1   **Title:** Phonological processing in speech perception: what do sonority differences tell
2   us?

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34   **Abstract**

35   Previous research has associated the inferior frontal and posterior temporal brain regions
36   with a number of phonological processes. In order to identify how these specific brain
37   regions contribute to phonological processing, we manipulated subsyllabic phonological
38   complexity and stimulus modality during speech perception using fMRI. Subjects
39   passively attended to visual or auditory pseudowords. Similar to previous studies, a
40   bilateral network of cortical regions was recruited during the presentation of visual and
41   auditory stimuli. Moreover, pseudowords recruited a similar network of regions as speech
42   sounds and letters under a similar passive paradigm. However, few regions in the whole-
43   brain results revealed neural processing differences associated with phonological
44   complexity independent of modality of presentation. In an ROI analysis, the only region
45   sensitive to phonological complexity was the posterior part of the inferior frontal gyrus
46   (IFGpo), with the complexity effect only present for print. In sum, the sensitivity of
47   phonological brain areas depends on the modality of stimulus presentation and task
48   demands.
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1. Introduction

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69   Neuroimaging studies have identified a distributed network of brain regions

70   involved in the processing of phonological information during the perception of speech

71   sounds. For example, studies that have investigated phonological processing by

72   contrasting the processing of syllables or phonemes to the processing of complex

73   auditory stimuli (e.g. environmental sounds (Giraud & Price, 2001), bird songs

74   (Tremblay, Baroni, & Hasson, 2012), tones (Demonet et al., 1992; Poeppel et al., 2004;

75   Rimol, Specht, & Hugdahl, 2006; Vouloumanos, Kiehl, Werker, & Liddle, 2001), and

76   unintelligible speech sounds (Benson, Richardson, Whalen, & Lai, 2006; Liebenthal,

77   Binder, Spitzer, Possing, & Medler, 2005; Obleser, Zimmermann, Van Meter, &

78   Rauschecker, 2007; Okada et al., 2010)) have consistently reported clusters of activation

79   within the supratemporal gyrus (STG) and superior temporal sulcus (STS). In addition,

80   the presentation of auditory and/or orthographic stimuli (word and/or pseudowords)

81   requiring a phonological judgment recruits regions located within the inferior frontal

82   gyrus (IFG), the middle frontal gyrus (MFG) and the inferior parietal lobules (IPL)

83   (Booth et al., 2002; Burton, Locasto, Krebs-Noble, & Gullapalli, 2005; Burton, Small, &

84   Blumstein, 2000; Jacquemot, Pallier, LeBihan, Dehaene, & Dupoux, 2003; Kareken,

85   Lowe, Chen, Lurito, & Mathews, 2000; Poldrack et al., 2001).

86   Of particular interest is the observation that the IFG, MFG and IPL are typically

87   not recruited during passive listening (Deschamps & Tremblay, 2014; McGettigan et al.,

88   2011; Tremblay & Small, 2011) or passive reading of single letters (Van Atteveldt,

89   Formisano, Goebel, & Blomert, 2004). For example, studies that have used a passive

90   paradigm to examine specific phonological processes such as print-speech convergence

91   of letters (Van Atteveldt et al., 2004), or manipulated phonological complexity by

92   comparing single consonants to consonant clusters in words (Tremblay & Small, 2011),

93   pseudowords (McGettigan et al., 2011) and syllable sequences (Deschamps & Tremblay,

94   2014) during passive listening have not reported clusters of activation within the IFG, the

95   MFG and the IPL (Deschamps & Tremblay, 2014; McGettigan et al., 2011; Tremblay &

96   Small, 2011; Van Atteveldt et al., 2004). In fact, Deschamps and Tremblay (2014) and

97   Tremblay and Small (2011) reported that activation magnitude increased as a function of

98   syllabic complexity with auditory stimuli only within supratemporal plane regions,

99   whereas McGettigan et al. (2011) did not find any positive correlations between syllabic

100   complexity and brain activation. In addition, Van Atteveldt et al. (2004) found that the

101   passive viewing of letters activated the bilateral lateral and inferior occipital cortex, and

102   the passive listening to single speech sounds activated the bilateral primary auditory

103   cortex, the STG and the STS. Interestingly, the bilateral posterior STS and STG were

104   activated during both the passive viewing of letters and the passive listening to speech

105   sounds, suggesting that this region might be involved in heteromodal phonological

106   processing (i.e. multisensory convergence).

107   Logically, measuring brain activation when subjects are passively attending to

108   stimuli can target more automatic and obligatory phonological processes, whereas more

109   cognitively demanding tasks (e.g. discrimination, rhyme judgments) recruit additional

110   processes (i.e. verbal working memory, segmentation, rehearsal). While passive

111   processing of spoken or printed letters and words in the absence of a task does activate a

112   number of auditory and visual areas, as well as regions involved in phonological

113   processing, it is not clear whether the same is true of pseudowords. One study by Burton

114   and colleagues (2005) using two different tasks (i.e. rhyming and same/different

115   judgments) with auditory and visually presented words and pseudowords identified

116   regions that were modality-specific (i.e. left STG for auditory stimuli and right lingual

117   gyrus for visual stimuli) and a number of regions that were recruited across modalities,

118   stimulus type (i.e. words and pseudowords) and tasks (e.g.. left IFG, bilateral posterior

119   STG, left fusiform). Of particular interest is that Burton and colleagues (2005) found

120   more activation across brain regions for pseudoword judgments and interpreted the result

121   as reflecting greater articulatory recoding demands. In fact, differences between the

122   processing of words and pseudowords during tasks requiring a judgment and reading are

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123 well documented (Mechelli, Gorno-Tempini, & Price, 2003; Shaul, Arzouan, &
124 Goldstein, 2012; Simos et al., 2002; Xiao et al., 2005). Notwithstanding the importance
125 of these results, the findings raise the issue of whether the brain regions outside of
126 STS/STG were recruited because of the task or because of the pseudowords. This is a
127 potentially important issue in that pseudowords are often used to evaluate reading ability
128 differences in fluent and dysfluent readers (Shaul et al., 2012) and in children with
129 specific speech and language impairments (Macchi, Schelstraete, & Casalis, 2014). In
130 order to investigate more automatic phonological processes, we used a passive print and
131 speech pseudoword paradigm. By minimizing the influence of non-linguistic cognitive
132 functions and semantic/conceptual activation, the neural correlates associated with
133 automatic modality-specific or heteromodal phonological processes were investigated.

134   In the current study we used a metric of phonological complexity to examine
135 obligatory phonological processing targeting the structure of the syllable. Because
136 phonological complexity reflects more than simple speech/non-speech distinctions,
137 differences in stimulus length, or the presence or absence of consonant clusters, we
138 focused on sonority. Sonority has been used to explain a wide range of linguistic and
139 psycholinguistic phenomena (Bastiaanse, Gilbers, & Van Der Linde, 1994; Clements,
140 Kingston, & Beckman, 1990; Goad, 2010; Romani & Galluzzi, 2005; Zec, 1995). In this
141 study, we varied the sonority values of consonants within the initial consonant cluster (i.e.
142 CC) of the first syllable in pseudowords. The principle of sonority stipulates that speech
143 sounds can be characterized according to their placement along a scale (Clements et al.,
144 1990; Steriade, 1990) that captures the relative resonance of speech sounds (Clements,
145 2009). For example, in English, vowels are the most sonorous and stop consonants are
146 the least sonorous (Dobrovolsky & Katamba, 1996). Since each consonant and vowel has
147 a sonority value, sonority differences between two phonemes (in our case consonants)
148 can be calculated (Gierut, 2007). In a consonant cluster, the smaller the difference

between the sonority of two consonants, the more phonologically complex the cluster (for more details, refer to Gierut, 2007; Steriade, 1990). While, the influence of sonority on speech perception, speech production and reading has been documented behaviorally during language acquisition (first or second) and in neuropsychological populations (Baum, 2002; Fabre & Bedoin, 2003; Miozzo & Buchwald, 2013; Morrisette, Farris, & Gierut, 2006; Romani & Calabrese, 1998; Sperbeck & Strange, 2010), the neural correlates underlying the processing of sonority, to our knowledge, have not yet been investigated.

Informed by the results from previous studies, we expected to find a subset of regions located within the supratemporal plane and STS that have been identified by prior neuroimaging studies as relevant to phonological processing that would be sensitive to syllabic complexity while subjects are passively attending to visually- and/or auditorily-presented pseudowords; such a finding would highlight regions that are involved in obligatory and mandatory phonological processes and distinguish modality-specific from heteromodal phonological processes.

2. Material and Methods

2.1 Participants
Eighteen healthy right-handed (Oldfield, 1971) native speakers of Canadian English participated in this experiment (mean age 24 years $\pm$ 7.7, range : 18-40 years, 11 females). The data from two participants could not be used due to technical problems during the acquisition of the high-resolution anatomical scan, leaving sixteen participants in the analysis. All participants had normal hearing and normal or corrected-to-normal vision. Subjects had no self-reported history of speech, language or neurological disorders. All

172   participants gave informed consent in accordance with the ethics committee of the

173   Montreal Neurological Institute (MNI). The study was approved by the Magnetic

174   Resonance Research Committee (MRRC) and the MNI Research Ethics Board.

175   **2.2 Stimuli**
176   The experiment consisted of four tasks: (1) passive listening, (2) passive reading, (3)

177   listening and repeating, and (4) reading aloud. Only the first two tasks (i.e. passive

178   listening and passive reading) were analyzed for the current report. The stimuli consisted

179   of a set of 40 pseudowords presented visually and auditorily. To create pseudowords,

180   initial word lists containing common two-syllable trochaic nouns, six to eight letters in

181   length, with onsets utilizing all legal two-consonant clusters of English were developed

182   using the UWA Psychology: MRC Psycholinguistic Database (Colheart, 1981). Words

183   were ordered by sonority ranking (Steriade, 1990) and divided into two categories on that

184   basis: low phonological complexity (LPC) and high phonological complexity (HPC). We

185   calculated the sonority ranking by measuring the absolute distance in sonority between

186   the two consonants in each word-onset cluster. Words with consonant cluster onsets that

187   had a sonority ranking of 4 or more (e.g. /pl/) were classified as LPC and words with

188   consonant cluster onsets that had a sonority ranking of 3 or less were classified as HPC

189   (e.g. /st/). Based on these words, pseudowords were then created by substituting the first

190   consonant of the onset of the second syllable for another English consonant (see

191   Supplementary material S1 for some examples). Pseudowords were compared for bigram

192   frequency of the first and second consonant of the onset of the second syllable to ensure

193   that they were legal and equally frequent combinations of English orthography and

194   phonology (Balota et al., 2007; Solso & Juel, 1980). Pseudowords in each phonological

195   category were matched in terms of number of orthographic neighbors and bigram

196 frequency mean (Balota et al., 2007). The auditory pseudowords were recorded by a

197 female native English speaker in a sound-treated room. Recordings were made at a 44

198 kHz sampling rate directly onto disk.

199 **2.3 Procedure**
200 The experiment consisted of 4 experimental runs (13.5 minutes each) that included two

201 perceptual runs and two production runs. Within each run, forty stimuli were presented in

202 the auditory modality and another forty in the visual modality, for a total of 80 stimuli per

203 run. The stimulus modality was randomized within each run. The perceptual runs were

204 always presented first in order to minimize the likelihood of covert rehearsal.

205 Participants were not aware until the beginning of the production runs when they would

206 have to speak in the scanner. The perceptual runs were separated from the production

207 runs by the acquisition of a high-resolution anatomical scan. For both the perceptual and

208 production runs, auditory stimuli were on average 1000ms in duration and the visual

209 stimuli remained on the screen for 1000ms. Both stimulus presentation and participants'

210 responses occurred during the interscan interval (i.e. silent interval). All stimuli were

211 presented using Presentation Software (Neurobehavioral System, CA, USA). A resting

212 condition signaled by a dark gray screen was also included as the baseline condition. In

213 order to verify that subjects were paying attention during the perceptual and production

214 runs, catch trials were included. Upon visual presentation of a fixation cross, subjects

215 were instructed to press a button on a MRI-compatible response box for the catch trials.

216 Rest trials were interleaved with the experimental conditions. Within each run, the

217 number   of   rest   trials   (10)   was   optimized   using   OPTseq2

218 (http://surfer.nmr.mgh.harvard.edu/optseq/).

219 **2.4 fMRI parameters**

220 The data were acquired on a 3T Siemens Trio scanner at the Montreal Neurological

221 Institute. Participants wore MR-compatible headphones (Sensimetrics Corporation,

222 Malden, MA) and their head was immobilized by means of a vacuum-bag filled with

223 polystyrene balls and a forehead-restraining device (Hybex Innovations, St-Leonard, Qc,

224 CAN). A T2-weighted gradient-echo multi-slice EPI interleaved sequence was used for

225 the fMRI scans (TE= 30ms, TR=2.04, Flip Angle 90º, matrix 64x64, FOV=256x256,

226 slice thickness 4mm, isotropic, no gap). Thirty-four axial slices oriented parallel to the

227 AC-PC line were acquired covering the whole brain. To eliminate movement artefact

228 associated with speaking and to ensure that subjects could clearly hear the auditory

229 stimuli, a clustered sparse temporal acquisition paradigm was used. For each trial, a

230 clustered acquisition of two volumes was completed, resulting in 208 functional volumes

231 per experimental run. The silent inter-scan interval was 4.04s (cluster-onset asynchrony:

232 8.08s). Stimulus presentation started during the inter-scan interval exactly 4 seconds

233 before the acquisition of the two successive volume scans. High-resolution T1-weighted

234 volumes were acquired for anatomical localization after the two perceptual runs.

235 **2.5 fMRI data analysis**

236 The four time series were spatially registered, motion-corrected (within and across runs),

237 de-spiked and converted to a percentage of signal change using AFNI (Cox, 1996). The

238 anatomical scan of each participant was aligned to their registered EPI time series using

239 local Pearson correlations (Saad et al., 2009). A linear least squares model was used to fit

240 to each time point of the hemodynamic response function for each of the conditions.

241 Each experimental condition had its own regressor. Additional regressors for the mean,

242 the linear and the quadratic trend components as well as the six motion parameters (x, y,

243   z, roll, pitch, yaw) were also included in the model. We modeled a 2.02s period

244   beginning at the start of the stimulus, using AFNI's TENT function. We used the first TR

245   for all subsequent analyses. To create a surface representation of each participant's

246   anatomy, Freesurfer was used (Dale, Fischl, & Sereno, 1999; Bruce Fischl, Sereno, &

247   Dale, 1999). For each participant, each hemisphere of the anatomical volume was inflated

248   to a surface representation and aligned to a template of average curvature. SUMA was

249   used to import the surface representation from Freesurfer and to project the functional

250   data from the first level analysis onto the 2D surface. Both the surface representations

251   and the functional data were standardized to a common mesh reference system (Saad,

252   Reynolds, Argall, Japee, & Cox, 2004). The functional data were smoothed on the

253   surface using a Gaussian 6-mm full-width at half-maximum filter. Whole-brain group

254   analyses were performed on the surface using SUMA on the subjects' beta values taken

255   from the first level analysis. The main focus of the whole-brain analyses was on the effect

256   of auditory and visual stimuli during speech perception as well as the effect of

257   phonological complexity during speech perception. The surface-based group analyses

258   were corrected for multiple comparisons, using a Monte Carlo simulation implemented in

259   Freesurfer. This correction implements a cluster-size threshold procedure to protect

260   against Type I error. Based on the simulation results, it was determined that a family-wise

261   error (FEW) rate of $p < 0.01$ is achieved with a minimum cluster size of 127 contiguous

262   surface nodes, each significant at $p < 0.01$. From the whole-brain contrasts (corrected for

263   multiple comparisons) we also identified brain areas that were sensitive to both auditory

264   and visual stimuli (auditory ∩ visual) using a conjunction mask of brain activity (Nichols,

265   Brett, Andersson, Wager, & Poline, 2005).

266 **2.6 Anatomical ROI analysis**

267 To further profile the role of regions typically reported in studies on phonological

268 processing (Burton et al., 2005; Okada & Hickok, 2006; Price, 2012; Vouloumanos et al.,

269 2001), we conducted an analysis of anatomical regions of interest (ROI). This subset of

270 ROIs included the inferior frontal gyrus (pars opercularis (IFGpo), pars triangularis

271 (IFGpt), and pars orbitalis (IFGporb), the planum temporale (PT), the superior temporal

272 sulcus (STS), the lateral superior temporal gyrus (STG), and the supramarginal gyrus

273 (SMG). Each ROI was defined on the subject's individual cortical surface representation

274 using an automated parcellation scheme (Desikan et al., 2006; B. Fischl et al., 2004). This

275 parcellation scheme relies on a probabilistic labeling algorithm based on the anatomical

276 convention of Duvernoy (1991) (Destrieux, Fischl, Dale, & Halgren, 2010). For some of

277 the ROIs selected, we edited the Freesurfer parcellation by sub-dividing it into smaller

278 ROIs (See supplementary S1). Details of the parcellation are described in Supplementary

279 Materials S2.

280   For each subject, we extracted the mean percentage of BOLD signal change in

281 each ROI. We first examined which ROIs were significantly active in perception by

282 testing the following hypothesis using FDR-corrected t-tests (Benjamini & Hochberg,

283 1995; Genovese, Lazar, & Nichols, 2002) (q=0.05): (i) perception > 0, (n=16, one-sample

284 t-tests). All the ROIs that were significantly active were submitted to statistical

285 evaluation in a repeated-measures ANOVA (rANOVA) with the factors modality

286 (auditory and visual) and complexity (high phonological complexity and low

287 phonological complexity). We investigated the main effects of modality and complexity

288 as well as two-way interactions.

3. Results

3.1 fMRI results

3.2.1 Whole brain analyses

The node-wise ANOVA showed a significant effect for the auditory and visual modality during speech perception (Fig. 1A). The activation associated with the auditory and orthographic stimuli revealed regions involved in the sensory processing of auditory or visual information, namely bilateral primary visual cortex and its corresponding association areas (e.g. lingual gyrus, fusiform gyrus, middle occipital gyrus and inferior occipital sulcus and gyrus) when pseudowords were presented orthographically and bilateral primary auditory cortex and its association areas (e.g. lateral superior temporal gyrus, transverse temporal gyrus and sulcus) when pseudowords were presented auditorily (for a review, Price, 2012). As illustrated in Figure 1A, the conjunction between the auditory and visual stimuli revealed overlapping activation for both modalities in numerous bilateral cortical regions including the posterior portion of the superior temporal sulcus, the inferior circular sulcus of the insula, the posterior cingulate gyrus and sulcus, the calcarine sulcus, and the medial superior frontal gyrus. Overlapping clusters of activation were also found in the left supramarginal gyrus, the left superior frontal gyrus and sulcus, the left middle frontal gyrus, the left postcentral gyrus, the left precentral gyrus, the left mid-portion of the superior temporal gyrus, the left posterior portion of the inferior temporal, the left cuneus, the left precuneus, the right superior parietal gyrus, and the right anterior portion of the cingulate gyrus and sulcus. The node-wise ANOVA showed a significant effect of complexity for speech perception (Fig. 1B). When we compared the HPC and LPC activation to investigate regions sensitive to phonological complexity, significant differences were observed in the left calcarine

313   sulcus, middle occipital gyrus, occipital sulcus and superior temporal sulcus as well as

314   the right occipital pole and calcarine sulcus (see Figure 1B, and Table 1 for a complete

315   list).

316   **3.2.2 ROI analysis**

317   Only the ROIs that were significantly activated for speech perception were included in

318   the subsequent analyses. Eight ROIs (bilateral IFGpo, PT, STGp, left SMGa and right

319   SMGp) were used to investigate the main effect of modality (i.e. auditory, visual), the

320   main effect of phonology (HPC, LPC), and the two-way interaction between

321   modality*phonology.

322   *Main effects*

323   A main effect of modality was found in the bilateral PT (left PT: $F_{1,15}=36.22$, $p<0.0001$;

324   right PT: $F_{1,15}=44.64$, $p<0.0001$) and bilateral STGp (left STGp: $F_{1,15}=34.60$, $p<0.0001$;

325   right STGp: $F_{1,15}=85.10$, $p<0.0001$). Paired sample t-tests revealed that both of these

326   regions were significantly more active for auditory stimuli relative to visual stimuli (left

327   PT: t=6.02, $p<0.0001$; right PT: t= 6.68, $p<0.0001$; left STGp: t=5.88, $p<0.0001$; right

328   STGp: t=9.23, $p<0.0001$). To determine whether the difference observed was due to a

329   lack of activation in one modality, we tested whether the activation level in each modality

330   was significantly different from 0 (one-sample t-test, one-tailed). The left PT was

331   significantly activated for both modalities (auditory: t=7.44, $p<0.0001$, visual: t=2.1,

332    $p=0.026$), while the bilateral STGp (left STGp auditory: t=6.2, $p<0.001$, left STGp visual:

333   t=1.19, $p=0.28$; right STGp auditory: t=9.4, $p<0.0001$; right STGp visual: t=0.34, $p=0.74$)

334   and the right PT (auditory: t=6.22, $p< .0001$; visual t=0.87, $p=0.40$) were not significantly

335   activated in the visual condition (for more details, refer to Figure 2A).

336   *Two-way interaction effects (Phonology x Modality)*

337   A two-way interaction was found for the bilateral IFGpo (left IFGpo: $F_{1,15}=5.11$, p=0.04;

338   right IFGpo: $F_{1,15}=5.62$, p=0.03), the left SMGa ($F_{1,15}=5.77$, p=0.03) and the right SMGp

339   ($F_{1,15}=8.461$, p=0.01). Paired sample t-tests revealed a significant HPC - LPC difference

340   in the visual modality ($t_{15}=2.368$, p=0.03) for the left IFGpo (refer to Figure 2B). A

341   significant difference between visual and auditory modalities for the HPC-LPC contrast

342   emerged in the right IFGpo (($t_{15}=2.371$, p=0.03) and right SMGp ($t_{15}=2.909$, p=0.01).

343   For the left SMGa, paired sample t-tests revealed a marginally significant effect of

344   complexity only in the visual modality ($t_{15}=2.127$, p=0.05).

345

346   **4. Discussion**

347   The findings from the current experiment demonstrate that in the absence of an explicit

348   task, only a subset of regions typically involved in phonological processing are sensitive

349   to sonority differences that modulate syllabic complexity. We focused on a subset of

350   brain regions within the posterior supratemporal plane and the inferior frontal cortex and

351   examined brain regions associated with the manipulation of phonological complexity

352   (sonority) and stimulus modality (orthographic and auditory) in pseudowords. The results

353   suggest that neural processing differences associated with phonological complexity

354   during passive listening are modality dependent. In the following, we discuss the findings

355   of the whole-brain analyses and ROI analyses in terms of the role of phonological

356   complexity and modality of presentation as an experimental tool to flesh out the neural

357   correlates of phonological processing.

358   Not surprisingly, the whole-brain phonological contrast yielded few regions in

359   which an effect of complexity was observed, suggesting that in the absence of an overt

360   task, regions typically involved in the processing of phonological information are not

361   modulated by complexity. This finding is congruent with two recent neuroimaging

362   studies in which phonological complexity was manipulated during passive listening. In

363   these studies, phonological complexity was manipulated by contrasting consonant

364   clusters (CCV) to single consonant vowel combination (CV) in words (Tremblay &

365   Small, 2011) and pseudowords (McGettigan et al., 2011). In the first study, the

366   phonological contrast during passive perception revealed one region within the right PT

367   in which the activity was scaled to the degree of complexity (Tremblay & Small, 2011),

368   whereas in the second study no effect of complexity was observed (McGettigan et al.,

369   2011). Nonetheless, Deschamps and Tremblay (2014) demonstrated that syllabic

370   complexity as defined by the absence or presence of consonant clusters in syllable

371   sequences recruits a broad network of regions within the supratemporal plane.

372   In the present study, consistent with previous neuroimaging studies (Binder et al.,

373   2000; Demonet et al., 1992; Giraud & Price, 2001; Liebenthal et al., 2005; Okada et al.,

374   2010; Poeppel et al., 2004; Vaden, Muftuler, & Hickok, 2010; Vouloumanos et al., 2001),

375   an effect of phonological complexity as indexed by sonority differences was observed in

376   the left STS. From our whole-brain analysis, we found the locus of activation in the mid

377   portion of the STS.   Previous studies have noted clusters of activation within the mid-

378   anterior STS during phonemic/non-phonemic discrimination tasks (Liebenthal et al.,

379   2005), passive listening to speech sounds (Binder et al., 2000) and repetition of words

380   varying in phonemic similarity between items (Vaden et al., 2010).   Mid-posterior STS

381 activation has been observed for manipulation of the neighborhood density of words

382 (Okada & Hickok, 2006) or the degree of intelligibility of sentences (Okada et al., 2010).

383 In contrast, reading studies report activation within the posterior STS (Turkeltaub, Eden,

384 Jones, & Zeffiro, 2002). Taken together, these results suggest that subregions within the

385 STS show markedly different patterns of activation depending on the kind of

386 phonological representations being processed (i.e. phonemes, syllables, whole-word) with

387 the mid-anterior STS appears sensitive to the processing of phonemic/syllabic

388 information whereas the mid-posterior STS appears more sensitive to lexical-

389 phonological information. We note that we did not find a complexity or a

390 modality*complexity effect within our STS ROI because the locus of activation observed

391 in the whole-brain analysis is located in the mid STS not the posterior STS. Thus, only

392 the mid STS is sensitive to sonority differences targeting syllabic structure, which is

393 congruent with the hypothesis that different subregions within the STS subserve different

394 phonological processes.

395 Interestingly, the only region sensitive to phonological complexity in the ROI

396 analysis was the posterior part of the left IFG (IFGpo) and only for print. Despite the

397 absence of an overt response, the orthographic presentation activated different brain areas

398 than passive listening suggesting that the processing of orthographic stimuli results in an

399 obligatory orthographic to phonological transformation or articulatory recoding, a

400 function previously attributed to this region by others (for more details, refer to: Burton et

401 al., 2005; Burton, Noll, & Small, 2001; Burton et al., 2000; Zatorre, Evans, Meyer, &

402 Gjedde, 1992; Zatorre, Meyer, Gjedde, & Evans, 1996). Interestingly, it appears that this

403 <mark>transformation/recoding is sensitive to sonority differences at the neural level even during</mark>

404 <mark>passive reading.</mark>

405   The whole-brain analysis and the ROI analysis also identified regions that were

406 significantly activated for both modalities for pseudowords despite not showing an effect

407 of phonological complexity. These regions are similar to the ones reported in Burton et al.

408 (2005) and Van Atteveldt et al. (2004), suggesting that pseudowords recruit a similar

409 network as words and letters under different task demands. Of particular interest is that

410 the lower bank of the bilateral STG/STS was activated for both auditory and visual

411 pseudowords, an area that has been previously implicated in automatic speech/print

412 convergence processes (i.e. integration) using letters and single speech sounds during

413 passive listening/viewing (Blau, van Atteveldt, Ekkebus, Goebel, & Blomert, 2009; Van

414 Atteveldt et al., 2004). In addition, the ROI analysis revealed that only the left PT was

415 significantly active in both modalities. One potential role of the PT in auditory processing

416 is as a computational hub, disambiguating complex sounds through the isolation of

417 different properties of the acoustic objects (e.g. temporal and spectral information) and

418 matching them to stored phonological spectro-temporal templates (Griffiths & Warren,

419 2002). However, given that PT was also recruited during the passive reading task, it

420 appears that the PT is involved in accessing cross-modal spectro-temporal profiles. In

421 others words, during passive listening and reading, the PT is involved in accessing stored

422 phonological representations. This is consistent with previous neuroimaging studies that

423 have reported activation within PT under a wide range of experimental paradigms that

424 require access to auditory phonological spectro-temporal templates, such as passive

425 listening to speech sounds (Mazoyer et al., 1993; Petersen, Fox, Posner, Mintun, &

426   Raichle, 1988; Tremblay, Deschamps, & Gracco, 2011; Wise et al., 1991), active

427   listening to speech sounds (Binder et al., 2000; Binder et al., 1997; Binder, Frost,

428   Hammeke, Rao, & Cox, 1996) and reading (Nakada, Fujii, Yoneoka, & Kwee, 2001).

429   **5. Conclusion**

430   In the present study we used sonority difference in pseudowords to evaluate the manner

431   in which differences in phonological properties activate brain regions for spoken and

432   written speech under passive stimulus conditions. The results of the present investigation

433   suggest that while sonority is an important concept in phonological theory, language

434   acquisition and language breakdown, at the neural level, sonority differences alone in

435   pseudowords do not modulate the entire network of regions typically involved in

436   phonological processing. The present results suggest that the phonological properties of

437   speech associated with sonority are insufficient to activate brain areas associated with

438   phonological processing as measured by fMRI. In the visual modality, sonority

439   differences modulated activation within the left IFGpo, suggesting a stronger association

440   between sonority differences and speech processing most likely due to an obligatory

441   decoding of orthographic features into phonological forms. It may be the case that the

442   lack of a sonority effect in the auditory modality might be related to the inherent

443   limitations of fMRI, that is, its poor temporal resolution. Further work using different

444   functional neuroimaging techniques with better temporal resolution, such as

445   electroencephalography (EEG) or magnetoencephalography (MEG) might be of value in

446   capturing sonority effects in speech perception.

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Legends

Figure 1: **Part A. Speech perception network.** The red color scheme represents nodes that are significantly active during the auditory condition (i.e. passive listening), the yellow color scheme represents nodes that are significantly active during the visual condition (i.e. passive reading) and the orange color scheme represents nodes that are significantly active for the conjunction of the two conditions (i.e. passive listening and passive reading). **Part B. Phonological contrast.** Clusters of significant differences between the HPC and LPC conditions. Positive activation is represented in yellow and negative activation is represented in blue. Activation is shown on the group average smoothed white matter folded surface.

Figure 2: Brain activity, expressed as a percentage of signal change. Single asterisk indicate a significant difference against zero (one-sample t-test). STGp = posterior superior temporal gyrus; PT = planum temporal; IFGpo = Inferior frontal gyrus pars opercularis.

490 **Supplementary material S1**

Words and pseudowords		
Sonority difference	Words	Pseudowords
High complexity	Slipper	Slinner
	Scallops	Scannops
	Smoker	Smoger
Low complexity	Precept	Premept
	Critter	Crimmer
	Blizzard	Bliffard

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Supplementary material S2

494   We divided the ROI from the automated Freesurfer parcellation into two sets: (i) frontal

495   regions and (ii) temporal-parietal regions. The frontal set included the inferior frontal

496   gyrus (pars opercularis (IFGpo), pars triangularis (IFGpt), and pars orbitalis (IFGporb)).

497   The regions from the frontal set were based on unedited Freesurfer parcellation. The IFG

498   is located between the circular sulcus of the insula and the inferior frontal sulcus. The

499   IFG is subdivided into three subregions by both the horizontal and vertical rami of the

500   anterior part of the lateral sulcus. The pars triangularis is bounded rostrally and caudally

501   by the horizontal and vertical rami, respectively. The pars opercularis is posterior to the

502   vertical ramus. The pars orbitalis is located anteriorly and inferiorly to the horizontal

503   ramus and the anterior segment of the circular sulcus of the insula binds it posteriorly.

504   The temporal-parietal set included the planum temporale (PT), the superior temporal

505   sulcus (STS), the lateral superior temporal gyrus (STG), and the supramarginal gyrus

506   (SMG). PT is located posteriorly to the transverse temporal sulcus, anteriorly to the

507   SMG, medially to the posterior segment of the lateral sulcus and laterally to the lateral

508   part of the STG. For PT, we used the unedited version of the Freesurfer parcellation.

509   The STS runs parallel to the lateral fissure from the temporal pole to the supramarginal

510   gyrus. For the STS, we modified the Freesurfer parcellation by dividing the sulcus into

511   two parts at the junction of the SMG and the lateral STG, creating the posterior STS

512   (STSp). The lateral STG has the rostral extent of the STS as its rostral boundary, the

513   caudal portion of the superior temporal gyrus as its caudal boundary, the lateral fissure

514   and SMG as its medial boundary, and for its lateral boundary, the superior temporal

515   sulcus. For the lateral STG, we edited the Freesurfer parcellation by dividing the gyrus at

516   the level of the anterior part of PT, thereby creating the posterior lateral STG (STGp).

517   The SMG curves around the posterior part of the lateral sulcus, it is bounded rostrally by

518   the caudal extend of the STG, caudally by the rostral extent of the superior parietal gyrus,

519   medially by lateral banks of the intraparietal sulcus and laterally by the lateral fissure.

520   The Freesurfer parcellation of the SMG was modified by dividing the gyrus into an

521   anterior (SMGa) and a posterior (SMGp) section based on location of the endpoint of the

522   lateral fissure (Desikan et al., 2006).

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