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Orthographic and phonological selectivity across the reading system in deaf skilled readers

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Abstract

People who are born deaf often have difficulty learning to read. Recently, several studies have examined the neural substrates involved in reading in deaf people and found a left lateralized reading system similar to hearing people involving temporoparietal, inferior frontal, and ventral occipito-temporal cortices. Previous studies in typical hearing readers show that within this reading network there are separate regions that specialize in processing orthography and phonology. We used fMRI rapid adaptation in deaf adults who were skilled readers to examine neural selectivity in three functional ROIs in the left hemisphere: temporoparietal cortex (TPC), inferior frontal gyrus (IFG), and the visual word form area (VWFA). Results show that in deaf skilled readers, the left VWFA showed selectivity for orthography similar to what has been reported for hearing readers, the TPC showed less sensitivity to phonology than previously reported for hearing readers using the same paradigm, and the IFG showed selectivity to orthography, but not phonology (similar to what has been reported previously for hearing readers). These results provide evidence that while skilled deaf readers demonstrate coarsely tuned phonological representations in the TPC, they develop finely tuned representations for the orthography of written words in the VWFA and IFG. This result suggests that phonological tuning in the TPC may have little impact on the neural network associated with skilled reading for deaf adults.

Keywords

word reading; deaf; orthography; phonology; fMRI; fMRIadaption; VWFA

Introduction

Learning to read can be challenging for people who are born deaf because they do not have full access to the spoken language encoded by print. Although reading outcomes are

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generally poor for deaf individuals, some deaf people do nonetheless achieve high levels of reading proficiency (Qi and Mitchell, 2012; Traxler, 2000). Numerous studies have examined reading in people who are deaf, yet to date there is no clear agreement of what contributes to these reading difficulties and why some deaf people are good readers and others are not. One theory is that those who are able to develop age-appropriate reading skills have strong phonological skills and are able to make strong connections between orthography and phonology (Mayer and Trezek, 2014). These authors purport that phonology is essential to reading regardless of hearing status. While a role for phonology in reading success for deaf individuals might make sense based on our understanding of reading in the hearing population, a recent meta-analysis showed that phonological skills account for only 11% of the variance in reading ability for deaf people. However, language ability accounts for 35% of the variance, making it a better predictor of reading skill (Mayberry et al., 2011).

Currently, little is known about the neural architecture supporting reading in deaf people, or the ways the brain responds and adapts to support reading when auditory input is limited (and thus access to phonology is restricted); nonetheless, several recent studies have shed some light on the neural underpinnings of reading in deaf adults (Corina et al., 2013; Emmorey et al., 2013, 2016; Wang et al., 2015). In order to situate those recent neuroimaging studies, we first briefly review the literature on hearing readers.

Over the past two decades understanding the neural components of reading in hearing children and adults has received much attention. As such, we have a better understanding of the neural circuitry involved in visual word recognition in the hearing population. Recent research has focused on three main neuroanatomical regions involved in single word reading: the occipitotemporal cortex (OTC), temporoparietal cortex (TPC), and inferior frontal gyrus (IFG; e.g., Carreiras et al., 2014). These studies provide evidence for a hierarchical organization in the ventral visual OT pathway for visual word form, leading to the proposal that, running posteriorly to anteriorly along this pathway, neurons are tuned to increasingly complex word features, namely from oriented bars, to letters, bigrams, and finally to quadragrams (Cohen and Dehaene, 2004; Vinckier et al., 2007). Glezer et al. (2009, 2015, 2016) provided evidence that an area within the ventral OT (vOT) region, the so-called visual word form area (VWFA), appears to function like an orthographic lexicon. Neurons in this part of the brain seem to be specialized to process written words we have learned, and not novel words. Additionally, this selectivity appears to be specific to the left hemisphere, as the homologous right hemisphere VWFA does not show this same selectivity (Glezer et al., 2015).

Although it is agreed that the VWFA is involved in reading, there have been conflicting reports about the specificity of this area, and it has been debated whether the OTC might also be involved in aspects of reading that go beyond just the visual /orthographic processing of words. A number of studies have shown that the vOT is activated when people engage in a host of language tasks and processes including (but not limited to) pseudoword rhyming and reading (Dietz et al., 2005; Hagoort et al., 1999, Xu et al., 2001), naming familiar pictures, reading Braille, processing auditory and tactile words (Price and Devlin, 2003, 2004), and processing phonological information (Price and Devlin, 2011; Twomey et al.,

2011; Yoncheva et al., 2010). Activity in this region has also been shown to be modulated by top down processing and task demands (Hellyer et al., 2011; Kherif et al., 2011). Interestingly, a study by Glezer and Riesenhuber (2013) found that when identified at the individual subject level, the VWFA shows selectivity for written words, but when the VWFA is defined at the group level, intersubject variability in the location and size of the VWFA causes this selectivity to be washed out. This result suggests that many of the conflicting findings may be accounted for by the type of analysis conducted.

In hearing readers, both TPC and IFG have been implicated in phonological and semantic aspects of written word reading (Binder et al., 2009; Katzev et al., 2013; Kircher et al., 2011); however, the exact nature of the processing that occurs within these regions is controversial. A recent meta-analysis sought to reconcile some of the conflicting findings (Vigneau et al., 2006). Vigneau et al. showed that both TPC and IFG have clusters of neurons that independently respond to semantics and phonology, as well as other clusters that respond to both, suggesting that single- and multi-domain processing occurs in these regions. However, the exact nature of the representations processed in these areas during word reading is still unclear. Recently, Glezer et al. (2016) showed that a region within the TPC appears to be finely tuned to phonological features during single word reading in typical hearing readers, and that this same region shows weak selectivity to phonological features in people with dyslexia (Glezer et al., 2018). These findings suggest that a region within the TPC does indeed engage in phonological processing during word reading, and moreover, that it shows altered tuning in hearing people with reading difficulties.

A number of fMRI studies have focused on the neural correlates associated with different levels of reading skill in hearing people, most notably in the area of dyslexia (Boets et al., 2013; Hasko et al., 2013; Mahé et al., 2013; Richlan et al., 2011; Sun et al., 2010; van der Mark et al., 2009). As mentioned earlier, a few recent studies examined the neural circuitry of reading in deaf adults (Aparicio et al., 2007; Corina et al., 2013; Emmorey et al., 2013, 2016; Wang et al., 2015). Generally, these studies indicate that skilled deaf readers engage a neural circuitry similar to that reported for hearing readers, particularly when engaged in semantic tasks. However, it appears that reading skill level and type of task (i.e., phonological vs. semantic) both modulate activity in the reading circuit for this population, suggesting different processing strategies as a function of skill and linguistic processing requirements. In regions known to be involved in skilled reading (IFG, TPC, VWFA) for hearing people, results have been mixed as to whether these regions are similarly engaged for deaf readers. We outline the findings for each of these regions below.

IFG.

The results regarding the role of the IFG during reading in deaf people are inconclusive. While some results show that the IFG is differentially engaged in deaf versus hearing readers, other findings indicate the IFG is similarly active for both groups. Evidence for differential engagement comes from Aparicio et al. (2007), who showed that deaf readers, when engaged in a phonological task, activated the left and right IFG more than hearing readers. Additionally, they showed that hearing people activated the left IFG more and deaf people activated the right IFG more during a lexical decision task. However, one thing to

note is that these differences may be due to the fact that the deaf group had a lower reading level than the hearing group. Controlling for reading level, Emmorey et al. (2013) showed that both deaf and hearing readers activated the left IFG during a semantic task (concreteness judgment) and a phonological task (syllable counting). However, when comparing the tasks directly, within each group, they found that the deaf group showed more activation in the left IFG for the semantic task than the phonological task, whereas the hearing group did not. This result suggests that while deaf readers are employing the same neural circuitry for reading as hearing people, the type of task has an impact on degree of activation, particularly when phonological processing is required. Emmorey et al., (2013) suggest deaf readers may be less likely than hearing readers to activate phonological representations when performing a semantic task (and vice versa for a phonological task). There are also mixed results concerning whether reading skill level affects activation in the IFG in deaf readers. Corina et al., (2013) reported that both proficient and less proficient readers activated the IFG during an implicit reading task, whereas Emmorey et al. (2016) found that during a semantic task the left IFG is activated more for skilled deaf readers compared to less skilled readers.

TPC.

Temporoparietal cortex findings are also quite mixed. While Aparicio et al. (2007) found more activation for deaf than hearing readers in the TPC region during a lexical decision task, Emmorey et al. (2013) did not observe a difference between groups during a semantic decision task. One fairly consistent finding, however, is that during phonological tasks, parietal regions within the TPC (inferior parietal lobule and supramarginal gyrus) are more active for deaf compared to hearing readers (Aparicio et al., 2007; Emmorey et al., 2013; Li et al., 2014). This result would suggest that, similar to the IFG, the type of task can affect activation in the TPC. One other consistent finding is that another region within the TPC, very near the TPC region of interest (ROI) used for the present study, activates more for skilled compared to less skilled deaf readers (Corina et al., 2013; Emmorey et al., 2016).

VWFA.

Results from studies of deaf readers are fairly consistent regarding VWFA activation. Generally, researchers have found no differences in VWFA activation between deaf and hearing readers (Aparicio et al., 2007; Emmorey et al., 2013; Wang et al., 2015). However, there are mixed results when comparing between skill levels. Corina et al. (2013) found greater activation for more proficient deaf readers, while Emmorey et al. (2016) found no difference between skilled and less skilled deaf readers in this region. Furthermore, Wang et al. (2015) examined how lack of auditory input in profoundly deaf readers impacts the location and functional connectivity of the VWFA and found that the location and extent of activation were similar between the deaf and hearing groups, but deaf readers showed reduced functional connectivity between vOT cortex and superior temporal cortex.

Preferential functional connectivity between the VWFA and TPC has been shown in the hearing population, and the strength of this connectivity predicts performance on a semantic reading task (Stevens et al., 2017). These results fit well with the reading model proposed by Pugh et al. (2001), who suggested that initially, during reading development, a dorsal circuit

(involving the VWFA, TPC and IFG) is dominant over the ventral route (involving the VWFA and IFG). This dorsal route allows for the direct mapping of graphemes to phonemes, which is needed for decoding to occur in the initial stages of reading development. The dorsal system also provides input to, and receives feedback from, the ventral system (vOT or VWFA); this reciprocal communication between the TPC and vOT helps to “train-up” the ventral system. Over time and with extensive experience, the ventral system becomes tuned to word forms and allows for the fast recognition of words. Wang et al. (2015) suggested that the reduced functional connectivity between the dorsal and ventral streams that they observed in profoundly deaf readers indicates that print may not be automatically associated with phonological representations for deaf individuals, and that phonological representations may not be needed to help develop the visual word form area, as theorized by models of reading development in hearing individuals (Pugh et al., 2001).

Interestingly, recent evidence suggests that orthographic representations can be established without a phonological system, and can be based solely on extensive exposure to print (Grainger et al., 2012), supporting Wang et al.'s proposal (2015) that selectivity for written words can occur independently of a well-developed phonological system. This hypothesis is in line with the idea that for skilled reading, the same neural circuitry is recruited in both hearing and deaf people, but that skilled deaf readers directly engage the orthographic and semantic systems, perhaps bypassing the phonological system entirely (Bélanger and Rayner, 2015; Bélanger et al., 2013). However, Gutierrez-Sigut et al. (2017) showed that deaf readers (in a transparent language) do automatically access phonological representations but the degree of phonological response didn't correlate with reading ability in contrast to hearing participants. This finding suggests that deaf readers do not rely on phonological information in the same way that hearing readers do (see also Fariña et al., 2017). Friesen and Joanisse (2012) found evidence for a weak pseudohomophone effect in deaf readers and suggested that deaf readers do have access to phonology, but the accessible phonological information is more coarsely tuned compared to hearing readers.

While brain imaging studies to date have provided valuable information about the neural reading network in deaf populations, all relied on an average BOLD-contrast response to examine the neural underpinnings of reading. However, relating BOLD-contrast signal change with neural selectivity (i.e., does a region specialize in a linguistic process) is complicated by the fact that both the density of selective neurons as well as the broadness of their tuning contribute to the average activity level in a voxel. That is, a given BOLD-contrast signal change in a voxel could arise from a large number of unselective neurons that all respond at a low level to a large set of stimuli, or from a population of highly active, more selective neurons, of which only subsets respond (those whose preferred stimuli most resemble the current stimulus). However, fMRI rapid adaptation (fMRI-RA) techniques can probe neuronal tuning more directly and selectively (for a review, see Grill-Spector et al., 2006). Given two sequentially presented stimuli, the BOLD-contrast response *to the pair* is taken to reflect similarity of the neuronal activation patterns corresponding to the two individual stimuli. Thus, the lowest response reflects activation of identical neuronal populations and maximum signal indicates activation of disjoint groups of neurons for the two stimuli (Jiang et al., 2006). Furthermore, as the technique exploits adaptation effects at

the neuronal level, its spatial resolution is not limited by the voxel resolution (Krekelberg et al., 2006).

Glezer et al. (2009, 2015, 2016) recently showed that this technique can be used to probe neuronal tuning for single-word reading at a level beyond what is possible by comparing the average BOLD-contrast level response to individually presented stimuli. While this technique has been used to examine word reading in hearing individuals, it has not been used to examine neural tuning in deaf readers. fMRI rapid adaptation can provide valuable information about the degree to which neural specificity in the VWFA, IFG, and TPC differs in individuals with varied reading skill and lead to a better understanding of where differences lie and what factors might contribute to reading skill differences.

In the present study, we present two independent fMRI-RA experiments that examine neural tuning to orthography and phonology during single word reading in skilled deaf readers. In order to separate and control for orthographic and phonological factors and keep scanning sessions within a reasonable time frame, each participant completed two scanning sessions, each with a different and independent experimental focus. Experiment 1 examined orthographic tuning, and Experiment 2 examined phonological tuning. In order to focus on regions known to be involved in orthography (VWFA) and phonology (IFG, TPC), we acquired a functional localizer for each participant to define regions of interest (ROIs). In Experiment 1 (Orthography), we used a localizer in which participants covertly read real words and made orthographic, phonological, and semantic decisions (blocked by task) about the words in order to define the VWFA in each individual. We then examined the response within this region to real word (RW) and pseudoword (PW) stimuli. The RW and PW stimuli were presented in prime-target pairs (RWs were paired with RWs and PWs were paired with PWs). There were three conditions of interest: (1) “same” (S) trials, in which the same stimulus was presented twice (as prime and target; e.g., *coat-coat*); (2) “one letter difference” (1L) trials, in which the prime and target differed by only one letter (e.g., *boat-coat*); and (3) “different” (DIFF) trials, in which the target shared no letters with the prime (e.g., *fish-coat*).

In Experiment 2 (Phonology), we used the same VWFA ROI and also identified phonological regions (TPC and IFG) using only the phonological word reading blocks from the localizer (see below). We then examined the response to real word pairs in each individually-defined ROI (VWFA, TPC, and IFG). There were three conditions of interest in which intra-pair stimulus similarity was varied: 1) the same target repeated (S), such as *hair-hair*; 2), a homophone of the target (H), such as *hare-hair*; and 3) a different word from the target (Control), such as *hear-hair*. See Figure 1 for examples of each stimulus type. The Control pairs were matched with the H and S pairs for linguistic factors, such as overlapping orthography and phonology (see Methods). Prior studies using the same techniques, design, and paradigm (Glezer et al., 2016, 2018), termed this Control condition “DIFF”, but for clarity between the current Experiments 1 and 2, we labeled this condition “Control”. Lastly, we used an oddball detection task, which engages the participants’ attention, yet avoids potential task-related confounds (Grady et al., 1996; Sunaert et al., 2000).

Our predictions were based on the prior fMRI-RA word processing studies of hearing readers that used the same procedures to individually localize and interrogate regions of interest for activation during the adaptation conditions of interest (Glezer et al., 2009, 2015, 2016). Although Experiment 1 and 2 were independent, we predicted that in both experiments and for all three ROIs (VWFA, TPC, and IFG), the same (S) condition would show maximum adaptation (i.e., the lowest signal, compared all other conditions) because two identical words should repeatedly activate the same neural populations. We also expected the least amount of adaptation for the DIFF and Control conditions, because the two words differ in orthography and phonology; thus, the second stimulus would activate a different subpopulation of neurons. Crucially, in Experiment 1 where we examined orthographic tuning in the VWFA, the critical condition of interest was the 1L condition. The 1L condition allows us to test for experience-dependent tuning to the orthography of word and word-like stimuli. That is, it allowed us to examine the degree to which neurons in this region are tuned to known words by comparing the response pattern within the VWFA to real words (RW) vs. pseudowords (PW). We hypothesized that in deaf skilled readers, like in hearing readers, the VWFA contains neurons tightly tuned to real words. As proposed by Glezer et al. (2009), this selective tuning for real words is the result of visual experience with words and the behavioral requirement to discriminate words from each other when they are visually highly similar (e.g., *farm* and *form*). This experience is hypothesized to produce RW-tuned neurons that come to show high selectivity to a specific RW, but show little response to other real words, even when orthographically similar.

In contrast, lack of experience with PWs and the lack of a need to discriminate real words from PWs (such as *farm* from *tarm*) during normal reading should lead neurons tuned to specific RWs to show weaker experience-driven response differentiation from orthographically similar PWs (see Figure 2A, B and C for hypothesized patterns of results). That is, these RW-tuned neurons not only respond strongly to their preferred RW, but also respond to a lesser degree to similar PWs. For example, neurons tuned to the word *farm* would respond very little to the real words *form*, *firm*, *harm*, etc. In contrast, the pseudoword *tarm* would elicit low-level activation of neurons tuned to orthographically similar real words (*farm*, *harm*, *term*, etc.). This similarity would lead to partial overlapping of neural firing patterns (i.e., '*farm*' and '*harm*' are activated by both '*karm*' and '*tarm*'), resulting in partial adaptation leading to a *gradual*/BOLD response increase with increasing dissimilarity (from Same to 1L to DIFF) in the PW pairs. In contrast, if neurons in the VWFA are tuned to sublexical features, one would predict a gradual response increase with increasing dissimilarity for *both* the RW pairs and the PW pairs. That is, because the S condition has maximal sublexical unit overlap there would be maximal adaptation, and because the 1L condition has partial sublexical unit overlap there would be partial adaptation. Lastly, because the DIFF condition has no sublexical overlap there would be no adaptation.

In Experiment 2, the key condition of interest that differentiates an orthographic representation from a phonological representation is the response of the homophone (H) condition. For regions tasked with phonological processing, the averaged response would be equivalent to that observed for processing of the identical word pairs (S) given the identical phonology of homophone pairs. That is, even though the two words in an H pair differ in orthography, a region selective for phonology should respond to them identically, leading to

maximum adaptation (or a reduced response), as in the S condition (Figure 2C). In contrast, in brain areas showing orthographic whole-word selectivity, like the VWFA (Glezer et al., 2009, 2016), responses to the H condition should be identical to the Control condition, given the orthographic differences of H word pairs.

Methods

Participants

Thirteen deaf adults participated in the study (see Table 1 for participant characteristics). One participant withdrew after experiencing peripheral nerve stimulation. All participants were right-handed, prelingually deaf (i.e., before age two), had a hearing loss of 70dB or greater, acquired ASL prior to age 5, used ASL as their primary and preferred language, and reported no history of a learning disability or a neurological or behavioral disorder. Informed consent was obtained according to procedures approved by the UCSD and SDSU Human Research Protection Programs.

We assessed participants' nonverbal IQ using the matrixes subtest of the Kaufman Brief Intelligence Test (Kaufman and Kaufman, 2004), which is a multiple-choice test of nonverbal reasoning that assesses nonverbal intelligence. Reading skill was measured with the reading comprehension subtest of the Peabody Individual Achievement Test-Revised (PIAT-R; Markwardt, 1989). In this subtest, participants read (silently) a sentence, then choose a picture (from among four choices) that best matches the sentence. Items increase in difficulty throughout the test, and the test is discontinued if a participant produces five errors among seven consecutive responses. We measured phonological processing skills using phonological awareness tests that do not require overt speech production, developed by Hirshorn et al. (2015) designed specifically for profoundly deaf adults. The tests examine the extent to which participants base phonological decisions on orthography and their ability to access phonological representations without useful orthographic cues. The test has three component tasks, each with "shallow" and "deep" trial types. The main difference between the shallow and deep trials in both parts of the test is that the shallow trials do not require participants to distinguish between phonological and orthographic regularity, while the deep trials do.

For the Sounds task, three pictures are displayed in a triangle formation, and participants select the "odd man out" – the item that has a different first sound or a different vowel (blocked conditions). For the shallow trials, the similar sounding pairs overlap in both phonology and orthography (e.g., *doll*, *door*, *belt*), and for the deep trials, the similar pairs share only phonology (e.g., *compass*, *kettle*, *lemon*). For the Manipulation task, participants see two pictures (e.g., a ring and a hat, or a bird and a toe) and must combine the first sound first object pictured with the rime of the second object pictured to make a new word (e.g., *rat*, *bow*). Participants type the new word on a keyboard. Scores on the Sounds task and the Manipulation task were combined to create scores for shallow awareness (correct answers can be determined based on orthography alone) and deep awareness (phonology must be accessed to answer correctly).

Table 1 details the average scores of participants as well as historical data from hearing participants from our lab, included for reference purposes. All participants were considered skilled deaf readers, based on the reading comprehension subtest of the PIAT-R.

Stimuli, design, and procedure

The fMRI paradigm consisted of two scanning sessions conducted on two separate days. As discussed in the introduction we used a similar design and procedure as in previous studies (Glezer et al., 2009, 2015, 2016). The stimuli and tasks for the localizer were identical to that used in Experiment 1 from Glezer et al. (2016). The fMRI-RA for Experiment 1 in the present study used the same stimuli and task as that used in Experiment 3 from Glezer et al. (2009). For Experiment 2 in the present study we used the same stimuli and task as in Experiment 1 from Glezer et al. (2016). On Day 1 participants completed the functional localizer (block design, one run) and Experiment 1 (fMRI-RA, six runs), and on Day 2 they completed the same functional localizer (block design, one run) and Experiment 2 (fMRI-RA, four runs). The localizers, Experiment 1, and Experiment 2 are described below, and example stimuli are shown in Figure 1. The purpose of conducting separate scans and using different tasks to localize the ROIs and to examine the experimental effects was to make sure the results from fMRI-RA were as independent as possible from the localizer. This procedure avoids any circularity or “double dipping” issues.

Functional Localizer Scans

Design and procedure—We acquired functional localizers for each participant in order to functionally define individually-based ROIs associated with orthographic (VWFA) and phonological processing (IFG, TPC). The purpose of these localizers was to identify regions involved in orthographic and phonological processing during silent reading. We have used this localizer successfully to identify orthographic and phonological areas in the hearing population with and without phonological problems, i.e., typical and dyslexic readers (Glezer et al., 2016, 2018). In addition, to ensure that we were obtaining ROIs of equivalent size (or activation extent) between participants in this study and in our previous studies, we used the same localizers and selection criteria.

Each block began with a 2000 ms cue, which instructed participants to perform one of following tasks throughout the block: Word Matching – participants needed to decide whether the two simultaneously presented words were the same or different; Word Rhyming – participants needed to decide whether the two words in a pair rhymed with each other; Word Meaning – participants needed to decide whether the two words in a pair belonged to the same or different semantic category; Scrambled Words – participants needed to decide whether the two visual patterns (pixel-scrambled words) in a pair had the same or different contrast. Participants were instructed to silently read the words and to press a button held in the right hand to indicate yes or press a button held in their left hand to indicate no.

Stimuli—For the Word Matching task, 60 three-to-six letter, high and low frequency words were used, and there were two conditions – 1) Same (two words were identical; e.g., desk-desk), and 2) Different (two words differed by one letter; e.g., desk-disk). For the Word Rhyming task, 80 three-to-six letter, low and high frequency words were used, and there

were four conditions – 1) words with the same orthography that rhymed (e.g., cave-save), 2) words with different orthography that rhymed (e.g., bows-toes), 3) words with the same orthography that did not rhyme (e.g., hose-lose), and 4) words with different orthography that do not rhyme (e.g., plow-fear). For the Word Meaning task, 40 high frequency animate and 40 high frequency inanimate four-to-eight letter words were used, and there were two conditions – both words in a pair belonged to 1) the same animate or inanimate category (e.g., lion-fish, or shoe-book), or 2) different categories (e.g., lion-book). Lastly, for the Scrambled Words task pixel-wise scrambled images from 60 three-to-six letter words were used, and there were two conditions – the two scrambled images were 1) the same image with the same contrast, or 2) different images with additional 30% difference in contrast. There were two runs and during each run, each condition was repeated twice in a pseudorandomized order with new stimuli. Each run lasted 6.49 minutes, and participants were asked to perform the tasks according to cues, while keeping their fixation at the center of the screen.

ROIs—We used the functional localizers to identify regions of interest as follows. The VWFA was identified using all of the word reading blocks with the contrast of Word Matching, Word Rhyming, and Word Meaning combined (referred to as “Word Processing”) versus Fixation, masked (inclusive) by the contrast of Word Matching, Word Rhyming, and Word Meaning combined (i.e., “Word Processing”) versus Visual Pattern (scrambled words). The goal was to identify a region in the ventral visual pathway that is highly selective for real words at the whole-word level. To do this it was crucial to use real words to identify the region. We chose not to use other stimuli (e.g. pseudowords) because that could lead to localizing a region that might be involved in something other than real word processing (e.g., sublexical bigram processing). While we localize and use the same VWFA region for both experiments, results obtained from Experiment 1 are independent of the results obtained from Experiment 2. In order to identify areas that were largely involved in phonological processing during reading we conducted contrasts that included only the word reading blocks where participants performed the phonological task (Word Rhyming > Fixation masked (inclusive) by Word Rhyming > Word Matching). We masked this contrast to help constrain selective regions to peak clusters of a reasonable size (see below). Finally, in order to be able to compare our current results with previous findings from hearing readers we used the same analysis methods as in Glezer et al. (2016, 2018).

Event-related fMRI-RA Experiment 1: Orthography

Design and procedure—We collected fMRI images over six event-related runs for each participant. Each run began and ended with a 30s fixation period. Between the two fixation periods, participants viewed a total of 115 trials at a rate of one every 4s. During each trial, a 1s fixation cross preceded two sequentially displayed words (400ms each, separated by a 200ms blank screen), followed by a 2s blank screen.

Stimuli—Real word (RW) and pseudoword (PW) stimuli were presented in prime-target pairs (RWs were paired with RWs, and PWs were paired with PWs) in three conditions of interest: S, IL, DIFF.

RW pairs were created by first obtaining 47 high frequency. The 1L condition was created by changing one letter of the target word to make another RW noun of comparable frequency. For the DIFF condition, we chose words of equal frequency in which no letters were repeated in any position. All RW conditions were matched for length, part of speech, bigram frequency, and neighborhood size (using the English Lexicon Project (Balota et al., 2007, see Table 2).

For PW pairs, 47 target PW stimuli were generated using the ARC Nonword Database (Rastle et al., 2002). The 1L condition was created by altering one letter of the PW target (matched to the target for bigram frequency). For the DIFF condition, we generated PWs using the ARC Nonword Database, with no letters repeated (as compared to the target) in any position. While the PW were generated using the ARC Nonword Database, for consistency purposes, the PWs were matched to RWs for length, bigram frequency, and neighborhood size (using the English Lexicon Project (Balota et al., 2007)).

Task—To engage participants' attention and keep task demands the same for all stimuli of interest, we asked participants to perform an “*oddball*” detection task during scanning (Glezer et al., 2009, 2015, 2016) by pressing a button whenever they saw the sequential letter string *xyz*. These *oddball* stimuli occurred on approximately 17% of the trials and were created by randomly replacing 3 sequential letters at the beginning, middle, or end of either the prime or the target stimuli (appearing 50% in prime and 50% in target position). Trial order was randomized and counterbalanced using M-sequences (Buras and Boynton, 2002), for a total of six runs, with 98-99 trials per condition. During scanning, participants read all words covertly but responded only to instances of the oddball words, by pressing a button with the right hand.

Event-related fMRI-RA Experiment 2: Phonology

Design and procedure.—We collected MRI images from four event-related scans for each subject. Each run lasted 9.47 minutes, with 30s fixation periods at the beginning and end of each. Between the two fixation periods, participants responded to a total of 127 trials at a rate of one every 4s. During each trial, following a 1 s fixation cross, two sequential words were displayed (400ms each with a 200ms blank screen in-between), followed by a 2s blank screen. Each run presented 25-26 trials per condition.

Stimuli—As noted in the Introduction, Experiment 2 (Phonology) had three conditions of interest: S, H, and Control (creating a triplet). All words in the triplet were one syllable, with the same number of letters and phonemes. All lists were matched for POS, frequency, bigram frequency and orthographic neighborhood based on the English Lexicon Project (Balota et al., 2007, see Table 3). Word lists were matched based on the most frequently occurring POS for each word. Trial order was randomized and counterbalanced using M-sequences (Buras and Boynton, 2002), and the number of presentations was the same for all stimuli.

Task—Similar to Experiment 1, we asked participants to read all words silently as they performed a phonological oddball detection task. Subjects pressed a button with their right

hand each time they saw a two-syllable word. All experimental stimuli were one-syllable words, and two-syllable words were *oddballs*. There were no differences in word length between *oddball* and non-*oddball* words. The two-syllable *oddball* stimuli appeared in approximately 17% of the trials and occurred equally often as either the prime or the target.

Data Acquisition—MRI data were collected at the Center for Functional MRI at the University of California, San Diego, on a 3-Tesla GE Discovery MR750 scanner equipped with an eight-channel head coil. For both the functional localizers and the fMRI-RA scans, we acquired 35 interleaved axial slices (4mm thick, no gap, $3.2 \times 3.2 \text{ mm}^2$ in-plane resolution) using a gradient echo-planar sequence (flip angle=90°, TR=2.0s, TE=29ms, FOV=205°, 64×64 matrix). The stimuli were projected onto a screen at the foot of the scanner bed using an XGA video projector and a MacBook Pro computer running PsyScope X Build 77 (psy.ck.sissa.it).

Data Processing and Analysis

General fMRI data preprocessing and analyses

For both the functional localizers and the fMRI-RA scans, all preprocessing and most statistical analyses were done using the SPM2 software package (<http://www.fil.ion.ucl.ac.uk/spm/software/spm2/>). After discarding the first five volumes of each run, EPI images were temporally aligned to the middle slice (for event-related scans only), spatially realigned, resliced to $2 \times 2 \times 2 \text{ mm}^3$, and spatially normalized to a standard MNI reference brain in Talairach space. Images were then smoothed with an isotropic 6mm Gaussian kernel. After removing low frequency temporal noise from the EPI runs with a high pass filter (1/128Hz), fMRI responses were modeled with a design matrix comprising the onset of trial types and movement parameters as regressors of interest and of no interest, respectively, using a standard canonical hemodynamic response function (HRF).

Participant ROI identification

The VWFA region was identified for each individual subject independently with the data from the localizer scan using the contrast of Word Processing (which included all word conditions, i.e., Word Matching, Word Rhyming and Word Meaning) versus Fixation ($p < 0.00001$, uncorrected), masked by the contrast of Word Processing versus Scrambled Words ($p < 0.05$, uncorrected). This contrast typically resulted in only one or two foci in the left ventral occipitotemporal cortex. ROIs were selected by identifying in each participant the most anterior cluster that was significant above the corrected cluster-level of $p < 0.05$ in the ventral occipitotemporal cortex (specifically, the occipitotemporal sulcus/fusiform gyrus region), in a location closest to the published location of the VWFA (approximate Talairach coordinates $-43 -54 -12 \pm 5$; Cohen and Dehaene, 2004). Thresholds were adjusted upward to obtain a cluster between 10-50 voxels in size. To determine if results were specific to the left VWFA, we performed the same analyses in the right hemisphere.

The TPC and IFG ROI were identified for each subject individually using the contrast of Word Rhyming > Fixation ($p < 0.00001$, uncorrected) masked by Word Rhyming > Word Matching ($p < 0.05$, uncorrected). In order to select ROIs that were of equivalent size across

subjects (Goh et al., 2010; Park et al., 2004), we adjusted thresholds upward until clusters were between 10 and 100 voxels.

fMRI-RA analysis

Following preprocessing and the general analysis described above, we extracted the mean percent signal change from the VWFA, TPC, and IFG ROIs for each participant using the MarsBar toolbox (Brett et al., 2002) and conducted repeated-measures ANOVAs. Greenhouse–Geisser correction was used and noted in the text when the assumption of sphericity was not met. All post-hoc pairwise comparisons use Bonferroni correction on the percent signal change.

Results

Participants ROI identification (VWFA, TPC, and IFG)

ROIs were identified in all participants for all three regions (VWFA was identified with the orthographic functional localizer, and TPC and IFG were identified with the phonological functional localizer). Across subjects, the MNI coordinates for each ROI's average location (and standard deviation) were as follows: In the VWFA: -45 ± 7 , -59 ± 7 , -15 ± 6 ; in the angular/superior temporal gyri of the TPC: -51 ± 7 , -53 ± 6 , 10 ± 7 ; and in the IFG: -53 ± 6 , 6 ± 4 , 13 ± 5 . Figure 3 shows the average location of each ROI along with the locations of ROIs from a similar study of hearing readers (Glezer et al., 2016); as can be seen, the location of the ROIs was quite similar for both studies. We were also able to identify a right VWFA (rVWFA) in 10 of 12 participants, which is a larger percentage of participants than what has been reported for hearing readers (e.g., 2 of 20 demonstrated a rVWFA in Baker et al., 2007; 14 of 34 in Glezer et al., 2009, and 6 of 12 using a loose threshold in Glezer et al., 2015). The average ROI location across subjects for the rVWFA was $(40 \pm 7 \text{ } -59 \pm 11 \text{ } -21 \pm 6)$. Paired t-tests revealed that these *x* and *y* coordinates were not significantly different from those in the left VWFA ROI ($p > 0.1$), but the rVWFA was slightly more ventral than the VWFA in the left hemisphere (*z* coordinates, $p = 0.013$). The next section presents results of the fMRI-RA signal extracted from each participant's ROIs.

Event-related fMRI-RA: Experiments 1 and 2

Experiment 1: Orthographic representation—Responses in the individually-defined left VWFA ROIs showed adaptation for words that were identical (S condition) but no adaptation for words that were completely different or only differed by one letter (1L condition, Figure 4). A repeated measures ANOVA revealed a significant difference between conditions ($F(2, 22) = 17.789$, $p < 0.0001$, $\eta_p^2 = 0.618$). Post-hoc pairwise comparison tests revealed a significant difference between the S and 1L conditions, and between the S and DIFF conditions ($p = 0.008$ and < 0.0001 , respectively), but there was no significant difference between the 1L and DIFF conditions ($p = 0.416$). However, for pseudowords, there was a graded adaptation pattern ($S < 1L < \text{DIFF}$), with S lower than 1L and DIFF. A repeated measures ANOVA revealed a significant difference between conditions ($F(2, 22) = 20.436$, $p < 0.0001$, $\eta_p^2 = 0.650$). Post-hoc pairwise comparison tests revealed a significant difference between S and 1L and S and DIFF ($p = 0.012$, $p < 0.0001$, respectively) and 1L was significantly lower than DIFF ($p = 0.031$). A 2×3 repeated-measures ANOVA with lexical

type (RW vs. PW) and experimental condition (S, 1L, and DIFF) revealed a significant effect of the three adaptation conditions ($F(2,22) = 20.281, p < 0.0001, \eta_p^2 = 0.691$), a significant difference between the two lexical types ($F(1,11) = 27.291, p < 0.0001, \eta_p^2 = 0.712$), and a significant interaction between the two factors ($F(2,22) = 3.650, p = 0.045, \eta_p^2 = 0.275$).

Interestingly, in the right VWFA (identified in a similar manner to the left VWFA, see Methods), a repeated measures ANOVA revealed a trend towards a significant difference between conditions ($F(2,18) = 3.332, p = 0.059, \eta_p^2 = 0.270$), (see Figure 5A). Whereas for PWs, there was a significant effect of condition ($F(2,18) = 20.118, p < 0.0001, \eta_p^2 = 0.691$). Post hoc pairwise comparisons reveal a significant difference between S and both DIFF and 1L ($p < 0.0001$ and 0.018 , respectively), but there was not a significant difference between 1L and D ($p = 0.168$). A 2×3 repeated-measures ANOVA with lexical type (RW vs. PW) and experimental condition (S, 1L, and DIFF) revealed a significant effect of the three adaptation conditions ($F(2,18) = 12.639, p = 0.001, \eta_p^2 = 0.584$), and a significant difference between the two lexical types ($F(1,9) = 10.030, p = 0.011, \eta_p^2 = 0.527$), but no significant interaction between the two factors ($F(2,18) = 1.704, p = 0.219, \eta_p^2 = 0.159$).

Experiment 2: Phonological Representation—In the TPC a repeated measures ANOVA with Greenhouse-Geisser correction revealed a significant effect of condition ($F(1.279,12.783) = 13.739, p = 0.002, \eta_p^2 = 0.579$) (Figure 6). Post-hoc pairwise comparisons revealed that S was significantly lower than H and Control ($p = 0.042, p = 0.004$, respectively) and H was significantly lower than Control ($p = 0.0224$). In the IFG, there was a significant difference between conditions ($F(2,18) = 8.477, p = 0.003, \eta_p^2 = 0.485$); and in post hoc pairwise comparisons S was significantly lower than H and Control ($p = 0.046, p = 0.028$, respectively), but H and Control were not significantly different from each other ($p = 1.0$).

Finally, the VWFA did not show adaptation for the H condition. A repeated measures ANOVA revealed a significant effect of condition ($F(2,22) = 9.160, p = .001, \eta_p^2 = 0.454$). Post-hoc pairwise comparisons revealed that S was significantly lower than H and Control ($p = 0.014, p = 0.011$, respectively), and H was not significantly lower than Control ($p = 1.0$); see Figure 5B. In the right VWFA a repeated measures ANOVA revealed a significant effect of condition ($F(2,18) = 21.825, p < 0.0001, \eta_p^2 = 0.708$). Post hoc pairwise comparisons revealed no significant difference between Control and H ($p = 1.0$), while both Control and H were significantly higher than S ($p = 0.001$ for both comparisons).

Discussion

The goal of this study was to examine in skilled deaf readers the orthographic and phonological selectivity to written words in regions known to be involved in reading for hearing people: the VWFA, TPC, and IFG. Using fMRI-RA in two independent experiments, we provide evidence that deaf adults who are skilled readers exhibit response selectivity to written words in the left hemisphere in the VWFA and IFG that is similar to what has been previously reported in typical hearing readers (Glezer et al., 2016). Additionally, skilled deaf readers showed selectivity in the right VWFA in Experiment 2, but there was only a trend for selectivity in Experiment 1; right VWFA selectivity has not been reported in typical hearing readers (Glezer et al., 2009, 2015). Importantly, while deaf

skilled readers show responsivity to phonology in the TPC, this region does not appear to be selectively tuned to phonological features, as has been shown in hearing readers (Glezer et al., 2016). These results support the idea that a fine-grained representation for phonology is not necessary for skilled reading to occur in deaf people. Our findings suggest that phonology is accessed during reading when deaf readers engage in a phonological task, but at a more coarse-grained level than for hearing readers. This supports the idea that skilled reading in people who are deaf does not require a finely-tuned phonological representation and may be accomplished via direct mapping from orthography to semantics. However, examining these questions in less-skilled deaf readers will be needed in order to confirm this hypothesis.

Orthography and the VWFA

In adult hearing readers the VWFA activates to words and word-like stimuli (Dehaene and Cohen, 2011; Dehaene et al., 2001; Fiebach et al., 2002; Kronbichler et al., 2004; Tagamets et al., 2000) and contains neurons highly selective for individual real words or learned pseudowords (Glezer et al., 2009, 2015). Previous research has shown that this region activates similarly for hearing and deaf readers in terms of the magnitude (Aparicio et al., 2007; Emmorey et al., 2013; Wang et al., 2015), the location, and the extent of VWFA activation (Wang et al., 2015). While these findings would suggest that this region is performing similarly in both populations, one cannot confidently deduce that its selectivity to written words is similar. As noted earlier, it is possible for the same signal within a region to be generated by differently tuned neurons; that is, a large number of nonselective neurons that respond broadly (i.e., to a large set of stimuli) could produce the same signal as a small number of highly active, but more selective neurons. Using fMRI-RA we were able to probe the neuronal tuning more precisely and directly than previous studies of deaf readers. Our results provide the first evidence that skilled deaf readers show similar selectivity to orthography in the VWFA as that reported for hearing readers, using the same experimental paradigm and stimuli in both groups (Glezer et al., 2009, 2016). Neurons in the VWFA of skilled deaf readers are experience-dependent and are tightly tuned to known whole written words but show broad tuning for novel words (pseudowords), just as in skilled hearing readers.

The literature contains conflicting findings about the impact of reading skill on activation in this region (Corina et al., 2013; Emmorey et al., 2016). Corina et al (2013) found a difference in activation between skilled and less-skilled deaf readers while Emmorey et al. (2016) found no difference. While the present study was not designed to examine this question, previous work using the same design and technique showed that in hearing adults with dyslexia (demonstrating phonological deficits), there is selectivity to written words in the VWFA as seen in previous studies with typical hearing readers (Glezer et al., 2018). This finding suggests that imprecise phonological representations may not impact visual word tuning in the ventral stream to the degree posited by Pugh et al (2001). However, because less-skilled deaf readers are not dyslexic, it is possible that the response profile in this region would differ between skilled and less-skilled deaf readers. It will be interesting in future studies to examine this question using fMRI-RA.

Unlike what has been found in hearing readers, the skilled deaf readers in this study showed selectivity to orthography in the right hemisphere VWFA in Experiment 2 (and a trend in Experiment 1). This result lends support for the *phonological mapping hypothesis* (Maurer and McCandliss, 2007), which posits that the characteristic left lateralization for reading is the result of the need to map left lateralized phonological information to visual information. This hypothesis predicts less left lateralization with lower phonological skill levels. This result was found for the N170 response in an ERP study of adult deaf readers, compared to hearing readers who were matched for reading ability but not for phonological skill (Emmorey et al., 2017). These authors found that for deaf readers, better reading ability was associated with a larger N170 over the right hemisphere, while for hearing readers better reading ability was associated with a smaller right N170. Emmorey et al. (2017) pointed out that while right-sided involvement for hearing readers tends to be maladaptive, it appears to be advantageous for deaf readers. They suggested that the difference in lateralization between deaf and hearing participants is likely due to a difference in the contribution of the left-lateralized phonological representations, as predicted by the phonological mapping hypothesis. Sacchi and Laszlo (2016) also provide support for the phonological mapping hypothesis, showing that left lateralization of the N170 response can be predicted by phonological awareness skills in hearing children. In the present study, we provide fMRI evidence that skilled deaf readers, who have less precise phonological skills than typical hearing readers (see Table 1), show selectivity in the left VWFA in both experiments and in the right VWFA in Experiment 2 (with a trend for selectivity in Experiment 1). In contrast, previous studies with typical and dyslexic hearing readers report selectivity only in the left VWFA (Gaillard et al., 2006; Glezer et al., 2009, 2018; Vinckier et al., 2007). In agreement with Emmorey et al., (2017), our results suggest that the involvement of the right hemisphere VWFA in the deaf participants does not appear to be maladaptive since they were all skilled readers. However, these conclusions will need to be further examined as only one of our Experiments solidly supported this claim. In addition, studies with less skilled hearing and deaf readers are needed to confirm this hypothesis.

Phonology and TPC

With the fairly well-established theory that strong phonological skills are needed for reading success in hearing people, a large focus of the research on reading in the deaf population has been on the degree to which phonology is required for reading success, and as detailed in the introduction, results regarding the importance of phonology to reading success is quite mixed. Findings on the neurological underpinnings of phonological processing and the degree of phonological activation during reading in deaf readers are similarly mixed.

Previously, it has been shown that for typical hearing readers, a region within the TPC exhibits selectivity to the phonology of written words (Glezer et al., 2016). Using the same methods, we examined the tuning to phonology of written words in skilled deaf readers. Our results show that while there is responsivity to phonology (i.e. the H condition adapts compared to the Control condition), the representation within the TPC of skilled deaf readers does not show the same specificity (i.e. the H condition did not fully adapt - it was significantly different than S) as has been shown in typical hearing readers (Glezer et al., 2016). This finding suggests that 1) skilled deaf readers have coarser-grained phonological

representations than skilled hearing readers, 2) deaf readers do not require fine-grained representations for reading success, and 3) phonology is engaged when making phonological judgments to written words. Our findings also support recent behavioral research showing that skilled deaf readers show the same sensitivity to orthography as skilled hearing readers (e.g., Fariña et al., 2017). Further, they support the idea that skilled deaf readers show some sensitivity—but less selectivity—to phonology when reading (Friesen and Joanisse, 2012). The neurons in the TPC showed sensitivity to the phonology of a written word when the participants were doing a phonological task (syllable counting). While the goal of the present study was to probe orthographic versus phonological tuning, and not to examine task effects, it does help to elucidate the role phonology plays in reading success in people who are deaf. Future studies will be required to more exactly determine the impact of task on activation of phonology when deaf people are reading.

Orthography and phonology in the IFG

While previous results regarding the involvement of the IFG during reading in people who are deaf are mixed, it does appear that skill level and task can affect activation level in this region. Our results indicate that skilled deaf readers show the same response profile as has been reported for typical hearing readers (Glezer et al., 2016). Skilled deaf readers show selectivity to written words with no adaptation for homophones, suggesting that this region is more responsive to whole word orthographic structure of the written word and not the phonological structure. The IFG is purported to have a role in phonological assembly, as well as in articulation of phonological representations (Démonet et al., 1992; Poldrack et al., 1999; Tan et al., 2005). In addition, the IFG has been implicated in articulatory recoding of print (Sandak et al., 2004). Interestingly, MacSweeney et al. (2009) showed that activation in this region is negatively correlated with phonological processing ability in both hearing and deaf adults when they performed a rhyme judgment task. However, Emmorey et al., (2016) recently identified an IFG cluster in a similar location to this study, which was positively correlated with task accuracy when the participants performed a syllable counting task. The present study, in conjunction with our previous fMRI-RA work (Glezer et al., 2009, 2016) therefore sheds light on these seemingly conflicting findings. While it looks as though skill level and type of task have an impact on the overall average BOLD response in this region, the underlying neural specificity (as measured with fMRI-RA) for written words in the IFG appears to be consistent in skilled readers regardless of hearing status (and thus phonological ability). That is, neurons in this region appear to be tightly tuned to whole written words. Therefore, the inconsistencies seen in overall activation in this region reported in previous studies cannot be attributed to differences in underlying representations or the degree of tuning/coding to orthographic or phonological components. Rather, it may reflect another cognitive skill important for completing the task (e.g. attention, effort, memory etc.).

It has been suggested that connections between the IFG and the VWFA are required for successful reading (Paulesu et al., 1996) and functional connectivity between these regions—and not the connectivity between the VWFA and sound-related regions—has been demonstrated in the deaf population (Wang et al., 2015). These findings, taken together with the results from the present study, suggest that skilled deaf readers develop a neural reading system quite similar to that of typical hearing readers, with selectivity to written words in the

VWFA and IFG, and that both groups of readers can use a direct route from orthography to semantics. However, unlike typical hearing readers, who require the development of and access to a finely tuned phonological system to develop into good readers, deaf readers do not appear to need to develop or access a finely tuned phonological system to become good readers.

In conclusion, we present evidence that skilled deaf readers show high selectivity to orthography in both the left and right VWFA and in IFG, and coarse tuning to phonology in the TPC. These findings indicate that skilled deaf readers present with a unique response profile. That is, while their response profile is similar to hearing readers in the left VWFA and IFG, the impact of coarsely tuned phonological representations in the TPC appears to have little impact on the neural network associated with skilled reading.

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References

- Allen T (1986). Patterns of academic achievement among hearing-impaired students In *Deaf Children in America*, Schildroth A, and Karchmer M, eds. (San Diego, CA: College Hill Press), pp. 161–206.
- Aparicio M, Gounot D, Demont E, and Metz-Lutz M-N (2007). Phonological processing in relation to reading: an fMRI study in deaf readers. *Neuroimage* 35, 1303–1316. [PubMed: 17329129]
- Baker CI, Liu J, Wald LL, Kwong KK, Benner T, and Kanwisher N (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proc. Natl. Acad. Sci. U. S. A* 104, 9087–9092. [PubMed: 17502592]
- Balota DA, Yap MJ, Cortese MJ, Hutchison KA, Kessler B, Loftis B, Neely JH, Nelson DL, Simpson GB, and Treiman R (2007). English Lexicon Project. *Behav. Res. Methods* 39, 445–459. [PubMed: 17958156]
- Bélanger NN, and Rayner K (2015). What Eye Movements Reveal about Deaf Readers. *Curr. Dir. Psychol. Sci* 24, 220–226. [PubMed: 26594098]
- Bélanger NN, Mayberry RI, and Rayner K (2013). Orthographic and phonological preview benefits: parafoveal processing in skilled and less-skilled deaf readers. *Q. J. Exp. Psychol. (Hove)* 66, 2237–2252. [PubMed: 23768045]
- Binder JR, Desai RH, Graves WW, and Conant LL (2009). Where Is the Semantic System? A Critical Review and Meta-Analysis of 120 Functional Neuroimaging Studies. *Cereb. Cortex* 19, 2767–2796. [PubMed: 19329570]
- Boets B, Op de Beeck HP, Vandermosten M, Scott SK, Gillebert CR, Mantini D, Bulthe J, Sunaert S, Wouters J, and Ghesquiere P (2013). Intact But Less Accessible Phonetic Representations in Adults with Dyslexia. *Science* 342, 1251–1254. [PubMed: 24311693]
- Brett M, Anton J-L, Valabregue R, and Poline J-B (2002). Region of interest analysis using an SPM toolbox. *Present. 8th Int. Conf. Funct. Mapp. Hum. Brain*
- Burav as GT, and Boynton GM (2002). Efficient Design of Event-Related fMRI Experiments Using M-Sequences. *Neuroimage* 16, 801–813. [PubMed: 12169264]
- Carreiras M, Armstrong BC, Perea M, and Frost R (2014). The what, when, where, and how of visual word recognition. *Trends Cogn. Sci* 18, 90–98. [PubMed: 24373885]
- Cohen L, and Dehaene S (2004). Specialization within the ventral stream: the case for the visual word form area. *Neuroimage* 22, 466–476. [PubMed: 15110040]
- Corina DP, Lawyer LA, Hauser P, and Hirshorn E (2013). Lexical processing in deaf readers: an FMRI investigation of reading proficiency. *PLoS One* 8, e54696. [PubMed: 23359269]

- Dehaene S, and Cohen L (2011). The unique role of the visual word form area in reading. *Trends Cogn. Sci* 15, 254–262. [PubMed: 21592844]
- Dehaene S, Naccache L, Cohen L, Bihan DL, Mangin JF, Poline JB, and Riviere D (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nat. Neurosci* 4, 752–758. [PubMed: 11426233]
- Démonet JF, Chollet F, Ramsay S, Cardebat D, Nespoulous JL, Wise R, Rascol A, and Frackowiak R (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain a J. Neurol* 115 (Pt 6), 1753–1768.
- Dietz NAE, Jones KM, Gareau L, Zeffiro TA, and Eden GF (2005). Phonological decoding involves left posterior fusiform gyrus. *Hum. Brain Mapp* 26, 81–93. [PubMed: 15934062]
- Emmorey K, Weisberg J, McCullough S, and Petrich J. a F. (2013). Mapping the reading circuitry for skilled deaf readers: an fMRI study of semantic and phonological processing. *Brain Lang* 126, 169–180. [PubMed: 23747332]
- Emmorey K, McCullough S, and Weisberg J (2016). The neural underpinnings of reading skill in deaf adults. *Brain Lang* 160, 11–20. [PubMed: 27448530]
- Fariña N, Dunabeitia JA, and Carreiras M (2017). Phonological and orthographic coding in deaf skilled readers. *Cognition* 168, 27–33. [PubMed: 28646750]
- Fiebach CJ, Friederici AD, Müller K, and von Cramon DY (2002). fMRI evidence for dual routes to the mental lexicon in visual word recognition. *J. Cogn. Neurosci* 14, 11–23. [PubMed: 11798383]
- Friesen DC, and Joanisse MF (2012). Homophone effects in deaf readers: Evidence from lexical decision. *Read. Writ* 25, 375–388.
- Gaillard R, Naccache L, Pinel P, Clémenceau S, Voile E, Hasboun D, Dupont S, Baulac M, Dehaene S, Adam C, et al. (2006). Direct intracranial, FMRI, and lesion evidence for the causal role of left inferotemporal cortex in reading. *Neuron* 50, 191–204. [PubMed: 16630832]
- Glezer LS, and Riesenhuber M (2013). Individual Variability in Location Impacts Orthographic Selectivity in the “ Visual Word Form Area .” *J. Neurosci* 33, 11221–11226. [PubMed: 23825425]
- Glezer LS, Jiang X, and Riesenhuber M (2009). Evidence for highly selective neuronal tuning to whole words in the “visual word form area”. *Neuron* 62, 199–204. [PubMed: 19409265]
- Glezer LS, Kim J, Rule J, Jiang X, and Riesenhuber M (2015). Adding Words to the Brain’s Visual Dictionary: Novel Word Learning Selectively Sharpens Orthographic Representations in the VWFA. *J. Neurosci* 35, 4965–4972. [PubMed: 25810526]
- Glezer LS, Eden G, Jiang X, Luetje M, Napoliello E, Kim J, and Riesenhuber M (2016). Uncovering phonological and orthographic selectivity across the reading network using fMRI-RA. *Neuroimage* 138, 248–256. [PubMed: 27252037]
- Glezer LS, Jiang X, Luetje M, Napoliello EM, Kim J, Riesenhuber M, and Eden GF (2018). An fMRI-Adaptation Study of Compromised Phonological Selectivity in Superior Temporal and Normal Orthographic Selectivity in Occipito-Temporal Cortices in Adults with Dyslexia. *Submiss*
- Goh JO, Suzuki A, and Park DC (2010). Reduced neural selectivity increases fMRI adaptation with age during face discrimination. *Neuroimage* 51, 336–344. [PubMed: 20139012]
- Goldin-Meadow S, and Mayberry RI (2001). How Do Profoundly Deaf Children Learn to Read? *Learn. Disabil. Res. Pract* 16, 222–229.
- Grady CL, Horwitz B, Pietrini P, Mentis MJ, Ungerleider LG, Rapoport SI, and Haxby JV (1996). Effect of task difficulty on cerebral blood flow during perceptual matching of faces. *Hum. Brain Mapp* 4, 227–239. [PubMed: 20408201]
- Grainger J, Dufau S, Montant M, Ziegler JC, and Fagot J (2012). Orthographic processing in baboons (*Papio papio*). *Science* 336, 245–248. [PubMed: 22499949]
- Grill-Spector K, Henson R, and Martin A (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci* 10, 14–23. [PubMed: 16321563]
- Gutierrez-Sigut E, Vergara-Martinez M, and Perea M (2017). Early use of phonological codes in deaf readers: An ERP study.
- Hagoort P, Indefrey P, Brown C, Herzog H, Steinmetz H, and Seitz RJ (1999). The neural circuitry involved in the reading of German words and pseudowords: A PET study. *J. Cogn. Neurosci* 11, 383–398. [PubMed: 10471847]

- Hasko S, Groth K, Bruder J, Bartling J, and Schulte-Körne G (2013). The time course of reading processes in children with and without dyslexia: an ERP study. *Front. Hum. Neurosci* 7, 570. [PubMed: 24109444]
- Hellyer PJ, Woodhead ZVJ, Leech R, and Wise RJS (2011). An Investigation of Twenty/20 Vision in Reading. *J. Neurosci* 31, 14631–14638. [PubMed: 21994379]
- Hirshorn EA, Dye MWG, Hauser P, Supalla TR, and Bavelier D (2015). The contribution of phonological knowledge, memory, and language background to reading comprehension in deaf populations. *Front. Psychol* 6, 1153. [PubMed: 26379566]
- Jiang X, Rosen E, Zeffiro T, Vanmeter J, Blanz V, and Riesenhuber M (2006). Evaluation of a shape-based model of human face discrimination using fMRI and behavioral techniques. *Neuron* 50, 159–172. [PubMed: 16600863]
- Katzev M, Tüscher O, Hennig J, Weiller C, and Kaller CP (2013). Revisiting the functional specialization of left inferior frontal gyrus in phonological and semantic fluency: the crucial role of task demands and individual ability. *J. Neurosci* 33, 7837–7845. [PubMed: 23637175]
- Kaufman AS, and Kaufman NL (2004). Kaufman brief intelligence test (2nd ed.) (Bloomington, MN: Pearson).
- Kherif F, Josse G, and Price CJ (2011). Automatic top-down processing explains common left occipito-temporal responses to visual words and objects. *Cereb. Cortex* 21, 103–114. [PubMed: 20413450]
- Kircher T, Nagels A, Kirner-Veselinovic A, and Krach S (2011). Neural correlates of rhyming vs. lexical and semantic fluency. *Brain Res* 1391, 71–80. [PubMed: 21447325]
- Krekelberg B, Boynton GM, and van Wezel RJA (2006). Adaptation: from single cells to BOLD signals. *Trends Neurosci* 29, 250–256. [PubMed: 16529826]
- Kronbichler M, Hutzler F, Wimmer H, Mair A, Staffen W, and Ladurner G (2004). The visual word form area and the frequency with which words are encountered: evidence from a parametric fMRI study. *Neuroimage* 21, 946–953. [PubMed: 15006661]
- Li Y, Peng D, Liu L, Booth JR, and Ding G (2014). Brain activation during phonological and semantic processing of Chinese characters in deaf signers. *Front. Hum. Neurosci* 8, 1–11. [PubMed: 24474914]
- MacSweeney M, Brammer MJ, Waters D, and Goswami U (2009). Enhanced activation of the left inferior frontal gyrus in deaf and dyslexic adults during rhyming. *Brain* 132, 1928–1940. [PubMed: 19467990]
- Mahé G, Bonnefond A, and Doignon-Camus N (2013). Is the impaired N170 print tuning specific to developmental dyslexia? A matched reading-level study with poor readers and dyslexics. *Brain Lang* 127, 539–544. [PubMed: 24148146]
- Maurer U, and McCandliss BD (2007). The development of visual expertise for words: the contribution of electrophysiology. *Single-Word Read. Biol. Behav. Perspect* 43–63.
- Mayberry RI, del Giudice AA, and Lieberman AM (2011). Reading achievement in relation to phonological coding and awareness in deaf readers: a meta-analysis. *J. Deaf Stud. Deaf Educ* 16, 164–188. [PubMed: 21071623]
- Mayer C, and Trezek BJ (2014). Is reading different for deaf individuals? Reexamining the role of phonology. *Am. Ann. Deaf* 159, 359–371. [PubMed: 25669018]
- Park DC, Polk TA, Park R, Minear M, Savage A, and Smith MR (2004). Aging reduces neural specialization in ventral visual cortex. *Proc. Natl. Acad. Sci. U. S. A* 101, 13091–13095. [PubMed: 15322270]
- Paulesu E, Frith U, Snowling M, Gallagher A, Morton J, Frackowiak RS, and Frith CD (1996). Is developmental dyslexia a disconnection syndrome? Evidence from PET scanning. *Brain* 119 (Pt 1), 143–157. [PubMed: 8624677]
- Poldrack RA, Wagner AD, Prull MW, Desmond JE, Glover GH, and Gabrieli JD (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage* 10, 15–35. [PubMed: 10385578]
- Price CJ, and Devlin JT (2003). The myth of the visual word form area. *Neuroimage* 19, 473–481. [PubMed: 12880781]

- Price CJ, and Devlin JT (2004). The pro and cons of labelling a left occipitotemporal region: “the visual word form area.” *Neuroimage* 22, 477–479. [PubMed: 15110041]
- Price CJ, and Devlin JT (2011). The Interactive Account of ventral occipitotemporal contributions to reading. *Trends Cogn. Sci* 15, 246–253. [PubMed: 21549634]
- Pugh KR, Mencl WE, Jenner a R., Katz L, Frost SJ, Lee JR, Shaywitz SE, and Shaywitz BA (2001). Neurobiological studies of reading and reading disability. *J. Commun. Disord* 34, 479–492. [PubMed: 11725860]
- Qi S, and Mitchell RE (2012). Large-Scale Academic Achievement Testing of Deaf and Hard-of-Hearing Students : Past, Present, and Future. *J. Deaf Stud. Deaf Educ* 17, 1–18. [PubMed: 21712463]
- Rastle K, Harrington J, and Coltheart M (2002). 358,534 nonwords: the ARC Nonword Database. *Q. J. Exp. Psychol. A* 55, 1339–1362. [PubMed: 12420998]
- Richlan F, Kronbichler M, and Wimmer H (2011). Meta-analyzing brain dysfunctions in dyslexic children and adults. *Neuroimage* 56, 1735–1742. [PubMed: 21338695]
- Stevens WD, Kravitz DJ, Peng CS, Tessler MH, and Martin A (2017). Privileged Functional Connectivity between the Visual Word Form Area and the Language System. *J. Neurosci* 37.
- Sun Y, Lee J, and Kirby R (2010). Brain Imaging Findings in Dyslexia. *Pediatr. Neonatol* 51, 89–96. [PubMed: 20417459]
- Sunaert S, Van Hecke P, Marchal G, and Orban GA (2000). Attention to speed of motion, speed discrimination, and task difficulty: an fMRI study. *Neuroimage* 11, 612–623. [PubMed: 10860790]
- Tagamets M. a, Novick JM, Chalmers ML, and Friedman RB (2000). A parametric approach to orthographic processing in the brain: an fMRI study. *J. Cogn. Neurosci* 12, 281–297. [PubMed: 10771412]
- Tan LH, Laird AR, Li K, and Fox PT (2005). Neuroanatomical correlates of phonological processing of Chinese characters and alphabetic words: a meta-analysis. *Hum. Brain Mapp* 25, 83–91. [PubMed: 15846817]
- Traxler CB (2000). The Stanford Achievement Test, 9th Edition : National Norming and Performance Standards for Deaf and Hard-of-. *J. Deaf Stud. Deaf Educ* 5, 337–348. [PubMed: 15454499]
- Twomey T, Duncan KJK, Price CJ, and Devlin JT (2011). Top-down modulation of ventral occipitotemporal responses during visual word recognition. *Neuroimage* 55, 1242–1251. [PubMed: 21232615]
- van der Mark S, Bucher K, Maurer U, Schulz E, Brem S, Buckelmüller J, Kronbichler M, Loenneker T, Klaver P, Martin E, et al. (2009). Children with dyslexia lack multiple specializations along the visual word-form (VWF) system. *Neuroimage* 47, 1940–1949. [PubMed: 19446640]
- Vigneau M, Beaucousin V, Hervé PY, Duffau H, Crivello F, Houdé O, Mazoyer B, and Tzourio-Mazoyer N (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *Neuroimage* 30, 1414–1432. [PubMed: 16413796]
- Vinckier F, Dehaene S, Jobert A, Dubus JP, Sigman M, and Cohen L (2007). Hierarchical coding of letter strings in the ventral stream: dissecting the inner organization of the visual word-form system. *Neuron* 55, 143–156. [PubMed: 17610823]
- Wang X, Caramazza A, Peelen MV, Han Z, and Bi Y (2015). Reading Without Speech Sounds: VWFA and its Connectivity in the Congenitally Deaf. *Cereb. Cortex* 25, 2416–2426. [PubMed: 24642423]
- Yoncheva YN, Zevin JD, Maurer U, and McCandliss BD (2010). Auditory selective attention to speech modulates activity in the visual word form area. *Cereb. Cortex* 20, 622–632. [PubMed: 19571269]

Highlights

- An fMRI rapid adaptation paradigm explored neural tuning in skilled deaf readers
- Both the left and right VWFA showed selectivity to whole word orthography
- Sensitivity, but not selectivity to phonology was found in temporoparietal cortex
- Skilled deaf readers develop finely tuned neural representations of written words
- Phonological tuning may have little impact on reading success for deaf adults

Figure 1.
Examples of each experimental paradigm for the fMRI-RA (A-C) and the localizers (D).

Figure 2.

Predictions for fMRI-RA response to each condition for an orthographic (A) and (B) whole word and (C) part word (sublexical) representation and (D) a phonological representation.

Figure 3.

Average ROI locations for A) VWFA, B) TPC and C) IFG. Yellow denotes the average location of the subjects from the current study and Cyan denotes the average location from hearing readers in Experiment 1 from Glezer et al. (2016). D) Average location of the rVWFA. Yellow denotes the average location of the subjects from the current study and Cyan and Blue denotes the average location from hearing readers from Glezer et al. (2009, 2015).

Figure 4. Percent signal change in Experiment 1 for A) real words and B) pseudowords in the VWFA. Box plot shows third (top) and first (bottom) quartile, box plot bars represent min and max, **x** = mean, line = median, **o** = subject. *** < 0.0001, ** < 0.01, * = 0.05.

Figure 5.

Percent signal change in Experiment 1 (A) and Experiment 2 (B) in the rVWFA. Box plot shows third (top) and first (bottom) quartile, box plot bars represent min and max, $\bar{x}$ = mean, line = median, $\bullet$ = subject. **** < 0.0001, *** = 0.001, ** < 0.01, * < 0.05.

Figure 6. Percent signal change in Experiment 2 in each ROI. Box plot shows third (top) and first (bottom) quartile, box plot bars represent min and max, **x** = mean, line = median, **o** = subject. *** < 0.005, ** < 0.01, * < 0.05

Table 1.

Assessment measures and scores. Historical data from hearing participants in previous studies from our lab is listed for reference purposes.

	Deaf Mean (SD) N = 12	Hearing Mean (SD) N = 60
Age	32 (5.7)	25 (6.6)
Gender	9M, 3F	34M, 56 F
KBIT	112 (15.1)	105 (15)
PIAT raw score	91 (4.5)	85 (10)
Range	82-97	64-99
Reading age (in years)	14 (1.3)	14 (1.6)
Hirshorn Total (percent correct)	0.67 (0.15)	0.92 (0.07)
Hirshorn deep (percent correct)	0.49 (0.25)	0.89 (0.11)
Hirshorn shallow (percent correct)	0.84 (0.07)	0.95 (0.05)

Table 2.

Psycholinguistic characteristics of the stimuli used in Experiment 1. Length = item length (number of letters); Freq = mean Hyperspace Analogue to Language (HAL) log frequency; N = number of orthographic neighbors; BG Freq = averaged bigram frequency.

Experiment 1					
Real Words					
		Length	Freq	N	BG Freq
SAME	Mean	4.13	10.73	10.45	1816
	SD	0.68	1.04	4.72	769
	Median	4	10.76	11	1701
	SEM	0.10	0.15	0.69	112
	Min	3	8.03	2	479
	Max	6	12.60	20	3895
1L	Mean	4.13	11.04	10.26	1880
	SD	0.68	0.96	4.48	871
	Median	4	11.17	11	1762
	SEM	0.10	0.14	0.65	127
	Min	3	8.78	1	481
	Max	6	13.10	18	4150
DIFF	Mean	4.13	10.74	9.36	1704
	SD	0.68	1.12	4.52	877
	Median	4	10.65	10	1517
	SEM	0.10	0.16	0.66	128
	Min	3	8.63	1	452
	Max	6	14.35	18	4563
Pseudowords					
		Length	Freq	N	BG Freq
SAME	Mean	4.13	n/a	10.51	1300
	SD	0.68		4.89	564
	Median	4		9.00	1207
	SEM	0.10		0.71	82
	Min	3		1	350
	Max	6		23	2586
1L	Mean	4.13	n/a	9.47	1279
	SD	0.68		4.73	586
	Median	4		9.00	1181
	SEM	0.10		0.69	86
	Min	3		1	177
	Max	6		19	2829
DIFF	Mean	4.13	n/a	9.34	1483
	SD	0.68		4.37	794
	Median	4		9.00	1283

Experiment 1				
Real Words				
	Length	Freq	N	BG Freq
SEM	0.10		0.64	116
Min	3		1	242
Max	6		19	3452

Table 3.

Psycholinguistic characteristics of the stimuli used in Experiment 2. Length = item length (number of letters); Freq = mean Hyperspace Analogue to Language (HAL) log frequency; N = number of orthographic neighbors; BG Freq = averaged bigram frequency.

Experiment 2					
		Length	Freq	N	BG Freq
SAME	Mean	3.96	9.16	10.27	1914
	SD	<i>0.64</i>	<i>1.80</i>	<i>5.21</i>	<i>764</i>
	Median	<i>4</i>	<i>9.07</i>	<i>11</i>	<i>1819</i>
	SEM	<i>0.09</i>	<i>0.26</i>	<i>0.74</i>	<i>109</i>
	Min	<i>3</i>	<i>5.20</i>	<i>1</i>	<i>756</i>
	Max	<i>5</i>	<i>13.27</i>	<i>20</i>	<i>3641</i>
H	Mean	3.96	8.32	9.35	1828
	SD	<i>0.64</i>	<i>1.91</i>	<i>5.75</i>	<i>869</i>
	Median	<i>4</i>	<i>8.21</i>	<i>8</i>	<i>1661</i>
	SEM	<i>0.09</i>	<i>0.27</i>	<i>0.82</i>	<i>124</i>
	Min	<i>3</i>	<i>4.19</i>	<i>0</i>	<i>166</i>
	Max	<i>5</i>	<i>12.51</i>	<i>23</i>	<i>3916</i>
CONTROL	Mean	3.96	8.88	9.59	1759
	SD	<i>0.64</i>	<i>1.91</i>	<i>4.42</i>	<i>839</i>
	Median	<i>4</i>	<i>8.82</i>	<i>10</i>	<i>1582</i>
	SEM	<i>0.09</i>	<i>0.27</i>	<i>0.63</i>	<i>120</i>
	Min	<i>3</i>	<i>4.71</i>	<i>1</i>	<i>156</i>
	Max	<i>5</i>	<i>12.72</i>	<i>19</i>	<i>4288</i>