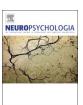


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The N170 ERP component differs in laterality, distribution, and association with continuous reading measures for deaf and hearing readers



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ABSTRACT

The temporo-occipitally distributed N170 ERP component is hypothesized to reflect print-tuning in skilled readers. This study investigated whether skilled deaf and hearing readers (matched on reading ability, but not phonological awareness) exhibit similar N170 patterns, given their distinct experiences learning to read. Thirty-two deaf and 32 hearing adults viewed words and symbol strings in a familiarity judgment task. In the N170 epoch (120–240 ms) hearing readers produced greater negativity for words than symbols at left hemisphere (LH) temporo-parietal and occipital sites, while deaf readers only showed this asymmetry at occipital sites. Linear mixed effects regression was used to examine the influence of continuous measures of reading, spelling, and phonological skills on the N170 (120–240 ms). For deaf readers, better reading ability was associated with a larger N170 over the right hemisphere (RH), but for hearing readers better reading ability was associated with smaller RH N170. Better spelling ability was related to larger occipital N170s in deaf readers, but this relationship was weak in hearing readers. Better phonological awareness was associated with smaller N170s in the LH for hearing readers, but this association was weaker and in the RH for deaf readers. The results support the phonological mapping hypothesis for a left-lateralized temporo-parietal N170 in hearing readers and indicate that skilled reading is characterized by distinct patterns of neural tuning to print in deaf and hearing adults.

1. Introduction

Reading is an essential skill of modern life that most citizens of industrialized countries master by late adolescence. However, the apparent ease with which the majority of children become fluent expert readers is somewhat deceiving – decades of research has shown that the neuro-cognitive processes involved in acquiring and then using this skill are extremely complex (e.g., Rayner et al., 2001). Although a full specification of the processes involved in reading and learning to read is still lacking, it is clear that a highly coordinated and rapid interplay of sensory, perceptual and linguistic processes all play a role.

Perhaps one factor contributing to the apparent ease of learning to read is the fact that many aspects of the skill are built on top of a preexisting and well-developed system of spoken language comprehension. It is therefore not surprising that theories of reading usually reserve a primary role for prior spoken word knowledge in the mechanics of learning to read as well as skilled adult reading (e.g., Frost, 1998). For hearing people, weak phonological skills are clearly linked to poorer reading ability in both children (e.g., Wagner and Torgesen,

1987) and adults (e.g., Macaruso and Shankweiler, 2010). Whether phonological skills are similarly critical to reading success for deaf individuals is currently under intense debate. Some argue that the process of learning to read is essentially the same for deaf and hearing children and that speech-based phonological skills are key to reading achievements for both groups (Easterbrooksetal., 2008; Paul et al., 2009; Perfetti and Sandak, 2000; Wang et al., 2014). Others have recently argued that phonology does not play a central role in the development or maintenance of skilled reading for deaf people (Mayberry et al., 2010; Miller and Clark, 2011). Mayer and Trezek (2014) maintain that interpreting this current research as suggesting a lack of importance for phonology is flawed because these studies were conducted with deaf readers who had not achieved reading success - perhaps because they had not developed strong phonological skills. To address some of these issues, the current study specifically targeted skilled adult deaf readers who are matched on reading level with their hearing peers, with both groups exhibiting a similar range of reading ability. Specifically, we will be interested in examining how deaf and hearing readers differ in the temporal dynamics of reading and what linguistic factors (reading

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ability, spelling skill, phonological awareness) impact these neural patterns.

Critical to all theories of reading is the specification of the neurocognitive processes involved in comprehending the elemental units of written language – visually encountered words. For over 50 years researchers have sought to elaborate the cascade of processes underlying our ability to rapidly recognize and comprehend visually presented words. The speed at which words are comprehended is perhaps one of the most remarkable aspects of reading – during typical reading we recognize between two and five words per second, which puts an upper bound on speed of recognition at 200–500 ms per word. Clearly, to track the rapid time-course of the processes underlying visual word recognition requires a methodology with high temporal resolution. Event-related potentials (ERPs) offer this kind of precision, showing sensitivity to differences in processing at the millisecond level (Luck, 2005).

A substantial body of research using ERPs has shown that this technique is sensitive to a cascade of sensory, perceptual and linguistic processes that unfold over the course of recognizing a word. While the largest group of studies have tended to focus on processes near the end of the recognition stream - in particular those involved in the processing of word meaning (e.g., the N400), more recently a growing number of studies have focused on the earliest perceptual mechanisms involved in processing the orthographic and phonological attributes of words (see Maurer and McCandliss, 2008, for a review). One line of research of particular relevance to the current study is a growing number of reports concerned with the response of a brain region hypothesized to underlie the initial processing of visually presented words - the socalled visual word form area (VWFA; Cohen and Dehaene, 2004). This region is generally localized in functional imaging studies to the left fusiform gyrus and has been shown in fluent adult readers to be significantly more active during the processing of visually presented words and word-like letter strings than to other classes of visual stimuli (Baker et al., 2005; Dehaene and Cohen, 2011). Recent fMRI studies with deaf readers indicate that the anatomical location and activation strength of the VWFA is similar for deaf and hearing adult readers, despite differences in reading skill and phonological awareness between these groups (Aparicio et al., 2007; Emmorey et al., 2013; Wang et al., 2014). However, it is unknown whether activation within the VWFA involves a different time course of visual word recognition for deaf compared to

Of direct relevance to the current study, an even larger literature has shown that an early ERP component peaking around 170 ms after a visual stimulus (the N1 or N170) shows a similar sensitivity to word and word-like stimuli. Specifically, visual words and word-like letter strings produce a larger N170 amplitude than do size and luminance matched visual stimuli from other categories (Maurer and McCandliss, 2008). Moreover, consistent with the fMRI VWFA effect, the N170 to visual words tends to be proportionally larger in amplitude over left hemisphere temporo-occipital scalp sites. One hypothesis concerning the functional significance of the N170 is that it reflects expertise in a particular domain of knowledge representation (Rossion et al., 2003). This notion comes from the observation that a family of N170 effects are seen across a variety of stimulus domains including words, faces, and some non-face objects (Rossion et al., 2003). What typically distinguishes these different varieties of N170 is their scalp distribution. So, while the word-based N170 is larger over left temporo-occipital scalp sites, the face-specific N170 has been shown to have either a more bilateral distribution or slightly right hemisphere predominance. In both cases the idea is that these areas are somehow "tuned" to preferentially process a specific domain of knowledge over the course of massive experience (in the case of words and reading) or perhaps from a combination of experience and evolutionary selection pressure (in the case of faces; Rossion et al., 2003).

With respect to words and the N170, one question that arises is what kind of knowledge and/or perceptual processing reflects the

specialization of this component? A variety of studies seem to converge on the possibility that this component is very sensitive to the differential activation of orthographic knowledge. Consistent with this hypothesis, Bentin et al. (1999) - in one of the first studies to systematically examine early visual correlates of letter and word perception using the fine temporal precision of ERPs - reported that an temporooccipital negativity peaking at 170 ms (N170) differentiated words, pseudowords and letter strings (orthographic stimuli) from strings of alphanumeric symbols (non-orthographic stimuli). While orthographic strings produced a larger left hemisphere N170, symbols strings tended to produce larger N170 activity over the right hemisphere. Numerous subsequent studies have interpreted the larger left hemisphere N170 to words as reflecting the expertise that adult readers have acquired from their substantial exposure to print (e.g., Brem et al., 2005; Cohen et al., 2000; Maurer et al., 2005b; Tarkiainen et al., 1999). More recently Maurer and colleagues (Maurer et al., 2005a, 2005b, 2006, 2007) have argued that the orthographic (letters) vs. non-orthographic (symbols) lateralization differences reflects an acquired differential sensitivity of left temporo-occipital brain regions to "coarse" tuning for print. In other words, during the process of becoming a skilled reader circuits in the left temporo-occipital region stabilize on the combination of features that make up letters. Consistent with this hypothesis Maurer et al. (2005b, 2006) found that children just prior to learning to read (while in kindergarten) did not show the adult pattern of left-lateralized N170 activity (in contrasts of letter string and symbol string stimuli). However, less than two years later when those same children were again tested during the second grade, a pattern more like that found in adults was present. In other words, second graders showed a larger left hemisphere N170 to letters strings than symbol strings. In contrast, "fine-tuning" for print, reflected by sensitivity to regular orthographic structure (e.g., N170 response to words > pseudowords > consonant strings) appears to develop later, possibly not until after 5th grade (Coch and Meade, 2016).

To our knowledge, no previous study has examined the nature or scalp distribution of the N170 to words and symbol strings in deaf readers, and there has been very little electrophysiological research investigating visual word recognition in the deaf population. An early study by Neville et al. (1982) found that congenitally deaf signers did not exhibit visual field asymmetries when reading English words, although their word recognition accuracy was equal to the hearing participants. In the hearing readers an early negativity over occipital regions (N200) was observed which was larger in the hemisphere contralateral to visual field presentation, but for deaf participants this response was symmetric for right visual field (RVF) presentations (and larger in the right hemisphere for left visual field (LVF) presentations). In addition, the response over anterior temporal regions (N160) was larger in the left hemisphere for hearing participants, but was symmetrical for deaf participants. The reading levels of the deaf and hearing groups in this study are unknown, and it is unclear whether the lack of hemispheric asymmetry in both the behavioral and ERP responses for the deaf participants reflects differences in reading skill, phonological ability, or neural reorganization arising from congenital deafness and/or sign language knowledge.

More recently, MacSweeney et al. (2013) contrasted ERP responses in deaf and hearing adults as they performed rhyme judgments to sequentially presented written words (e.g., chair/bear pairs in which the rhyme decision could only be made using phonological knowledge). Only data from deaf participants who performed above chance (n=9) were analyzed (hearing participants were at ceiling). MacSweeney et al. (2013) observed no significant group differences in laterality for ERP responses to the first word in the pair (the "contingent negative variation" response between 600 and 1200 ms), although the left laterality effect was significant for the subgroup of nine hearing participants (p < .01), and this effect was only a trend for the deaf participants (p = .083). Both deaf and hearing participants showed greater negativity to nonrhyming than rhyming pairs between 300–600 ms, with a similar

onset latency of the "N450" for both groups. However, in the hearing group, the N450 was largest over the right hemisphere (the neural generator for this response is thought to be in left temporal and frontal regions; Khateb et al., 2007). In contrast, no interactions involving hemisphere approached significance in the deaf group. This pattern is consistent with the results of D'Hondt and Leybaert (2003) who found a left hemisphere (RVF) advantage for hearing participants making rhyme judgments ("yes" responses) but no hemispheric asymmetry for deaf participants who were matched on rhyme ability and reading level. Thus, the existing ERP literature with adult deaf readers suggests a more bilateral neural response to visual words compared to hearing readers, but the factors that lead to reduced left lateralization in this population remain unclear.

The left-lateralization of the N170 for hearing readers is often explained by the phonological mapping hypothesis which proposes that the emergence of left hemisphere processing of visual word forms is the result of linking printed words to left hemisphere auditory language regions in order to perform the linking of orthography with phonology (phonological mapping) that occurs during the process of learning to read (McCandliss and Noble, 2003). Recently, Sacchi and Laszlo (2016) explicitly tested the hypothesis that the N170 becomes increasingly left lateralized because phonological mapping processes drive early reading mechanisms towards the left hemisphere. They argued that an important prediction of the phonological mapping hypothesis is that greater phonological awareness should go along with more left lateralized visual word processing. They tested this idea by collecting ERPs while children in grades five and six viewed words and objects. Consistent with the phonological mapping hypothesis they reported that the degree of left lateralization of the N170 was predicted by phonological awareness (but not by vocabulary size).

Phonological awareness is also associated with general reading ability for hearing people. While awareness of phonology might be at the heart of the N170 lateralization, it is also possible that some other factor that drives both reading skill and phonological awareness is behind the increase in N170 lateralization found in readers with better phonological awareness. The population of deaf readers can help address this question because for deaf readers, phonological awareness is not as clearly linked to reading success (e.g., Mayberry et al., 2010), phonological knowledge is relatively coarse-grained (e.g., McQuarrie and Parilla, 2009), and phonological codes may not be automatically accessed during word reading (e.g., Bélanger et al., 2013). If a leftlateralized temporo-occipital N170 to word stimuli (compared to symbol strings) is still apparent in deaf readers, then phonological mapping from letters to sound cannot be the sole driving force behind N170 lateralization. On the other hand, if the N170 to word stimuli is bilateral or has right temporo-occipital distribution for deaf readers, it would lend support to the phonological mapping account of N170 distribution in hearing readers.

In the current study we compared ERPs in the N170 epoch (120-240 ms) to words and symbols strings in two groups of adult readers. One group was composed of 32 hearing adults who learned to read via standard instructional techniques whereby visual words are taught by mapping letters onto sounds. In this group we predict that the now typical pattern of left lateralized temporo-occipital N170s for visually presented words and a right lateralized temporo-occipital N170 for symbols strings should emerge. A second group of participants were 32 profoundly deaf adults matched in reading ability with the hearing readers, but who because of the lack of auditory input did not learn to read via letter to sound mapping. In contrast, the deaf readers may have acquired knowledge of spoken language phonology via speech-reading (lipreading) and articulatory information (e.g., Charlier and Leybaert, 2000; MacSweeney et al., 2008), and reading instruction occurred in the context of American Sign Language (ASL) where written English words can be learned through connections with signs and fingerspelled words (e.g., Humphries and MacDougall, 1999). If the leftlateralized temporo-occipital N170 seen in hearing readers is due to effects of mapping sounds to letters during the process of learning to read, then we do not expect to see a similar pattern to words/letter strings compared to symbol strings in deaf readers especially over the scalp sites that have typically shown the largest N170 response (i.e., those over temporo-parietal and to a lesser degree occipital scalp sites). Further, this study will allow us to more rigorously test the expertise hypothesis of the N170 – that is, that the overall difference between letter string and symbol string stimuli (regardless of laterality) will be reflected in expert readers that acquire reading skill via different learning strategies. If ERPs in the N170 epoch to words reflect a general tuning process due to extensive exposure to text, then we should see a difference in the ERPs during this time-period to words and symbols for deaf readers, but perhaps with a different characteristic scalp pattern than hearing readers.

Finally, we examined whether and how reading skill, phonological awareness, and orthographic sensitivity (assessed as spelling ability) modulate ERP responses in the two groups. Because the deaf and hearing groups were matched on reading ability, we can tease apart deafness-related from skill-related modulations. If we observe parallel patterns for both groups (e.g., larger or more left-lateralized ERP effects for better readers), it will indicate invariance in neural responses associated with visual word recognition and will highlight the stability of the reading system across populations. On the other hand, if we find that reading-skill is associated with distinct neural patterns for deaf and hearing readers, it will indicate that the optimal end-state for the reading system differs when access to auditory speech is significantly reduced due to hearing loss. Such a result would point to deaf-specific adaptations of the reading circuit. As noted above, we will also assess whether better phonological awareness skill is associated with greater left-lateralization of ERPs in the N170 epoch for hearing adults, paralleling the Sacchi and Laszlo (2016) results with children, and whether this pattern also holds for deaf adults who have much weaker phonological awareness ability. Finally, we hypothesize that orthographic sensitivity may play a larger role in learning to read for deaf compared to hearing readers because deaf readers may rely more on direct orthographic-to-semantic mappings due to weaker phonological skills. Therefore, we also examined whether spelling ability differentially modulated ERP components for deaf versus hearing readers in the N170 epoch. In sum, this study aimed to tease apart temporal neural patterns that reflect general effects of reading, phonological, and spelling skill (found across the two populations) from those patterns that are specific only to deaf readers.

2. Methods

2.1. Participants

Sixty-four volunteers participated in this experiment. Thirty-two were congenitally deaf adults (15 female; mean age = 29 years, range = 18–46 years) who were either native signers of ASL (born into deaf signing families; N = 23) or acquired ASL before age seven (N = 8); one deaf participant learned ASL after age seven. The other 32 were typical hearing adults (27 female; mean age = 22 years, range = 19–32 years) who were native speakers of English (none knew ASL). The deaf participants were severely to profoundly deaf (db loss \geq 70 db), and all were congenitally or prelingually deaf. The mean number of years of education for the deaf participants was 17 (SD = 2.7) and for the hearing participants, it was 15 years (SD = 1.7). All participants had normal or corrected to normal vision. Three deaf and four hearing participants were left-handed.

2.2. Behavioral tests

All participants underwent an assessment battery that measured reading comprehension, print exposure, spelling recognition, and phonological awareness. The battery included the following tests:

2.2.1. Peabody Individual Achievement Test (PIAT) – revised; reading comprehension subtest (Markwardt, 1998)

In this subtest, participants read (silently) a sentence, then choose from four pictures the one that best matches the sentence. Items increase in difficulty throughout the test, and the test is discontinued if a participant produces seven consecutive responses containing five errors. The mean PIAT raw score for deaf readers was 85 (SD = 9.6), and the mean score for the hearing readers was 85 (SD = 9.2). The deaf and hearing groups did not differ in their reading comprehension ability, t (62) = .12, p = .89.

2.2.2. Author Recognition Test (ART; Acheson et al., 2008)

This test provides a measure of print exposure. Participants read a list of 130 names (65 real authors and 65 foils) and indicate which ones they know to be authors. Scores are computed as the number of hits (correctly identified authors) minus false alarms (incorrect identifications). The mean ART score was 17 (SD = 14) for the deaf participants and 12 (SD = 7) for the hearing participants. The difference in print exposure was marginally significant, t(62) = 1.9, p = .06.

2.2.3. Spelling recognition test (Andrews and Hersch, 2010)

The test contains 88 items, half correctly spelled and half misspelled. Misspellings change one to three letters of the word and often preserve the pronunciation of the base word (e.g., *addmission, seperate*). Items are printed in columns, and participants are instructed to circle items they think are incorrectly spelled. The recognition test score is the number of correctly classified items, both hits and correct rejections. The mean spelling score for deaf readers was 75 (SD = 7.6), and the mean spelling score for the hearing readers was also 75 (SD = 7.8). The deaf and hearing groups did not differ in their spelling ability, t(62) = .18, p = .86.

2.2.4. Phonological awareness test (Hirshorn et al., 2015)

This test was specifically designed for profoundly deaf adults and does not require overt speech production. For one 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). In a second task, participants are shown two pictures (e.g., a bird and a toe) and are asked to combine the first sound of the word in the first picture with the rime of the word in the second picture to make a new word (e.g., bow). Participants type the new word that is created on a keyboard. The mean total accuracy for deaf readers on this phonological awareness test was 64% (SD = 14.7%), and the mean accuracy for the hearing readers was 91% (SD = 8.3%). The hearing readers scored significantly higher than the deaf readers, t(62) = 9.23, p < .0001.

2.3. ERP stimuli

The 180 experimental stimuli for this experiment were all composed of five character ASCII strings. One hundred and twenty of these strings were common English words (nouns and adjectives) and the remaining 60 were five-character non-alphanumeric symbol strings. The words varied in lexical frequency between 4.14 and 13.7 log HAL frequency (English Lexicon Project: Balota et al., 2007). The symbol strings were each a unique pseudorandom arrangement of five characters drawn from a pool of 26 typical ASCII characters (e.g., \$\%^#@ and \circ?*/*). The words and symbol strings were pseudorandomly intermixed in a single list which was used to form the 180 trial sequence for this experiment.

2.4. Procedure

Stimuli were presented in the center of a 24-in. LCD monitor (ASUS VG248) set to resolution of 1920×1080 pixels with a refresh rate of 100 Hz. The monitor was located approximately 145 cm directly in front of the participant. Stimuli were displayed as white lower case

letters (in the case of words) or white symbol strings on a black background in the fixed width New Courier font (40 \times 80 pixel character cells). The critical stimuli subtended 2° of horizontal and .75° vertical visual angle.

Each trial began with a fixation cross that was displayed in the center of the screen for 500 ms followed by a 500 ms blank screen and a 300 ms stimulus (i.e., a word or symbol string). Following each stimulus, a 700 ms blank screen and trial ending response cue were displayed. The response cue indicated that one of four buttons on a game pad resting in the participant's lap was to be pressed. Five-hundred ms after the participant's behavioral response, the next trial began.

With the onset of the response cue participants were instructed to make a rating judgment of the previous critical stimulus using a four-point familiarity scale. They were told that their highest rating (pressing a button marked with "f++") was to be used to indicate that they found the previous critical stimulus "very familiar" while their lowest rating was to be used to indicate they found the stimulus "not at all familiar" (a button marked with an "X"). The two intermediate judgments were to be used for "familiar" (f+) and "less familiar" (f-) ratings. Participants were told to withhold their rating responses until the response cue stimulus was displayed (i.e., after the critical ERP epoch). We selected this task because it required participants to make a range of judgments on the same scale for both the word and symbol string stimuli. Approximately every 40 trials participants were given a brief rest break of about two minutes.

2.4.1. EEG recording procedure

Participants were seated in a comfortable chair in a sound attenuated darkened room. An electro-cap fitted with tin electrodes was used to record continuous electroencephalogram (EEG) from 29 sites on the scalp (see Fig. 1). Four additional electrodes were attached: one below the left eye (LE, to monitor for vertical eye movement/blinks), one to the right of the right eye (HE, to monitor for horizontal eye movements), one over the left mastoid (A1, reference), and one over the right mastoid (A2, recorded actively to monitor for differential mastoid activity). All EEG electrode impedances were maintained below 5 k Ω (impedance for eye electrodes was less than 10 k Ω). The EEG was amplified by an SA bioamplifier with a bandpass of .01–40 Hz, and the EEGs were continuously digitized at 250 Hz (12 bit A/D). Trials with blinks and eye movement artifacts were rejected before averaging.

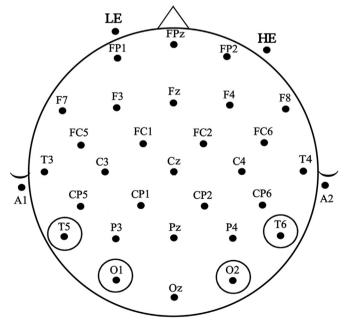


Fig. 1. The modified 10–20 system electrode montage used in this study. The four sites used in the average reference data analyses are circled.

2.4.2. Data analysis

Separate ERPs were averaged starting 100 ms pre-stimulus onset and continuing on for 300 ms. In a preliminary set of analyses, we contrasted ERPs to words low and high in lexical frequency. None of these analyses revealed any significant or marginal differences on the P1 or N170 amplitude as a function of word frequency. Therefore, to equate the number of items used to contrast ERPs recorded to words and symbol strings, only the 60 words with the lowest lexical frequency were included in the word condition. All 60 symbol string items went into the averages for these items. The resulting ERPs were then baselined to the average of 100 ms pre-stimulus period and low-pass filtered at 20 Hz. Only trials without muscle artifact or eye movement/blink activity were included in averages (less than 10% of trials were rejected).

In keeping with the standard procedure for studies focusing on the N170, all sites were re-referenced off-line to the average of the 29 scalp sites (i.e., average reference; Joyce and Rossion, 2005). The resulting ERP data were quantified by calculating mean amplitudes within two latency windows: 50–120 ms (P1), and 120–240 ms (N170). After an initial set of analyses indicated that the scalp distribution of both the P1 and N170 differed considerably we used separate sets of mixed design ANOVAs to analyze the data at the temporo-parietal (T5/T6) and occipital (O1/O2) sites. Each of these analyses included between-subject factors of Hearing Status (Deaf vs. Hearing) as well as two withinsubject factors of Stimulus Type (Words vs. Symbol Strings) and Laterality (left hemisphere vs. right hemisphere).

Finally, to explore the relationship between ERP measures of word processing and behavioral indices of reading, spelling, and phonological abilities we also employed a less common approach to analyzing ERP data. We used linear mixed effects regression modeling (LMER) to explore whether our online neural measures of word processing were related to these behavioral test scores (Baayen et al., 2008). Independent variables included one discrete fixed effect factor of Hearing Status (Deaf = 0 vs. Hearing = 1) and three continuous factors: Reading Skill (each participant's raw score on the PIAT test), Spelling Skill (each participant's score on the spelling recognition test), and Phonological Awareness (each participant's total score on the phonological awareness test). Test scores were normalized prior to analysis as recommended by Payne et al. (2015). Also included in the model were two factorial scalp site variables of Laterality (left hemisphere = 0 vs. right hemisphere = 1) and temporo-parietal/occipital (T/O) distribution (T = 0 vs. O = 1). Our first attempts at specifying the random effects structure for the LMER models involved the recommendation of keeping it maximal (Barr et al., 2013). However, all such models failed to converge for either component, so based on the recommendations of Bates et al. (2015) and Payne et al. (2015) we instead formulated models using random intercepts for subjects and stimulus items and random slopes for the covariances of the highest order interaction term (Hearing Status \times Reading Skill \times Spelling Skill \times Phonological Skill \times Laterality \times T/O distribution with Subjects: (0 + Hearing-Status:ReadingSkill:SpellingSkill:Laterality:T/O | Subjects)). In reporting LMER results we included the t-test values for comparisons of interest as well as the 95% confidence intervals (CIs) for effects that did not include 0 in the CI (see Payne et al., 2015). CIs are now the recommended way to report significance with LMER analyses (Bates et al., 2015).

3. Results

3.1. ERP results - words vs. symbols

As can be seen in Figs. 2 and 3, the ERPs from this study produced a clear pattern of early ERP components including an occipital maximum positivity peaking near 100 ms post stimulus onset (i.e., P1) and a subsequent temporo-parietally distributed negativity peaking near 200 ms (i.e., N170).

3.1.1. 50-120 ms (P1 epoch)

The ERPs in the P1 epoch were maximally positive (> 4 microvolts) at occipital sites and substantially smaller at temporo-parietal sites (main effect of T/O: F(1,62) = 64.02, p < .0001 – see Fig. 2) so separate ANOVAs for the two sets of sites were used in all subsequent analyses. Importantly, there were no significant differences in the amplitude of the positivity in this epoch between words and symbol strings at either set of electrode sites (all ps involving the stimulus Type variable > .11). The positivity was however, significantly larger in hearing (2.5 microvolts) than deaf (1.45 microvolts) readers at occipital sites (main effect of Hearing Status at occipital sites: F(1,62) = 4.44, p = .039; temporo-parietal: p > .49 – see Figs. 3 and 4), but not temporoparietal sites (all ps involving the Hearing Status variable > .13).

3.1.2. 120-240 ms (N170 epoch)

As can be seen in Fig. 2B there were also large differences between the occipital and temporo-parietal sites (main effect of site: F(1,62) = 22.02, p < .0001) in this time-period. We therefore analyzed the two scalp locations in separate ANOVAs.

In analyses of the temporo-parietal sites the left hemisphere was significantly more negative-going than the right hemisphere (main effect of Laterality, F(1,62) = 14.15, p = .0004). Words produced larger negativities than symbol strings (main effect of Stimulus Type: F(1,62) = 9.93, p = .0025) and importantly, this pattern was more apparent over the left than right hemisphere (Stimulus Type × Laterality interaction: F(1,62) = 12.91, p = .0006). There was also a higher order interaction between Hearing Status, Stimulus Type, and Laterality (F (1,62) = 4.02, p = .049). To better understand this interaction, we ran two sets of follow-up analyses. In the first we examined the two participant groups separately. Only the hearing readers produced a significant Stimulus Type × Laterality interaction at temporo-parietal sites, F(1,62) = 21.68, p = .0001, indicating that the laterality effect (left hemisphere more negative than right) was greater for words (1.9 microvolts) than that for symbol strings (.63 microvolts - see Fig. 3). Although overall the left hemisphere was significantly more negativegoing than the right for deaf readers (main effect of Laterality: F(1,31) = 5.33, p = .028), there was no evidence of a significant differential hemispheric asymmetry for the two stimulus types (see Fig. 3, stimulus Type \times Laterality p > .32) at temporo-parietal sties. This interpretation of the interaction is supported by a second set of follow-up analyses comparing the two groups separately at the left and right hemisphere temporo-parietal sites. Only the left hemisphere analysis produce a significant Hearing Status × Stimulus Type interaction (left hemisphere: F(1,62) = 6.01, p = .017; right hemisphere: p > .86).

In analyses of the occipital sites the left hemisphere was again more negative-going overall than the right (F(1,62) = 9.98, p < .0024) but as can be seen in Fig. 2, ERP differences between words and symbol strings were primarily due to words being more negative over the left than right hemisphere, while symbol strings produced a more bilaterally symmetrical response (Stimulus Type \times Laterality interaction: F (1,62) = 14.21, p = .0004 – see Fig. 2A). Unlike the temporo-parietal analysis, at occipital sites there was not a significant difference in amplitude between the two groups as a function of Stimulus Type and Laterality (i.e., the Hearing Status × Stimulus Type × Laterality interaction: p > .8). We nevertheless did the follow-up analyses on the groups separately to determine if the critical Stimulus Type × Laterality interaction was significant in both groups. Unlike the temporoparietal sites, analyses at occipital sites indicated that both groups produced a pattern of more negative left than right hemisphere ERPs for words compared to symbol strings (Stimulus Type × Laterality interaction, Hearing: F(1,31) = 8.39, p = .007; Deaf: F(1,31) = 5.97, p = .007.02 - see Fig. 3).

3.1.3. LMER analyses of the effects of continuous variables

To examine the influence of continuous measures of reading, spelling and phonological skills on the two ERP analysis epochs (P1, N170),

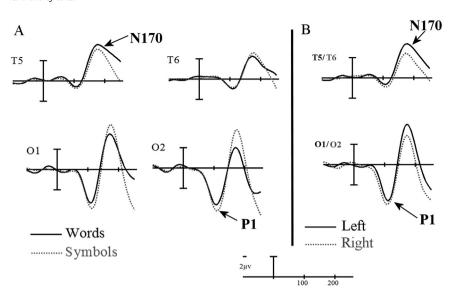


Fig. 2. Grand mean ERPs from all 64 participants. Panel A overplots ERPs for words and symbol strings at the four analysis electrode sites and panel B over-plots ERPs for the left and right hemispheres averaged across all stimuli.

we used linear mixed effects regression (LMER - Baayen et al., 2008). Rather than using averaged ERPs for these analyses, we used single trial EEG data from individual stimuli. For each stimulus, we calculated the mean amplitude in two epochs (50-120 ms and 120-240 ms) at each scalp site. We used the LMER function in the lme4 package (CRAN project; Bates et al., 2015) to model the influence of reading, spelling, and phonological skills on the two ERP measures. To increase statistical power, we used all 120 of the word stimuli (the 60 Symbol strings were not included in these analyses). Also included in each LMER model were the grouping factor of Hearing Status (0 = deaf vs. 1 = hearing) as well as scalp site factors of Laterality (left = 0 vs. right = 1) and T/O distribution (0 = Temporo-parietal, 1 = Occipital). To help visualize and interpret the effects from these analyses we included LMER solutions using the above scheme across all 29 scalp sites and plotted the LMER Estimate values for the two temporal epochs as scalp maps (referred to as LMEerps in Figs. 4-6).

Because LMER Estimate values are in units of the dependent variable (Payne et al., 2015), such scalp maps are something like scalp voltage maps typically used to display the distribution of effects in ERP studies. However, because the LMER approach models – as well as controls for – the effects of multiple independent variables, these maps reflect effects in the data that are not easily visualized in standard ERP or voltage map comparisons. For example, using this approach it is possible to examine the range of influence of a variable such as reading skill, while at the same time controlling for the effects of other variables such as spelling and phonological skill. Nonetheless, one caveat in using

such LMEerp maps (and LME in general as applied with ERPs) is that the relationship between the dependent variable and the various predictor variables is not as transparent as in traditional factorial ANOVA designs where the effects of independent variables can usually be directly visualized in the appropriate grand average or difference waves. In particular, the polarity (color) of the LMEerp effects might be ambiguous because of the complex nature of the modeling process used in the LMER models. Therefore, as a check on the nature of the effects visible in the LMEerp maps we also included in Figs. 4-6 traditional ERP contrasts formed from median split ERPs as a function of the variable of interest (e.g., for the reading skill variable we formed separate grand averaged ERPs for the 16 deaf participants with higher reading test scores and for the 16 deaf participants with lower reading test scores). These plots while not an ideal parallel to LMEerp maps can be used to help interpret the distribution and polarity of effects seen in the LMEerp maps.

3.1.3.1. Reading skill effects. In the P1 epoch both the Hearing Status by T/O distribution and Hearing Status by Laterality interactions with Reading Skill were significant (t = 2.15, CI [.03, .77] and t = -2.31 m CI [.80, -.07], respectively). As can be seen in the topographic LMER estimate and ERP median split plots in Fig. 4A, these interactions are consistent with a different reading skill effect in the deaf readers compared to the hearing readers over left occipital sites (note in particular the blue values for deaf and red values for hearing readers at the O1 site). There were also significant effects of reading skill in the

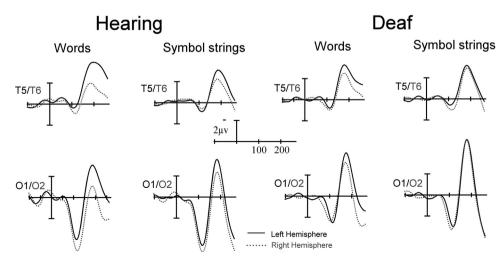


Fig. 3. ERPs from four posterior electrode sites plotted separately for hearing and deaf readers.

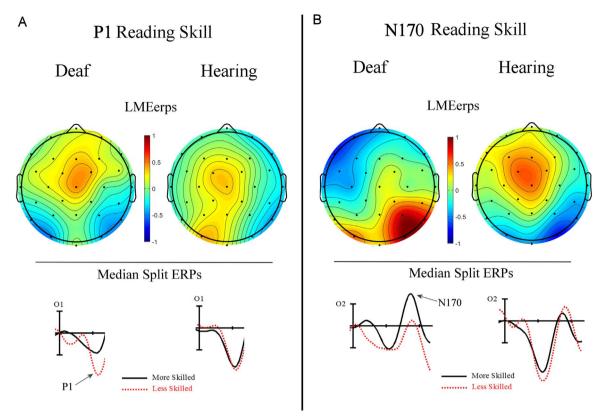


Fig. 4. (A) LMEerp estimate maps (top) and median split ERPs at the O1 site (bottom) for the P1 epoch in deaf and hearing readers. LMEerp voltage maps are based on the Estimate statistic at each electrode site for the effect of the reading skill variable (see text for an explanation). The median split ERPs contrast the 16 most skilled and 16 least skilled readers. (B) same as (A) but for the N170 epoch and the O2 electrode site. (For color figures, the reader is referred to the web version of this article).

N170 epoch as revealed by an interaction between Reading skill, Hearing status, and T/O distribution (t = -4.50, CI [-1.21 -.47]). As can be seen in the LMEerp maps and median split ERPs in Fig. 4B, the reading skill effect was of opposite polarity for hearing and deaf readers in this epoch especially over the right occipital site (O2). The median split ERPs suggest that this pattern is indicative of increases in reading skill being associated with larger right occipital negativities in deaf readers and smaller right occipital negativities in hearing readers. ¹

3.1.3.2. Spelling skill effects. While there were no significant effects of spelling skill on the P1, there was a significant Hearing Status by T/O distribution by Spelling Skill interaction later during the N170 ms epoch (t = 5.54, CI [.68, 1.42]). As can be seen in Fig. 5, better spelling scores in both groups were associated greater right hemisphere ERP negativity in this epoch. However, the LME analysis (but not the median split ERP waves) indicates that this relationship was stronger for deaf than hearing readers (Fig. 5 top).

3.1.3.3. Phonological awareness effects. Like spelling skill there were no significant effects of phonological awareness in the P1 epoch; however, there were effects in the subsequent N170 epoch. Here, there were interactions of phonological skill between Hearing Status and both T/O distribution (t=2.61, CI [.11, .79]) and Laterality (t=-4.36, CI [-1.09, -.42]). As can be seen in Fig. 6, higher phonological

awareness scores were associated with smaller ERP negativities in both groups, although the effect was much more pronounced in hearing readers over the left hemisphere and in the deaf readers over the right hemisphere.

4. Discussion

In the current study, we compared early ERP components to word and symbol string stimuli in hearing and deaf adults who were matched on their overall reading ability. We first summarize the results and then discuss possible interpretations of the differences we observed between the deaf and hearing readers.

As expected, the early occipitally distributed P1 did not differ as a function of stimulus type (words vs. symbols strings) or recording hemisphere (left vs. right). However, a few tens of millisecond later during the epoch of the N170, the left hemisphere became significantly more negative-going than the right hemisphere (see Fig. 2B) and words differed significantly from symbol strings. At temporo-parietal sites words produced larger N170s than symbol strings especially over the left hemisphere, while at occipital sites symbol strings produced larger N170s than words – especially over the right hemisphere (see Fig. 2).

There were also differences in the P1 and the N170 between the deaf and hearing readers. Hearing readers produced larger occipitally distributed P1s than deaf readers (see Fig. 3). The N170 differences between the groups emerged as a function of laterality and stimulus type but only at temporo-parietal sites. While there were clear lateral asymmetries during the N170 epoch for words compared to symbols strings in hearing readers (words much larger on the left, symbol strings only slightly larger on the left), the laterality effects in the deaf readers were smaller and did not significantly differentiate between the two stimulus types. However, at occipital sites both groups showed reliably larger left than right hemisphere N170s for words compared to symbol strings (symbols strings tended to produce more bilaterally symmetrical

 $^{^{\}rm 1}$ One seemingly contradictory effect in the LMEerp maps in Fig. 4B is the opposite polarity of the relationship between test scores and the N170 measurements for reading in hearing and deaf readers. The relationship for deaf readers is positive (red) and for hearing it is negative (blue). As we explain in the text, such ambiguity in the LMEerp maps could be due to the complex nature of the LMER modeling approach and this is where using median split ERPs to supplement the LME analyses can be useful. The median split ERPs clearly suggest that the polarity of the O2 N170 effect is in the interpreted direction – larger right occipital negativities associated with better test scores in the deaf readers and lower test scores in the hearing readers.

Spelling Effects

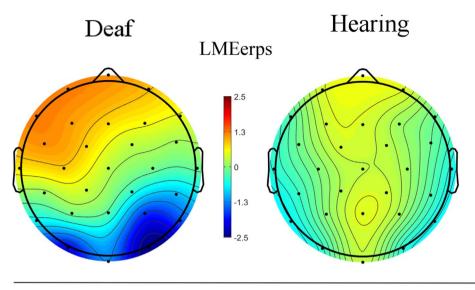
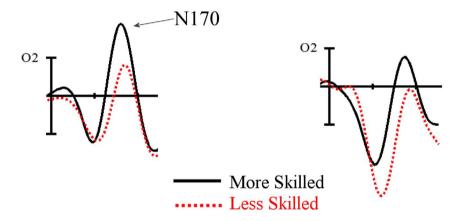


Fig. 5. (Top) LMEerp estimate maps for the N170 epoch showing the spelling skill effect for deaf and hearing readers. (Bottom) median split ERPs at the O2 site. (For color figures, the reader is referred to the web version of this article).

Median Split ERPs



N170 responses in both groups - see Fig. 3).

Turning to the effects of continuous test score variables on ERP amplitudes, we found clear differences for deaf and hearing readers as a function of all three variables (reading ability, phonological awareness, spelling skill). In the case of reading skill while increasing scores were associated with a smaller occipital P1 over the left hemisphere and a larger N170 over the right hemisphere in deaf readers, almost the exact opposite pattern was found in hearing readers – that is, at occipital sites a slightly larger left-sided P1 and a smaller right sided N170 were associated with better reading scores (see LME and median split ERPs in Fig. 4). Better spelling ability was related with larger occipital N170s in both groups (see Fig. 5), although the LME analyses suggest this pattern was stronger for deaf readers especially over right occipital sites. Finally, higher scores on the phonological awareness test were associated with smaller N170s, especially over left occipital sites in hearing readers. A similar but weaker pattern was found in the deaf readers, and the distribution of the effect was over the right occipital site (Fig. 6).

Overall, we suggest that the general pattern of results supports the phonological mapping hypothesis as an explanation for the left-lateralization of the temporo-parietal N170 ERP component in hearing individuals. While this N170 response was strongly left lateralized in hearing readers, the comparable effect was more bilateral for deaf participants who had similar reading ability but much poorer

phonological awareness than the hearing participants. Thus, the left-lateralized N170 to words at sites near auditory language centers in the left hemisphere in hearing individuals may arise from the developmental process of consistently mapping orthographic representations to phonological representations of speech. The finding that both hearing and deaf readers showed comparable left lateralization to words compared to symbol strings at occipital sites suggests that this more posterior portion of the N170, which is closer to visual processing regions, might reflect aspects of word processing more tied to visual/orthographic mechanisms. Deafness would presumably not disadvantage beginning readers as they tune neural circuits in brain regions sensitive to these mechanisms.

Further, phonological awareness ability had a much larger impact on the N170 in hearing than deaf readers, and the effect was left-lateralized in the hearing group but right lateralized in the deaf group (Fig. 6). For both groups of readers, individuals with poorer phonological awareness exhibited a larger N170 over occipital electrode sites (left for hearing and right for deaf readers). This pattern differs somewhat from the Sacchi and Laszlo (2016) results with hearing children. For children, better phonological awareness was associated with a larger left-lateralized N170 (also over occipital sites). The difference in the direction of the relationship of N170 and phonological awareness for hearing children and adults may reflect a shift in the role that

Phonological Awareness Effects

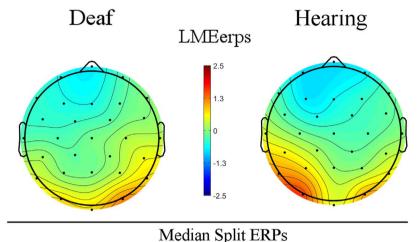
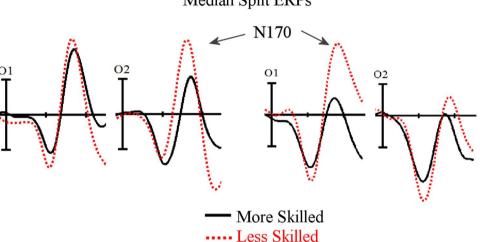


Fig. 6. (Top) The LMEerp phonological awareness effect in the N170 epoch for deaf and hearing readers. (Bottom) median split ERPs (based on phonological awareness scores) for deaf (left) and hearing (right) readers at occipital sites. Note in particular the different lateral distribution of the N170 effect for hearing and deaf readers which shows up as a positivity (better scores, more positive ERPs) in the LMEerps (top). (For color figures, the reader is referred to the web version of this article).



phonology plays in visual word recognition. For children, word reading is emerging as a left-lateralized process due at least in part to emerging phonological awareness and the ability to map speech sounds to orthographic representations. These data are broadly consistent with the hypothesis that phonological mapping skills are actively tuning the visual response to printed words in children, leading to a positive correlation between phonological awareness and N170 amplitude in the left hemisphere. For hearing adults, neural tuning to words is essentially complete such that readers with good phonological awareness have already established fine-tuned and stable orthographic word representations. However, hearing adults with weaker phonological awareness may exhibit larger N170 amplitude in the left hemisphere because more neural resources are required to recognize printed words due to weaker top-down modulation from phonology. The fact that the relationship between phonological awareness and N170 amplitude was minimal for deaf adults is consistent with this hypothesis since strong top-down modulation from phonology is not expected for deaf readers.

An additional factor that could contribute to a more symmetrical N170 response in the deaf participants is that they were all bilingual, and most acquired English as a second language. All (but one) of the deaf participants acquired ASL from birth or in early childhood, and none had attended an oral-only school. A bilateral N170 response has been reported for L2 readers of both alphabetic and non-alphabetic scripts (etal., 2004; Maurer et al., 2008; Proverbio et al., 2002). However, a left-lateralized N170 is generally observed in early bilinguals who learned both languages in childhood (e.g., Grossi et al., 2010; Maurer et al., 2008). The fact that ASL is not written means that for deaf

readers there is no competition between orthographies across their two languages and different grapheme-to-phoneme mappings that do not need to be distinguished. Thus, we suggest that it is unlikely that the symmetrical temporo-parietal N170 for deaf readers is due to bilingualism.

In addition, the effects of reading skill on the N170 were distinct for hearing and deaf readers, with better deaf readers, but poorer hearing readers, exhibiting larger right occipital N170 amplitudes. Since the groups were matched on reading ability, this finding suggests that the optimal neural dynamics of visual word processing differs for skilled deaf and hearing readers. Specifically, for hearing readers, increased engagement of the right hemisphere was associated with poorer reading ability, consistent with previous studies (e.g., Shaywitz and Shaywitz, 2005; Laszlo and Sacchi, 2015). Recruitment of the right hemisphere has been argued to be maladaptive for hearing readers, possibly because right occipitotemporal regions may process words more as visual objects, which may result in less differentiated orthographic representations (Laszlo and Sacchi, 2015). In contrast, for deaf readers, recruitment of the right hemisphere appears to be beneficial rather than maladaptive. Furthermore, for deaf readers, better spelling ability was also associated with larger N170 amplitudes over the right occipital site, whereas for hearing readers this effect was much smaller and bilaterally symmetrical. Thus for deaf readers, recruitment of right hemisphere regions is not indicative of poorly specified orthographic representations, possibly because orthographic representations are not fine-tuned by left-lateralized phonological mappings - in contrast to hearing readers.

The fact that deaf participants did not exhibit a significantly larger N170 to words than to symbol strings (in contrast to the hearing participants) suggests that temporo-parietal cortex in deaf readers does not strongly differentiate between words and symbols, indicating less specialization for print in these regions. Laszlo and Sacchi (2015) reported that less experienced hearing adult readers (i.e., those with less print exposure) differentiated words less strongly from objects and ambiguous word/objects (e.g., the word "smile" shaped like a smile), particularly over the right hemisphere. However, if anything, the deaf readers in our study had slightly more reading experience than the hearing readers (the deaf participants scored better on the Author Recognition Test than the hearing participants). Thus, reading experience does not appear to tune the N170 response to words in the same way as hearing readers. We suggest at least two possible explanations for why the N170 is less specialized for words in skilled deaf readers. One possibility is that the N170 tuning for print is specifically modulated by the mapping from orthography to phonology and is strongly influenced by the grapheme-to-phoneme conversion established when learning to read (e.g., Maurer and McCandliss, 2008). Under this hypothesis, coarse phonological representations of speech and weaker links between orthographic and phonological representations result in less word-specific neural tuning for deaf readers in the temporo-parietal N170 response.

Another possible explanation, which is not mutually exclusive, is that deaf readers' experience with fingerspelling alters the tuning of the N170 such that this ERP component comes to respond to orthographic stimuli that are more object-like (i.e., handshapes). ASL uses a onehanded fingerspelling system in which distinct handshapes represent letters of the English alphabet, and these handshapes are rapidly combined to spell-out words (e.g., proper names, technical jargon, concepts that do not have an established lexical sign). This system is not universal; for example, other signed languages, like British Sign Language (BSL), use a two-handed fingerspelling system. Previous fMRI studies with both ASL and BSL have shown that the VWFA responds more to fingerspelled words than to lexical signs (Emmorey et al., 2015; Waters et al., 2007), suggesting that this region plays a general role in mapping orthographically structured input onto lexical representations. Furthermore, several studies have documented a strong positive relationship between fingerspelling ability and reading skill in deaf readers (Emmorey and Petrich, 2012; Morere and Allen, 2012; Padden and Ramsey, 2000; Stone et al., 2015). Fingerspelling might serve an important function in orthographic segmentation whereby deaf children learn to identify fingerspelled handshapes and map them onto letters in English words (Chamberlain and Mayberry, 2000; Haptonstall-Nykaza and Schick, 2007; Hirsh-Pasek, 1987; Padden and Ramsey, 2000). This segmentation and mapping process has been hypothesized to aid deaf children in learning to analyze and segment printed words (Stone et al., 2015). It is currently unknown whether fingerspelled letters or words elicit an N170 response; but if so, then the N170 may be much more broadly tuned for deaf individuals who sign.

We also found differences between the two groups for the amplitude of the P1, although this effect did not interact with the stimulus type variable suggesting more macro level differences in visual stimulus processing. The occipitally distributed P1 was larger in hearing than deaf participants. Careful examination of Figs. 3 and 4 suggests that the difference at occipital sites is likely due to the deaf participant ERPs being more negative-going in the first 180 ms after stimulus onset and hearing participant ERPs being more positive-going in this same epoch. A number of previous studies have reported differences in amplitudes between either the P1 or the N1 in hearing compared to deaf adults while processing other types of non-linguistic visual stimuli (e.g., Bottari et al., 2011). These differences have usually been attributed to differences in early sensory experiences of the two groups, such that congenitally deaf individuals are hypothesized to exhibit enhanced perceptual and attentional processing (e.g., Bavelier and Neville, 2002). Prior studies showing deaf individuals exhibiting an enhanced N1 compared to hearing participants over posterior sites broadly fits the pattern we are seeing. However, those studies have shown group differences only for peripheral stimuli and/or stimuli that involve the processing of motion (e.g., Neville and Lawson, 1987). The one study that demonstrated P1 differences (Bottari et al., 2011) reported *larger* occipital P1s for deaf individuals detecting a non-linguistic stimulus (an opening circle), which is the reverse of the pattern seen in the current study.

Interestingly, there was evidence from the LME analysis suggesting that individual differences in reading ability might be contributing to some of the variance in the time range of the P1. The median split ERP and LMEerp plots in Fig. 4 appear to show that it is the more skilled deaf readers who contributed to the smaller P1s and larger N170s at occipital sites. Hearing readers on the other hand showed a small reversed (LMEerp) or equivalent (median split ERPs) pattern of reading skill P1 effects. Neither spelling skill nor phonological awareness showed any relationship with P1 amplitude which suggests that the differences in this early epoch are related to some other aspect of visual processing that may influence reading skill. Clearly, this result will need to be further explored in future studies, but it does suggest an interesting very early difference between hearing and deaf readers for processing linguistic stimuli.

Recently, Dufau et al., 2015 have shown similarly early effects on visual word processing due to the visual complexity of words in hearing readers. To explain such early effects, they argued for a model of word recognition where there is an initial fast feed-forward sweep of neural activity which cascades through the visual system and then higher language systems. This feed-forward sweep reflects a weak initial state of the networks at each level of processing prior to stabilization through feedback (Grainger and Holcomb, 2009). DuFau et al. (2015) also pointed out that reactive feedback needs to be complemented with proactive mechanisms that enable preparatory activity prior to stimulus presentation. Such an account has been used to explain differences in the time course of word processing in different tasks. For example, Strijkers et al. (2015) showed that variables like word frequency influence the time course of ERP effects starting at very different time points depending on the demands of the task. Such differential proactive mechanisms might also explain differences in early ERP responses in different groups of participants. For example, differences in attentional processes resulting from altered visual experiences in deaf individuals (e.g., Neville and Lawson, 1987) might underlie different patterns of early ERP responses to visual stimuli. Attentional differences could change the nature of early visual feed-forward networks involved in the initial stage of word processing. Or alternatively, how one achieves a high skill level in reading using different learning mechanisms might also differentially influence either the organization of early visual processes or the top-down mechanisms used to stabilize feedforward activity. For example, skilled deaf and hearing readers might use different proactive strategies during reading that in turn bias early cortical networks that process visual stimuli.

In conclusion, the pattern of results suggests that skill-related neural adaptations to processing written words differs for deaf and hearing adults who have similar reading ability, but who differ in phonological skill and knowledge. Specifically, neural adaptations that are maladaptive for hearing readers may actually be beneficial for deaf readers. A larger N170 in the over right occipital sites was associated with better reading ability in deaf (but not hearing) readers. A larger right occipital N170 was also linked to orthographic precision (as measured by spelling ability) for both deaf and hearing readers, although the relationship may be stronger in the deaf group (as suggested by the LME analysis). For hearing (but not deaf) readers, phonological ability was linked to the N170 response in the left hemisphere (although with the opposite correlation as hearing children). The lack of a strong N170 left-lateralization for deaf readers supports the hypothesis that for hearing readers, left-lateralization of the N170 is driven by the establishment of strong and stable sound-letter mappings. Finally, we suggest that the weaker N170 differentiation at temporo-parietal sites between

words and symbol strings observed for the deaf readers in our study may be due to a lack of top-down modulation from sound-based phonological representations for words and/or to a more broadly tuned N170 response to orthographic stimuli that might include more "object like" fingerspelled words.

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References

- Acheson, D.J., Wells, J.B., MacDonald, M.C., 2008. New and updated test of print exposure and reading abilities in college students. Behav. Res. Methods 40, 278–289 (PMCID: PMC3022331).
- Andrews, S., Hersch, J., 2010. Lexical precision in skilled readers: individual differences in masked neighbor priming. J. Exp. Child Psychol.: Gen. 139 (2), 299–318. http:// dx.doi.org/10.1037/a0018366.
- Aparicio, M., Gounot, D., Demont, E., Metz-Lutz, M.N., 2007. Phonological processing in relation to reading: an fMRI study in deaf readers. NeuroImage 35, 1303–1316.
- Baayen, R.H., Davidson, D.J., Bates, D.M., 2008. Mixed-effects modeling with crossed random effects for subjects and items. J. Mem. Lang. 59, 390–412.
- Baker, C.I., Liu, J., Wald, L.L., Kwong, K.K., Benner, T., Kanwisher, N., 2005. Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. Proc. Natl. Acad. Sci. USA 104, 9087–9092.
- Balota, D.A., Yap, M.J., Cortese, M.J., Hutchison, K.A., Kessler, B., Loftis, B., Neely, J.H., Nelson, D.L., Simpson, G.B., Treiman, R., 2007. The English Lexicon project. Behav. Res. Methods 39, 445–459.
- Barr, D.J., Levy, R., Scheepers, C., Tily, H.J., 2013. Random effects structure for confirmatory hypothesis testing: keep it maximal. J. Mem. Lang. 68, 255–278.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using (lme4). J. Stat. Softw. 67, 1–48.
- Bavelier, D., Neville, H.J., 2002. Cross-modal plasticity: where and how? Nat. Rev. Neurosci. 3 (6), 443–452.
- Bélanger, N.N., Mayberry, R.I., Rayner, K., 2013. Orthographic and phonological preview benefits: parafoveal processing in skilled and less-skilled deaf readers. Q. J. Exp. Psychol. 66 (11), 2237–2252. http://dx.doi.org/10.1080/17470218.2013.780085.
- Bentin, S., Mouchetant-Rostaing, Y., Giard, M.H., Echallier, J.F., Pernier, J., 1999. ERP manifestations of processing printed words at different psycholinguistic levels: time course and scalp distribution. J. Cogn. Neurosci. 11 (3), 235–260.
- Bottari, D., Caclin, A., Giard, M.H., Pavani, F., 2011. Changes in early cortical visual processing predict enhanced reactivity in deaf individuals. Plos one 6 (9), 25607.
- Brem, S., Lang-Dullenkopf, A., Maurer, U., Halder, P., Bucher, K., Brandeis, D., 2005. Neurophysiological signs of rapidly emerging visual expertise for symbol strings. Neuro Rep 16, 45–48.
- Chamberlain, C., Mayberry, R.I., 2000. Theorizing about the relationship between ASL and reading. In: Chamberlain, C., Morford, J., Mayberry, R. (Eds.), Language Acquisition by Eye. Lawrence Erlbaum and Associates, Mahwah, NJ, pp. 221–260.
- Charlier, B.L., Leybaert, J., 2000. The rhyming skills of deaf children educated with phonetically augmented speechreading. Q. J. Exp. Psychol.: Sect. A Hum. Exp. Psychol. 53, 349–375.
- Coch, D., Meade, G., 2016. N1 and P2 to words and wordlike stimuli in late elementary school children and adults. Psychophysiology 53, 115-128.
- Cohen, L., Dehaene, S., 2004. Specialization within the ventral stream: the case for the visual form area. NeuroImage 22, 466–479 (PMID:15110040).
- Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.A., Michel, F., 2000. The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain 123, 291–307.
- D'Hondt, M., Leybaert, J., 2003. Lateralization effects during semantic and rhyme judgement tasks in deaf and hearing subjects. Brain Lang. 87 (2), 227–240.
- Dehaene, S., Cohen, L., 2011. The unique role of the visual word form area in reading. Trends Cogn. Sci. 15, 254–262.
- Dufau, S., Grainger, J., Midgley, K.J., Holcomb, P.J., 2015. A thousand words are worth a picture: Snapshots of printed-word processing in an event-related potential megastudy. Psychological Sci. 26 (12), 1887–1897.
- Easterbrooks, S.R., Lederberg, A., Miller, E.M., Bergeson, J.P., Connor, C.M., 2008. Emergent literacy skills during early childhood in children with hearing loss: strengths and weaknesses. Volta Rev. 108, 91–114.
- Emmorey, K., Petrich, J.A.F., 2012. Processing orthographic structure: associations between print and fingerspelling. J. Deaf Stud. Deaf Educ. 17 (2). http://dx.doi.org/10.1093/deafed/enr051.
- Emmorey, K., Weisberg, J., McCullough, S., 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.
- Emmorey, K., McCullough, S., Weisberg, J., 2015. Neural correlates of fingerspelling, text, and sign processing in deaf ASL-English bilinguals. Lang. Cogn. Neurosci. 30 (6),

- 749-767
- Frost, R., 1998. Toward a strong phonological theory of visual word recognition: true issues and false trails. Psychol. Bull. 123 (1), 71.
- Grainger, J., Holcomb, P.J., 2009. Watching the word go by: on the time course of component processes in visual word recognition. Lang.linguist. compass 3 (1), 128-156
- Grossi, G., Savill, N., Thomas, E., Thierry, G., 2010. Posterior N1 asymmetry to English and Welsh words in early and late English–Welsh bilinguals. Biological Psychol. 85 (1), 124–133.
- Hirshorn, E.A., Dye, M.W.D., Hauser, P., Supalla, T.R., Bavelier, D., 2015. The contribution of phonological knowledge, memory, and language background to reading comprehension in deaf populations. Front. Psychol. 6 (1153). http://dx.doi.org/10.3389/fpsyg.2015.01153.
- Hirsh-Pasek, K., 1987. The metalinguistics of fingerspelling: an alternate way to increase reading vocabulary in congenitally deaf readers. Read. Res. Q. 22 (4), 455–474. http://dx.doi.org/10.2307/747702.
- Humphries, T., MacDougall, F., 1999. "Chaining" and other links: making connections between American Sign Language and English in two school settings. Vis. Anthropol. Rev. 15 (2), 84–94.
- Joyce, C., Rossion, B., 2005. The face-sensitive N170 and VPP components manifest the same brain processes: the effect of reference electrode site. Clin. Neurophysiol. 116, 2613–2631.
- Khateb, A., Pegna, A.J., Landis, T., Michel, C.M., Brunet, D., Seghier, M.L., et al., 2007. Rhyme processing in the brain: an ERP mapping study. Int. J. Psychophysiol. 63, 240–250.
- Kim, K.H., Yoon, H.W., Park, H.W., 2004. Spatiotemporal brain activation pattern during word/picture perception by native Koreans. Neuroreport 15 (7), 1099–1103.
- Luck, S.J., 2005. An Introduction to the Event-Related Potential Technique. MIT Press, Cambridge, MA.
- Macaruso, P., Shankweiler, D., 2010. Expanding the simple view of reading in accounting for reading skills in community college students. Read. Psychol. 31, 454–471.
- MacSweeney, M., Waters, D., Brammer, M.J., Woll, B., Goswami, U., 2008. Phonological processing in deaf signers and the impact of age of first language acquisition. NeuroImage 40, 1369–1379.
- MacSweeney, M., Goswami, U., Neville, H., 2013. The neurobiology of rhyme judgment by deaf and hearing adults: an ERP study. J. Cogn. Neurosci. 25 (7), 1037–1048.
- Markwardt, F.D., 1998. Peabody Individual Achievement Test-Revised (PIAT-R).

 American Guidance Service, Circle Pines, MN.
- Maurer, U., McClandiss, B.D., 2008. The development of visual expertise for words: the contribution of electrophysiology. In: Grigorenko, E.L., Naples, A.J. (Eds.), Single-Word Reading: Behavioral and Biological Perspectives. Lawrence Erlbaum Associates, New York, NY, pp. 43–63.
- Maurer, U., Brandeis, D., McCandliss, B.D., 2005a. Fast, visual specialization for reading in English revealed by the topography of the N170 ERP response. Behav. Brain Funct. 1, 13.
- Maurer, U., Brem, S., Bucher, K., Brandeis, D., 2005b. Emerging neurophysiological specialization for letter strings. J. Cogn. Neurosci. 17, 1532–1552.
- Maurer, U., Brem, S., Kranz, F., Bucher, K., Benz, R., Halder, P., Steinhausen, H., Brandeis, D., 2006. Coarse neural tuning for print peaks when children learn to read. NeuroImage 33, 749–758.
- Maurer, U., Brem, S., Bucher, K., Kranz, F., Benz, R., Steinhausen, H., Brandeis, D., 2007. Impaired tuning of a fast temporo-occipital response for print in dyslexic children learning to read. Brain 130, 3200–3210.
- Mayberry, R.I., del Giudice, A.A., Lieberman, A.M., 2010. Reading achievement in relation to phonological coding and awareness in deaf readers: a meta-analysis. J. Deaf Stud. Deaf Educ. 16, 164–188 (PMCID: PMC3739043).
- Mayer, C., Trezek, B.J., 2014. Is reading different for deaf individuals? Reexamining the role for phonology. Am. Ann. Deaf 159, 359–371.
- McCandliss, B.D., Noble, K.G., 2003. The development of reading impairment: a cognitive neuroscience model. Ment. Retard. Dev. Disabil.: Res. Rev. 9, 196–205.
- McQuarrie, L., Parilla, R., 2009. Phonological representations in deaf children: rethinking the "functional equivalence" hypothesis. J. Deaf Stud. Deaf Educ. 14, 137–154 (PMID: 18635579).
- Miller, P., Clark, M.D., 2011. Phonological awareness is not necessary to become a skilled deaf reader (review). J. Dev. Phys. Disabil. 23, 459–476.
- Morere, D.A., Allen, T.E., 2012. Fingerspelling. In: Morere, D.A., Allen, T.E. (Eds.), Assessing Literacy in Deaf Individuals: Neurocognitive Measurement and Predictors. Springer, New York, NY, pp. 179–189.
- Neville, H., Kutas, M., Schmidt, A., 1982. Event-related potential studies of cerebral specialization during reading: II. Studies of congenitally deaf adults. Brain Lang. 16, 316–337.
- Neville, H.J., Lawson, D., 1987. Attention to central and peripheral visual space in a movement detection task: an event-related potential and behavioral study. II. Congenitally deaf adults. Brain Res. 405, 268–283.
- Padden, C., Ramsey, C., 2000. American Sign Language and reading ability in deaf children. In: Chamberlain, C., Morford, J., Mayberry, R. (Eds.), Language Acquisition by Eye. Lawrence Erlbaum Associates, Mahwah, NJ, pp. 165–189.
- Paul, P.V., Wang, Y., Trezek, B.J., Luckner, J.L., 2009. Phonology is necessary, but not sufficient: a rejoinder. Am. Ann. Deaf 154, 346–356.
- Payne, B.R., Lee, C., Federmeier, K., 2015. Revisiting the incremental effects of context on word processing: evidence from single-word event-related brain potentials. Psychophysiology 52, 1456–1469.
- Perfetti, C.A., Sandak, R., 2000. Reading optimally builds on spoken language: implications for deaf readers. J. Deaf Stud. Deaf Educ. 5 (1), 32–50.
- Proverbio, A.M., Čok, B., Zani, A., 2002. Electrophysiological measures of language processing in bilinguals. J Cog Neuro 14 (7), 994–1017.

- Rayner, K., Foorman, B.R., Perfetti, C.A., Pesetsky, D., Seidenberg, M.S., 2001. How psychological science informs the teaching of reading. Psychol. Sci. Public Interest 2 (2) 31–74
- Rossion, B., Joyce, C.A., Cottrell, G.W., Tarr, M.J., 2003. Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. NeuroImage 20, 1609–1624.
- Sacchi, E., Laszlo, S., 2016. An event-related potential study of the relationship between N170 lateralization and phonological awareness in developing readers. Neuropsychologia 91, 415–425.
- Shaywitz, S.E., Shaywitz, B.A., 2005. Dyslexia (specific reading disability). Biol. Psychiatry 57 (11), 1301–1309.
- Stone, A., Kartheiser, G., Hauser, P.C., Petitto, L.-A., Allen, T.E., 2015. Fingerspelling as a novel gateway into reading fluency in deaf bilinguals. PLoS One 10 (10). http://dx.doi.org/10.1371/journal.pone.0139610.
- Strijkers, K., Bertrand, D., Grainger, J., 2015. Seeing the same words differently: the time

- course of automaticity and top-down intention in reading. J. Cogn. Neurosci. 27, 1542-1551.
- Tarkiainen, A., Helenius, P., Hansen, P.C., Cornelissen, P.L., Salmelin, R., 1999. Dynamics of letter string perception in the human occipitotemporal cortex. Brain 122, 2119–2132.
- Wagner, R.K., Torgesen, J.K., 1987. The nature of phonological processing and its causal role in acquisition of reading skills. Psychol. Bull. 101, 192–212.
- Wang, X., Caramazza, A., Peelen, M.V., Han, Z., Bi, Y., 2014. Reading without speech sounds: VWFA and its connectivity in the congenitally deaf. Cereb. Cortex. http://dx. doi.org/10.1093/cercor/bhu044. (first published online March 18, 2014).
- Waters, D., Campbell, R., Capek, C.M., Woll, B., David, A.S., McGuire, P.K., et al., 2007. Fingerspelling, signed language, text and picture processing in deaf native signers: the role of the mid-fusiform gyrus. NeuroImage 35 (3), 1287–1302. http://dx.doi. org/10.1016/j.neuroimage.2007.01.025.