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The VWFA is the home of orthographic learning when houses are used as letters

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Running head: ORTHOGRAPHIC LEARNING AND THE VWFA

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Abstract

43 Learning to read specializes a portion of the left mid-fusiform cortex for printed
44 word recognition, the putative "visual word form area" (VWFA). This study examined
45 whether a VWFA specialized for English is sufficiently malleable to support learning a
46 perceptually atypical second writing system. The study utilized an artificial orthography,
47 "HouseFont," in which house images represent English phonemes. House images elicit
48 category-biased activation in a spatially distinct brain region, the so-called
49 "parahippocampal place area" (PPA). Using house images as letters made it possible to
50 test whether the capacity for learning a second writing system involves neural territory
51 that supports reading in the first writing system, or neural territory tuned for the visual
52 features of the new orthography. Twelve human adults completed two-weeks of training
53 to establish basic HouseFont reading proficiency and underwent functional neuroimaging
54 pre and post-training. Analysis of three functionally defined regions of interest, the
55 VWFA, and left and right PPA, found significant pre- versus post-training increases in
56 response to HouseFont words only in the VWFA. Analysis of the relationship between
57 the behavioral and neural data found that activation changes from pre- to post-training
58 within the VWFA predicted HouseFont reading speed. These results demonstrate that
59 learning a new orthography utilizes neural territory previously specialized by the
60 acquisition of a native writing system. Further, they suggest VWFA engagement is driven
61 by orthographic functionality and not the visual characteristics of graphemes, which
62 informs the broader debate about the nature of category-specialized areas in visual
63 association cortex.

64

65

66 **Significance Statement**

67 Fluent reading recruits a portion of the brain known as the visual word form area
68 (VWFA), but it is less well understood how malleable the VWFA remains after acquiring
69 literacy in a native language. There is also debate about the type of visual information the
70 VWFA can process as orthographically meaningful. We tested whether native English-
71 speaking adults could learn a second, visually atypical writing system for English and
72 used neuroimaging data to assess the location of any learning effects. Participants
73 acquired basic reading ability and learning effects were found in the neural territory that
74 underlies English reading. This suggests that the VWFA remains plastic after initial
75 literacy and is not restricted by the visual features of a writing system.

76

77 Acquiring a second language in adulthood is challenging, in part because neural
78 resources become specialized for native language processing (Hull & Vaid, 2007; Tan et
79 al., 2003). This specialization can make it difficult to use the same neural tissue to
80 support fluency in a second language (Klein, Mok, Chen, & Watkins, 2014; Mårtensson
81 et al., 2012). In this paper we examined a related question: to what degree can adults
82 acquire a second writing system for their native language? To address this question, we
83 taught adult native English speakers a perceptually atypical artificial orthography for
84 English. We used behavioral and functional magnetic resonance imaging (fMRI) methods
85 to ascertain if their newly learned reading skill involved a region already specialized for
86 reading English, the putative “visual word form area” (VWFA).

87 The VWFA is a region in the left fusiform gyrus that preferentially responds to
88 orthographic visual stimuli (Cohen & Dehaene, 2004; Cohen et al., 2002; Glezer, Kim,
89 Rule, Jiang, & Riesenhuber, 2015; McCandliss, Cohen, & Dehaene, 2003; Szwed et al.,
90 2011) (but see Price and Devlin (2003) and Vogel, Petersen, and Schlaggar, (2014) for
91 alternative accounts of the VWFA). This response specialization emerges with the
92 acquisition of literacy (Saygin et al., 2016), even when native language literacy is
93 acquired in adulthood (Dehaene et al., 2010), suggesting an absence of a “critical” period
94 of plasticity (Bornstein, 1989).

95 Less is known about the degree to which the VWFA remains plastic once it has
96 become specialized to support a native writing system, and to what extent its recruitment
97 depends upon the perceptual characteristics of a writing system. The widespread
98 acquisition of second language literacy suggests the VWFA can support skilled reading
99 for multiple orthographies (Tschirner, 2016). However, this apparent ease may be

100 misleading due to the high degree of visual similarity between naturally occurring
101 orthographies (Hirshorn & Fiez, 2014). This visual similarity may reflect the cultural
102 evolution of writing systems to use forms that are optimized for the representational
103 capacities of the VWFA (Dehaene, 2009), in which case the VWFA may be poorly
104 equipped to respond to a perceptually atypical orthography. Further, the high degree of
105 visual similarity between natural writing systems may allow any literacy-driven
106 specialization of the VWFA to readily transfer to another orthography, thereby
107 overestimating the plasticity of the VWFA for orthographies that are perceptually distant
108 from the native orthography.

109 A strong test of the VWFA’s plasticity therefore requires acquisition of a
110 perceptually atypical orthography by an individual whose VWFA has already been
111 specialized by a native orthography. The need to disentangle factors that are intertwined
112 in naturally occurring orthographies motivates the use of an artificial orthography in the
113 present study. We build upon a previously reported study that used face images as
114 “letters” to represent English phonemes (Moore, Durisko, Perfetti, and Fiez, 2014). In
115 this previous study, orthographic learning effects were observed in the left mid-fusiform
116 cortex, but there was ambiguity whether these effects localized to the VWFA or to tissue
117 specialized for face processing, the left “fusiform face area” (FFA). Thus, it remains
118 unclear whether orthographic learning effects localize to tissue that is specialized for
119 processing the visual characteristics of the grapheme forms (e.g., words printed with face
120 letters to the FFA) or whether visual stimulus with orthographic functionality may induce
121 plasticity within the VWFA, even when it has already been specialized for a perceptually
122 typical native orthography.

123 To address this question, we trained English speakers to read an artificial
124 orthography in which images of houses represent English phonemes (HouseFont). We
125 chose houses because they are preferentially processed in a region known as the
126 parahippocampal place area (PPA), which is spatially distant from the VWFA. The
127 PPA's distinctiveness allows us to identify the neural tissue dedicated to processing the
128 graphemes of our new orthography. We employed a localizer scan to functionally
129 identify the PPA and VWFA, and pre- and post-training scans to isolate neural changes
130 associated with HouseFont learning. This allowed for a clear test of whether a VWFA
131 tuned to a native orthography (English) has the flexibility to respond to a second
132 orthography (HouseFont), even when this second orthography uses graphemes that are
133 highly distinctive from those used in the Roman alphabet. If the perceptual characteristics
134 of grapheme forms drive the locus of orthographic learning, significant learning effects
135 should be observed in the PPA. Alternatively, if the functional use of visual forms as
136 orthographic symbols drives the locus of orthographic learning, and the neural tissue that
137 supports this learning remains malleable, significant learning effects should be observed
138 in the VWFA.

139

140

141

Method

Participants

143 Fourteen University of Pittsburgh undergraduate students were originally enrolled
144 in the study. This sample size was selected based on research showing that imaging
145 research can achieve power of roughly 80% using a threshold of .05 and 12 subjects

146 (Desmond & Glover, 2002), and results for our prior study (Moore et al., 2014) in which
147 significant differences in the VWFA territory were observed for between-group
148 comparisons (N=11 and 12) of the response to a trained versus untrained orthography.
149 One participant dropped out on the second day of training and one dropped out after
150 having completed everything except the post-training imaging session. Data from the
151 final sample of 12 individuals (8 female, 4 male) are reported (M age = 19.17 years, SD =
152 1.19). All participants were recruited from a database of individuals interested in
153 participating in research studies. All study participants were right-handed, native English
154 speakers, and had no history of second language fluency, hearing or vision issues,
155 learning or reading problems, drug or alcohol abuse, mental illness, neurological issues,
156 or contraindications for fMRI. All participants provided informed consent and were
157 compensated for their time. All procedures were approved by the institutional review
158 board (IRB) of the University of Pittsburgh.

159

160 **Study Overview**

161 The study involved a two-week training protocol to learn HouseFont. Training
162 occurred after two pre-training fMRI sessions and before a post-training fMRI session.
163 The first of the pre-training fMRI sessions was designed to localize three regions of
164 interest (ROIs): the VWFA and the left and right PPA. The purpose of the second pre-
165 training fMRI session was to measure the response to words printed in HouseFont before
166 training. The final fMRI session measured the response to HouseFont after training.
167 Behavioral measures of post-training reading skill were also acquired as part of this final
168 session. Participants were debriefed and paid following the post-training scan. Figure 1

169 provides an overview of the study timeline and the design of specific tasks. Table 1

170 summarizes the HouseFont training protocol. Further details are provided below.

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176 **Table 1**

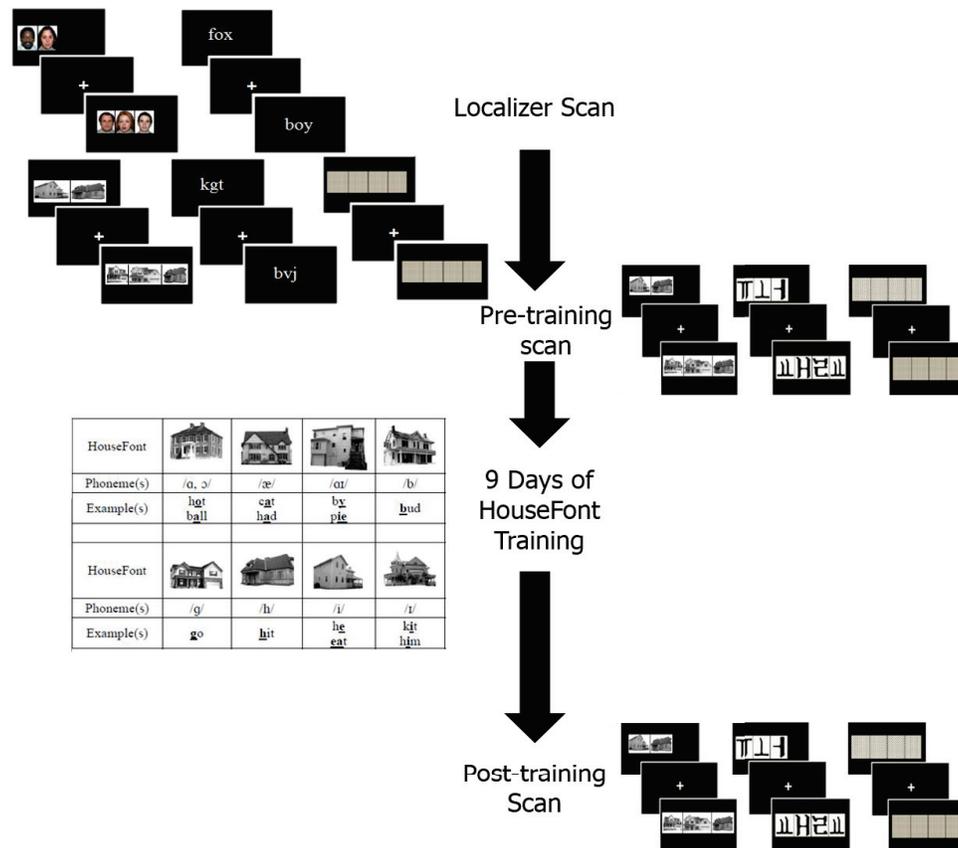
177 *HouseFont Training Protocol*

<i>Week</i>	<i>Session</i>	<i>Tasks</i>
Baseline		Localizer fMRI Pre-training fMRI
Week 1	Session 1	Phoneme Training Phoneme Test
	Session 2	Phoneme Training Review Word Level Training Word Test (1)
	Session 3-5	Word Level Training Word Test (2-4)
Week 2	Session 6-9	Story Level Training Word Test (5-8)
	Session 10	Reading Test (GORT-4) Post-training fMRI

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183 **Fig. 1.** Participants completed a localizer scan, a pre-training scan, HouseFont training,

184 and a post-training scan. The images alongside each point on the timeline are examples of

185 the stimuli used for the neuroimaging sessions.

186

187 **Pre-training fMRI Sessions**

188 **Localizer session.** Participants started the study by completing a localizer fMRI
189 session and a battery of standardized reading tests. The localizer session was conducted
190 using a Siemens Medical Systems 3T Magnetom TIM Trio scanner with a 32-channel
191 radio frequency coil. High-resolution structural scans were collected using an axial
192 MPRAGE with 192 slices and 1 mm isotropic voxels. Functional data were collected
193 across 29 interleaved slices in the same plane as the structural data (TR= 1500 ms, TE =
194 25 ms, FOV = 200 mm, FA = 70°).

195 During functional data acquisition, participants completed a 1-back task with five
196 categories of visual stimuli: 1) houses, 2) faces, 3) words, 4) letter-strings, and 5) patterns
197 (Figure 1). Following similar localizer protocols used in prior studies (Fox, Iaria, &
198 Barton, 2009; Rossion, Hanseeuw, & Dricot, 2012), stimuli were drawn from sets of 40
199 exemplars for each of the non-orthographic (houses, faces, and patterns) categories, and
200 sets of 157 exemplars for the orthographic (word and letter-string) categories. The scan
201 consisted of four functional runs each lasting 6 minutes. Every run had a total of 15
202 blocks (three of each category, randomly ordered). Blocks consisted of 15 trials, with the
203 stimulus for each trial presented for 200 ms followed by an 800 ms fixation cross.
204 Participants were asked to press a key when they detected a stimulus that repeated the
205 one shown previously (i.e., 1-back). A 1-back target was presented for 12.5% of each
206 block. A 9 s baseline condition followed each block. During this baseline, participants
207 attended to a fixation cross at the center of the screen. During each run, the sets of house,
208 face, and pattern stimuli were distributed pseudorandomly within each of the three blocks
209 for each condition. With the exception of 1-back trials, the word and letter-string stimuli

210 did not repeat. None of the house images used in the localizer task were used as stimuli in
211 the subsequent parts of the study.

212 **Pre-training session.** The pre-training scan was completed within a week of the
213 localizer session. For logistical reasons, the scanner, a 3T Siemens Allegra equipped with
214 a standard radio frequency coil, differed from that used for the localizer session. High-
215 resolution structural scans were collected using a sagittal MPRAGE with 192 slices and 1
216 mm isotropic voxels. Functional data were collected across 38 interleaved slices (3.125 x
217 3.125 x 3.2 mm voxels) parallel to the anterior-posterior commissure (TR= 2000 ms, TE
218 = 25 ms, FOV = 200 mm, FA = 70°).

219 During the pre-training scan participants passively viewed 140 words printed in
220 HouseFont and an untrained artificial orthography, KoreanFont. KoreanFont is an
221 artificial alphabetic orthography that borrows graphemes from Hangul, the Korean
222 writing system, and assigns them to English phonemes. They also saw 16 pattern displays
223 that were repeated over 140 trials. Word and pattern stimuli were matched for length.
224 Participants completed two runs, which consisted of seven blocks of each stimuli type for
225 a total of 21 blocks. Each block contained 10 trials of the same stimulus type. For each
226 trial, participants saw one HouseFont or KoreanFont word or pattern set for 1500 ms,
227 followed by 500 ms of a centrally located fixation cross (Figure 1). They were instructed
228 to attend to the stimuli, but were not asked to perform an overt task. The same set of
229 HouseFont words were presented during the pre-training and post-training sessions;
230 individuals were not exposed to this set of HouseFont words at any other time.

231 **HouseFont Training**

232 HouseFont consists of 35 grapheme-to-phoneme mappings, where each grapheme
233 is a particular house image that is used to represent a single phoneme or (in a few cases)
234 two very similar sounds (e.g., /ɑ/ in *hot* and /ɔ/ in *ball*). All of the house images used for
235 HouseFont were 300 x 300 pixels, normalized, and lightened to a light grey. Participants
236 were trained to read HouseFont across nine sessions, which were broken into three
237 phases: house-phoneme mapping (Session 1), word-level training (Sessions 2-5), and
238 story-level training (Session 6-9). Each training session lasted from 1-2 h. These training
239 phases are summarized.

240 **Session 1: House-phoneme mapping.** Participants began their training by
241 learning to map each HouseFont grapheme with a corresponding phoneme using a self-
242 paced computer program. The 35 house graphemes were visually presented in random
243 order, and participants pressed a spacebar to hear the corresponding sound after each
244 grapheme was displayed. Participants completed five cycles of the phoneme training,
245 followed by a test of their ability to produce the phoneme associated with each grapheme.
246 Participants who achieved less than 90% accuracy repeated the training. All participants
247 passed in three or fewer attempts.

248 **Sessions 2-5: Word-level training.** After a brief refresher on the house-phoneme
249 mapping, participants learned how to read aloud short words printed in HouseFont. Each
250 session of the word-level training involved reading 400 1-2 syllable words, which were 2
251 to 5 phonemes in length. The same set of 400 words was used in Sessions 2-5, with the
252 word order randomized across sessions. For each trial, participants were encouraged to
253 attempt to read the word when it appeared; they had the option to hear any individual
254 phoneme or the entire word if necessary. At the end of each session, a computer-based,

255 single-word-reading test was administered. Each word test consisted of three conditions
 256 presented in a block design, with the order of blocks randomized across test sessions: old
 257 HouseFont words (words included in word-level training), new HouseFont words, and
 258 pronounceable HouseFont non-words. There were 20 trials per condition. A trial
 259 consisted of a 1-syllable word that was 3 to 4 phonemes in length. The pronunciation
 260 accuracy was scored for each item, and reading latency was measured from the time a
 261 word first appeared on the screen to when the participant pressed the space bar to
 262 advance to the next word.

263 **Sessions 6-9: Story-level training.** In the final training stage, participants
 264 advanced to reading aloud short stories printed in HouseFont (Figure 2). For each
 265 session, participants read 10 early reader stories of similar difficulty from the “Now I’m
 266 Reading!” series (Gaydos, 2003). The story level increased in difficulty with each
 267 successive session. Performance on story reading was measured by words read per
 268 minute. At the end of each session, participants completed a single-word-reading test
 269 identical in design and scoring to those used during word-level training.

270



271

272 **Fig. 2.** An example of part of a story printed in HouseFont. It reads, ‘See father. Father is
 273 here.’

274

275 **Post-training Behavioral and fMRI Session**

276 During the final session (Session 10), participants completed behavioral testing to
277 assess their final HouseFont reading skill and an fMRI session to measure learning-
278 related changes in the neural response to HouseFont. For the behavioral testing,
279 participants' reading speed and accuracy were assessed using six passages (Form A
280 Stories 1 – 6) from the Gray Oral Reading Test – 4 (GORT-4) (Wiederholt & Bryant,
281 2001) that were transcribed into HouseFont. Number of words read per minute and
282 number of errors made per word were calculated as an index of reading speed and
283 accuracy respectively. The number of errors made per word was determined by dividing
284 the number of errors (e.g., omissions, phoneme substitutions, whole word or part word
285 repetitions, etc.) made by the number of words in each passage. The post-training scan
286 was completed during Session 10 immediately after administration of the behavioral
287 tests, using the same scanner and fMRI protocol as in the pre-training scanning session.

288

289 **fMRI Data Analysis**

290 **fMRI data preprocessing.** Preprocessing of the fMRI data was completed using
291 the Analysis of Functional NeuroImages (AFNI) software package (Cox, 1996). The first
292 two brain volumes from the localizer runs and the first brain volume from the pre-training
293 and post-training runs were removed to allow for stabilization of the signal. The
294 functional images were slice time corrected (3dTshift), and all data were motion
295 corrected (3dvolreg). The data were smoothed using a Gaussian filter set to a smoothing
296 kernel of 5.5 mm full width at half maximum. Next, the functional images were
297 registered to the skull stripped high-resolution structural images. Images were then
298 transformed into standard Talairach space using a non-linear warping procedure in AFNI

299 to allow for group analysis (Talairach & Tournoux, 1988). Functional images were scaled
300 to a mean global intensity.

301 **Regions of interest (ROI) identification.** The central question of this study is
302 whether HouseFont learning is supported by neural tissue specialized by the acquisition
303 of a native (English) orthography (i.e., territory at or near the VWFA) or tissue that
304 shows selectivity for the perceptual characteristics of the non-native HouseFont
305 orthography (i.e., the territory at or near the PPA). To address this question, the data from
306 the localizer session were used to functionally localize *a priori* ROIs in the left fusiform
307 and bilateral parahippocampal cortices.

308 Multivariate pattern analysis (MVPA) was used to identify each of the three ROIs
309 within MATLAB using the Princeton Multi-Voxel Pattern Analysis toolbox (Detre et al.,
310 2006). For this analysis, the functional data preprocessing was the same as described
311 above, with one exception: as is common in MVPA, the data were not spatially smoothed
312 (Mur, Bandettini, & Kriegeskorte, 2009). MVPA has been found to be more sensitive to
313 fine grain differences between stimuli (for a review see Coutanche (2013)). This
314 increased sensitivity allowed us to successfully localize the left fusiform ROI using a the
315 hallmark contrast used in early work characterizing the VWFA: words and letter-strings
316 (Cohen et al., 2002; Dehaene, Le Clec'H, Poline, Le Bihan, & Cohen, 2002; Petersen,
317 Fox, Snyder, & Raichle, 1990). To localize the PPA ROIs, a house and word contrast was
318 used.

319 For each run, we z-scored the pre-processed activity values (beta-weights) for
320 each voxel, accounting for the hemodynamic delay by shifting the condition time course
321 by two TRs. A Gaussian Naive Bayes (GNB) classifier was trained and tested on the

322 activity patterns for the contrasts of interest (words vs letter-strings and houses vs words)
 323 using a leave-one-run-out cross-validation procedure, where each iteration was trained on
 324 data from all-but-one run (e.g., three runs), and tested on data from the held-out run.
 325 Classification performance from the iterations was averaged to give a single accuracy
 326 value. The resulting accuracy for the contrasts (where chance is 50%) was then allocated
 327 to the central voxel of a 3-voxel radius searchlight sphere, which was moved serially
 328 across the brain.

329 We identified the voxel with peak decoding accuracy for the words vs. letter-
 330 strings contrast within AFNI's anatomical mask of the left fusiform cortex and for the
 331 houses vs. words contrast within anatomical masks of the left and right parahippocampal
 332 cortex for each subject. To generate the group level ROIs for the VWFA and PPAs, we
 333 created a 6 mm radius sphere centered on the location of average peak accuracy across all
 334 subjects for the respective contrast in each anatomical mask (Table 2).

335

336 **Table 2**337 *Functionally defined ROIs that were applied to the pre- and post-training data*

Localizer ROI	Cluster Size (Voxels)	Center of Mass Coordinates (X,Y,Z)
Left Parahippocampal Gyrus (L PPA)	33	-28, -43, -7
Right Parahippocampal Gyrus (R PPA)	33	26, -43, -4
Left Fusiform Gyrus (VWFA)	33	-34, -55, -13

338 Coordinates are in Talairach space.

339

340 **Analysis of behavioral and neural learning effects**

341 **Analysis of behavioral learning effects.** To test if participants showed
342 improvements in HouseFont reading during training, reading accuracy and reading speed
343 were assessed for each of the word tests. A one-way repeated measures ANOVA was
344 performed on the average reading latency scores for correct responses across the eight
345 word tests to determine if reading speed changed over the course of training.

346 **Analysis of neural training effects.** To test if participants showed neural changes
347 associated with training (i.e., changes in the neural responses to HouseFont words), the
348 pre- and post-training data were modeled using AFNI's 3dDeconvolve to estimate the
349 BOLD response (average beta-weight value) for HouseFont and KoreanFont. The motion
350 estimates from preprocessing were included as regressors of no interest. Then, we
351 compared the resulting t-values for HouseFont and KoreanFont across the pre- and post-
352 training sessions, using both an ROI-based and a whole-brain (vowel-wise) group
353 analysis.

354 For the ROI analysis, the VWFA and PPA ROIs identified from the localizer
355 (Table 2) were applied to the pre-and post-training session data. Using AFNI 3dROIstats,
356 the averaged beta weight value for the voxels within each ROI was obtained for each
357 participant's response to HouseFont and KoreanFont before and after HouseFont training.
358 These values were exported to IBM Statistical Package for the Social Sciences (SPSS)
359 version 25. To determine if there were training and ROI based differences in HouseFont
360 activation, a 2 x 2 x 3 repeated measures analyses of variance (ANOVA) was performed
361 with orthography (HouseFont, KoreanFont), session (pre-training, post-training), and
362 region (VWFA, left PPA, and right PPA) specified as within-subject variables. It was
363 expected that there would be a significant three-way interaction, which would suggest

364 there was a differential change in HouseFont activation between ROIs that resulted from
365 HouseFont reading training. A significance threshold of $p < .05$ was used, with correction
366 for all violations of normalcy in the data.

367 As a complementary analysis approach, a whole brain voxel-wise analysis was
368 used to identify pre- versus post-training changes in the response to HouseFont without *a*
369 *priori* constraints. The computed t-values for the HouseFont versus KoreanFont contrast
370 for each participant were contrasted across the pre- versus post-training sessions for each
371 voxel using AFNI 3dClustSim, with a significance threshold of $p = 0.005$ (corrected $p =$
372 0.05) and a cluster size threshold of 60 contiguous voxels.

373 **Relationship between behavioral and neural measures.** To examine the
374 relationship between behavioral and neural measures of learning, each participant's
375 reading speed score from the final word test was standardized and combined with the
376 standardized reading speed score from the GORT-4. This composite reading speed score
377 was examined using a regression analysis, to determine whether the pre- vs. post-training
378 change in the estimated BOLD responses within the VWFA ROI accounted for
379 HouseFont reading speed variability.

380 Because the sample size of the current study is small, we performed a similar
381 analysis that combined data from the participants in the current study ($N = 12$) with data
382 from two participant groups reported by Moore et al. (2014): one group that learned an
383 artificial orthography with face images as letters (FaceFont; $N = 12$) and one group that
384 learned an artificial orthography with borrowed Korean graphs mapped to English
385 phonemes (KoreanFont; $N = 11$). For each participant from the Moore et al. study, the
386 final reading speed was calculated in the same way as it was for HouseFont, by

387 averaging the z-score of the GORT reading speed and the inverse z-score of the final
388 word test reading speed. The imaging data from the Moore et al. study were acquired
389 using the same design and scanner as in the current study, with the exception that only a
390 post-training session was acquired, and instead of viewing HouseFont and KoreanFont
391 words, participants viewed FaceFont and KoreanFont words. Because the data from the
392 Moore et al. study were previously analyzed using a different software package, they
393 were reprocessed using the same methods as in the current study.

394 Next, we used an ROI analysis to extract the average estimated BOLD response
395 within the VWFA territory for each participant across our three groups (HouseFont,
396 FaceFont, KoreanFont). To avoid biasing the results by using the VWFA ROI identified
397 using data from only the HouseFont participants, we drew upon the literature to define an
398 unbiased ROI for this across-group analysis. Specifically, we used a coordinate from a
399 recent study by Lerma-Usabiaga, Carreiras, and Paz-Alonso, (2018), where real words
400 and consonant strings were contrasted to localize a specific VWFA subregion in the
401 middle occipitotemporal sulcus (mOTS) that exhibits lexical-level orthographic
402 selectivity, and which can be distinguished from a more posterior VWFA subregion that
403 is more generally responsive to visual word forms (pOTS). The average peak coordinate
404 reported by Lerma-Usabiaga and colleagues for their mOTS subregion was rounded to
405 the closest whole number, transformed into Talairach space, and used as a center of a 6
406 mm sphere (-42, -57, -4). Using AFNI 3dROIstats, the averaged beta weight value for the
407 voxels within this mOTS ROI was obtained for each participant's response to their
408 trained orthography during the post-training scan. These values were entered into a

409 regression analysis, along with the orthography learned by the participant, to predict
410 participants' reading speed following training.

411

412 **Results**

413 **Behavioral Measures of HouseFont Learning**

414 Average accuracy for trained participants across all of the word tests performed
415 during training was 90%. This is not surprising, because HouseFont is a transparent
416 orthography and so once the grapheme-phoneme mappings have been mastered, they can
417 in theory be used to decode English words and pronounceable nonwords with perfect
418 accuracy. For this reason, the focus of the behavioral training analyses was reading
419 latency. To test if participants showed improvements in HouseFont reading over the
420 course of their training, a one-way repeated measures ANOVA was performed on the
421 average reading latency score for correct responses on the eight word tests. Two
422 individuals were missing a single word test and were excluded from the analysis. The
423 Greenhouse-Geisser correction was applied because Mauchly's test of sphericity was not
424 met, $p = .01$. There was a significant effect of test session $F(2.28, 20.48) = 10.47$, $p =$
425 $.001$, which reflects a decrease in reading latencies over the course of HouseFont training.
426 From the first word test (Session 2) to the final word test (Session 9), the average reading
427 latency dropped from 6288 ms ($SD = 1963$ ms) to 4670 ms ($SD = 1126$ ms). This 25%
428 reduction in reading latency indicates that participants became more skilled at reading
429 HouseFont across the two weeks of training.

430 Improvements in HouseFont reading were also evident in the context of story
431 reading. Participants maintained a relatively steady rate of reading across story level

432 training (Sessions 6-9), even though the stories became increasingly more difficult across
 433 sessions (Figure 3). By the end of story-level training (Session 9), participants were
 434 reading an average of 21.85 words per minute ($SD = 2.88$). Participants also read six
 435 passages of a standardized reading assessment, the GORT, to assess final reading
 436 accuracy and speed. On this measure participants attained a mean fluency of 21.15 ($SD =$
 437 5.13) words per minute, with a mean error rate of 2% ($SD = 0.02$) per word. These
 438 proficiency results are similar to those observed for 1st grade children learning English
 439 (Hasbrouck & Tindal, 2006).

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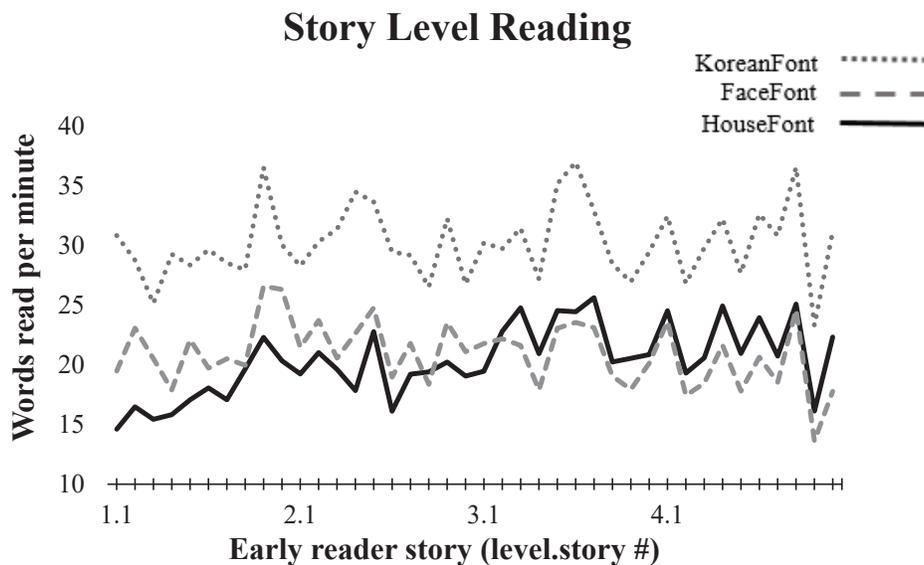
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Fig. 3. Stories increased in difficulty over the four days of story-level reading, but participants maintained a similar rate of words read per minute. The performance of

455 HouseFont participants on the early reader training stories was consistent with
456 performances seen for other artificial orthographies, KoreanFont and FaceFont.
457 KoreanFont and FaceFont data adapted with permission from “Learning to read an
458 alphabet of human faces produces left-lateralized training effects in the fusiform gyrus,”
459 by M. W. Moore, C. Durisko, C. A. Perfetti, J. A. Fiez, 2014, Journal of Cognitive
460 Neuroscience, 26(4), p. 901.

461

462 **Neural Measures of HouseFont Learning**

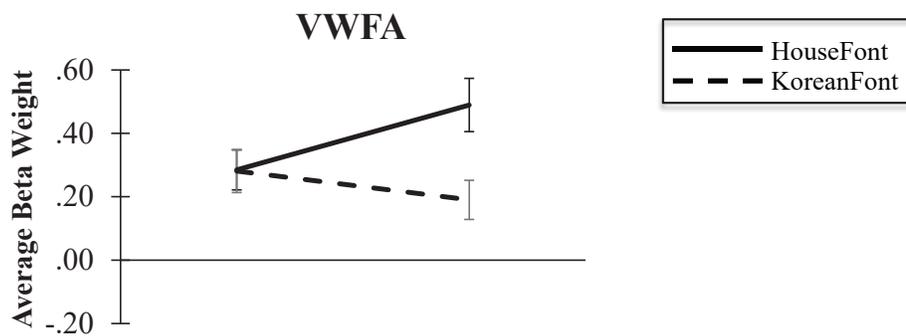
463 **ROI analysis.** A 2 x 2 x 3 repeated measures ANOVA was used to examine the
464 effect of orthography (HouseFont, KoreanFont), session (pre-training, post-training), and
465 region (VWFA, left PPA, and right PPA) on neural activity. This analysis revealed a
466 main effect of orthography, $F(1,11) = 97.07, p < .001, \eta_p^2 = .90$, and region, $F(1.37,22) =$
467 $7.97, p = .008, \eta_p^2 = .42$, with no effect of session, $F(1,11) = .11, p = .749, \eta_p^2 = .01$. There
468 was a significant interaction between orthography and region, $F(1.79,22) = 10.41, p =$
469 $.001, \eta_p^2 = .49$, and trend level interactions for orthography and session, $F(1,11) = 4.32, p$
470 $= .062, \eta_p^2 = .28$, and training and region, $F(1.49,22) = 3.20, p = .079, \eta_p^2 = .23$. Most
471 importantly, the predicted three-way interaction was also significant, $F(1.44,22) = 6.25, p$
472 $= .016, \eta_p^2 = .36$.

473 In order to examine the three-way interaction and address our *a priori* hypothesis
474 that HouseFont-elicited activity in the VWFA would change after training, we ran a
475 separate 2x2 repeated measures ANOVA (orthography [HouseFont, KoreanFont], session
476 [pre-training, post-training]) for each region. Within the VWFA there was a main effect
477 of orthography, $F(1,11) = 15.23, p = .002, \eta_p^2 = .58$ and no effect of session, $F(1,11) =$

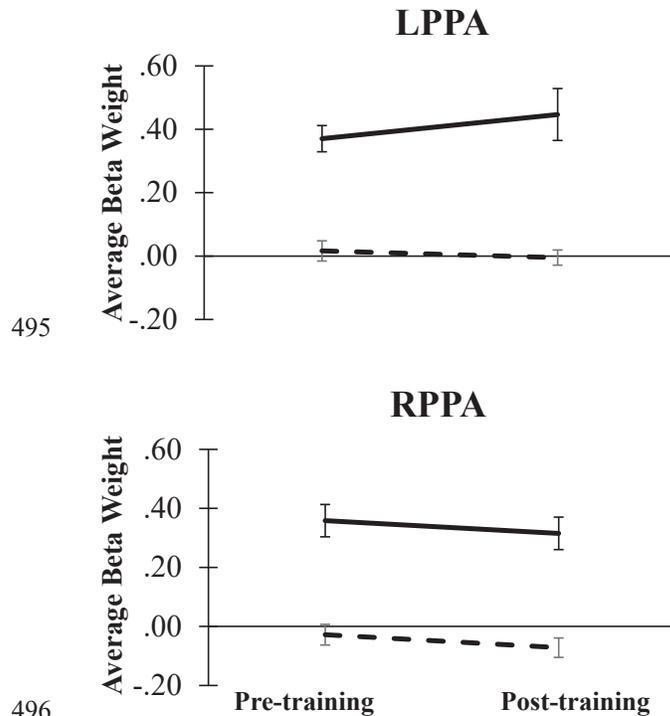
478 .86, $p = .374$, $\eta_p^2 = .07$ (Figure 4). Critically, however, there was a significant interaction
 479 between orthography and session, $F(1,11) = 9.79$, $p = .010$, $\eta_p^2 = .47$, in the VWFA. Post-
 480 hoc comparisons of the interaction revealed that the response to KoreanFont decreased
 481 across sessions, $p = .100$, while HouseFont evoked greater activation in the post-training
 482 session compared to pre-training session, $p = .059$. These are the expected results if the
 483 HouseFont training tuned the VWFA to treat strings of HouseFont images as
 484 orthographic information.

485 In the left PPA there was an effect of orthography, $F(1,11) = 55.43$, $p < .001$, $\eta_p^2 =$
 486 .83, no effect of session, $F(1,11) = .47$, $p = .507$, $\eta_p^2 = .04$, and no significant interaction
 487 between orthography and session, $F(1,11) = 1.91$, $p = .194$, $\eta_p^2 = .15$. Similarly, in the
 488 right PPA there was an effect of orthography, $F(1,11) = 62.12$, $p < .001$, $\eta_p^2 = .85$, no
 489 effect of session, $F(1,11) = 1.31$, $p = .276$, $\eta_p^2 = .11$, and no interaction between
 490 orthography and session, $F(1,11) = .00$, $p = .993$, $\eta_p^2 = .00$. The expected main effects of
 491 orthography and the lack of other effects show that the PPA bilaterally responded more to
 492 HouseFont than KoreanFont and that HouseFont training did not alter this difference.

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497 **Fig. 4.** The VWFA showed no main effect for session or orthography, but there was a
498 significant interaction of session and orthography. The left and right PPA showed the
499 expected significant main effect of orthography, no main effect of training, and no
500 significant interaction between session and orthography. Error bars indicate standard
501 error.

502
503 **Whole brain voxel-wise analysis.** To investigate if HouseFont training altered the
504 response to HouseFont strings in areas outside of the *a priori* ROIs, a whole brain voxel-
505 wise analysis was conducted with the pre- and post-training fMRI data. HouseFont
506 activation was compared to KoreanFont activation in both the pre- and post-training
507 scans separately. Then, the difference in pre-training was compared to the difference in

508 post-training. This comparison yielded 10 significant training effect clusters, nine of
 509 which were negative, indicating more activation in post-training. The one positive cluster,
 510 which was located in the left middle temporal gyrus (BA19), indicates more activation
 511 during pre-training (see Table 3). Several of the clusters are in regions known to be
 512 involved in reading (Bolger, Perfetti, & Schneider, 2005), including the left inferior
 513 frontal gyrus, the left superior parietal lobe, and the left fusiform gyrus. Portions of the
 514 left fusiform gyrus training effect cluster overlapped with the VWFA ROI (Figure 5),
 515 which is not surprising given the significant interaction effect found in the VWFA ROI.
 516 No training effect clusters were identified within the left or right parahippocampal gyrus.

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524 **Table 3**

525 *Clusters identified by the whole brain voxel-wise analysis (trained orthography*
 526 *[HouseFont] versus untrained orthography [KoreanFont], pre- to post-training)*

Cluster Location	Cluster Size (Voxels)	Peak Coordinates (X,Y,Z)
Left superior parietal lobe (BA7)	418	-28, -64, 44
Left precentral/inferior frontal gyrus (BA6/BA8)	322	-49, 2, 14
Right posterior cerebellum	233	17, -64, -22

ORTHOGRAPHIC LEARNING AND THE VWFA

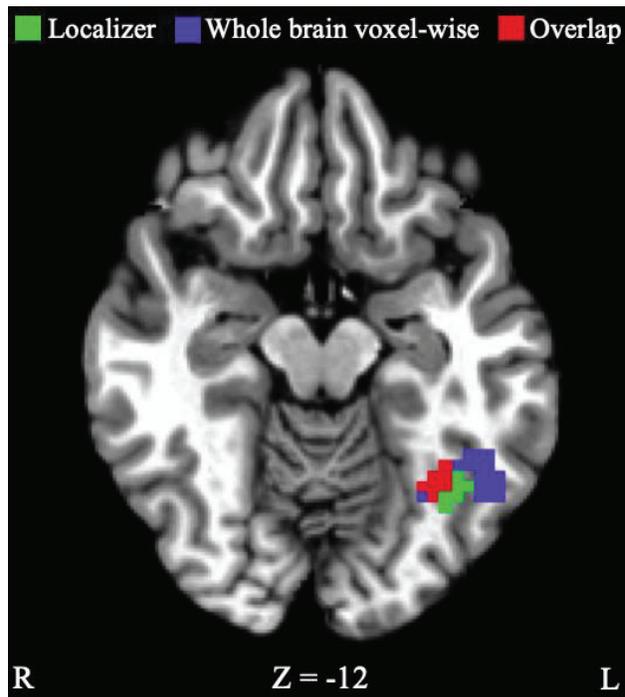
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Left thalamus/ left caudate nucleus	197	-7, -13, 14
Right caudate	95	17, 14, 14
Left medial frontal gyrus (BA6)	95	-1, 14, 44
Left middle frontal gyrus (BA46)	81	-43, 29, 20
Left middle temporal gyrus (BA19)*	72	-49, -61, 17
Left fusiform gyrus (BA37)	68	-40, -49, -10
Left insula (BA13)	65	-31, 17, 11

527 All clusters were identified with a corrected $p = .05$. Coordinates are in Talairach space.

528 BA – Brodmann area *Indicates the cluster that displayed more activation during pre-
529 training.

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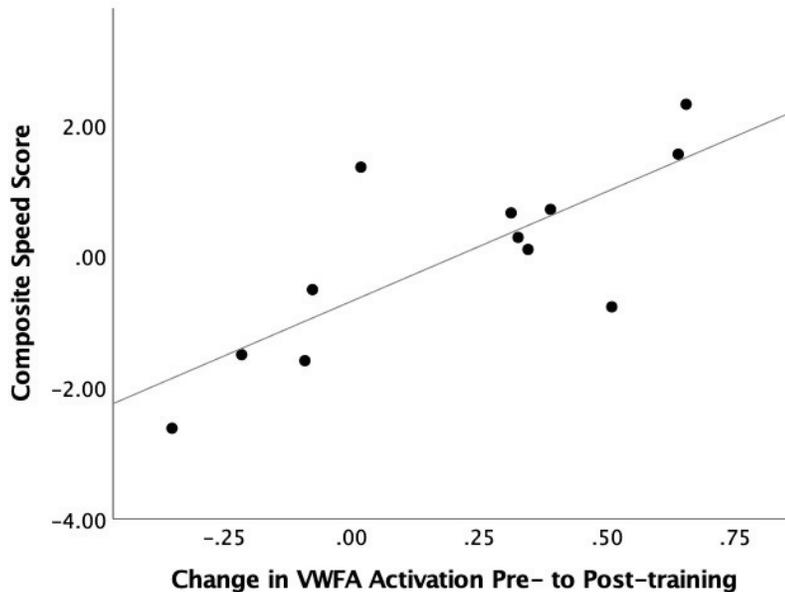


532 **Fig. 5.** VWFA ROI (green) identified by the localizer scan (-34, -55, -13), and the
533 learning effect cluster (blue) identified from the whole brain voxel-wise analysis of
534 activation for HouseFont versus KoreanFont from pre- to post-training (-40, -49, -10).
535 Red represents the overlap. Coordinates are in Talairach space.

536

537 **Relationship between Behavioral and Neural Measures of HouseFont Learning**

538 To probe the relationship between neural and behavioral measures of HouseFont
539 learning effects, we performed a regression to test the contribution of training related
540 activation change in the VWFA to HouseFont reading speed. A HouseFont reading speed
541 score was calculated by averaging the z-score of the number of words read per minute on
542 the GORT and the inverse z-score (z-score multiplied by -1) of the response time per
543 word on the final word test. The change in activation from pre- to post-training in the
544 VWFA did significantly predicted reading speed $b = 3.34$, $t(10) = 3.90$, $p = .003$, and it
545 explained a significant proportion of variance in reading speed scores, $R^2 = .60$, $F(1, 10)$
546 $= 15.24$, $p = .003$ (Figure 6). Based on these results, we conclude that the VWFA is
547 critical for rapid HouseFont reading.

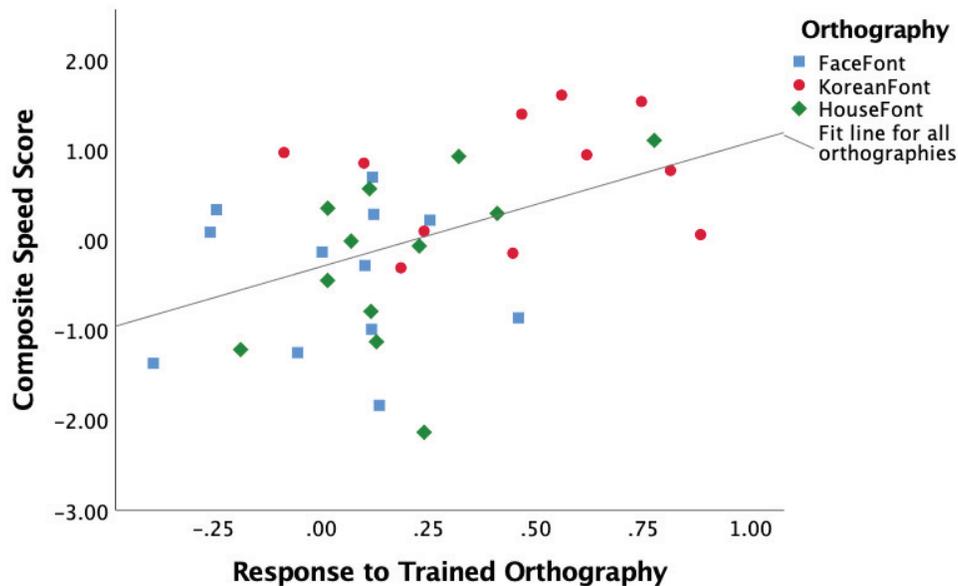


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549 **Fig. 6.** Scatter plot of the variance explained by the pre- to post-training change of the
550 VWFA for reading speed. The VWFA change showed a significant positive relationship
551 with reading speed. Reading speed scores were zero-centered.

552 We obtained convergent results using data from the HouseFont-trained
553 participants in the current study, and the FaceFont- and KoreanFont-trained participants
554 previously reported by Moore et al. (2014). While the three orthographies differ in the
555 graphs they use and in their average reading speed (see Figure 3), we expected that
556 behavioral measures of reading speed would be significantly predicted by the VWFA
557 activation in response to the trained orthography. We assessed this using a specific
558 VWFA subregion reported in the literature (mOTS; Lerma-Usabiaga et al., 2018) as an
559 ROI (to avoid biasing our ROI localization to the HouseFont group). The post-training
560 response to the trained orthography within the mOTS ROI significantly predicted reading
561 speed $b = 1.38$, $t(32) = 2.82$, $p = .008$. On the other hand, which orthography a participant

562 learned (FaceFont, KoreanFont, or HouseFont) did not significantly predict reading speed
563 $b = -.00$, $t(32) = -.01$, $p = .992$. These results align with previous reports of FaceFont and
564 KoreanFont learning effects (Moore et al., 2014) and the findings from HouseFont.
565 Moreover, the significant relationship between the neural and behavioral measures of
566 learning suggest that despite the visual differences in the graphs used, reading speed
567 variation across all three artificial orthographies can be predicted by learning effects seen
568 within the VWFA territory (see Figure 7).
569



570
571 **Fig. 7.** Scatter plot of the variance in reading speed explained by the response to trained
572 orthography within the VWFA ROI. The response to the trained orthography showed a
573 significant positive relationship with reading speed. Reading speed scores were zero-
574 centered across all three orthographies.
575

576

Discussion

577 This study tested whether acquisition of a perceptually atypical second writing
578 system recruits the same neural tissue already tuned by native-English reading, or if
579 instead the locus of orthographic learning tracks with the perceptual characteristics of the
580 grapheme forms. More specifically, we were interested in the presence or absence of
581 artificial orthography (HouseFont) learning effects within three functionally defined
582 areas: an orthographic area (VWFA) within the left mid-fusiform gyrus (Cohen &
583 Dehaene, 2004), and bilateral place areas (left PPA, right PPA) within the
584 parahippocampal gyri (Epstein & Ward, 2010). We hypothesized that orthographic
585 learning effects would be observed in either the VWFA or the PPA, but not in both
586 regions. Significant learning effects were found only within the VWFA, and individual
587 differences in the magnitude of pre- vs. post-training changes in VWFA activation
588 correlated with differences in HouseFont reading speed. We conclude the VWFA was
589 recruited to support HouseFont literacy acquisition in our adult participants.

590 The results from this study converge with Moore et al. (2014), who also observed
591 training-related increases in the VWFA territory when participants learned one of two
592 artificial alphabets for English: FaceFont, in which face images were used as letters, and
593 KoreanFont, in which letters were borrowed from the Korean alphabet and mapped to
594 English phonemes. Taken together, the results from the current study and Moore et al.
595 (2014) point towards three principles of VWFA function: 1) learning a new alphabetic
596 orthography uses VWFA tissue already specialized by acquisition of English literacy, 2)
597 orthographies with a wide range of visual forms can induce neural plasticity in the

598 VWFA, 3) the laterality of the VWFA is influenced by the mapping principles of an
599 orthography.

600

601 **New orthographic learning uses the same tissue as English**

602 The HouseFont training effects demonstrate that the VWFA in native English
603 speakers was modified by HouseFont learning. Similarly, Moore et al. (2014) found a
604 left-lateralized training effect for FaceFont in the vicinity of the VWFA. However, they
605 could not conclusively assign FaceFont learning to the same territory that supports
606 English reading for two reasons. First, a putative left homologue of the right-lateralized
607 face processing area (Kanwisher et al., 1997) falls in close proximity to the VWFA
608 (Nestor, Behrmann, & Plaut, 2013). Consequently, the locus of observed FaceFont
609 learning effects could arguably reflect the use of neural tissue specialized for face or
610 orthographic processing. Second, Moore et al. (2014) did not localize the response to
611 printed English in their participants, so they were unable to directly compare the
612 functional response to English and FaceFont. The present study circumvented these
613 problems by using house graphs associated with category-specific activation in tissue that
614 is spatially distant from the VWFA and by functionally localizing the VWFA prior to
615 HouseFont training.

616 While we attribute the change in HouseFont activation within the VWFA to
617 orthographic learning, alternative accounts warrant consideration. It is possible that
618 repetitive exposure to a small set of visual images could be sufficient to increase the
619 VWFA response to the frequently experienced images. We cannot completely discount
620 this possibility because none of our studies have involved a control group with similar

621 exposure to the image sets in a non-literacy context. However, we favor the idea that the
622 activation changes in the VWFA are related to literacy acquisition. This is because the
623 regions in which activation increased were selective, the learning effects in the fusiform
624 gyrus correlate with reading (Figure 6 and see Moore et al. (2014), and the connectivity
625 of the VWFA is suited for visual-phonological mapping (Alvarez & Fiez, 2018).

626 It is also important to remember that imaging is a correlational, rather than a
627 causal, method. It is possible that part or all of the increased VWFA activation following
628 training could be from accessing the English orthographic representations of the
629 HouseFont words. If this were the case, it could mean the VWFA is not necessary for
630 accurate HouseFont reading, but rather is activated as a byproduct of accurately decoding
631 the HouseFont word. We took extra care to ensure that HouseFont graphemes were never
632 equated with an English grapheme and no English appeared during the training phase.
633 Additionally, prior work with artificial orthographies found that a patient with acquired
634 alexia was unable to learn a small set of face-phoneme pairings but was able to learn
635 face-syllable pairings (Moore, Brendel, & Fiez, 2014). This finding suggests that the
636 VWFA territory is critical rather collateral to learning an artificial alphabetic
637 orthography.

638

639 **Visual and brain constraints on orthographic learning**

640 Our findings also demonstrate that there is considerable flexibility in the type of
641 visual forms that can serve as letters of an alphabet. This is not a trivial point, as this
642 observed flexibility is counter to some theories of how the brain and reading shape one
643 another. Most notably, Dehaene (2009, p. 184) conjectured that orthographies have

644 culturally evolved to be visually similar to each other because they are forced to conform
645 to the abilities of the available neural tissue. As part of this argument, Dehaene
646 specifically suggested that both face and house images are avoided almost entirely by
647 writing systems because the VWFA, which supports skilled reading, is not the preferred
648 processing area for this kind of visual information (Dehaene, 2009). The findings of this
649 study, and those of Moore et al. (2014), challenge this idea, because they show that
650 participants can readily obtain basic reading proficiency for an orthography with
651 perceptually atypical forms (house or face images).

652 One potentially important caveat is that individuals tend to read FaceFont and
653 HouseFont more slowly than an artificial orthography made of more typical graphs
654 (KoreanFont) (Figure 3). This could reflect intrinsic limitations, such as those posited by
655 Dehaene (2009). Alternatively, it could reflect differences in the visual complexity and
656 discriminability of faces and houses, as compared to the simpler and higher-contrast letter
657 forms in KoreanFont, or that tissue tuned for printed English might better transfer this
658 tuning to a visually similar orthography (e.g., KoreanFont) as compared to a visually
659 dissimilar (e.g., FaceFont, HouseFont) orthography. Transfer effects also might occur for
660 other characteristics of an orthography, such as its grouping of graph elements (such as
661 the dots in Arabic words) (Abadzi, 2012). This transfer effect hypothesis could be tested
662 by comparing the learning of artificial orthographies in which graphemes are borrowed
663 from natural orthographies varying in perceptual distance from a reader's native
664 orthography. For example, we might predict native English speakers would read an
665 artificial orthography with Korean graphemes more quickly than one with Arabic
666 graphemes because Korean letters are more visually similar to English letters.

667 Despite baseline differences in reading speed, similar rates of learning are found
668 across HouseFont, FaceFont, and KoreanFont (Figure 3) and there is no evidence of a
669 learning plateau across six weeks of training (Martin et al, 2018). Taken together, these
670 results support Moore et al.'s (2014) conclusion that tuning of the VWFA for English
671 creates a “perceptual bottleneck” that slows the visual discrimination of a perceptually
672 atypical second orthography, without preventing accurate reading and fluency gains with
673 continued reading experience. In sum, the weight of evidence suggests that learnable
674 orthographies are not constrained by the brain, but instead that experience with an
675 orthography shapes the brain.

676

677 **Laterality effects in orthographic learning**

678 Finally, our results demonstrate that alphabetic orthographic learning recruits left-
679 lateralized brain regions, regardless of the perceptual characteristics of the orthography.
680 In the whole brain voxel-wise analysis, a strong pattern of left-lateralized regions showed
681 HouseFont training effects (Table 3), and a similar set of regions showed training effects
682 in FaceFont (unpublished findings). Most notably, both the current study and Moore et al.
683 (2014) found training effects in the left fusiform gyrus. The lack of a training effect in the
684 right fusiform gyrus in Moore et al. (2014) is particularly striking as face processing has
685 been associated with right-lateralized visual processing (Grill-Spector, Knouf, &
686 Kanwisher, 2004; Kanwisher, McDermott, & Chun, 1997).

687 HouseFont, FaceFont, and KoreanFont differ visually, but share the same
688 alphabetic mapping principle. To clarify whether the principle of left-lateralization holds
689 true for non-alphabetic orthographies, we turn to Hirshorn et al.'s (2016) Faceabary

690 training study in which face images represented English syllables. The study found
691 Faceabary training effects in both the left and right mid-fusiform gyrus, with more
692 bilateral patterns of activation correlated with higher Faceabary reading fluency. In
693 contrast, Hirshorn et al. (2016) found a strong pattern of left-lateralization outside of the
694 fusiform gyrus when comparing pre- to post-training activation for Faceabary, which is
695 consistent with results from both the current study and Moore et al. (2014). This leads us
696 to conclude that a key driver of left-lateralized fusiform gyrus recruitment is whether an
697 orthography implements an alphabetic mapping principle, while a broader left-lateralized
698 reading network is recruited irrespective of an orthography's mapping principle.

699

700 **Conclusions**

701 The current study found that adult acquisition of a perceptually atypical
702 alphabetic orthography induced left-lateralized neural plasticity in the VWFA. We
703 conclude that the VWFA remains highly malleable in adulthood. Further, our results, in
704 combination with other work, indicate that the localization of orthographic learning to the
705 VWFA is driven by orthographic functionality rather than the visual characteristics of a
706 script, while the lateralization of the VWFA is influenced by the mapping principles of a
707 script.

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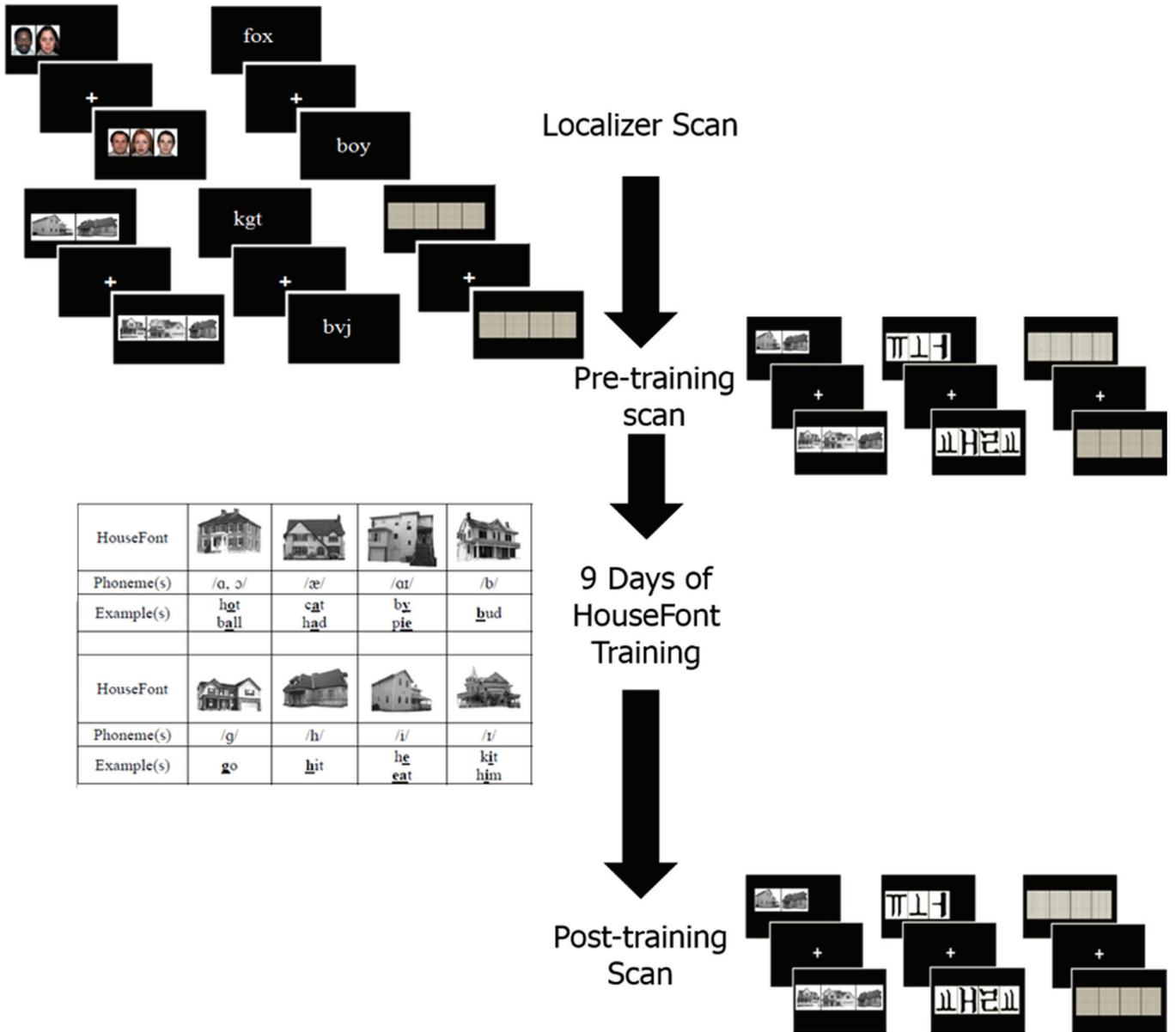
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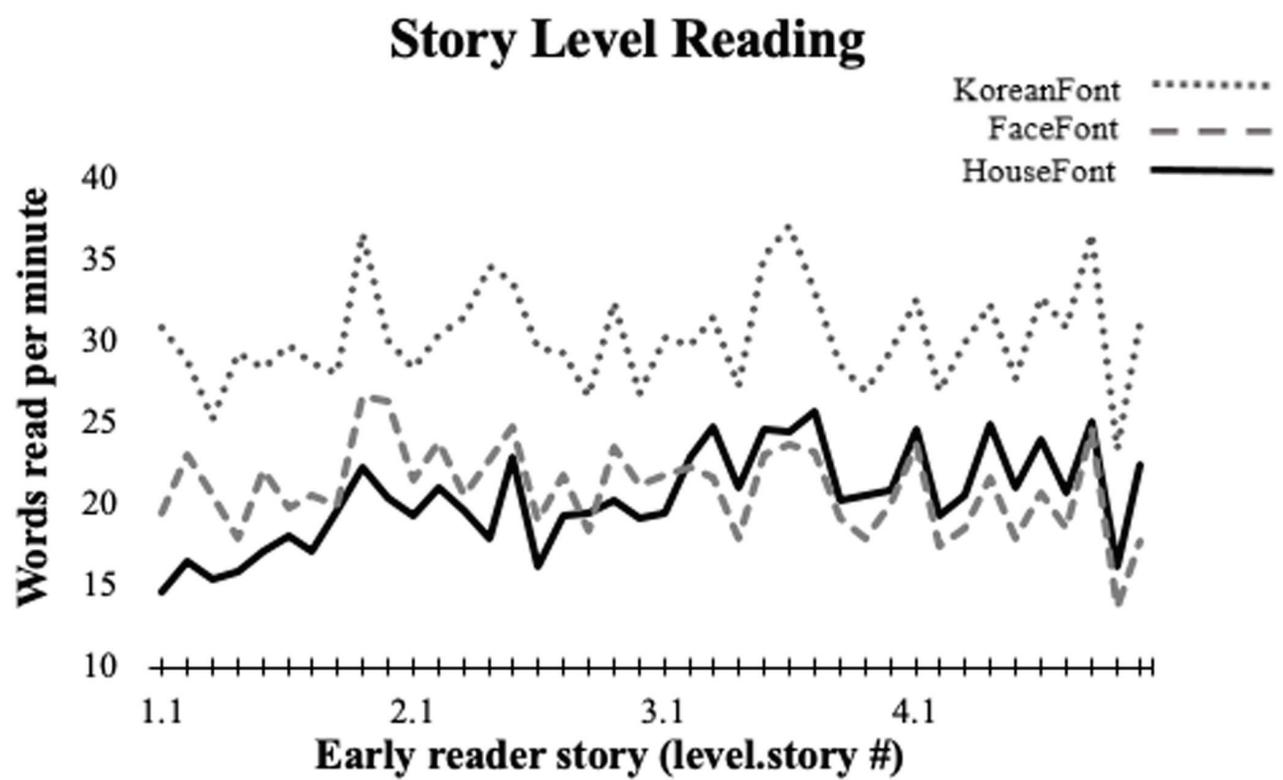
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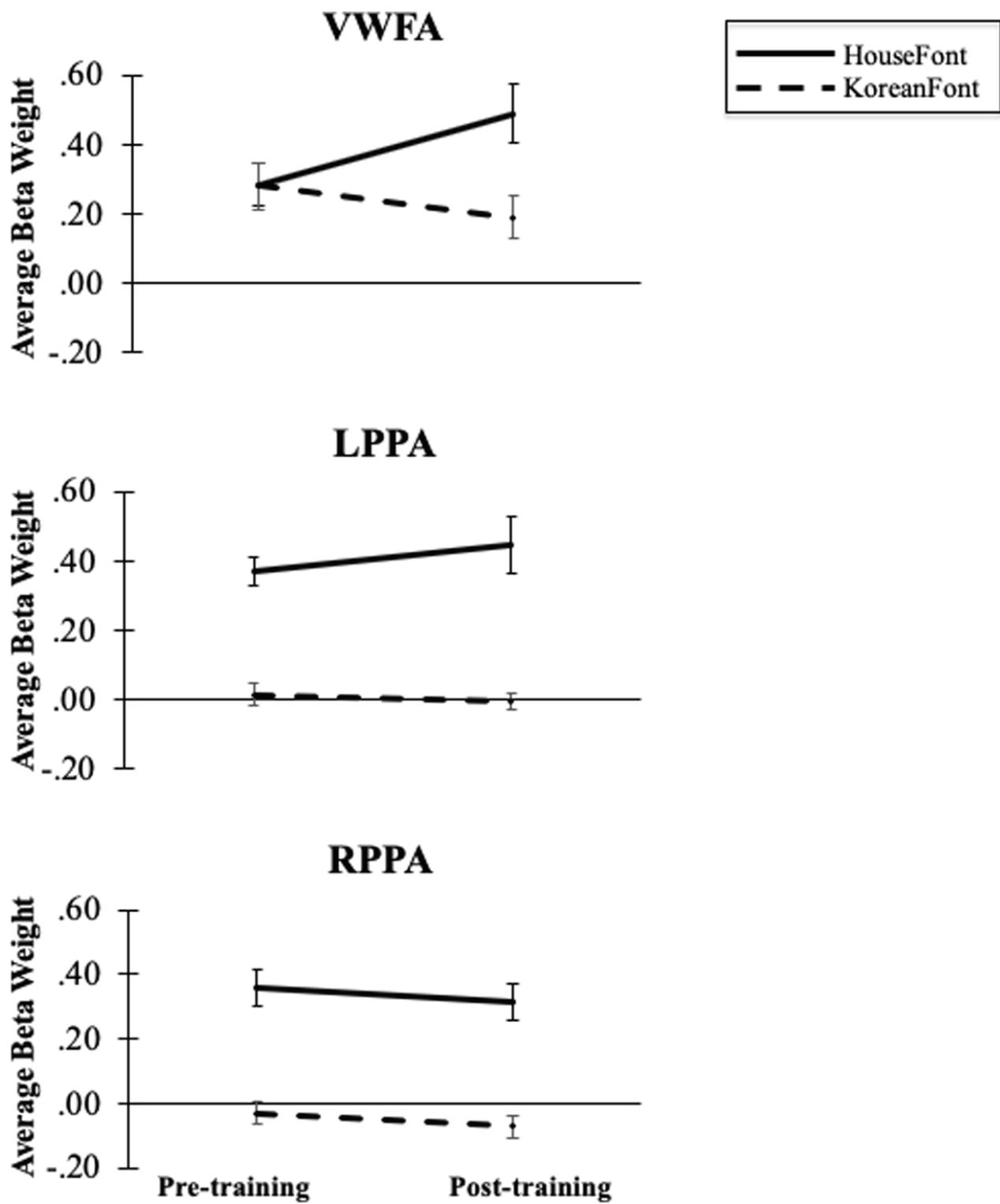
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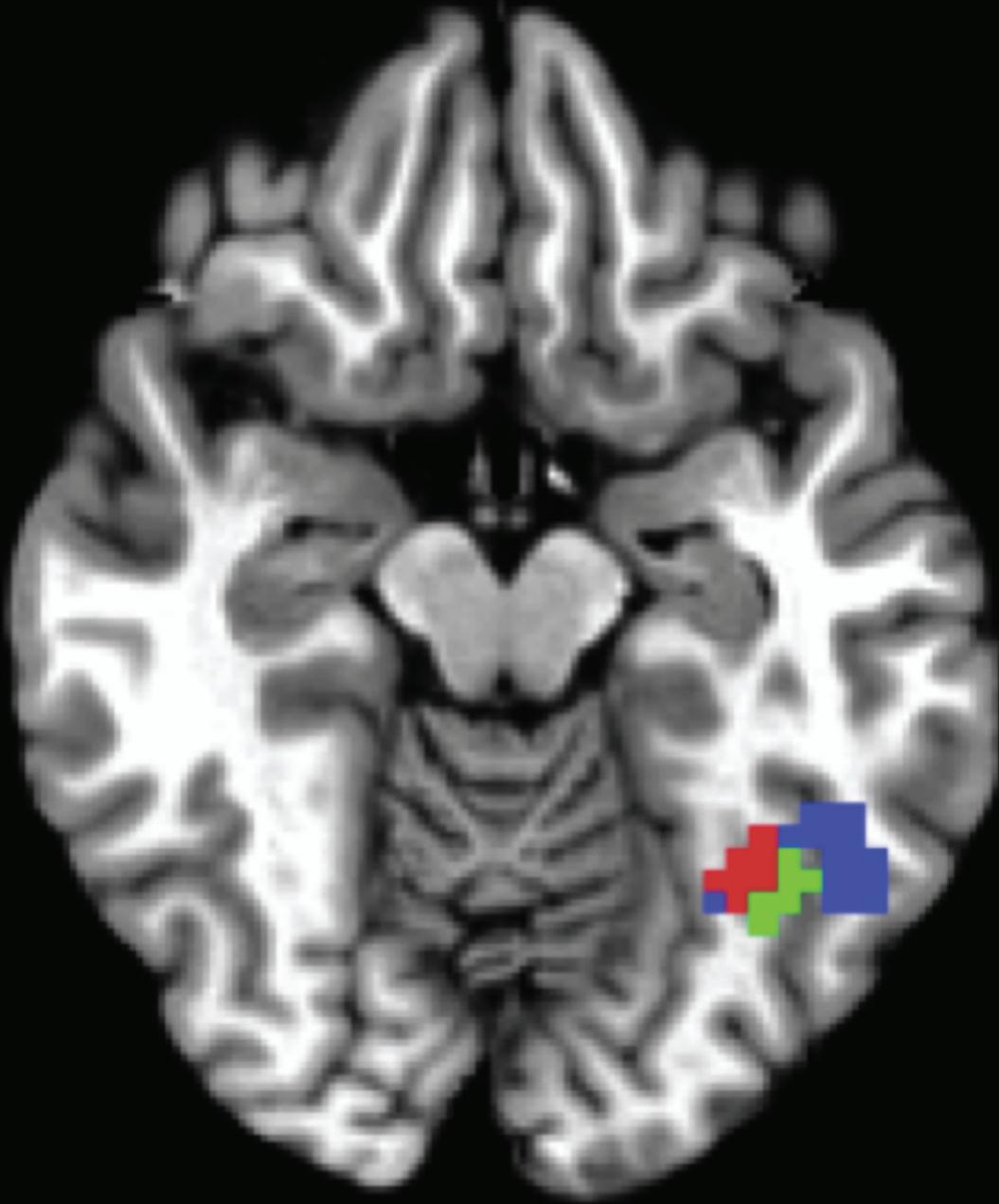








■ Localizer ■ Whole brain voxel-wise ■ Overlap



R

Z = -12

L

