listening to
662 speech. *Neuropsychologia*, *49*(7), 2045–2054.
663 <https://doi.org/10.1016/j.neuropsychologia.2011.03.034>
- 664 Muthukumaraswamy, S. D., & Singh, K. D. (2008). Modulation of the human mirror neuron system
665 during cognitive activity. *Psychophysiology*, *45*(6), 896–905. <https://doi.org/10.1111/j.1469-8986.2008.00711.x>
- 667 Nuttall, H.E., Kennedy-Higgins, D., Devlin, J. T., & Adank, P. (2018). Modulation of intra- and inter-
668 hemispheric connectivity between primary and premotor cortex during speech perception.
669 *Brain and Language*. <https://doi.org/10.1016/j.bandl.2017.12.002>
- 670 Nuttall, H.E., Kennedy-Higgins, D., Hogan, J., Devlin, J. T., & Adank, P. (2016). The effect of speech
671 distortion on the excitability of articulatory motor cortex. *NeuroImage*, *128*, 218–226.
672 <https://doi.org/10.1016/j.neuroimage.2015.12.038>
- 673 Nuttall, H.E., Kennedy-Higgins, D., Devlin, J. T., & Adank, P. (2017). The role of hearing ability and
674 speech distortion in the facilitation of articulatory motor cortex. *Neuropsychologia*, *94*, 13–22.
675 <https://doi.org/10.1016/j.neuropsychologia.2016.11.016>
- 676 Nuttall, H.E., Kennedy-Higgins, D., Devlin, J. T., & Adank, P. (2018). Modulation of intra- and inter-
677 hemispheric connectivity between primary and premotor cortex during speech perception.
678 *Brain and Language*. <https://doi.org/10.1016/j.bandl.2017.12.002>
- 679 Panouillères, M. T. N., & Möttönen, R. (2018). Decline of auditory-motor speech processing in older
680 adults with hearing loss. *Neurobiology of Aging*, *72*, 89–97.
681 <https://doi.org/10.1016/j.neurobiolaging.2018.07.013>
- 682 Peelle, J. E., Troiani, V., Grossman, M., & Wingfield, A. (2011). Hearing loss in older adults affects
683 neural systems supporting speech comprehension. *The Journal of Neuroscience : The Official*
684 *Journal of the Society for Neuroscience*, *31*(35), 12638–12643.
685 <https://doi.org/10.1523/JNEUROSCI.2559-11.2011>
- 686 Peelle, J. E., & Wingfield, A. (2016). The Neural Consequences of Age-Related Hearing Loss. *Trends in*
687 *Neurosciences*, *39*(7), 486–497. <https://doi.org/10.1016/j.tins.2016.05.001>

- 688 Perry, A., & Bentin, S. (2010). Does focusing on hand-grasping intentions modulate
689 electroencephalogram μ and α suppressions? *Neuroreport*, *21*(16), 1050–1054.
690 <https://doi.org/10.1097/WNR.0b013e32833fcb71>
- 691 Pichora-Fuller, M. K. (2003). Cognitive aging and auditory information processing. *International*
692 *Journal of Audiology*, *42*(sup2), 26–32. <https://doi.org/10.3109/14992020309074641>
- 693 Pichora-Fuller, M. K., Kramer, S. E., Eckert, M. A., Edwards, B., Hornsby, B. W. Y., Humes, L. E., ...
694 Wingfield, A. (2016). Hearing Impairment and Cognitive Energy. *Ear and Hearing*, *37*, 5S-27S.
695 <https://doi.org/10.1097/AUD.0000000000000312>
- 696 Plomp, R., & Mimpen, A. M. (n.d.). Improving the reliability of testing the speech reception threshold
697 for sentences. *Audiology : Official Organ of the International Society of Audiology*, *18*(1), 43–52.
698 Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/760724>
- 699 Plomp, R., & Mimpen, A. M. (1979). Speech-reception threshold for sentences as a function of age
700 and noise level. *The Journal of the Acoustical Society of America*, *66*(5), 1333–1342.
701 <https://doi.org/10.1121/1.383554>
- 702 Puglisi, G., Leonetti, A., Cerri, G., & Borroni, P. (2018). Attention and cognitive load modulate motor
703 resonance during action observation. *Brain and Cognition*, *128*, 7–16.
704 <https://doi.org/10.1016/j.bandc.2018.10.006>
- 705 Pulvermüller, F., & Fadiga, L. (2010). Active perception: sensorimotor circuits as a cortical basis for
706 language. *Nature Reviews. Neuroscience*, *11*(5), 351–360. <https://doi.org/10.1038/nrn2811>
- 707 Sato, M., Buccino, G., Gentilucci, M., & Cattaneo, L. (2010). On the tip of the tongue: Modulation of
708 the primary motor cortex during audiovisual speech perception. *Speech Communication*, *52*(6),
709 533–541. <https://doi.org/10.1016/j.specom.2009.12.004>
- 710 Schwartz, J.-L., Basirat, A., Ménard, L., & Sato, M. (2012). The Perception-for-Action-Control Theory
711 (PACT): A perceptuo-motor theory of speech perception. *Journal of Neurolinguistics*, *25*(5),
712 336–354. <https://doi.org/10.1016/j.jneuroling.2009.12.004>
- 713 Schwartz, Z. P., & David, S. V. (2018). Focal Suppression of Distractor Sounds by Selective Attention
714 in Auditory Cortex. *Cerebral Cortex*, *28*(1), 323–339. <https://doi.org/10.1093/cercor/bhx288>
- 715 Skipper, J. I., Devlin, J. T., & Lametti, D. R. (2017). The hearing ear is always found close to the
716 speaking tongue: Review of the role of the motor system in speech perception. *Brain and*
717 *Language*, *164*, 77–105. <https://doi.org/10.1016/j.bandl.2016.10.004>
- 718 Smalle, E. H. M., Rogers, J., & Möttönen, R. (2014). Dissociating Contributions of the Motor Cortex to
719 Speech Perception and Response Bias by Using Transcranial Magnetic Stimulation. *Cerebral*
720 *Cortex (New York, N.Y. : 1991)*. <https://doi.org/10.1093/cercor/bhu218>
- 721 Thomson, R. S., Auduong, P., Miller, A. T., & Gurgel, R. K. (2017). Hearing loss as a risk factor for
722 dementia: A systematic review. *Laryngoscope Investigative Otolaryngology*, *2*(2), 69–79.
723 <https://doi.org/10.1002/lio2.65>
- 724 Tremblay, P., Sato, M., & Small, S. L. (2012). TMS-induced modulation of action sentence priming in
725 the ventral premotor cortex. *Neuropsychologia*, *50*(2), 319–326.
726 <https://doi.org/10.1016/j.neuropsychologia.2011.12.002>
- 727 Vaden, K. I., Kuchinsky, S. E., Ahlstrom, J. B., Dubno, J. R., & Eckert, M. A. (2015). Cortical activity
728 predicts which older adults recognize speech in noise and when. *The Journal of Neuroscience :
729 The Official Journal of the Society for Neuroscience*, *35*(9), 3929–3937.
730 <https://doi.org/10.1523/JNEUROSCI.2908-14.2015>

- 731 Wassermann, E. M. (2002). Variation in the response to transcranial magnetic brain stimulation in
732 the general population. *Clinical Neurophysiology : Official Journal of the International*
733 *Federation of Clinical Neurophysiology*, 113(7), 1165–1171. Retrieved from
734 <http://www.ncbi.nlm.nih.gov/pubmed/12088713>
- 735 Watkins, K. E., Strafella, a. P., & Paus, T. (2003). Seeing and hearing speech excites the motor system
736 involved in speech production. *Neuropsychologia*, 41(8), 989–994.
737 [https://doi.org/10.1016/S0028-3932\(02\)00316-0](https://doi.org/10.1016/S0028-3932(02)00316-0)
- 738 Woodruff, C. C., & Klein, S. (2013). Attentional distraction, μ -suppression and empathic perspective-
739 taking. *Experimental Brain Research*, 229(4), 507–515. [https://doi.org/10.1007/s00221-013-](https://doi.org/10.1007/s00221-013-3612-3)
740 [3612-3](https://doi.org/10.1007/s00221-013-3612-3)
- 741