

Neuroimaging and Reading Comprehension

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ABSTRACT

In this paper, we first introduce functional magnetic resonance imaging (fMRI), followed by a review of three themes of neuroimaging research on the neural correlates of reading-related skills: (1) typical and struggling readers, including developmental dyslexics, (2) an inverted U-shaped function in second language reading that portrays an increased activation in the reading network during learning phases and a decrease in activation as participants were more familiar with the exercise, and (3) cognitive capacity and syntactic complexity. Our intent is to show that interdisciplinary work involving how language operates in the brain, including the neural basis of reading comprehension, can provide a deeper understanding of some of the mechanics, processes, and behavioral data associated with reading comprehension.

Keywords: functional magnetic resonance imaging (fMRI), inverted U-shaped function, neurolinguistics, reading network

INTRODUCTION/BACKGROUND

Interdisciplinary studies typically involve a combination of two or more academic disciplines to achieve a common task that is related to various

disciplines (Ausburg, 2006). The use of Magnetic Resonance Imaging (MRI) to study brain activity is approximately 20 years old according to the Center for Functional MRI (2019); therefore, it is a relatively new field in cognitive neuroscience, medicine, and neuropsychology. One outcome of MRI studies of brain activity is neuroimaging research on the neural correlates of reading-related skills which can provide an indication of the neural regions involved in language processing.

The purpose of this paper is to present an overview of three themes in the neuroimaging research literature on the neural correlates of reading-related skills. We believe that selected brief overviews of research on the neurobiology of reading can provide a deeper understanding of mechanics, processes, and behavioral data in reading comprehension. These overviews can further complement what is taught about these mechanics and processes in contemporary courses and programs in reading comprehension. The three themes addressed in this paper are (1) typical and struggling readers, including developmental dyslexics, (2) an inverted U-shaped function in second language reading that portrays an increased activation in the reading network during learning phases and a decrease in activation as participants were more familiar with the exercise., and (3) cognitive capacity and syntactic complexity.

FUNCTIONAL MAGNETIC RESONANCE IMAGING

Neuroimaging refers to various noninvasive techniques which are used to produce images of the brain. Those techniques include positron emission tomography (PET), functional magnetic resonance imaging (fMRI), and multichannel electroencephalography (EEG), and magnetoencephalography (MEG). There are two broad categories of neuroimaging: functional imaging which provides visual images of the information processing centers of the brain and structural imaging which focuses on the structure of the nervous system (Center for Functional MRI, 2019). For the sake of brevity and coherence, we will focus on fMRI studies of language processing in this paper because the technique provides a means to (a) study the cortical representations of language in the brain and (b) produce an indication of the neural regions that are thought to be involved in language processing.

MRI involves a person lying inside a circular tunnel which is surrounded by a whirling magnet that produces a magnetic field. A radio frequency (RF) pulse is directed to the person's head, and the tissues emit signals which are measured and are used by a computer to construct a two-dimensional image that displays energy levels (Jay, 2003). MRI depends on the fact that the nucleus of a hydrogen atom behaves like a small magnet. The

MRI device produces a strong magnetic field which causes the hydrogen nuclei in the person's body to align with that magnetic field. A RF magnetic pulse at the correct frequency causes the hydrogen nuclei to absorb energy and to use that energy to create a brief magnetic resonance signal. The RF coils in the MRI machine detect that signal (Center for Functional MRI, 2019).

The key to understanding how MRI functions is that a magnetic resonance (MR) signal increases by a small amount as the result of an increase in neural activity in a particular area of the brain. Changes in the MR signal are the result of an increase in neural activity. Stowe and Sabourin (2005) depicted how fMRI produces brain images:

When a given task causes increased neuronal processing, there is an increased demand for blood to supply oxygen and glucose to that area which causes a (relatively slow) increase in the amount of blood delivered to that area over the next several minutes. fMRI measures changes over time in the proportion of deoxygenated blood to various areas on the brain, so that the beginning of processing of a particular kind of stimulus can be used as a baseline. (p. 330)

There are three major areas of inquiry in the neural basis of language, according to Fedorenko, Hshieh, Niteo-Castanon, Whitfield-Gabrieli, and Kanwisher (2010), "What brain regions are involved? Are any of these regions specialized for particular aspects of linguistic processing (e.g., phonological, lexico-semantic, or structural processing)? Are any of these regions specific to language?" (p. 1177). Based on Fedorenko et al.'s (2010) inquires, we explore the connection between neuroimaging research and reading comprehension in the subsequent sections.

Neuroimaging techniques have assisted cognitive neuroscientists identify and explore (1) the brain's processing of written language, (2) neural subpopulations and the cognitive processes that critically support reading, (3) the connection and interaction of discrete cortical brain regions, referred to as the reading network, that broadly support reading-related audiovisual processing (Edwards, Burke, Booth, & McNorgan, 2018), (4) the neural bases of reading comprehension component processes by integrating cognitive behavioral data with brain-imaging research (Mason & Just, 2004), and (5) measures of the intensity of cognitive processing during reading (Just, Carpenter, Keller, & Thulborn, 1996).

THE READING NETWORK

In the cognitive neuroscience and neuroimaging fields of research, the reading network refers to four dominantly left-lateralized, anatomically distributed brain regions, each of which supports different reading-critical

processes. These otherwise independent processes, according to Edwards et al. (2018), must be coordinated and integrated during the overall reading process. Edwards et al. (2018) describe the components of the reading network as follows:

The fusiform gyrus (FG), which is involved in processing orthographic information [Blau, Reithler, van Atteveldt, Seitz, Gerretsen, Goebel, et al. (2010); Dehaene & Cohen (2011); McCandliss, Cohen, & Dehaene (2003)], the posterior superior temporal gyrus (pSTG), which is involved in processing phonology [Pugh, Mencl, Jenner, Katz, Frost, Lee et al. (2001); Demont, Chollet, Ramsay, Cardebat, Nespoulous, Wise et al. (1992); Paulesu, Frith, Snowling, Gallagher, Morton, Frackowiak et al. (1996)], the posterior superior temporal sulcus (pSTS), which is involved in cross-modal integration of visual and auditory information [Blau, Reithler, van Atteveldt, Seitz, Gerretsen, Goebel et al. (2010); Gullick & Booth (2014); van Atteveldt, Blau, Blomert & Goebel (2010)], and the inferior frontal gyrus (IFG), which has been associated with later high-level phonological recoding while reading [Pugh, Mencl, Jenner, Katz, Frost, Lee et al. (2001); Herbster, Mintun, Nebes, & Becker (1997); Shaywitz, Shaywitz, Pugh, Fulbright, Constable Mencl et al. (1998); van Atteveldt, Formisano, Goebel, & Blomert (2007)]. (p. 1)

Cognitive neuroscientists have also identified three neural pathways that have been shown to be involved in reading. Arrington et al. (2019) mentioned a dorsal, a ventral, and an anterior system. The dorsal system consists of left temporoparietal areas including the angular gyrus, supramarginal gyrus, and posterior superior temporal gyrus. These areas map orthographic information to phonological and semantic properties of the printed words (Xu et al., 2001). The ventral pathway connects the left ventral occipitotemporal cortex to the middle and inferior temporal gyri where orthography is mapped to word recognition (Cohen et al., 2000). The anterior system where phonological recoding and semantic integration occur has its focus in the left inferior frontal gyrus (Poldrack et al., 1999; Zhu et al., 2012; Zhu et al., 2013).

An appendix contains a list of cortical components and associated terms and their cortical location. Friederici's (2011, p. 1359) figure of anatomical details of the left hemisphere is also helpful in locating the different lobes, the major language relevant gyri, and coordinate labels.

TYPICAL AND STRUGGLING READERS

In this section, we begin with a summary of the locations of neural activations captured while typical and struggling readers were engaged in reading tasks. Next, we present the details of one study to give the reader of this paper a brief introduction to the kinds of prompts that are used in neuroimaging studies of reading. We conclude this section with a brief description of developmental dyslexia.

Neural Activations of Typical, Struggling, Atypical, and Impaired Readers

Pollack, Luk, and Christodoulou (2015) conducted meta-analyses separately for typical and atypical readers, including children and adults. They used Activation Likelihood Estimation (ALE) to analyze contrasts for tasks involving rhyming or reading visually presented letter or word stimuli in Dutch, English, French, German, Italian, or Norwegian. ALE determines the convergence of foci reported from different studies and is a widely used technique for coordinate-based meta-analysis of neuroimaging data (Eickhoff, Bzok, Laird, Kurth, & Fox, 2012). Typical readers “showed reliable activation in only left lateralized regions, including the inferior frontal area, precentral area and middle temporal gyrus” (Pollack et al., 2015, p. 2).

For impaired readers, Fletcher et al. (2000) reported “more activation of anterior portions (inferior frontal gyrus) and reversed (right greater than left) hemispheric asymmetries activation in posterior or temporal regions compared to non-impaired readers” (p. 49). Two other studies report the loci of reliable activation or higher activation than that reported for struggling readers: bilateral inferior frontal gyrus, left inferior parietal gyrus, right postcentral gyrus, bilateral fusiform gyrus, bilateral superior temporal gyrus, thalamus, left precuneus, and left middle occipital area (Maisog et al., 2008, p. 5); temporoparietal areas, with increasing task-induced demands for phonological analysis (angular gyrus), Wernicke’s area and basal temporal areas (Fletcher et al., 2000).

fMRI Used to Study Good and Poor Readers

Meyler et al. (2007) used fMRI to study brain activation of good and poor readers in the third and fifth grades during a visual sentence comprehension task. The subject samples consisted of 18 third grade poor readers and 14 good readers, and 23 fifth grade poor readers and 12 good readers. “Good” readers were identified by their teachers as average to above average. Criteria for inclusion in the study included a score at or below the 30th percentile on the combination of the Sight Word Efficiency and

Phonological Decoding Efficiency subtests of the *Test of Word Reading Efficiency* (Torgesen, Wagner, & Rashotte, 1999) and a score at or above the fifth percentile on the *Peabody Picture Vocabulary Test* (Dunn & Dunn, 1997). During the sentence comprehension test, the children had to decide whether the presented stimulus sentences “made sense” or not. Example sentences in the exercise were “The wind blew the leaf” and “The man fed the dress”. Meyler et al. (2007) reported that “participants with lower reading scores had less activation in the left middle temporal gyrus (Wernicke’s area), the right inferior parietal lobule, and the left postcentral gyrus” (p. 2783). Meyler et al. (2007) also found that “poorer reading ability is associated with less parietotemporal activation in the left middle temporal gyrus, the right inferior parietal lobule, and the left postcentral gyrus” (p. 2784) and that “the parietotemporal area, particularly in the left hemisphere, appears to be a key locus of dysfunction in children who experience difficulty in learning to read” (p. 2785).

In summary, a broad generalization for this section of the paper is that typical readers exhibit more activation than struggling readers in the left hemisphere frontal and temporal regions while reading; struggling readers show activation in both hemispheres but under-activate left hemisphere temporoparietal and occipitotemporal networks. As a result, struggling readers may have to compensate by increased activation in the right hemisphere posterior regions. This spillover of activation to the right hemisphere may be due to cognitive constrained comprehension in the left hemisphere. Cognitive constrained comprehension will be addressed in another section of the paper.

Dyslexic Readers

Dyslexic readers often manifest reduced or absent activation in the left hemisphere temporoparietal and occipitotemporal networks and often increased activation in the right hemisphere posterior regions (Pugh et al., 2013). Different researchers have reported activation in the right hemisphere homologous regions in the posterior temporo-parietal and temporo-occipital regions in dyslexic readers (Shaywitz et al., 2002) and higher activation than in typical readers in the right hemisphere and thalamus (Maisog et al., 2008).

Developmental dyslexia is a brain-based reading disorder characterized by difficulty with decoding and encoding phonological structures at the single-word level, poor spelling, and phonological awareness (Arrington et al., 2019; Lyon, Shaywitz, & Shaywitz, 2003; Pugh et al., 2013; Snowling, 2000; Vellutino, Fletcher, Snowling, & Scanlon, 2004). Phonological awareness refers to the understanding that phonemes (sound units that distinguish but do not convey meaning) and syllables make up

words. Impaired phonological processing ability and poor word recognition ability are believed to be the most common cause of reading difficulty. These deficits affect a reader’s ability to master the alphabetic principle, that is, the mapping of phonemes (units of sound) to graphemes (written symbols) and are expressed as difficulties in identifying and manipulating basic speech sounds (Meyler et al., 2007; Pugh et al., 2000).

As we noted in the previous paragraph, children with dyslexia have difficulties with the audiovisual integration of information required in reading. Edwards et al. (2018) note that “individuals with dyslexia show under-activation in [the fusiform gyrus] during word reading tasks...” (p. 1), and “in typically developing readers, activation in the posterior superior temporal gyrus increases during rhyming judgment tasks ..., whereas dyslexics have been shown to have an under-activation in this region” (p. 2).

EXPERIENCE, EXPERTISE, FAMILIARITY, AND THE INVERTED U-SHAPE FUNCTION

Functional and structural changes in the brain are often related to the ability to learn a second language (Cao, 2016). Researchers have proposed an inverted U-shaped function in neural responses to account for an increase in activation in the reading network during learning and a decrease in activation in the reading network as a result of the learner’s expertise, experience, and familiarity with the script, that is, the orthography in second language reading comprehension (Cao, 2016; Price & Devlin, 2011).

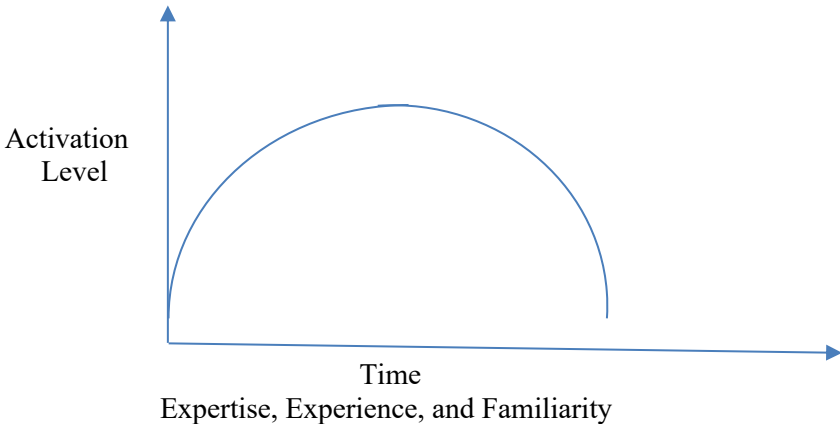


Figure 1. U-shaped Function

In this context, a function is any action of a group of related actions that contribute to a larger action. Related actions could refer to the activation of the four anatomically distributed brain regions, referred to as the reading network, that broadly support reading-related audiovisual processing. Reading-related audiovisual processing could refer to the larger action mentioned in the explanation of a function.

Figure 1 portrays the inverted U-shaped function mentioned above. In the graph, the horizontal axis is called the x -axis. In this example, the horizontal axis represents points in time and increases in the learner's expertise, experience, and familiarity, from the left (less expertise, experience, and familiarity) to the right of the graph (more expertise, experience, and familiarity). The vertical axis is the y -axis, and it portrays increases in activation levels in the reading network from the bottom of the graph (low activation) to the top of the graph (high activation). To graph a point, one must first locate its position on the x -axis, then find its location on the y -axis, and finally plot where these lines meet and intersect. It is unrealistic to expect to find such a "smooth" inverted U with real data, but our intention is to explain how U-function graphs are constructed. Our example shows an illustration of increased activation in the reading network during learning phases and a decrease in activation as participants were more familiar with the exercise.

Price (2013) offered the following evidence to support the claim that neural activation in the left temporo-occipital region increases during initial learning and decreases with increased experience and expertise. Responses are higher after adults learn a new script (Mei et al., 2013). Young children, ages 5-8, having better performance on phonological awareness, pseudo-word decoding, and word reading ability exhibit higher activation in active reading networks (Pugh et al., 2013). As the readers' experience and expertise with a script increases, activation in the left ventral occipito-temporal cortex decreases (Twomey et al., 2013). Activation in adults is less than activation in children because adults have more experience and expertise with the orthography (Olulade, Flowers, Napoliello, & Eden, 2013). Additionally, increases in word frequency co-occur with decreases in inferior frontal activation and with decreases for words relative to pseudo-words (Heim, Wehnelt, Grande, Huber, & Amuts, 2013).

In this section, we will present brief descriptions of some studies that led to the postulation of the inverted U-shaped function, with respect to comparisons of alphabetic and logographic features, visual word recognition, and visual word form system.

Mei et al. (2013) trained two matched groups of 44 Chinese college students, 19-25 years old, to read an artificial language either as a transparent,

alphabetic orthographic language (grapheme-to-phoneme mapping) or a nontransparent logographic language (word-to-sound mapping). The stimuli were 60 Chinese words and 60 artificial words which were constructed using 22 Korean Hangul letters, including 12 consonants and 10 vowels. Subjects received eight hours of training on the association between sounds of the 60 artificial language words and visual forms. Mei et al. (2013) reported:

phonological training resulted in increased activation in the fusiform gyrus ... with more left-lateralized activation after alphabetic training than after logographic training. This difference manifested in the posterior portion of the fusiform gyrus, decreased in the middle portion, and diminished in the anterior portion. (p. 169)

The left ventral occipito-temporal cortex (VOT) is involved in visual word recognition. Twomey et al. (2013) reported that activation is greater for low frequency words than high frequency words. Price and Devlin (2011) proposed that high frequency written words have more familiar visual patterns than low frequency written words, and that is why high frequency written words evoke less activation. Twomey et al. (2013) conducted a study using Japanese to differentiate between the effects of frequency of a word and the visual familiarity of the word. The stimuli for the study were written in morphographic Kanji and syllabographic Hiragana. Half of the words were in the more commonly written Kanji (30 words) and the other half were more commonly written in Hiragana (30 words). The stimuli also contained an equal number of nonwords divided equally between Kanji and Hiragana. Forty native Japanese speakers born and educated in Japan through at least secondary school viewed strings of characters and determined whether each string of characters formed a legitimate, existing Japanese word. Twomey et al.'s (2013) results indicated that visual familiarity had a greater effect on the activation of the least frequent words with virtually no effect on the most frequent words. In addition, "lexical frequency was found to significantly modulate activation in a region of the left inferior temporal gyrus lateral to the area in VOT showing a visual familiarity effect" (Twomey et al., 2013, p. 191).

The visual word form system (VWFS) is located in the occipito-temporal cortex and is believed to be involved in the orthographic processing of visually presented words. Olulade et al. (2013) conducted an fMRI study and an implicit word-processing task, the purpose of which was to determine whether differences exist between older experienced and younger novice readers in selectivity for words along the VWFS. Fifteen adult and 11 child monolingual native speakers of English were asked to identify tall graphemes within visually printed words. There is an ascending grapheme in the word *solve* but no ascending grapheme in the word *cease*. "Our results showed

differences between children and adults during word processing in the anterior left occipito-temporal cortex, providing evidence of developmental refinement for word recognition along the VWFS” (Olulade et al., 2013, p. 134).

Overall, the studies presented in this section show evidence that there was an increased activation in the reading network during learning phases and a decrease in activation in the reading network as participants were more familiar with the exercise. An interesting longitudinal study would be to determine whether there is a meaningful relationship between the falling part of the inverted U and a learning plateau which is a period of little or no progress, indicated by a flat place in a learning curve.

COGNITIVE CAPACITY AND SYNTACTIC COMPLEXITY

We begin this section with a brief introduction to cognitive capacity and then continue with an introduction to some syntactic phenomena that are believed to cause increases in neural activation during sentence comprehension. The phenomena to be presented and to be discussed are argument structure information, structures that entail movement such as topicalization, cleft sentences, and WH-questions, and centered and right branching subject/object relative clauses.

Cognitive Capacity

Learners can only attend to a finite amount of information at a given time due to the limited capacity of the working (short-term) memory system (Sweller, 1988). Originally, Miller (1956) advanced the notion that a person could hold from five to nine pieces of unrelated information (i.e., numbers) in short-term memory for processing, but more recent research now indicates that that estimate should be lowered to as few as four, when it comes to words instead of numbers (Cowan, 2001; Janssen, Kirshner, Erkens, Kircher, & Pass, 2010).

According to Feldon (2010, p. 18), cognitive load is “conceptualized as the number of separate chunks” or schemas “processed concurrently in working memory” while performing a task, plus “the resources necessary to process the interaction between them”. Cognitive load is experienced as mental effort. When cognitive load, that is, the information to be processed, exceeds working memory’s capacity to process it, readers will have difficulties comprehending the text.

Cognitive load is very similar to Just and Carpenter’s (1992) capacity theory of comprehension, that is, “cognitive capacity constrains comprehension” (p. 122). Hasegawa, Carpenter, and Just (2002) suggest that

the quantitative computational demand imposed by a cognitive process affects the amount of brain activation. Language comprehension is defined as a task that “demands extensive storage of partial and final products in the service of complex information processing” (Just & Carpenter, 1992, p. 123). When language comprehension has high demand “(either because of storage or computational needs), the speed of processing will decrease and some partial results may be forgotten” (Just & Carpenter, 1992, p. 123).

Just et al. (1996) provide a more detailed explanation:

At the cognitive level, sentence comprehension requires combining information from a sequence of words and phrases, computing their syntactic and thematic relations, and using world knowledge to construct a representation of the sentence meaning. These processes require the consumption of computational resources to perform the comprehension operations and also to maintain the representations of the component word meanings, propositions, and relational structures in an activated state during the processing. (p. 114)

Syntactic Complexity

We provide a list of grammatical features which increase syntactic complexity. Such an exemplary list should raise or enhance classroom teachers’ consciousness of the linguistic phenomena that can impact sentence and text comprehension.

Argument structure. Verbs play an important role in the comprehension of sentences for the following reasons. In order to comprehend a sentence, a reader must establish the predicate-argument relationship between a verb and the phrases associated with it. Verbs determine the number of arguments, their thematic roles, their syntactic category, and their semantic role in a sentence (Meltzer-Asscher, Mack, Barbieri, & Thompson, 2015).

An intransitive verb is classified as a one-place verb, having only one thematic role, e.g., *John slept*. A transitive verb is a two-place verb with two arguments, e.g., *Sam baked a cake*. A ditransitive verb is a three-place verb with three arguments, e.g., *Helen baked Mary a cake*.

Verbs determine the syntactic category of the phrases that co-occur with them, e.g., noun phrases, adjective phrases, adverb phrases, prepositional phrases. Verbs also determine the semantic role of noun phrases co-occurring with them, e.g., agent and theme. The agent, i.e., the logical subject, is the cause of the action of the event, or the being, whereas the theme is the recipient of the action, that is, the logical object. Meltzer-Asscher et al. (2015) refer to this information as argument structure information.

Research has shown that an increased number of thematic roles elicited greater activation in the left posterior perisylvian regions (Meltzer-Asscher et al., 2015). Bilateral superior sulcus activation co-occurred with an increased number of arguments in a sentence (Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003). The right anterior cingulate and medial precuneus were sensitive to the number of arguments (Shetreet, Palti, Friedman, & Hader, 2007). The processing cost of verbs with multiple thematic options increases as the number of thematic options increases (Shapiro, Zurif, & Grimshaw, 1987).

Movement. Movement has been found to contribute to the perceptual complexity of sentences (Neville, Nicol, Barss, Forster, & Garrett, 1991). Syntactic movement is involved when certain sentence constituents are moved from their base, canonical positions in the deep structure representation of a sentence to other noncanonical positions in the surface structure representation of a sentence, i.e., the hierarchical structure of a sentence as it is overtly pronounced. Movement of constituents leaves “traces”; a trace fills the base position of the transformed or moved argument. A trace is a phonetically empty, abstract, syntactically effective entity that “transmits the thematic role of the transformed argument via co-indexation. The representation of a trace is therefore necessary to comprehend sentences in which the canonical word order is changed” (Wartenburger et al., 2004, p. 73).

Movement phenomena can be seen in topicalization, cleft sentences, and WH-questions. In a topicalization sentence, the moved element becomes the semantic “topic” of the sentence.

Boys, Sarah Weinstein doesn't like.

For entertainment, we watch ballet.

That broccoli, George won't eat.

A cleft sentence also involves movement of a constituent from its canonical position into a separate clause to give it greater emphasis. There are two varieties of cleft sentences, *it*-clefts and *wh*-clefts. The *it*-cleft is introduced by the non-pronoun expletive *it*, usually followed by *be*, the focused constituent and the remainder of the sentence is introduced by a relative clause.

Base sentence: *Tom went to the baseball game last week.*

It was Tom who went to the baseball game last week.

It was to the baseball game that Tom went last week.

It was last week that Tom went to the baseball game.

Stowe, Tanenhaus, and Carlson (1991) contend that “to determine the meaning of a WH-phrase, a ‘gap’ must be located and the role associated with the gap assigned to the WH-phrase” (p. 319). Gaps can be thought of as

involving long-distance dependencies. The following sentence illustrates a gap. The *t* indicates the position in which a phrase bearing the role assigned to the question would appear in a declarative sentence:

Which book did the teacher say that the student stole t from the library?

WH-questions involve movement of constituents from a variety of canonical locations in declarative sentences:

The waiter asked [which tourist] [t ordered salad for lunch] (subject WH-Q)

The waiter asked [which salad] [the tourist ordered t for lunch] (object WH-Q)

Which book did the student say t disappeared from the library? (subject of an embedded clause)

Which book did the teacher say that the student stole t from the library? (object of an embedded clause)

Some researchers have reported activation in left inferior frontal cortex due to syntactic movement (Caplan & Waters, 1999; Cooke et al., 2001; Just et al., 1996), while Caplan and Waters (1999) and Just et al. (1996) have found activation in right inferior frontal gyrus, left and right posterior superior temporal cortex, left superior parietal and left angular cortex. Ben-Shachar, Palti, and Grodzinsky (2004) also reported that “topicalization sentences evoked significantly higher activation in left interior frontal gyrus and left precentral sulcus” (p. 1328). And WH-questions also evoked stronger activations than yes/no questions in the same areas (Ben-Shachar et al., 2004).

Centered and right branching subject/object relative clauses.

There has been extensive research conducted on restrictive subject-object center embedded relative clauses and restrictive object-subject right branching relative clauses. The following sentence contains a subject-object center embedded relative clause:

The juice that the child enjoyed stained the rug.

This is a complex sentence consisting of a main clause—*the juice stained the rug*—and a relative clause—*that the child enjoyed*—which modifies the subject of the main clause. The relative pronoun *that* serves as the direct object of the relative clause—*that the child enjoyed*. The relative clause is embedded in the main clause separating the subject of the main clause—*the juice*—from its predicate—*stained the rug*.

The next sentence contains an object-subject right branching relative clause:

The child enjoyed the juice that stained the rug.

In this sentence, the relative clause modifies the direct object of the main clause, and the relative pronoun serves as the subject of the relative

clause. There is no movement of constituents, and the canonical word order (subject-verb-object) of the main clause is not interrupted. A branching tree diagram of the sentence would show the relative clause branching off the noun phrase object of the main clause.

Previous research has shown that normal readers make more errors and require more time to process sentences containing center-embedded relative clause sentences than to process sentences containing right branching relative clauses (Berwick & Weinberg, 1984; Caplan, Alpert, Waters, & Oliverieri, 2000; Just & Carpenter, 1992; King & Just, 1991). Memory load associated with holding the relative clause subject noun phrase in a parsing buffer until it is assigned a thematic role and structuring the relative clause may account for the results (Constable et al., 2004).

Subject vs. object relative clauses. Previous research has shown that object relatives are more difficult to process than subject relatives (Hamburger & Crain, 1984; Just et al., 1996; Ni, Shankweiler, & Crain, 1996). The prevailing theoretical explanation concerns the assignment of thematic role (subject or object) to the head noun of the relative clause, which was discussed in the previous section of the paper.

Constable et al. (2004) conducted a study with 10 male and 10 female right-handed subjects, aged 18 to 40 years old, who were required to read and to listen to stimuli sentences and then to make a sentence goodness judgment following each sentence. The stimuli were 120 center embedded relative clause sentences, with half of the stimuli containing subject relatives (1 below) and half of the stimuli containing object relatives (2 below).

1. *The biologist-who showed the video-studied the snake.*
2. *The biologist-who the video showed-studied the snake.*

Prescriptively, sentence 2 is ungrammatical, because the objective form of *who* is *whom*, but unfortunately the distinction between *who* and *whom* is disappearing in English. The researchers found that the object relative sentences evoked more neural activity than subject relative sentences, primarily in Broca's area which is located in the inferior frontal lobe.

CONCLUSION

This is an interdisciplinary paper that discusses some applications of neuroimaging, a relatively new field in cognitive neuroscience and medicine, to the neural correlates of reading-related skills and the neural regions involved in language processing. Our intent is to show that interdisciplinary work involving how language operates in the brain, including the neural basis of reading comprehension, can provide a deeper understanding of some of the mechanics, processes, and behavioral data associated with reading

comprehension. We provide a brief introduction to functional magnetic resonance imaging, the reading network, the neural activations of typical and struggling, atypical, impaired readers, an inverted U-shaped function, and a discussion of some syntactic phenomena that may cause increases in neural activation during sentence comprehension due to cognitive capacity constraints on comprehension.

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Appendix Location of Components

Component	Location	Component	Location
Gyrus	The top part of a fold in the cortex	Sulcus	The trough below a gyrus
Anterior (rostral)	Toward the front of the brain	Posterior (caudal)	Toward the back of the brain
Superior (dorsal)	Toward the top of the brain	Inferior (ventral)	Toward the bottom of the brain
Temporal lobe	Beneath the lateral fissure on both cerebral hemispheres, toward the base of the center of the cortex, in proximity of the temples	Occipital lobe	Behind the parietal and temporal lobes, at the rear portion of the skull
Angular gyrus	In the parietal lobe	Supramarginal gyrus (SMG)	A portion of the parietal lobe, anterior to the angular gyrus
Superior temporal gyrus (STG)	At the topmost part of the temporal lobe, lateral to the head, somewhat above the external ear	Occipitotemporal gyrus	Part of the temporal and occipital lobes, also known as fusiform gyrus
Inferior frontal gyrus (IFG)	In the frontal lobe, part of the prefrontal cortex in the lowest part of the frontal lobe	Pars triangularis	Triangular shaped region in the frontal lobe
Pars opercularis	In the inferior frontal gyrus	Wernicke's area	In the left hemisphere, in the posterior section of the superior temporal gyrus
Broca's area	In the lower part of the left frontal lobe	Inferior parietal lobe	Behind the lower part of the postcentral sulcus
Occipital lobe	Posterior to the temporal and parietal lobes	Inferior longitudinal fasciculus	Connects the occipital and temporal lobes
Inferior fronto-occipital fasciculus	Connects the frontal, occipital and temporal lobes	Ventro prefrontal cortex	In the prefrontal cortex
Parietal lobe	Under the skull's parietal bone		

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