Automaticity in the reading circuitry

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Abstract

Skilled reading requires years of practice to learn to associate visual symbols (graphemes) with speech sounds (phonemes). Over the course of the learning process, this association becomes almost effortless and automatic. Here we hypothesize that automatic activation of phonological processing circuits in response to a visually presented word is a hallmark of skilled reading. We used magnetoencephalography (MEG) to measure cortical evoked responses to printed words while children engaged in an attention-demanding fixation task in which their attention was directed away from the words. We found strong activation in brain regions involved in speech sound processing, namely the superior temporal gyrus (STG). This automatic response to visually presented words in a canonical language region was indicative of good reading skills: the visual stimulus-driven STG response was only present in skilled readers but not in children with dyslexia. Our results suggest that automatic recruitment of phonological processing circuits is a hallmark of skilled reading; with practice, reading becomes effortless as the brain learns to automatically translate letters into sounds and meaning.

Highlights

- The superior temporal gyrus shows automatic responses to unattended printed words.
- In the inferior frontal gyrus, the response to printed words depends on the task.
- Only skilled readers showed cortical activity reflecting visually-driven, automatic responses in classical language regions.
- The strength of automaticity in the superior temporal gyrus correlated with individual reading skills.

Mastering spoken language is natural but learning written language is not (Saffran et al., 2001; Wandell et al., 2012). Infants learn to understand spoken language through statistical regularities in natural speech starting from the earliest stages of development (Saffran et al., 1996). Indeed, encoding phonetic information during speech perception (Mesgarani et al., 2014; Yi et al., 2019) seems to be an automatic process in infants, and specialized circuits for processing spoken language located in the superior temporal gyrus (STG) are activated by speech sounds irrespective of attention, and even during sleep in infants as young as three months (Dehaene-Lambertz et al., 2002). However, learning to read is an effortful process, which requires formal instruction on how to map arbitrary visual symbols (i.e., letters or graphemes) onto speech sounds (i.e., phonemes). Only after years of practice does this association become automatic and effortless allowing for fluid and deep reading (Norton and Wolf, 2012; Wolf, 2020).

Behaviorally, the difference between a child who struggles to apply knowledge of grapheme-phoneme correspondence to decode text and a child who fluidly reads a paragraph of text is striking. But neurally, what it means to automate the grapheme to phoneme conversion process is less clear. Cognitive models of reading have proposed that, for the literate brain, viewing printed words produces widespread and automatic activation of phonological and semantic representations (Harm and Seidenberg, 1999, 2004; Van Orden and Goldinger, 1994; Seidenberg and McClelland, 1989). These models posit that literacy involves automatizing the connections between orthographic (visual), phonological and semantic codes in the brain. Consistent with the prediction of these models, adult skilled readers show activation in canonical language processing areas such as the left inferior frontal gyrus (i.e., Broca's area) and supeior temporal cortex (i.e., Wernicke's area) in response to visually-presented words regardless of whether or not the task requires them to actively read the words (Kiefer and Martens, 2010; Klein et al., 2015; Mechelli et al., 2005; Van Orden, 1987; Pattamadilok et al., 2017; Paulesu et al., 2001; Price, 2012; Turkeltaub et al., 2003; Wilson et al., 2004). Furthermore, there is ample behavioral evidence suggesting automatic involvement of phonological processing in response to printed words (Dennis and Newstead, 1981; Frost, 1998; Perfetti and Bell, 1991; Perfetti et al., 1988; Stroop, 1935). Indeed, in a series of studies examining the construction of "audiovisual objects" from text, Blomert and colleagues have suggested that automatization of letter-sound knowledge is a hallmark of skilled reading and the lack of automatization is a critical component of the struggles observed in children with developmental dyslexia (Blau et al., 2009, 2010; Blomert, 2011; van Atteveldt et al., 2004).

An intriguing conjecture is that neurons throughout the reading circuitry become automatically responsive to text, regardless of whether a subject intends to read the text, as a result of long-term simultaneous neural activity occurring in visual and language regions over the course of schooling. Akin to Hebbian learning (Hebb, 1949), becoming a skilled reading might involve automatizing the information transfer between visual and language circuits such that canonical speech processing regions in the STG start

responding to written language even in the absence of attention. To test this hypothesis, it is essential to disentangle bottom-up, visually-driven responses from top-down, task-related responses, and to assess whether and how components of the reading circuitry are activated in an automatic manner by bottom-up signals from visual cortex. Here, we used magnetoencephalography (MEG) and source localization to define brain regions that were activated during a lexical decision task (active reading) and, within those regions, we characterized the time course of neural responses to text during a reading-irrelevant task in which words were placed outside the focus of attention. Using this paradigm, we first tested whether canonical speech processing regions shows automatic responses to printed words. We then assessed whether the strength of automaticity in those regions depends on an individual's reading skill.

Results

We measured cortical responses to printed words in children (n = 42, age = 7.16 to 12.7 years, mean±sd = 9.6±1.5) with a range of reading skills (including struggling readers with dyslexia) while they were conducting (1) a lexical decision task and (2) an attention-demanding color-judgement task on the fixation dot (fixation task) in separate runs of an MEG experiment. Figure 1 shows the procedure of the experiment. During runs of the lexical decision task, children were instructed to press a button as quickly as possible when they detected a made-up word (pseudoword). In the fixation task, children were instructed to focus on the fixation dot and press a button as quickly as possible when the fixation dot color changed to red. Importantly, across these two independent task runs, the stimuli remained identical and the only difference was the task. This allowed us to separately measure cortical responses that were automatically evoked by the stimuli (fixation task) as well as cortical responses that were associated with the cognitive task. The word stimuli were embedded in phase-scrambled noise with two different noise levels: 20% phase scramble in which the words were clearly visible and 80% phase scramble where the words were not visible but the contrast and spatial frequency of the image was maintained (Figure 1).

To assess automaticity in the reading circuitry, we first localized regions of interest (ROIs) that were engaged during the lexical decision task, and then assessed the timing and magnitude of visually evoked responses to text during the fixation task. This allowed us to dissociate visual, bottom-up responses to printed words from active reading related responses. To correct for multiple comparisons in both space (20,484 vertices) and time (301 time points), we employed the conservative spatiotemporal clustering algorithm (Maris and Oostenveld, 2007): ROIs were defined as significant vertices resulting from a permutation t-test (2-tailed) between the word and noise conditions in the lexical decision task (word > noise, Figure 2).

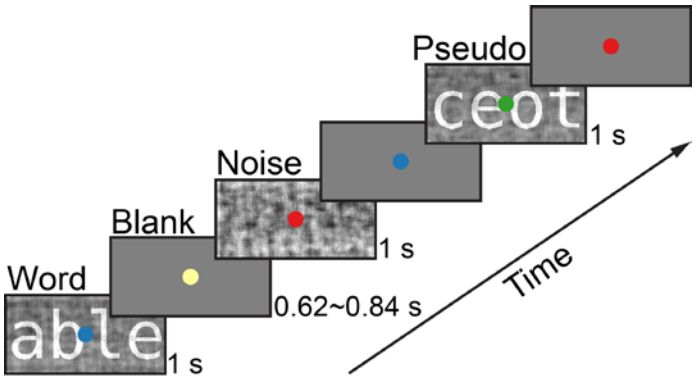

Figure 1. The experimental procedure. *On a given trial, a word, a noise patch, or a pseudoword was displayed for 1 s, followed by a gray blank screen. The next trial started after an inter-trial interval chosen randomly from a uniform distribution ranging from 0.62 to 0.84 seconds. Children conducted (1) a lexical decision task and (2) an attention-demanding fixation task in separate runs. The stimuli remained identical across both runs. During the lexical decision task, children were instructed to press a button when a pseudoword was presented. During the fixation task, they were instructed to press a button when the color of the fixation dot changed to red. Our analysis focused on a comparison of the response to words versus noise patches since there were stimulus locked button-presses in response to the pseudowords that might interfere with MEG source localization.*

Lexical decision making activates language processing network

Figure 2 shows the spatiotemporal extent of significant neural activity to words compared to noise patches in the left hemisphere during the lexical decision task. Each inset shows the time course of individual ROIs computed using dynamic statistical parametric mapping (dSPM) (Dale et al., 2000), averaged across all subjects for word (red) and noise (black) conditions. Consistent with previous literature, we found that canonical language processing regions are engaged while subjects performed a lexical decision task on visually presented words (Helenius et al., 1998). We defined four main ROIs based on this cortical activation map (word > noise): inferior frontal gyrus (IFG), temporoparietal junction (TPJ), and superior temporal gyrus (STG) and sensorimotor cortex. The posterior regions (STG and TPJ) are the conventional loci associated with phonological processing and are activated across auditory speech perception and reading tasks (Pugh et al., 2001, 2010). The IFG (Broca's area) is associated with different components of linguistic functions such as semantic, lexical, and phonological processing in both spoken and written languages (Sahin et al., 2009).

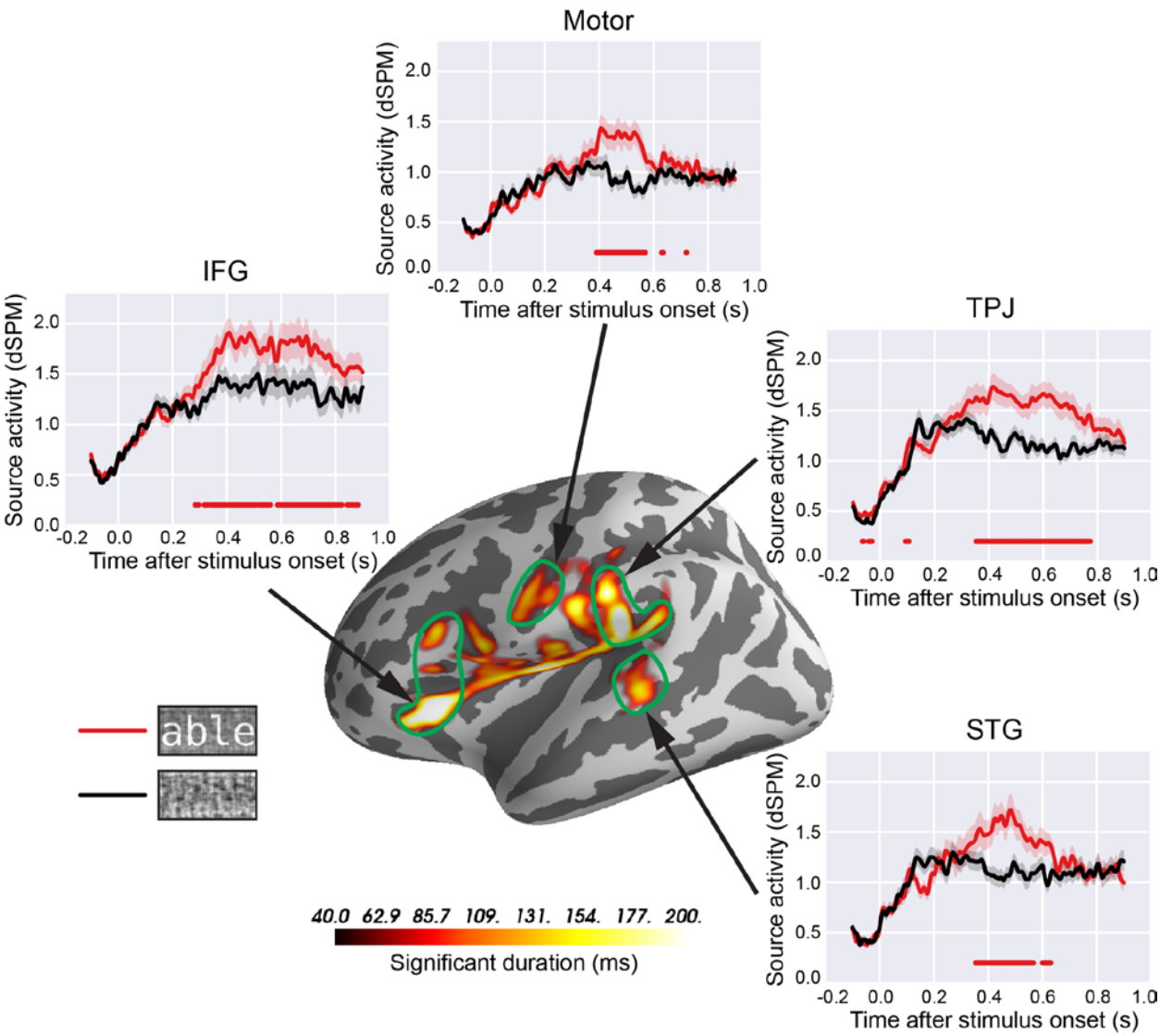

Figure 2. Canonical language regions respond to printed words during the lexical decision task. *cortical activation map in the left hemisphere during the lexical decision task projected into the freesurfer averaged cortical surface template (fsaverage), and thresholded based on spatial temporal clustering to correct for multiple comparisons. The color bar represents the duration of time that each vertex shows a significantly greater response to words compared to noise patches after correcting for multiple comparisons. The red and black lines show the source activity for words and noise, respectively. The red dots at the bottom of the plot indicate timepoints where the response is significantly different between the two conditions (determined by bootstrapping analysis p< 0.05).*

The difference in responses to words (red) and noise (black) began to diverge around 350 ms after stimulus onset in posterior ROIs (Figure 2 insets; STG: 353 ms, TPJ: 356 ms, motor: 390 ms, bootstrapping analysis $p < 0.05$). In contrast, there was earlier neural activity in IFG starting at ~280 ms, consistent with previous evidence for early MEG source synchronization and electrocorticography recordings during lexical processing (Cornelissen et al., 2009; Klein et al., 2015; Sahin et al., 2009; Wheat et al., 2010).

To examine the relationship between reading skill and neural activity in ROIs during the lexical decision task, we divided our subjects into two groups based on TOWRE Index standard scores (typical readers > 80, n = 17; struggling readers <= 80, n = 25). Figure 3 shows each group's time course of MEG source estimates. To characterize neural activity associated with the lexical decision task, we calculated the average differences in MEG source estimates between the word and noise condition during the 100 ms temporal window (Figure 3A and 3B; shaded areas), timepoints showing significantly greater responses to words at the group level across ROIs.

In the IFG, struggling readers showed a slower, the enhanced response to words at 400 ms that was sustained until 800ms post-stimulus onset (Figure 3A). In comparison, typical readers showed a markedly faster and shorter enhanced response to words beginning at 277 ms and lasting up to 500 ms after stimulus onset. IFG mean response magnitude in the 400-500ms post-stimulus interval of interest did not correlate with reading skill ($r = 0.23$, $p = 0.15$) suggesting that task-related activity in the IFG does not differ substantially between good versus poor readers.

In the STG (Figure 3B) and TPJ, there were robust and highly significant responses to words compared to noise in typical readers, while struggling readers showed much weaker responses. Within these regions, individuals' difference score in MEG response magnitudes (word - noise) strongly correlated with reading skill (STG: $r = 0.54$, $p = 0.0002$; TPJ: $r = 0.46$, $p = 0.002$). These results suggest different roles for each of these regions in the lexical decision task: the IFG was engaged in the lexical decision task irrespective of reading skill, while neural activity in the STG and TPJ depended on reading skill. Next, we capitalize on the independent data set obtained during the fixation task to (a) examine which of these responses to text are task-dependent and (b) whether the correlation with reading skill depends on the task performed by the subject or reflects the strength of the bottom-up response to text.

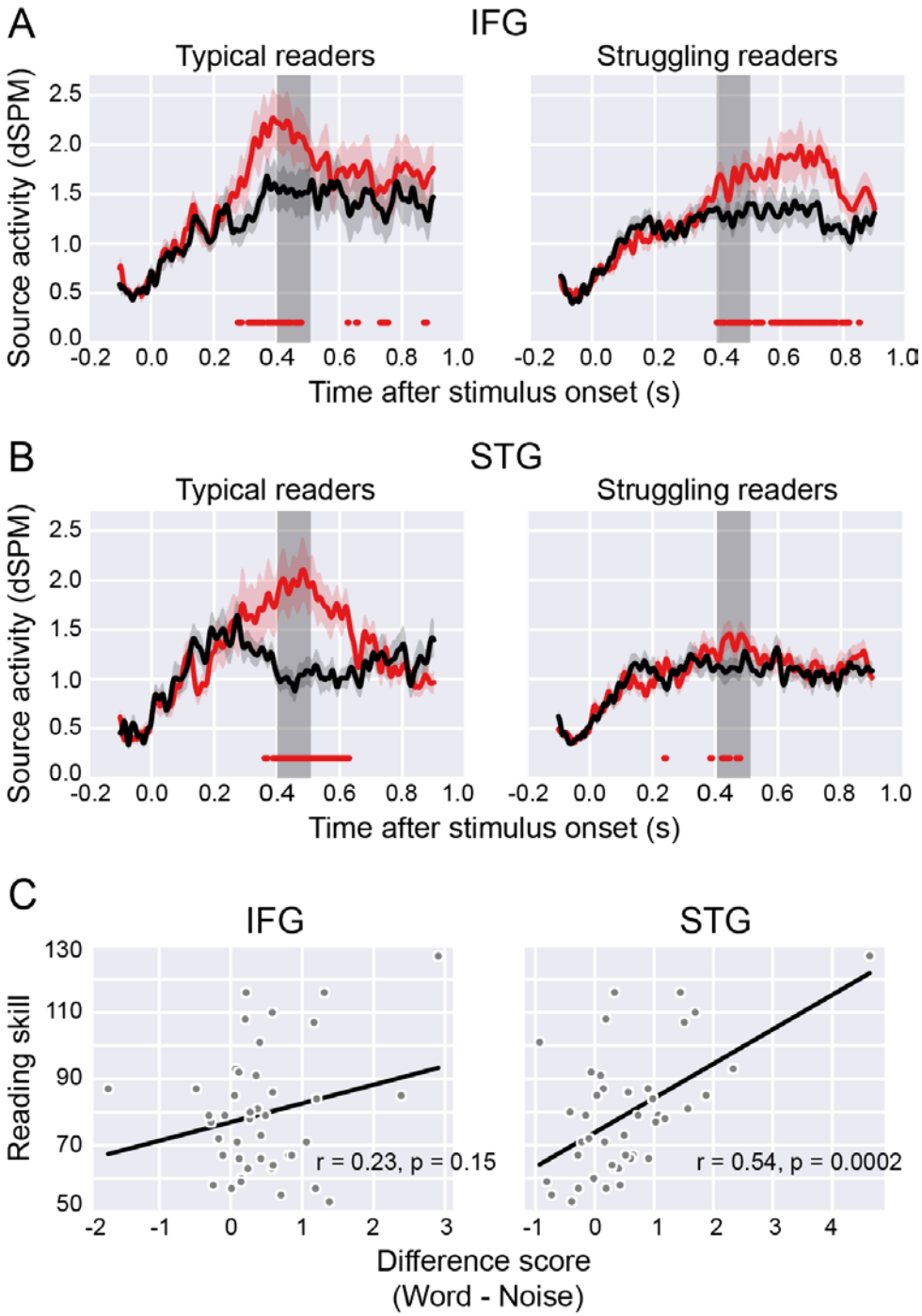

Figure 3. Cortical activity during the lexical decision task correlates with reading skill. *Responses within each functionally-defined region of interest are shown separately for Typical versus Struggling readers in the (A) Inferior Frontal Gyrus (IFG) and (B) Superior Temporal Gyrus (STG). In the IFG, there is larger response to words than noise for both Typical and Struggling readers. In the STG there is a robust difference in the response to words versus noise only for Typical readers. In struggling readers, STG activity does not differ for the two stimulus types. The red and black lines show the source activity for words and noise, respectively. The shaded areas represent s.e.m. across participants. Red dots represent timepoints showing significantly larger responses to words compared to noise (determined by bootstrapping analysis* $p < 0.05$*). The gray shaded rectangles are the time windows used to calculate the averaged response. (C)*

Only the STG response correlates with reading skill. The Y-axis is the standardized reading score (mean = 100, sd = 15) and the x-axis is the difference score of source activity for the two conditions (word-noise). The black line is the best-fitting repression line.

Automatic responses to text in speech processing regions

Next, we tested the hypothesis that, for skilled readers, there is an automatic, bottom-up response to visually presented words in language regions, even in the absence of attention or conscious reading. We reasoned that if neural activity in the regions identified in the lexical decision task is equivalent during the fixation task, then it is evidence for an automatic, stimulus-driven, task-independent response. Based on results from the lexical decision task, we predicted that IFG would show task-dependent responses to printed words whereas STG and TPJ would show task-independent responses to printed words indicative of the automatic association between graphemes and phonemes.

We found that the STG showed highly significant responses to words during the fixation task and the strength of the response depended on reading skill whereas other areas showed no responses to word stimuli (Figure 4A). Only in typical readers, MEG responses to words (red) were greater compared to noise (black), and the difference between the two diverged earlier (at ~300 ms) compared to the lexical decision task (Figure 4B). Importantly, like active reading-related MEG responses in the lexical decision task, the averaged MEG response magnitudes in the [300, 400] ms post-stimulus interval strongly correlated with reading skills (Figure 4C; $r = 0.50$, $p = 0.0008$). In fact, individual MEG responses in the lexical decision and fixation tasks were highly correlated (Figure 4D; $r = 0.69$, $p = 0.4\times10^{-6}$), suggesting that STG responded similarly to words regardless of whether subjects were actively reading them and performing a lexical decision task, or ignoring them and engaging in an attention-demanding task on the fixation dot (Figure 4D). Thus, even though the STG response might be modulated by task demands in some cases, a subject showing a weak response to words on the fixation task still shows a weak response when prompted to actively attend to and analyze the text. This finding underscores the importance of automaticity for skilled reading; akin to the visual system where attention and task demands modulate the automatic bottom-up response of neurons that code specific features of the visual stimulus, task demands might serve to modulate the automatic bottom-up response in the STG but only to the extent that the STG is responsive to text.

Although the TPJ showed greater responses to words than noise during the lexical decision task, we did not find a similar pattern during the fixation task. Typical readers showed some separation in responses to words compared to noise, but the difference was much smaller than in the STG. There was a trend, but no significant correlation between MEG response magnitudes and reading skill ($r = 0.29$, $p = 0.07$). Furthermore, in the IFG, there was an equivalent response to words and noise stimuli during the fixation task, and this response did not differ by group or relate to reading skill. Together, these

results suggest that the left STG is automatically engaged in response to visually presented words, and that the strength of neural activity is associated with reading skills in children. The IFG, on the other hand, is important for carrying out the lexical decision task, but is not critically involved in automatic grapheme-phoneme conversion processing.

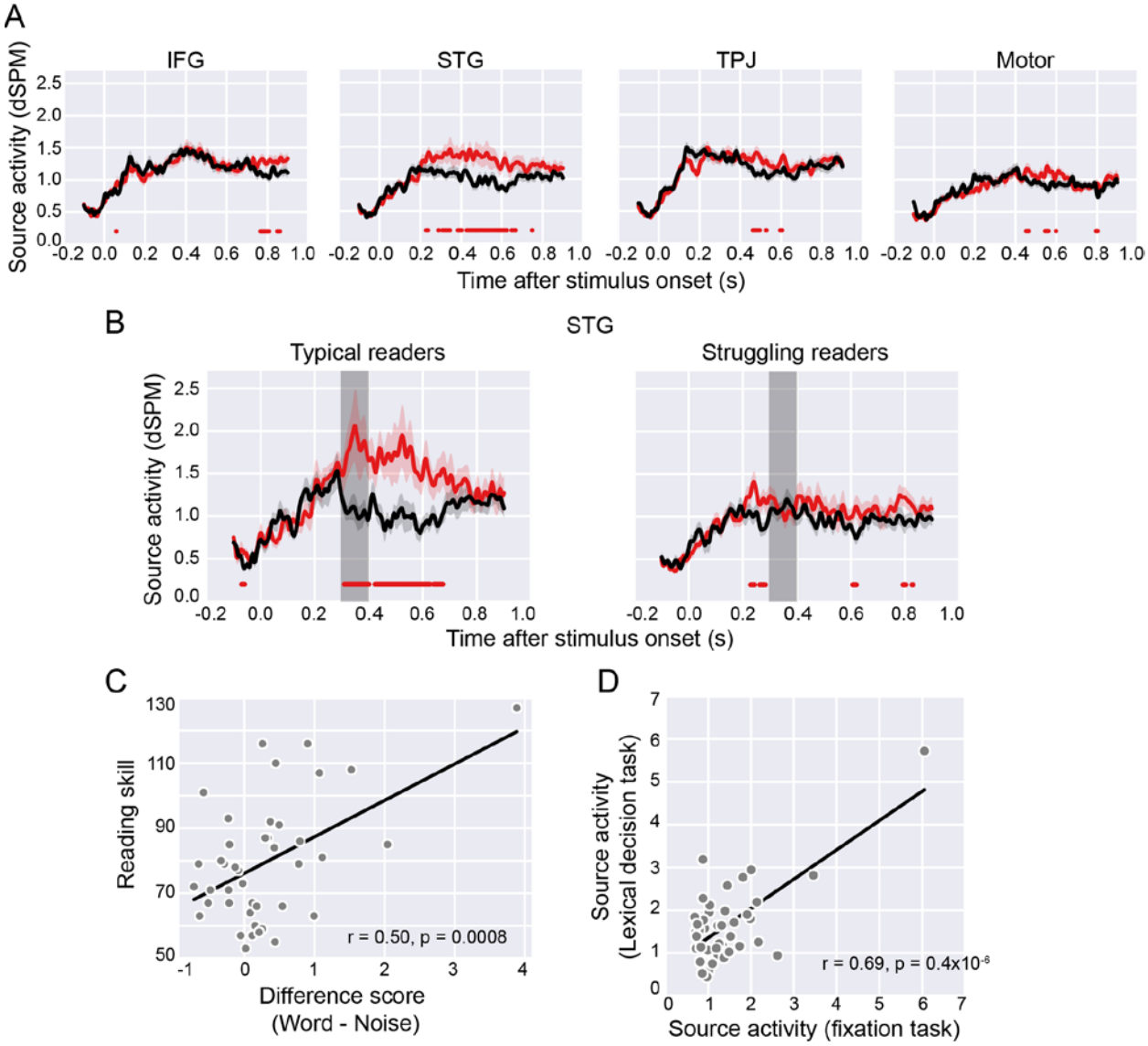

Figure 4. Automaticity in the superior temporal gyrus is related to reading skill. *(A) The response to words (red) and noise patches (black) for the full sample (N=42) during the fixation task is shown within the four regions that were localized independently with data from the lexical decision task (see Figure 2). At the level of the full sample, only the superior temporal gyrus (STG, second plot) shows a greater response to words versus noise when attention is diverted from the stimuli. (B) This "automatic" response in the STG is driven by the children with relatively strong reading skills and is not present in the struggling readers. Gray shaded rectangles are the time window used to calculate the averaged source activity. (C) The response of the STG during the fixation task correlates with reading skill. The Y-axis is the standardized reading score (mean = 100, sd = 15) and the x-axis is the difference score of source activity for the two conditions (word-noise). The black line is the best-fitting repression line. (D) Individual STG responses on the fixation*

task (x-axis) are highly correlated with responses on the lexical decision task (y-axis). The black line is the best-fitting repression line.

Reading disability versus reading level

So far we have shown that, in strong readers, there are robust and automatic responses to text in canonical speech processing regions (i.e., STG). Struggling readers show little or no activation in STG on the fixation or lexical decision tasks. Since our sample included children of different ages (between first and fourth grade) and, across those ages, we include both typical and struggling readers, we next seek to determine the relative contributions of age versus reading ability to the STG response. In other words, is the lack of STG response indicative of a deficit in the circuit in children with reading difficulty? Or, does automaticity steadily increase over each year as children's reading skills improve? To answer these questions we first examined the correlation between age and the STG response. We found that the STG response to words did not increase with age (fixation task: $r = 0.06$, $p = 69$; lexical task: $r = 0.19$, $p = 0.24$). Next we used a multivariate regression model to test the additive contributions of age and reading ability (indexed by age-normed scores on the TOWRE) to the STG response. We found a highly significant relationship between reading ability and STG response, irrespective of age and, once again, found no contribution of age in the model (Table 1). Thus, automaticity in the STG response to text is likely to develop early in literacy learning for typically reading children, establishing a foundation for children to hone their reading accuracy, rate and fluency. For struggling readers, the lack of response in the STG is likely to represent a barrier that continues to affect their ability to learn reading skills. In line with this perspective, every measure of reading skills including real and pseudoword reading accuracy and speed and fluency all correlated with the STG after controlling for the age of the subjects (Table 1).

	Coef	Std. error	p-value
Model 1			
Age	0.077	0.07	0.293
TOWRE	0.020	0.01	0.002
Model 2			
Age	0.076	0.07	0.311
BRS	0.019	0.01	0.006

Model 3			
Age	0.062	0.08	0.412
RF	0.014	0.01	0.015

Table 1. Superior temporal gyrus response is related to reading skills but not age. *Coefficients from regression models examining the relationship between scores on the Test of Word Reading Efficiency (TOWRE, Model 1), Woodcock Johnson Basic Reading Skills Composite (BRS, Model 2), Woodcock Johnson Reading Fluency (RF, Model 3) and the STG response (words - noise), controlling for age.*

Discussion

We have demonstrated that a part of canonical circuitry for processing spoken language, the left superior temporal gyrus (STG), is automatically engaged when skilled readers view text. It has long been hypothesized that automating the association between printed symbols and spoken language is at the foundation of skilled reading (Blau et al., 2009, 2010; Blomert, 2011; Harm and Seidenberg, 1999; Seidenberg and McClelland, 1989; van Atteveldt et al., 2004) and our results formalize this concept of automaticity and its relationship to reading skill: In skilled readers, text evokes a response in the STG even in the absence of attention, and even when subjects are performing a distracting task and actively trying to ignore the text. Furthermore, the magnitude of the STG response is strongly correlated with reading skill and largely consistent across both the fixation and the lexical decision task. In contrast, neural activity in the IFG depends on the task. The IFG is active during the lexical decision task but not during the fixation task. This dissociation indicates that the STG response on the fixation task is a bottom-up, stimulus-driven response while the IFG response is associated with the specific task the subject performs.

Our results provide clear evidence of automaticity in language processing regions in response to printed words by dissociating bottom-up responses from task-driven, top-down responses. These results are right in line with the prediction made by classic cognitive models of the reading architecture (Harm and Seidenberg, 1999; Pugh et al., 2010; Seidenberg and McClelland, 1989). In previous experiments attempting to measure the automatic response to printed words, attention was still directed to visual stimuli while subjects were engaged in a task other than reading (i.e., visual feature detection on word stimuli), making word stimuli task-irrelevant but still inside the focus of attention (Brunswick et al., 1999; Paulesu et al., 2001; Price et al., 1996; Turkeltaub et al., 2003). Thus, it is difficult to disambiguate the extent to which attention to the words provoked unwanted reading. In fact, in these previous experiments printed words activated brain regions (e.g., the IFG) that our data indicate are only active during reading tasks (e.g., lexical decision). By diverting attention from printed words, we show a dissociation between the IFG and STG response: while both areas are robustly activated during the

lexical task, automatic responses to printed words (fixation task) are only found in the STG.

Our findings stand in contrast to previous work in which words that were rendered invisible due to rapid visual backward masking. In the case of masking, words do not elicit measurable functional magnetic resonance imaging (fMRI) responses in language regions despite clear behavioral priming effects (Dehaene et al., 2001). The discrepancy between our results and previously reported priming effects might be due to the difference between fMRI and MEG measurements. MEG might be a more sensitive to measure small and brief neural activity compared to fMRI because of the sluglish nature of fMRI responses. Indeed, neural activity related to behavioral priming effects was found using EEG measurements (Luck et al., 1996), which have similar temporal resolution as MEG.

Another possibility is that the connectivity between visual and language circuits depends on the visibility of words. In the work by Dehaene and colleagues (Dehaene et al., 2001), a briefly presented word (30 ms) was rendered invisible due to visual backward masking. In contrast, words (83 ms) in the Luck et al.'s experiment were not invisible although the word detectability was reduced in the attentional blink paradigm (Luck et al., 1996). In our experiment, words were displayed for 1 s and had a high contrast, making them visible although attention was removed from them. It is an interesting future direction to study how the visibility of words affects automaticity in the language processing areas by manipulating noise levels (Ben-Shachar et al., 2011) and timing of the stimuli as well as task-demands (Kay and Yeatman, 2017).

In canonical perisylvian language processing regions, only the STG but not the TPJ (which is near proximity of supramarginal gyrus), showed automaticity. Many authors consider these two regions to have a similar function for reading and traditional "Wernicke's area" is often presumed to include both regions. While both regions are associated with phonological processing during auditory word processing (Binder et al., 1994a; DeWitt and Rauschecker, 2012, 2013), the supramarginal gyrus might be involved in further cognitive processing beyond phonological decoding such as storing information for conducting tasks (Caramazza et al., 1981; Paulesu et al., 1993; Warrington et al., 1971) whereas neural activity in the STG is often found to occur independently of the cognitive task (Binder et al., 1994a, 1994b, 1997; Millen et al., 1995; Wise et al., 1991).

Our findings suggest that there might be automatic mapping of speech sounds from visually presented words. Based on our results, we can formulate a hypothesis that there might be similar neural activity in response to printed words as to auditory word stimuli in the STG. Future work should test whether automatic responses to printed words in the STG share similar neural codes to the responses to auditory words.

Overall, our study demonstrated automatic responses to printed words in the STG, a part of canonical language processing areas. Skilled reading seems to require coactivation in the reading network for spoken and written language (McCandliss et al., 2003; Price, 2012; Pugh et al., 2010). Interestingly, the level of coactivation in the left

hemisphere reading network in early readers could be a predictor of reading outcomes after two years (Preston et al., 2016), suggesting that becoming a skilled reader relies on shared neural responses to both print and speech. Our results, showing the magnitude of automaticity depends on reading skills, suggests that automaticity in the STG may be a hallmark of skilled reading; with practice, reading becomes effortless as the brain learns to automatically translate letters into sounds and meaning.

Method

Participants

A total of 45 native English-speaking children ages 7-12 participated. We discarded data from 3 participants because their MEG signals were noisy and we included data from the remaining 42 participants for our analysis (see below). Children without histories of neurological or sensory disorders were recruited from a database of volunteers in the Seattle area (University of Washington Reading & Dyslexia Research Database; http://ReadingAndDyslexia.com). Parents and/or legal guardians of all participants provided written informed consent under a protocol approved by the University of Washington Institutional Review Board. All participants reported normal or corrected-to-normal vision.

Reading ability assessment

Participants participated in a behavioral session in which they completed a series of behavioral tests. Reading scores were measured using the Test of Word Reading Efficiency (TOWRE-2), which measures the number of sight words (sight word efficiency, SWE) and pseudowords (phonemic decoding efficiency, PDE) read in 45 s. They also were assessed using subtests from the Woodcock-Johnson IV (WJ), which measures untimed sight word and pseudoword reading. Each test produces age-normed, standardized scores with a population mean of 100 and standard deviation of 15. TOWRE and WJ measures of reading are highly correlated, but also index slightly different aspects of skilled reading. The TOWRE measures the speed and automaticity or word recognition, while the WJ measures the ability to apply orthographic knowledge to decoding difficult words and pseudowords. Thus, for the purpose of our study, we used TOWRE scores. We divided our participants into two groups: typical readers and struggling readers based on TOWRE score of 80. This is a typical cut-point that is used to define children with dyslexia as it represents roughly the bottom 10% of the continuum. Applying the same analysis using WJ scores did not change the pattern of the results.

Stimuli and experimental procedure

All the procedure was controlled by in-house python software (expyfun: https://github.com/LABSN/expyfun). The stimuli (real and pseudo words) were generated by manipulating the phase coherence of black word stimuli with contrast of 25.4% on a gray background. Specifically, a Fourier transform of the image was computed, the phase component was shuffled, and a new image was generated by mixing a percentage of the scrambled image with the original image. The amount of phase scramble was 20% (clearly visible) and 80% (unreadable), corresponding to word and noise condition, respectively. The stimuli were displayed on a gray background (50 cd/m^2) of a back-projected screen using a PT-D7700U-K (Panasonic) projector. The stimuli subtended 2.7° at a viewing distance of 1.25 m.

On a given trial, the stimulus was displayed for 1 s followed by a blank screen with a random duration between 620 and 840 ms sampled from a uniform distribution. The fixation color changed every 500 ms during the stimulus presentation. The fixation color could be green, blue, yellow, cyan, or red. With this identical procedure, participants conducted two tasks (lexical decision task and fixation task) in separate sessions. Thus, on each run the visual stimuli were identical but the task instructions changed. In the lexical decision task, participants were asked to press a designated button as soon as possible when the word was a made up word (pseudo word). In the fixation task, they were instructed to press the button as soon as possible when the fixation dot turned red (ignoring the images). Each session had four experimental blocks and in each block, there were 20 trials of the word condition, 20 trials of the noise condition, and 7 trials of the pseudo word condition.

D-primes for the lexical decision task suggest that all our participants performed the task as instructed (typical readers:1.74±0.23; struggling readers: 1.08±0.17, mean±sem, $p = 0.03$, independent t-test). All word stimuli had high lexical frequency to encourage our young participants, including struggling readers, to do the task. Despite the low performance compared to typical readers, the d-prime of struggling readers is above 1 suggesting that they also performed the task well. For the fixation task, typical readers and struggling readers performed the task equally well. The reaction times were 520±17 ms (typical readers) and 592±29 ms (struggling readers) ($p = 0.15$, independent t-test). The hit rates were 84±4 % (typical readers) and 73±4 % (struggling readers) ($p = 0.10$, independent t-test). Thus, differences in MEG responses during the fixation task could not be attributed to differences in task performance.

MEG and MRI data acquisition

MEG data were recorded inside a magnetically shielded room (IMEDCO) using a 306-channel dc-SQUID VectorView system (Elekta-Neuromag). Neuromagnetic data were sampled at 1kHz with a passband of 0.01 to 600 Hz. A 3D position monitoring system (Polhemus, Colhester, VT) was used to record the locations of head position indicator (HPI) coils, cardinal (nasion, left/right preauricular) anatomical landmarks. At least 100

digitized scalp points were used to coregister the MEG sensors with individual structural MRI. HPI coils were used to record the subject's head position continuously relative to the MEG sensors. Individual structural MRIs were obtained at The University of Washington Diagnostic Imaging Science Center (DISC) on a Philips Achieva 3T scanner for the boundary-element models that accurately characterize MEG forward field patterns. A whole-brain anatomical volume at 0.8×0.8 x 0.8mm resolution was acquired using a T1-weighted MPRAGE (magnetization prepared rapid gradient echo) sequence.

MEG data processing

The MEG data were analyzed using MNE-Python {Cite MNE paper}. Data were first denoised using signal space separation (Taulu and Kajola, 2005) to remove environmental artifacts. The continuous HPI data were used to compensate for subjects' head movements using the initial head position as the target MEG coordinate frame. Data were then low-passed (cutoff frequency at 40 Hz) and signal space projection was used to suppress heartbeat and eye-blink artifacts identified using electro-cardiogram and electro-oculogram (EOG) data. Noisy MEG channels were excluded from subsequent processing, which should have a minimal impact on localization due to the spatial redundancy of MEG measurements (Nenonen et al., 2007). Each trial epoch was 1 s including 100 ms before the stimulus onset and 900 ms after the stimulus onset. The original data was downsampled to 300 Hz to reduce the size of the data. The first 100 ms time interval served as a baseline and the averaged signal during the baseline was used for baseline correction. Noisy trials were rejected based on a criterion for peak-to-peak amplitude of MEG signals (30 pT for magnetometers, 4 pT/cm for gradiometers). Based on the number of trials in each condition after artifact rejection, we discarded data from 3 participants because there were not enough trials (< 40 trials in any of the conditions) for estimating average responses.

A cortical MEG source space was constructed using dipoles with 3 mm spacing, yielding 10242 dipoles per hemisphere. These were constrained to be normal to the cortical surface located along the gray/white matter boundary segmented from the structural MRI (Dale et al., 1999) using Freesurfer (http://surfer.nmr.mgh.harvard.edu/). Combining this structural information with subject colocation information, a three-compartment boundary element model (BEM) was used to provide an accurate calculation of the forward solution (Mosher et al., 1999) mapping dipole currents in the brain (source space) to observable MEG signals (sensor space). Dipole currents in this whole-brain source space were estimated from the evoked MEG response. To do this, we used an anatomically constrained minimum-norm linear estimation (MNE) approach (Dale et al., 1999; Hämäläinen and Ilmoniemi, 1994; Hämäläinen and Sarvas, 1989) with sensor noise covariance estimated from 100 ms epochs prior to each trial onset. Source localization data were then mapped to an average brain (freesurfer averaged brain) using

a non-linear spherical morphing procedure (20 smoothing steps) that optimally aligns individual sulcal–gyral patterns (Fischl et al., 1999).

To assess automatic responses to printed word stimuli, we used a region of interest (ROI) approach to increase statistical power and limit the number of statistical comparisons used to test our main hypothesis. We defined brain regions (ROIs) that were activated during the lexical decision task by finding spatiotemporal clusters in which MEG source activation was higher for the word stimuli compared to the scrambled noise stimuli. We calculated pairwise t-statistics corrected for multiple comparisons using 1024 permutations and cluster level correction. The resulting significant ($p < 0.05$) clusters in space and time were then visualized on the cortical surface. We further restricted vertices by selecting vertices that had significant duration greater than 100 ms. We then used these regions that were localized during the lexical-decision experiment to examine MEG responses during the fixation task experiment (which were independently ran in separate sessions).

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