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1   **Functional hierarchy for tactile processing in the visual cortex of sighted adults**

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25   **Abstract**

26   Perception via different sensory modalities was traditionally believed to be

27   supported by largely separate brain systems. However, a growing number of studies

28   demonstrate that the visual cortices of typical, sighted adults are involved in tactile

29   and auditory perceptual processing. Here, we investigated the spatiotemporal

30   dynamics of the visual cortex's involvement in a complex tactile task: Braille letter

31   recognition. Sighted subjects underwent Braille training and then participated in a

32   transcranial magnetic stimulation (TMS) study in which they tactually identified

33   single Braille letters. During this task, TMS was applied to their left early visual

34   cortex, visual word form area (VWFA), and left early somatosensory cortex at five

35   time windows from 20 to 520 ms following the Braille letter presentation's onset. The

36   subjects' response accuracy decreased when TMS was applied to the early visual

37   cortex at the 120–220 ms time window and when TMS was applied to the VWFA at

38   the 320–420 ms time window. Stimulation of the early somatosensory cortex did not

39   have a time-specific effect on the accuracy of the subjects' Braille letter recognition,

40   but rather caused a general slowdown during this task. Our results indicate that the

41   involvement of sighted people's visual cortices in tactile perception respects the

42   canonical visual hierarchy—the early tactile processing stages involve the early visual

43   cortex, whereas more advanced tactile computations involve high-level visual areas.

44   Our findings are compatible with the metamodal account of brain organization and

45   suggest that the whole visual cortex may potentially support spatial perception in a

46   task-specific, sensory-independent manner.

47   **Keywords:** perception; cross-modal interactions; Braille; visual cortex;

48   somatosensory cortex; TMS

49

1. Introduction

Until recently, perception via different sensory modalities was thought to be supported by largely separate brain systems—it was generally assumed that the visual cortex processes solely visual input, the somatosensory cortex processes solely tactile input, and so on (e.g., Fig. 18-2 in Kandel et al., 2012). Departures from this rule and the "unmasking" of cross-modal interactions during perceptual processing were reported mainly following sensory loss or injury (Bavelier and Neville, 2002; Lomber et al., 2011; Merabet and Pascual-Leone, 2010; Rauschecker, 1995; Sur et al., 1990). However, a growing number of studies demonstrate that tactile and auditory tasks involve the visual cortex even in typical adults (Amedi et al., 2007, 2001; Campus et al., 2017; Deshpande et al., 2010; Eck et al., 2016, 2013; Hagen et al., 2002; Kim and Zatorre, 2011; Lacey et al., 2014, 2010, Merabet et al., 2008, 2006; Poirier et al., 2005; Saito et al., 2006; Sathian et al., 2011, 1997; Siuda-Krzywicka et al., 2016; Stilla and Sathian, 2008; Tal et al., 2016; Zangenehpour and Zatorre, 2010) and that this involvement is functionally relevant (Amemiya et al., 2017; Merabet et al., 2008, 2004; Siuda-Krzywicka et al., 2016; Zangaladze et al., 1999). These findings suggest that cross-modal interactions between sensory systems are not an exception, possible only in the context of sensory deprivation or brain injury, but are rather a general mechanism that supports human perception.

The exact way in which the functioning visual cortex interacts with other sensory systems during tactile and auditory perception remains to be elucidated. Nevertheless, previous studies have already indicated that these interactions might follow a specific spatial pattern. In sighted adults, early visual areas are recruited through relatively simple tactile and auditory discrimination, such as through comparing the shape of single Braille characters, exploring various textures, or

75   perceiving noise bursts (Eck et al., 2013; Merabet et al., 2008; Sathian et al., 2011;

76   Stilla and Sathian, 2008; Zangenehpour and Zatorre, 2010; see also Merabet et al.,

77   2006; Saito et al., 2006). Tasks that require a more complex perceptual analysis, such

78   as tactile or auditory object recognition, tactile or auditory motion perception, or

79   whole-word Braille reading, activate relevant high-level visual regions in the ventral

80   and dorsal visual streams (Amedi et al., 2007, 2001; Hagen et al., 2002; Kim and

81   Zatorre, 2011; Lacey et al., 2014, 2010; Poirier et al., 2005; Siuda-Krzywicka et al.,

82   2016). These results suggest that, in a sighted person, the visual cortex's involvement

83   in tactile and auditory tasks might respect the typical visual processing hierarchy

84   (Reddy and Kanwisher, 2006; Riesenhuber and Poggio, 2000; Rolls, 2000); this

85   possibility is also suggested by our recent studies (Bola et al., 2017a; Siuda-

86   Krzywicka et al., 2016), which demonstrated that, in sighted adults, learning to read

87   Braille—a tactile task encompassing both spatial and linguistic processing—results in

88   both the anatomical reorganization of the early visual cortex as well as the functional

89   recruitment of the left ventral visual cortex, especially the visual word form area

90   (VWFA; Dehaene and Cohen, 2011; Price and Devlin, 2011). Based on the conjecture

91   described above, one may expect that these visual regions are involved in tactile

92   Braille reading in a hierarchical manner to support the different types of computations

93   necessary to accomplish this task. The early visual cortex would be firstly involved to

94   perhaps support the construction of a spatial representation of Braille dots and signs;

95   only then would the Braille reading involve the high-level ventral visual cortex, which

96   may support the creation of an abstract representation of a Braille letter (see, e.g., the

97   visual reading model proposed by Dehaene et al., 2005). Here, we put these

98   predictions to the test.

99   A group of seventeen sighted subjects, independent of the group described in
100 our previous studies (Bola et al., 2017b, 2017a, 2016; Siuda-Krzywicka et al., 2016),
101 received training in tactile Braille reading for eight months and then enrolled in a
102 chronometric transcranial magnetic stimulation (TMS) experiment. In chronometric
103 TMS, magnetic pulses are applied at specific time windows to investigate at which
104 time each brain area is involved in a given task (reviewed in Pascual-Leone et al.,
105 2000). In this study, we used this method to test whether and at which point neural
106 activity in the early visual cortex and the ventral visual cortex is causally linked with
107 successful tactile Braille letter recognition. Subjects were asked to read aloud single
108 Braille letters presented in the tactile modality while TMS was applied to the left
109 early visual cortex, the VWFA, or the left early somatosensory cortex at five different
110 time windows spanning from 20 to 520 ms following the Braille letter presentation's
111 onset (Fig. 1).

112   Previous studies suggest that Braille letter recognition should not be disrupted
113 by the stimulation of visual areas applied as early as 20–120 ms following the letter
114 presentation's onset (i.e., the earliest time window in our experiment). Zangaladze et
115 al. (1999), for example, reported that the visual cortex's most pronounced
116 involvement in tactile perception occurs well after this time (i.e., 150–200 ms
117 following the stimulus presentation) even in the case of a relatively low-level tactile
118 task (discriminating grating orientations). We thus hypothesized that, relative to the
119 earliest TMS time window, Braille letter recognition will be specifically disrupted by:
120 (1) TMS applied to the early visual cortex in intermediate (i.e., 120–220 or 220–320
121 ms) but not in late (i.e., 320–420 or 420–520 ms) time windows; and (2) TMS applied
122 to the VWFA in late (320–420 or 420–520 ms) but not intermediate (120–220 or 220–
123 320 ms) time windows. Establishing this temporal double dissociation will constitute

124 evidence of the visual cortex's hierarchical involvement in tactile processing in a way

125 that respects the canonical visual processing hierarchy from early to high-level visual

126 cortices.
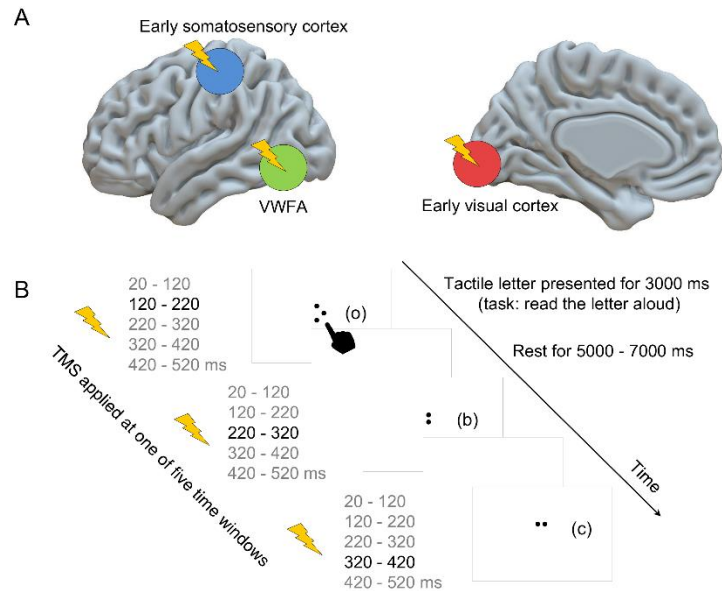
127

128 ***Figure 1.*** *Experimental design. (A) Subjects read aloud single Braille letters*

129 *presented in the tactile modality while TMS was applied to their left early visual*

130 *cortices, visual word form areas (VWFAs,) and left early somatosensory cortices; (B)*

131 *each trial consisted of a 3-s Braille letter presentation, followed by a 5- to 7-s rest*

132 *period with no stimuli presented. During each trial, three TMS pulses with an*

133 *interpulse interval of 50 ms (20 Hz) were applied at one of five time windows—20–*

134 *120, 120–220, 220–320, 320–420, or 420–520 ms—following the Braille letter*

135 *presentation's onset. Note that the representation of TMS sites in the figure is*

136 *schematic and reflects neither their exact localization nor the exact focus of TMS in*

137 *the experiment.*

138

139   **2.   Materials and Methods**

140 *2.1. Subjects*

141   Twenty-one healthy, right-handed female subjects were initially recruited for

142   the study (mean age = 23.7 years; SD = 3.3 years; range = 20–31 years). To ensure

143   appropriate statistical power, we decided to recruit at least fifteen to twenty subjects

144   prior to the data collection—a sample size that has been proven sufficient for

145   detecting TMS effects on reading and language processing (Pattamadilok et al., 2015;

146   Schuhmann et al., 2012; Sliwinska et al., 2015). All subjects were native Polish

147   speakers and had normal or corrected-to-normal vision. They were students studying

148   special education and specializing in blindness and related disabilities who were

149   visually familiarized with Braille signs as part of their curriculum. As in our previous

150   studies (see, e.g., Bola et al., 2016; Siuda-Krzywicka et al., 2016), subjects were

151   recruited from such a population for two reasons: (1) they were highly professionally

152   motivated to participate in the tactile Braille reading course and (2) their familiarity

153   with visual Braille reading was expected to facilitate a process of learning that would

154   result in their ability to recognize Braille letters by touch. Interestingly, behavioral

155   tests performed upon the tactile Braille training's onset revealed that the subjects'

156   visual familiarity with Braille only narrowly affected their initial ability to tactually

157   read this script. While most subjects were able to recognize some Braille letters in the

158   tactile modality, only five managed to read even a single word in one minute (see

159   Supplementary Information for the comparison of subjects' visual and tactile Braille

160   reading abilities). Apart from the TMS experiment reported in this paper, the subjects

161   participated in a longitudinal magnetic resonance imaging (MRI) study, the results of

162   which will be described in a separate publication. All tests and procedures described

163   in this paper were approved by the Committee for Research Ethics of the Institute of

164   Psychology of the Jagiellonian University (approval granted on 02/22/2016).

165 Informed consent and consent to publish were obtained from each subject prior to

166 their testing.

167   During the TMS experiment, four subjects were excluded because they found

168 the VWFA stimulation uncomfortable, even when its intensity was reduced from

169 110% (target intensity in the study; see Section 2.5) to 100% of their resting motor

170 threshold; 100% is the lowest intensity that has proven to be effective in interfering

171 with neural processing in this area (Duncan et al., 2010; Pattamadilok et al., 2015,

172 2010; Siuda-Krzywicka et al., 2016). Thus, data from the remaining seventeen

173 subjects (mean age = 24 years; SD = 3.4 years; range = 20–31 years) were included in

174 the analysis.

175   The reason why female subjects were exclusively recruited was related to the

176 gender distribution in the special education student population in Poland, wherein

177 such studies are primarily undertaken by women. It is important to note that previous

178 work has demonstrated the existence of gender differences in the Braille reading

179 abilities of visually impaired subjects (Argyropoulos and Papadimitriou, 2015). Thus,

180 it is possible that the inclusion of only female subjects modulated either the Braille

181 training's behavioral outcomes or the overall performance in the TMS experiment.

182 Nevertheless, such modulation would be orthogonal to effects of interest in our study.

183 It is unlikely that gender influences mechanisms of cross-modal interactions in the

184 brain or affects how TMS impacts these mechanisms.

185

186 *2.2. Tactile Braille reading course and behavioral tests*

187   Before participating in the TMS experiment, all subjects completed an eight-

188 month-long tactile Braille reading course and were administered tactile Braille word

189 and tactile Braille letter reading tests both prior to and following the course in a

190 manner similar to that of our previous studies (for a detailed description, see Bola et

191 al., 2016; Siuda-Krzywicka et al., 2016). In addition, their visual Braille reading skills

192 were tested both prior to and following the tactile Braille reading course. These tests

193 involved reading aloud in the visual modality as many Braille words as possible

194 within one minute. A list of 116 unrelated Polish words was employed, and both the

195 word list and a testing procedure were adapted from a standard Polish reading speed

196 test designed for school-aged children (seven to twelve years; Konopnicki, 1961).

197 *2.3. TMS study: task and stimuli*

198   In the TMS experiment, subjects were instructed to read aloud single Braille

199 letters presented in the tactile modality using an Active Star display (HandyTech,

200 Horb-Nordstetten, Germany). Single letter recognition was chosen rather than whole-

201 word reading to minimize within-subject and between-subject variance in

202 performance, which may mask TMS effects—especially in chronometric designs. At

203 the same time, reading aloud ensured that subjects were truly accessing a letter's

204 representation and were not solving the task based solely on a low-level spatial

205 representation of dots.

206   Each trial consisted of a 3-s-long Braille letter presentation, followed by a 5-

207 to 7-s rest period with no stimuli presented on the display. Subjects were asked to

208 identify Braille letters with the right-hand index finger. Each subject's finger was

209 placed upon the Braille display before the letter was presented, and subjects were free

210 to tactually explore a letter after it was presented. Subjects were not blindfolded, and

211 no instructions were given regarding whether they should keep their eyes closed or

212 open. This choice was motivated by two reasons: (1) our pilot experiments indicated

213 that blindfolding subjects decreases the precision of TMS and, consequently, the

214 quality of collected data (a TMS coil easily slips from a blindfold, especially during

215   the early visual cortex stimulation; subjects' facial movements move a blindfold,

216   which in turn moves neuronavigation trackers attached to subjects' heads; wearing a

217   blindfold during a relatively long experiment increases subjects' discomfort); and (2)

218   this design allowed us to test whether or not the tactile recognition of Braille letters

219   can involve the visual cortex when the visual input is unconstrained—that is, in a

220   situation that arguably resembles sighted people's everyday perceptual functioning

221   more closely than do experiments that require blindfolding. The Braille display was

222   covered to prevent subjects from visually recognizing stimuli. Vocal responses were

223   recorded via a microphone for 4 s following the Braille letter presentation's onset.

224   Overall, 300 trials were administered to each subject. Trials were divided into three

225   equal runs, corresponding to three TMS sites. Within each run, trials were further

226   divided into five subsets, corresponding to five TMS time windows. Consequently, all

227   experiment trials were divided into fifteen equal subsets (3 TMS sites x 5 TMS time

228   windows), each of which included twenty trials.

229   During Braille training, the subjects' tactile recognition of Braille letters was

230   trained in a specific order. The first half of the Polish alphabet (sixteen letters, which

231   are generally easier to recognize in the Braille alphabet: A, B, C, D, E, I, K, L, Ł, M,

232   O, P, S, T, U, Y) was introduced at the beginning of the course, while the second half

233   of the alphabet was introduced after the subjects' recognition of the first half was

234   mastered (see Bola et al., 2016). To increase within-subject and between-subject

235   consistency in performance, only letters that were introduced at the beginning of the

236   Braille reading course—those that were practiced the most extensively—were

237   employed in the TMS experiment as stimuli. The letter "A" was excluded from the

238   list of stimuli because it is the only Braille letter that consists of one dot and may be

239   processed using different mechanisms than other Braille letters (e.g., the recognition

240 of "A" does not involve combining dots into a coherent, spatial representation as the

241 recognition of other Braille letters does); as a result, fifteen letters were used as

242 stimuli (B, C, D, E, I, K, L, Ł, M, O, P, S, T, U, Y). Within each condition, the same

243 set of Braille letters was presented. The letters B, C, E, K, L, M, O, S, T, and Y were

244 presented once per condition, while the letters D, I, Ł, P, and U were randomly

245 chosen to be presented twice in order to reach a target number of trials per condition

246 (i.e., twenty trials; see above). The letter presentation's order was randomized for

247 each subject alongside the rule that the same letter could not be presented twice in a

248 row. Stimulus presentation and response recording were controlled using a program

249 written in Python that relied upon the PsychoPy package (Peirce, 2007).

250 *2.4. Localization of TMS sites*

251 During the TMS experiment, the left early visual cortex, the VWFA, and the

252 left early somatosensory cortex were targeted using a neuronavigation system. Prior

253 to the experiment, those sites were localized and marked on each subject's MRI scan.

254 The early visual cortex and the early somatosensory cortex were localized based on

255 each subject's brain anatomy. The early visual cortex was defined as a posterior

256 termination of the calcarine sulcus (Chambers et al., 2013; Merabet et al., 2008). The

257 early somatosensory cortex was marked within the postcentral gyrus, roughly 1–2 cm

258 posteriorly from "the omega knob" in the precentral gyrus (i.e., a canonical location

259 of the hand area in the primary motor cortex; Merabet et al., 2004; Vidoni et al.,

260 2010). In contrast, the VWFA was localized using individual, functional MRI

261 activations during tactile and visual lexical decision tasks acquired prior to the TMS

262 study. The localization tasks were part of a separate longitudinal MRI study

263 performed on the same group of subjects, which will be described in another

264 publication (see Supplementary Information for details that might be relevant to the

265 present study). In order to localize the VWFA in the TMS experiment, a two-step

266 procedure was employed. Firstly, brain activations enhanced by the visual lexical

267 decision task (performed in the Latin alphabet)—a task that is known to strongly

268 activate the VWFA (e.g., Rauschecker et al., 2011)—relative to the detection of hash

269 signs in the string of consonants were employed to broadly localize an area sensitive

270 to orthographic processing in the left ventral occipitotemporal region. Secondly, an

271 activation peak enhanced by the tactile lexical decision task (performed in the Braille

272 alphabet) relative to the detection of meaningless Braille signs in the string of

273 consonants written in the Braille alphabet was used to define the stimulation's

274 localization within the region of interest obtained during the first step. To verify the

275 accuracy of our VWFA localization procedure, single-subject data were normalized to

276 the Montreal Neurological Institute (MNI) space, and the chosen VWFA coordinates

277 were averaged across subjects. The mean MNI coordinates obtained using this

278 procedure (mean ± standard error of the mean: x = -39 ± 1, y = -62 ± 1, z = -11 ± 1)

279 agreed with the VWFA's location as reported in the literature (e.g., Cohen et al.,

280 2002; Glezer et al., 2009), which indicates that our localization procedure was

281 accurate.

282   TMS was expected to affect the subjects' Braille letter recognition at different

283 time points across the three sites (see Section 2.9); consequently, the sites could serve

284 one another as inherent control, and the inclusion of a separate control site was not

285 required.

286 *2.5. TMS protocol*

287   TMS was administered using a MagPro X100 stimulator (MagVenture,

288 Hückelhoven, Germany) with a 70-mm figure-eight coil. Stimulation was guided with

289 a Brainsight 2 neuronavigation system (Rogue Research, Montreal, Canada) and a

290 Polaris Vicra infrared camera (Northern Digital, Waterloo, Canada). In each trial,

291 three pulses with an interpulse interval of 50 ms (20 Hz) were applied at one of five

292 time windows, namely 20–70–120 ms, 120–170–220 ms, 220–270–320 ms, 320–370–

293 420 ms, or 420–470–520 ms, following the Braille letter presentation's onset.

294 Stimulation was administered in relatively wide time windows lasting 100 ms rather

295 than the 10–40 ms, which is the usual TMS time window width in studies of visual

296 reading (Amassian et al., 1989; Duncan et al., 2010; Salminen-Vaparanta et al., 2012).

297 This was done in order to account for the difficult nature of tactile reading and

298 expected between-subject variability in the task performance. Previous studies have

299 shown that chronometric TMS with the adjusted time window width can be

300 successfully applied to interfere with complex mental processes, even when between-

301 subject variability is high (e.g., Sack et al., 2005).

302 TMS intensity was initially set to 110% of each participant's resting motor

303 threshold. The motor threshold was indicated by the lowest stimulator output needed

304 to elicit a visible twitch of the relaxed hand in at least five of ten trials during the

305 contralateral primary motor cortex stimulation. The average individual motor

306 threshold was 37% (SD = 6%; range 24–48%) of the maximum stimulator output

307 power. Prior to the actual data collection, TMS was applied with a target intensity to

308 each site, and subjects were surveyed for any side effects of the stimulation. Six

309 subjects reported hand movements during the early somatosensory cortex stimulation,

310 and five subjects reported uncomfortable head muscle twitches during the VWFA

311 stimulation. In these cases, the stimulation's intensity for a given site was reduced to

312 100% of the individual motor threshold. As a result, in the actual TMS experiment,

313 hand movements during the early somatosensory cortex stimulation were neither

314 reported by any participant nor observed by an experimenter. For the VWFA

315   stimulation, residual head muscle twitches were at times observed, even when the

316   TMS intensity was adjusted. Provided that this condition was comfortable for a given

317   subject, the study was performed normally. Since the VWFA stimulation was

318   expected to interfere with tactile Braille letter recognition at a specific time window,

319   TMS within this site at other time windows controlled for these peripheral effects.

320   Subjects did not report any side effects during the early visual cortex stimulation.

321   The TMS time windows' order was randomized for each subject and

322   experimental run alongside the rule that, in adjacent experimental trials, TMS was

323   applied at adjacent time windows (e.g., 120–170–220 ms, 20–70–120 ms, 120–170–

324   220 ms, 220–270–320 ms, 320–370–420 ms). Such a randomization procedure

325   assured that timing differences between time windows—especially the early and late

326   time windows—were difficult to notice (see also Pattamadilok et al., 2015; Sliwinska

327   et al., 2012). The TMS sites' order was counterbalanced across subjects.

328   *2.6. MRI protocol*

329   MRI data were acquired using a Siemens Trio 3T scanner and a twelve-

330   channel coil. A high-resolution, structural T1-weighted image was acquired with the

331   following parameters: field of view: 256 x 256 mm, isometric voxel size: 1 mm, TR:

332   2530, TE: 3.32, flip angle: 7°, 176 slices. Functional data were acquired using an echo

333   planar imaging pulse sequence with the following parameters: field of view: 216 x

334   216 mm, isometric voxel size: 3 mm, matrix 72 x 72, TR: 2500 ms, TE: 28 ms, flip

335   angle: 80°, 41 slices in the AC–PC plane with an odd interleaved order.

336   *2.7. Procedure*

337   After providing informed consent and completing a safety screening

338   questionnaire, the subjects were familiarized with TMS and the neuronavigation

339   system. The structural MRI scan with the marked TMS target sites was subsequently

340 co-registered to a participant's head. Next, the resting motor threshold was measured

341 with single TMS pulses administered to the hand area in the left primary motor

342 cortex. Afterwards, two short training sessions were performed without and with

343 TMS, respectively, to familiarize subjects with the task and the triple-pulse TMS

344 protocol. The actual TMS experiment was subsequently conducted. All three target

345 sites were tested one by one in three separate runs and with five-minute breaks

346 between each run. Prior to each run, TMS was applied to the target site to test for

347 potential side effects of the stimulation (see Section 2.5). The whole procedure lasted

348 approximately 120 minutes.

349 *2.8. Data preprocessing*

350 For every trial, accuracy and reaction times were manually marked from the

351 recorded vocal responses in a blind fashion (i.e., a judge did not know to which

352 experimental condition a given trial belonged). One trial was excluded from all

353 further analyses due to an unexpected interruption of the experimental procedure that

354 took place during this trial; thus, 5,099 trials were included in the further steps.

355 Unusually accelerated or delayed responses, defined as those that were 2.5 SD faster

356 or slower than individual subjects' means within each experimental condition, were

357 treated as missing responses to minimize variance in the data and improve statistical

358 power (seventy trials; 1.4% of the data). Additionally, a log transformation was

359 applied to individual reaction time data to ensure the distributions' normality

360 (McDonald, 2009).

361 The Audacity software (www.audacityteam.org) and in-house Python scripts

362 were employed to perform accuracy and reaction time marking. All statistical

363 analyses were performed in the SPSS 25 package (IBM, USA).

364 *2.9. Data analysis: accuracy*

365   Given that the analysis of variance (ANOVA) applied to variables with

366 binomial distribution (e.g., subjects' accuracy quantified binomially as either a correct

367 or incorrect response) might produce spurious results (Jaeger, 2008), a statistical

368 analysis of the accuracy data was performed within the generalized linear mixed

369 model (GLMM). All valid trials (N = 5099; see Section 2.8) were entered into the

370 GLMM and were modeled as a binomial dependent variable using a logit link

371 function (correct answers vs. all errors—i.e., incorrect and missing answers modelled

372 jointly; see Supplementary Information for additional analyses, in which incorrect and

373 missing answers were modelled separately). The TMS site (the early visual cortex,

374 VWFA, and early somatosensory cortex), the TMS time window (0–70–120, 120–

375 170–220, 220–270–320, 320–370–420, and 420–470–520 ms), the TMS site x TMS

376 time window interaction, and an intercept were included in the model as fixed effects.

377 Additionally, a subject intercept was included as a random effect with the "variance

378 component" covariance type, to account for interpersonal variability. The early

379 somatosensory cortex, the first TMS time window, and their combination were used

380 as reference categories for TMS site, TMS time window, and TMS site x TMS time

381 window interaction coefficients, respectively. The model was estimated using the

382 SPSS "robust estimation" procedure to account for potential violations of the model

383 assumptions and with degrees of freedom fixed for all tests.

384   Pairwise comparisons were performed on estimated marginal means

385 reflecting the probability of a subject's correct recognition of a Braille letter under a

386 given condition. A significant TMS time window x TMS site interaction effect was

387 investigated across both TMS time windows and TMS sites. In comparisons between

388 TMS time windows within each site, the first time window (20–120 ms following the

389   Braille letter presentation's onset) was compared to every other time window. This

390   choice was motivated by several reasons. Firstly, such an early stimulation of the

391   visual cortex is unlikely to affect tactile processes in sighted subjects (Zangaladze et

392   al., 1999; see Section 1). We thus expected that TMS applied to the early visual

393   cortex and the VWFA in later time windows would disrupt subjects' performances

394   relative to the stimulation in the first time window. Secondly, the early somatosensory

395   cortex is critical for the initial tactile perception stage. It was demonstrated, for

396   example, that TMS applied to this site 30 ms following the presentation of a tactile

397   grating strongly interfered with judgments on its orientation (Zangaladze et al., 1999).

398   Based on the early somatosensory cortex's location in the tactile processing hierarchy,

399   one may expect that a disruptive effect of TMS applied to this site should be observed

400   in the first time window and vanish in later time windows; our planned comparisons

401   allowed us to test this prediction (i.e., test for an increase in accuracy in later time

402   windows relative to the accuracy in the first time window). Thirdly, contrasts made

403   against a TMS time window in which no effect is expected provide greater control for

404   unspecific stimulation effects than contrasts against no-TMS or sham conditions

405   because they control for both noise and tactile sensations (see De Graaf and Sack,

406   2011; Duncan et al., 2010; Pattamadilok et al., 2015; Sliwinska et al., 2012). Within

407   each TMS site, a Bonferroni correction was applied to correct the results for four

408   comparisons that were made (i.e., the first time window vs. every other time window).

409   Direct comparisons between time windows other than the first were not performed

410   because we did not have any specific hypothesis regarding such contrasts (for a

411   similar analytical strategy, see, e.g., Duncan et al., 2010; Pattamadilok et al., 2015;

412   Sliwinska et al., 2012). In comparisons between TMS sites within each time window,

413   all sites were compared with one another. Consequently, a Bonferroni correction was

414   applied to correct the results for three comparisons that were made within each time

415   window.

416   An additional analysis was performed to specifically test our hypothesis

417   regarding the temporal double dissociation between effects of the early visual cortex

418   stimulation and the VWFA stimulation on the subjects' Braille letter recognition

419   accuracy. Given that this hypothesis did not concern the early somatosensory cortex,

420   this TMS site was excluded, thus resulting in a 2 TMS site x 5 TMS time window

421   GLMM model (3,399 trials included; all other model parameters were maintained as

422   they were in the main analysis). In order to provide a stringent test for the double

423   dissociation, the pairwise comparisons' results were corrected for all tests performed,

424   considered jointly across factors (i.e., the results were corrected for thirteen

425   comparisons: four comparisons between the first and every other TMS time window

426   within each TMS site and five comparisons between TMS sites). A correction for

427   multiple comparisons was performed using the false discovery rate (FDR; Benjamini

428   and Hochberg, 1995), which provides more balanced p-value estimates than does a

429   Bonferroni correction when the number of comparisons is high.

430   *2.10. Data analysis: reaction time*

431   Median reaction times from correct responses were entered into a repeated-

432   measure 3 x 5 ANOVA with the TMS site (the early visual cortex, VWFA, and early

433   somatosensory cortex) and the TMS time window (0–70–120, 120–170–220, 220–

434   270–320, 320–370–420, and 420–470–520 ms) as within-subject factors. Pairwise

435   comparisons were performed using the same analytical logic as was described above.

436   While the actual reaction time analysis was performed on log-transformed data,

437   reaction times prior to log transformation are reported in the text and presented in

438   Figure 4 in order to enhance the presented results' interpretability.

439 *2.11. Data availability*

440   The accuracy and reaction time data, obtained as a result of the marking of

441 participants' vocal responses, are provided as supplementary material. Raw vocal

442 responses contain personally identifying information (i.e., the participants' voices)

443 and therefore cannot be made publicly available. This data-sharing strategy complies

444 with the requirements of the current study's funders and with the institutional ethics

445 approval.

446

447   **3. Results**

448   Our subjects progressed significantly in tactile reading during their Braille

449 training, reaching an average performance of 8.5 Braille words read per minute

450 (WPM; SD = 4.2 WPM; range = 3–16 WPM) and 17.3 Braille letters read per minute

451 (LPM; SD = 4.2 LPM; range = 11–29 LPM) (see Supplementary Information for

452 detailed behavioral results related to the Braille training). In the TMS experiment

453 itself, the overall Braille letter recognition accuracy was 83% (SD = 12%; range =

454 57–96%) and the overall reaction time was 1907 ms per Braille letter (SD = 522 ms;

455 range = 927–3051 ms).

456 *3.1. TMS effects on Braille letter recognition accuracy*

457   The GLMM applied to the analysis of the accuracy data (see Section 2.9; see

458 also Jaeger, 2008) correctly classified 83% of all subjects' responses. The corrected

459 model (i.e., including all independent variables; see Section 2.9) classified the data

460 significantly more efficiently than did the null model (which solely included an

461 intercept; $F_{(14,5084)} = 11.2$, $p < 0.001$). In the corrected model, no significant main

462 effects were detected for either the TMS site ($F_{(2,5084)} = 1.2$, $p = 0.311$) or the TMS

463 time window ($F_{(4,5084)} = 1.4$, $p = 0.236$), although we observed a significant TMS site

464   x TMS time window interaction ($F_{(8, 5084)} = 13.3$, $p < 0.001$). Fixed coefficients for the

465   GLMM are presented in Supplementary Table S1. The random effect included in the

466   model (reflecting between-subject variability; see Section 2.9) was also significant

467   with the intercept of 0.74 (SE = 0.28; Wald Z = 2.71, $p = 0.007$).

468   Pairwise comparisons within each TMS site revealed that, relative to the

469   earliest TMS time window (20–120 ms), the probability of recognizing a Braille letter

470   correctly decreased when TMS was applied at the 120–220 ms time window to the

471   early visual cortex ($t_{(5084)} = 2.97$, $p_{uncorr} = 0.003$, $p_{corr} = 0.012$; Fig. 2A) and at the

472   320–420 ms time window to the VWFA ($t_{(5084)} = 3.52$, $p_{uncorr} < 0.001$, $p_{corr} = 0.001$;

473   Fig. 2B). Interestingly, no significant effects were detected for the early

474   somatosensory cortex stimulation (all $p_{corr} > 0.25$; Fig. 2C).

Accuracy - comparisons between TMS time windows
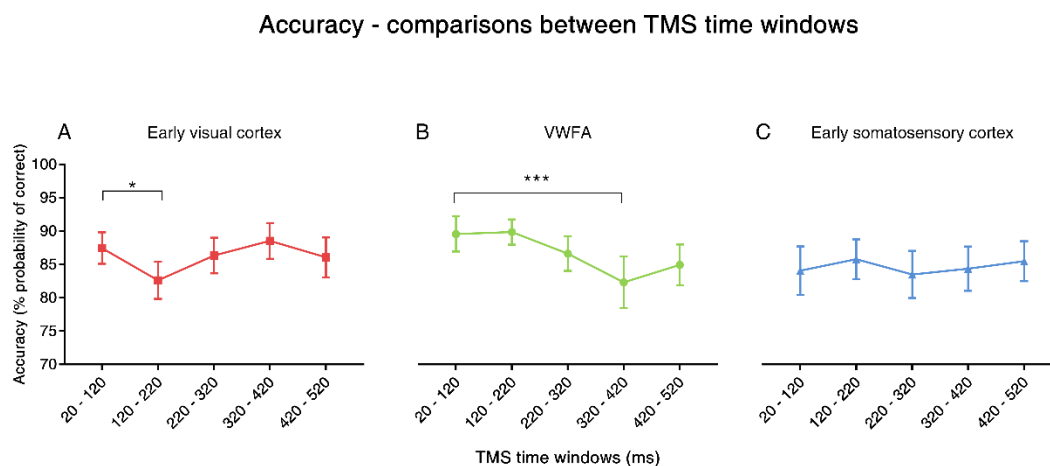
475

476   ***Figure 2.*** *Results of the Braille letter recognition accuracy analysis—comparisons*

477   *within each TMS site. Comparisons between the earliest TMS time window and every*

478   *other time window were performed for (A) the left early visual cortex stimulation; (B)*

479   *the visual word form area (VWFA) stimulation and (C) the left early somatosensory*

480   *cortex stimulation. The analysis was performed on marginal means reflecting the*

481   *probability of a subject's correct recognition of a Braille letter under a given*

482   *condition, which were estimated using a generalized linear mixed model (GLMM). **

483   *p < 0.05, *** p = 0.001, Bonferroni-corrected for multiple comparisons. Error bars*

484   *represent the standard error of the mean.*

485

486   Pairwise comparisons between TMS sites within each TMS time window

487   revealed a significantly decreased probability that a subject would recognize a Braille

488   letter correctly for the early visual cortex stimulation relative to the VWFA

489   stimulation in the 120–220 ms TMS time window ($t_{(5084)} = 4.14$, $p_{uncorr} < 0.001$, $p_{corr} <$

490   0.001). An inverse pattern was observed at the 320–420 ms time window, with the

491   probability of a subject correctly recognizing a Braille letter being lower for the

492   VWFA stimulation than for the early visual cortex stimulation ($t_{(5084)} = 2.49$, $p_{uncorr} =$

493   0.013, $p_{corr} = 0.039$). No significant differences were found in comparisons including

494   the early somatosensory cortex or other TMS time windows (all $p_{corr} > 0.08$).

495   Supplementary analyses suggest that detected decreases in the probability that a

496   subject would provide a correct answer were largely driven by an increase in the

497   probability that a subject would provide an incorrect answer rather than an increase in

498   the probability of a missing response (see Supplementary Figures S1–S2).

499
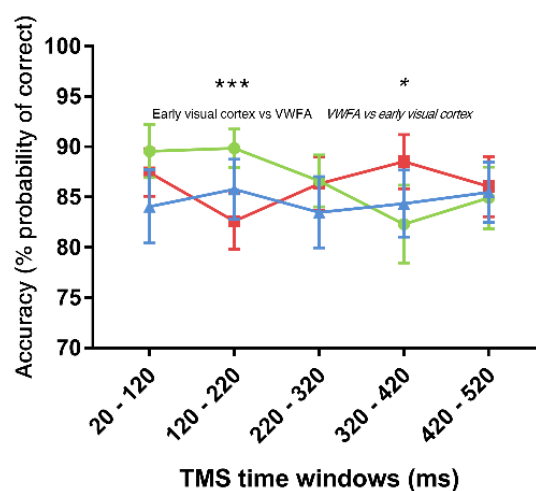
500 ***Figure 3.*** *Results of the Braille letter recognition accuracy analysis—comparisons*

501 *between TMS sites. Asterisks indicate significant accuracy differences between the*

502 *two TMS sites in a given time window. * p < 0.05, *** p = 0.001, Bonferroni-*

503 *corrected for multiple comparisons. Error bars represent the standard error of the*

504 *mean.*

505

506 In line with the results obtained within the main model, in the GLMM that

507 solely included the early visual cortex and the VWFA as TMS sites we detected a

508 significant interaction between the TMS site and the TMS time window ($F_{(4, 3389)}$ =

509 13.7, $p < 0.001$) and no significant main effects of either the TMS site ($F_{(1, 3389)}$ = 0.2,

510 $p = 0.652$) or TMS time window ($F_{(4, 3389)} = 1.77$, $p = 0.132$). In the pairwise

511 comparisons, FDR-corrected across all tests performed within a model (i.e., thirteen

512 tests; see Section 2.9), we replicated all effects obtained in the main analysis (Table

513 1).

514

515 ***Table 1***. *Results of the Braille letter recognition accuracy analysis—pairwise*

516 *comparisons including the early visual cortex and the VWFA, FDR-corrected for*

517 *multiple comparisons. Significant results are bolded; TMS TW–TMS time window.*

| Contrast	Contrast estimate	Standard error	t-value	p-value	FDR-adjusted p-value
Early visual: TMS TW 1 vs. TMS TW 2	**-0.048**	**0.016**	**2.97**	**0.003**	**0.013**
Early visual: TMS TW 1 vs. TMS TW 3	-0.011	0.021	0.52	0.604	0.785
Early visual: TMS TW 1 vs. TMS TW 4	0.011	0.017	0.65	0.519	0.75
Early visual: TMS TW 1 vs. TMS TW 5	-0.014	0.017	0.81	0.419	0.681
VWFA: TMS TW 1 vs. TMS TW 2	0.003	0.016	0.18	0.855	0.901
VWFA: TMS TW 1 vs. TMS TW 3	-0.030	0.020	1.51	0.130	0.282
VWFA: TMS TW 1 vs. TMS TW 4	**-0.072**	**0.021**	**3.53**	**< 0.001**	**0.003**
VWFA: TMS TW 1 vs. TMS TW 5	-0.046	0.025	1.88	0.06	0.156
TMS TW 1: early visual vs. VWFA	0.021	0.018	1.2	0.232	0.431
TMS TW 2: early visual vs. VWFA	**0.72**	**0.018**	**4.11**	**< 0.001**	**< 0.001**
TMS TW 3: early visual vs. VWFA	0.003	0.022	0.12	0.901	0.901
TMS TW 4: early visual vs. VWFA	**-0.062**	**0.025**	**2.5**	**0.012**	**0.039**
TMS TW 5: early visual vs. VWFA	-0.11	0.029	0.39	0.697	0.824

518

3.2. TMS effects on Braille letter recognition speed

The ANOVA for the reaction time data exhibited no significant TMS site x TMS time window interaction ($F_{(8, 128)}$ = 1.12, p = 0.357, η_p^2 = 0.065). However, significant main effects of the TMS site ($F_{(2, 32)}$ = 7.92, p = 0.002, η_p^2 = 0.331) and TMS time window ($F_{(4, 64)}$ = 2.58, p = 0.046, η_p^2 = 0.139) were detected. Pairwise comparisons between TMS sites (Fig. 4A) revealed that reaction times were significantly greater when TMS was applied to the early somatosensory cortex rather than the VWFA (+208 ms; $t_{(16)}$ = 4.34, p_{uncorr} = 0.001, p_{corr} = 0.003; d = 0.35) and, at trend level of significance, when TMS was applied to the early somatosensory cortex rather than the early visual cortex (+137 ms; $t_{(16)}$ = 2.67, p_{uncorr} = 0.017, p_{corr} = 0.051; d = 0.24). Pairwise comparisons between TMS time windows (Fig. 4B) did not reveal any significant differences in reaction times (the first time window vs. every other time window: all p_{corr} > 0.13; Fig. 4B).

The ANOVA that solely included the early visual cortex and the VWFA as TMS sites did not reveal any significant effects (all p > 0.18).

RTs - comparisons between areas
(TMS time windows combined)

A

RTs - comparisons between TMS time windows
(TMS areas combined)

B
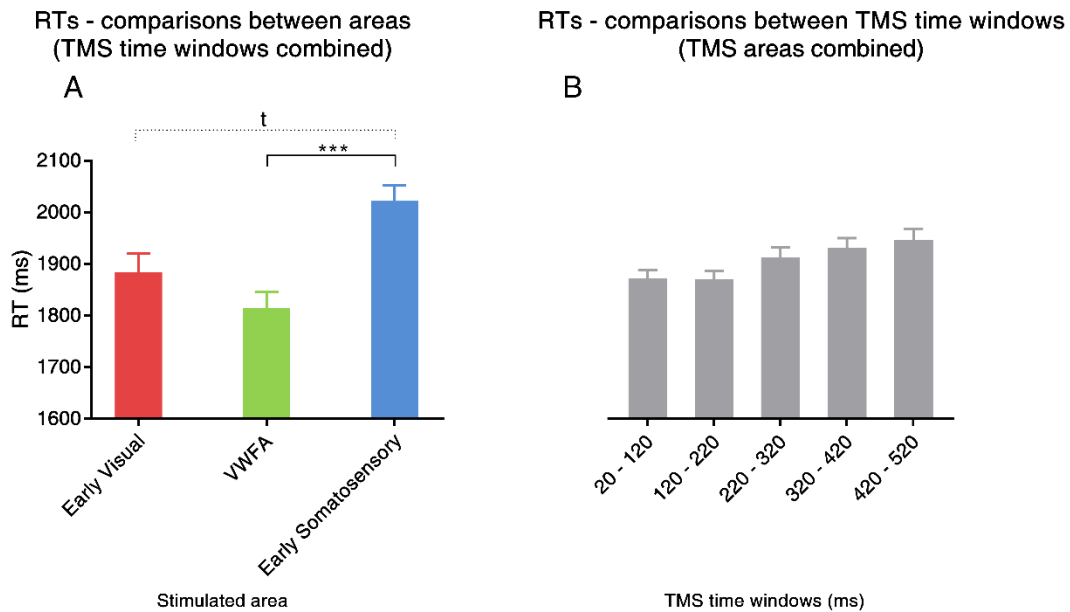
534

535 ***Figure 4.*** *Results of the Braille letter recognition speed analysis. To explore the*

536 *significant main effects of a TMS site and a TMS time window on subjects' reaction*

537 *times (represented as "RTs" in the images above), comparisons were performed*

538 *between: (A) all TMS sites, with data from TMS time windows combined within each*

539 *site; and (B) the first TMS time windows and every other time window, with data from*

540 *all TMS sites combined within each TMS time window. *** p = 0.001, ^{t} p = 0.051,*

541 *Bonferroni-corrected for multiple comparisons. Error bars represent the standard*

542 *error of the mean, adjusted to reflect between-subject variance in changes in reaction*

543 *times across (A) TMS sites or (B) TMS time windows using a method proposed by*

544 *Cousineau (2005). While the actual reaction time analysis was performed on the log-*

545 *transformed data, reaction times prior to the log transformation are presented to*

546 *enhance the figure's interpretability.*

547

548 **4. Discussion**

549 In this study, we employed a chronometric TMS to demonstrate that the early

550 and ventral visual cortices support tactile Braille letter recognition in sighted adults.

551   We observed specific spatiotemporal dynamics of this cross-modal involvement; the

552   early visual cortex was critically involved in the Braille letter recognition 120–220 ms

553   following the letter presentation, whereas the VWFA was critical for this task 320–

554   420 ms following the letter presentation. These results indicate that sighted people's

555   visual cortices are involved in tactile perception in a hierarchical manner.

556   Furthermore, our findings suggest that this cross-modal involvement respects the

557   canonical visual processing hierarchy; early stages of tactile processing are supported

558   by the early visual cortex, whereas more advanced tactile computations involve high-

559   level visual areas.

560   Our results align with previous studies that have documented cross-modal

561   activations at the various visual processing hierarchy stages in sighted people. Some

562   of these responses emerge as a result of learning new tactile or auditory skills (Amedi

563   et al., 2007; Saito et al., 2006; Siuda-Krzywicka et al., 2016; Zangenehpour and

564   Zatorre, 2010), while others are observed without any specific training, thus

565   suggesting they are part of a functional repertoire allowed by the default cortical

566   organization (Amedi et al., 2001; Campus et al., 2017; Eck et al., 2016, 2013, Lacey

567   et al., 2014, 2010; Sathian et al., 2011; Stilla and Sathian, 2008; Tal et al., 2016). In

568   the context of our work, it is particularly interesting that the fMRI study of Snow et

569   al. (2014) has already suggested that neural populations responsive to tactually

570   perceived shapes exist both in the early visual cortices and in higher-level ventral

571   visual regions (i.e., V4 and the lateral occipital complex) of sighted subjects. Our

572   results advance this finding by demonstrating that early and ventral visual cortices'

573   involvement in tactile perception is hierarchical and functionally relevant. The fact

574   that the visual cortex's stimulation disrupted tactile letter recognition in sighted

575   subjects—despite their not having been blindfolded—raises the possibility that cross-

576   modal interactions between the tactile and visual system occur in many everyday

577   situations.

578   We believe our results contribute to a discussion concerning the extent to

579   which the brain can be viewed as "metamodal"—that is, composed of areas showing

580   preference for specific computations independently of sensory input modality (Amedi

581   et al., 2017; Pascual-Leone and Hamilton, 2001). The metamodal account of brain

582   organization has recently received considerable support from research on blind and

583   deaf individuals (Amedi et al., 2017; Benetti et al., 2017; Bola et al., 2017c; Heimler

584   et al., 2015; Lomber et al., 2010; Meredith et al., 2011; for counter-arguments, see

585   Bedny, 2017). Several studies suggest that a metamodel account can be also applied

586   to the non-deprived brain; for example, the lateral occipital complex, which is

587   strongly activated during visual object recognition (Malach et al., 1995), is also

588   preferentially recruited for tactile and auditory object recognition (Amedi et al., 2007,

589   2001; Kim and Zatorre, 2011; Lacey et al., 2014, 2010), whereas the VWFA, an area

590   that develops functional preference for visual words and letters (Dehaene and Cohen,

591   2011; Price and Devlin, 2011), is strongly activated by tactile Braille reading (Siuda-

592   Krzywicka et al., 2016). Similarly, the V5/MT area, which exhibits functional

593   preference for moving visual stimuli (Zeki et al., 1991), becomes activated by

594   dynamic tactile and auditory stimuli (Hagen et al., 2002; Poirier et al., 2005). While

595   most of these studies focus on the high-level visual cortex, one recent work (Campus

596   et al., 2017) demonstrates that the early visual cortex can be recruited for spatial

597   although not temporal auditory processing, thus increasing the possibility that the

598   metamodal principle can be applied to low-level visual cortices to some extent. By

599   demonstrating that the early visual cortex was causally involved in a specific early

600   stage of tactile letter recognition, our results further support this possibility.

601 Moreover, our work supports the idea of the visual cortex's metamodal organization

602 from a more general perspective of the propagation of cross-modal information in this

603 cortical system. While previous studies have primarily focused on specific visual

604 regions, our findings suggest that early and high-level visual cortices can be gradually

605 engaged in tactile processing depending upon the task at hand's current computational

606 demands.

607 Based on the metamodal account of the visual system's organization, we

608 hypothesized that, during tactile Braille reading, the early visual cortex participates in

609 the construction of a spatial representation of Braille dots and signs, whereas the

610 VWFA supports the creation of an abstract representation of a Braille letter. In line

611 with this proposal, previous TMS studies have shown that sighted people's early

612 visual cortex supports spatial, non-linguistic tasks performed in the tactile modality,

613 such as discrimination of Braille signs' shapes (same/different decision; Merabet et

614 al., 2008), discrimination of tactually presented gratings' orientations (Zangaladze et

615 al., 1999), and distance judgments performed on Braille-like dots (Merabet et al.,

616 2004). Furthermore, fMRI experiments documented the early visual cortex's

617 recruitment for tactile texture perception (Eck et al., 2016, 2013; Sathian et al., 2011;

618 Stilla and Sathian, 2008). The VWFA's role in tactile perception was investigated in

619 our previous study (Siuda-Krzywicka et al., 2016), wherein we demonstrated that,

620 relative to touching strings of nonsense Braille characters, whole-word tactile Braille

621 reading activates this cortical region in sighted subjects and that TMS applied to

622 sighted subjects' VWFA disrupts performance in a tactile lexical decision task

623 similarly to the way it disrupts performance in a visual lexical decision task

624 performed in the Latin alphabet (as reported by Duncan et al., 2010). To our

625 knowledge, no study on sighted subjects has proven this cortical area's involvement

626 in tactile tasks that do not involve recognizing letters or words, which suggests that

627 the VWFA's cross-modal involvement might be specific to this cognitive domain.

628 The present results seem to generally agree with the available literature as well as our

629 initial hypothesis regarding the division of labor between the early visual cortex and

630 the VWFA. Notably, the early visual cortex's involvement in the tactile recognition of

631 Braille signs was observed relatively quickly (i.e., 120–220 ms following the Braille

632 letter presentation's onset). This is particularly interesting given the fact that tactile

633 recognition is usually much slower than visual recognition (see, e.g., Kitada et al.,

634 2014). Moreover, our subjects' tactile letter and word reading speeds were massively

635 slower than the typical visual reading speeds of sighted people (around 200–250

636 WPM; Hunziker, 2006) or even the typical Braille reading speeds of blind people

637 (Legge et al., 1999). Several studies have demonstrated that TMS applied to the early

638 visual cortex at comparable time windows disrupts non-linguistic processing in the

639 visual (Koivisto et al., 2011; Koivisto and Silvanto, 2012) and tactile modality

640 (Zangaladze et al., 1999), which supports our hypothesis regarding the early visual

641 cortex's relatively basic, spatial role in tactile reading. Only significantly later (320–

642 420 ms following the Braille letter presentation's onset) did the Braille letter

643 recognition involve the VWFA, which is suggestive of this area's qualitatively

644 different role in this task.

645 The identification of specific neural mechanisms underlying the visual

646 cortex's involvement in tactile perception remains a field of intensive inquiry. From a

647 theoretical perspective, two broad families of processes should be considered: (1)

648 "bottom-up" mechanisms, which directly map certain kinds of tactile information

649 onto the visual cortex processing machinery, and (2) indirect "top-down"

650 mechanisms, which take the form of either conscious visual imagery or unconscious

651   feedback signals propagating from higher-level cortical regions to the visual cortex.

652   In recent years, empirical evidence was provided in support of both these possibilities

653   (see, e.g., Amedi et al., 2001; Deshpande et al., 2010; Lacey et al., 2014, 2010;

654   Merabet et al., 2006; Siuda-Krzywicka et al., 2016). As proposed by Lacey et al.

655   (2009), these two types of mechanisms may very well act in concert, and their relative

656   contributions (and an exact type of top-down influences) to the visual cortex's

657   involvement in tactile perception might to some extent depend upon a subject's

658   familiarity with an object that is touched. This theoretical proposal was largely

659   confirmed in a series of studies concerning the role of the lateral occipital complex

660   (LOC) in tactile shape processing. The authors revealed that, during a tactile

661   exploration of familiar objects, the LOC activation's magnitude was correlated with

662   the magnitude of activation evoked in this area by a visual object imagery condition

663   (Lacey et al., 2010). Moreover, an effective connectivity analysis indicated that, under

664   both these conditions, the LOC's activation was primarily driven by inputs from the

665   prefrontal cortex (Deshpande et al., 2010). In contrast, the LOC activation's

666   magnitude during the tactile exploration of unfamiliar objects was not correlated with

667   the magnitude of activation evoked in this region by either visual object imagery or

668   spatial imagery (Lacey et al., 2014, 2010). Furthermore, the LOC's activation during

669   the tactile exploration of unfamiliar objects was primarily driven by inputs from the

670   somatosensory system and the intraparietal sulcus (Deshpande et al., 2010; Lacey et

671   al., 2014). The authors concluded that the LOC hosts a modality-independent

672   representation of an object's shape, which can be accessed both by bottom-up and

673   top-down mechanisms.

674   We believe our results might contribute to the development of the above-

675   described model in several ways. Firstly, we revealed that the ventral visual stream's

676   involvement in tactile perception can be preceded by the involvement of the visual

677   processing hierarchy's earlier stages. Based on our results, we cannot establish

678   whether the information computed in the early visual cortex during Braille letter

679   recognition is then transferred to the VWFA or whether the information processed in

680   these two regions is integrated outside the visual cortex. Nevertheless, our study

681   raises the possibility that inputs from early visual cortices are another important driver

682   of high-level visual areas' involvement in tactile perception—a hypothesis that, to our

683   knowledge, has not yet been directly tested. Secondly, our results suggest that

684   mechanisms of the visual cortex's involvement in the same tactile task might

685   significantly vary as a function of time following the stimulus presentation, thus

686   suggesting that this parameter should perhaps be included in the model. Based on a

687   distinction between the tactile perception of familiar and unfamiliar objects made by

688   Lacey et al. (2009), one might specifically expect to observe a stronger contribution

689   of bottom-up mechanisms to the visual cortex's cross-modal involvement at the onset

690   of a subject's interactions with a tactile object, when information about its shape and

691   identity is limited; in contrast, top-down mechanisms should gain importance with

692   time. Finally, based on these considerations, one might also expect that the bottom-up

693   mechanisms' contribution is more pronounced in the case of early visual areas, which

694   seem to be engaged in tactile perception at earlier time windows than are high-level

695   visual areas. Overall, our study reveals that the visual cortex's cross-modal

696   involvement is a dynamic process that develops within both space and time.

697   The subjects recruited for this study were able to visually read Braille signs

698   even prior to the initiation of their tactile Braille reading training. During their

699   training, the subjects often visually checked Braille exercises performed in the tactile

700   modality, which perhaps explains why they improved their visual Braille reading

701 speed following our study (see Supplementary Information for behavioral results

702 related to the tactile Braille training; for details regarding how the tactile Braille

703 training was designed, see Bola et al., 2016). This result might raise a question

704 regarding whether their visual familiarity with Braille signs may have influenced the

705 results of our TMS experiment. From the theoretical standpoint, studying tactile

706 perception without any form of contamination by the visual experience with the

707 object that is touched is perhaps exclusively possible when congenitally blind subjects

708 who have not developed the visual imagery mechanism are studied; arguably, every

709 sighted person would instantly start to imagine a tactually explored object, which

710 should likely be treated as a form of visual experience even if triggered internally.

711 Nevertheless, one might specifically wonder whether the subjects' training in the

712 visual Braille reading—a visual counterpart of the tactile task they performed in the

713 present experiment—may have influenced the mechanisms of the visual cortex's

714 cross-modal involvement that we have reported herein. Within the framework of the

715 model developed by Lacey et al. (2009) that was described above, it seems likely that

716 prior training in visual Braille reading amplifies the process of the visual cortex's

717 cross-modal involvement in tactile Braille reading observed in our study—perhaps by

718 priming neuronal populations in the visual cortex with Braille-like shapes or by

719 making the conceptual representation of the Braille script more salient and thereby

720 increasing the strength of top-down signals reaching the visual cortex during tactile

721 Braille reading. However, unless one assumes that learning to visually recognize

722 Braille signs leads to the emergence of neuronal populations responsive to the shape

723 of Braille dots or signs in the visual cortex, which then take over the processing of the

724 same shapes conveyed by the tactile modality—a possibility we consider highly

725 unlikely, especially given that our subjects were adults and their prior training in

726 visual Braille reading constituted a very small portion of their overall visual

727 experience—there exists no reason to believe that the visual Braille training

728 qualitatively changes mechanisms of the visual cortex's cross-modal involvement in

729 the process of reading this script tactually. In summary, we would expect to find

730 similar (possibly less pronounced) effects even in subjects with no formal visual

731 Braille training. Consistent with this line of reasoning, a considerable number of

732 studies have already indicated that the visual cortex is involved in various forms of

733 tactile perception (including the perception of Braille and Braille-like stimuli), even in

734 subjects without any specific visual experience with objects they have touched (for

735 studies including Braille and Braille-like shapes, see, e.g., Debowska et al., 2016;

736 Merabet et al., 2008, 2004).

737   Finally, contrary to the visual system stimulation, we found that TMS applied

738 to the early somatosensory cortex did not have any specific influence on the accuracy

739 of our subjects' Braille letter recognition; rather, the early somatosensory cortex

740 stimulation induced a general slowdown of subjects' reaction times independently of

741 the TMS time window. Such a pattern of results is unexpected; based on the early

742 somatosensory cortex's location in the tactile processing hierarchy, one might rather

743 expect that a disruptive effect of TMS applied to this area would be present in the

744 earliest time window and vanish in later time windows. Indeed, Zangaladze et al.

745 (1999) demonstrated that the TMS of the early somatosensory cortex, applied 30 ms

746 following the tactile presentation of a grating strongly disrupts the accuracy of

747 judgments on its orientation. Our results might suggest that effective tactile

748 perception critically depends upon the early somatosensory cortex's involvement even

749 at much later time points—a possibility that seems counterintuitive although, to our

750 knowledge, has not yet been specifically tested. It is important to stress, however, that

751 any interpretation of the effect found for the early somatosensory cortex stimulation

752 in our study should be made with caution, as our design was optimized for the

753 detection of time-specific effects and thus lacks optimal control conditions for

754 probing TMS effects present at all time windows. Notably, a recent study conducted

755 by Holmes et al. (2019) argues that localizing the somatosensory hand area by

756 moving a TMS coil posteriorly from the motor hand area is far from optimal. In that

757 paper, the authors defined the motor hand area as a site at which TMS induces the

758 strongest hand muscle response. In contrast, the localization of both the hand motor

759 area and the early somatosensory site in our study was constrained by anatomical

760 landmarks (see Section 2.4), which allowed us to avoid bias related to the imprecise

761 localization of the "omega knob"—a problem that seems to be common among

762 studies that employ the hand muscle response as an indicator of this region's location

763 (see Ahdab et al., 2016)—and ensure that we localized the early somatosensory cortex

764 within the postcentral gyrus. Nevertheless, given that the interindividual variability in

765 the somatosensory hand area's location within the postcentral gyrus seems

766 considerable (Holmes et al., 2019; Merzenich et al., 1987 Geyer et al., 1999; Grefkes

767 et al., 2001; Schweisfurth et al., 2018), we cannot fully exclude the possibility that our

768 method of localizing the early somatosensory cortex lacked the precision necessary to

769 detect a true time-specific effect of neural activity disruption in this area, and that the

770 observed general slowdown of reaction times reflects some confounds for which

771 comparisons with other TMS sites cannot account. This concern does not apply,

772 however, to our key results of the visual cortex stimulation, which are controlled

773 across both TMS time windows and TMS sites.

774   In conclusion, we provide causal evidence that, in sighted adults, tactile

775 Braille letter recognition is supported by the early visual and ventral visual cortices.

776 Moreover, our results indicate that, in sighted people, the visual cortex's involvement

777 in tactile perception respects the canonical visual hierarchy—that is, the early stages

778 of tactile processing involve the early visual cortex whereas more advanced tactile

779 computations involve high-level visual areas. In combination with our previous

780 studies (Bola et al., 2017a; Siuda-Krzywicka et al., 2016), these findings reveal the

781 visual cortex's remarkable multimodal potential to support tactile perception even

782 when the visual input is unconstrained.

783

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1024

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1026   Ł.B., J.M., M.S., M.W.S., M.P., K.J., M.S. and A.M. designed research; Ł.B. and J.M

1027   performed research; Ł.B., J.M., M.S. and D.D. analyzed data; Ł.B., J.M., K.J., M.S.

1028   and A.M wrote the paper.

1029

1030   **Competing interests**

1031   The authors declare that no competing interests exist.

1032