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Neural substrates of sublexical processing for spelling

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ABSTRACT

We used fMRI to examine the neural substrates of sublexical phoneme-grapheme conversion during spelling in a group of healthy young adults. Participants performed a writing-to-dictation task involving irregular words (e.g., choir), plausible nonwords (e.g., kroid), and a control task of drawing familiar geometric shapes (e.g., squares). Written production of both irregular words and nonwords engaged a left-hemisphere perisylvian network associated with reading/spelling and phonological processing skills. Effects of lexicality, manifested by increased activation during nonword relative to irregular word spelling, were noted in anterior perisylvian regions (posterior inferior frontal gyrus/operculum/precentral gyrus/insula), and in left ventral occipito-temporal cortex. In addition to enhanced neural responses within domain-specific components of the language network, the increased cognitive demands associated with spelling nonwords engaged domain-general frontoparietal cortical networks involved in selective attention and executive control. These results elucidate the neural substrates of sublexical processing during written language production and complement lesion-deficit correlation studies of phonological agraphia.

1. Introduction

Cognitive models of written language postulate two distinct mechanisms that support reading and spelling: lexical-semantic and sublexical. Lexical-semantic processing relies on interactions between conceptual knowledge of word meanings and word-specific phonological and orthographic representations. The lexical-semantic procedure is typically used when reading/spelling familiar words, and is especially important for generating correct pronunciations or spellings of irregular words that contain atypical sound-letter (phoneme-grapheme) correspondences (e.g., choir). By contrast, sublexical processing relies on the systematic application of letter-to-sound or sound-to-letter conversion rules critical for reading/spelling unfamiliar words or novel nonwords that are not represented in lexical-semantic memory.

Initial evidence regarding the neural underpinnings of lexical-semantic and sublexical processing came from lesion-deficit correlation studies of individuals with acquired surface and phonological alexia/agraphia (Beauvois & Derouesne, 1981; Rapcsak & Beeson, 2004, 2015; Rapcsak et al., 2009; Rapp, Purcell, Hillis, Capasso, & Miceli, 2016; Roeltgen & Heilman, 1984; Shallice, 1981). Surface alexia/agraphia reflects the breakdown of lexical-semantic procedures and is manifested as a disproportionate deficit in reading/spelling irregular words relative to regular words and nonwords that contain predictable phoneme-grapheme mappings. Surface alexia/agraphia have been associated with lesions involving left ventral occipito-temporal (lvOT) cortex encompassing the visual word-form area (VWFA) implicated in lexical orthographic processing, but the syndrome can also be produced by damage to a distributed network of extrasylvian cortical regions involved in semantic processing, including left anterior temporal lobe structures and posterior temporo-parietal cortex (middle temporal gyrus/angular gyrus) (Binder et al., 2016; Graham, Patterson, & Hodges, 2000; Rapcsak & Beeson, 2004, 2015; Wilson et al., 2009). By contrast, phonological alexia/agraphia is characterized by disproportionate impairment in nonword reading/spelling due to dysfunction of sublexical procedures, and has been associated with damage to a network of perisylvian cortical regions implicated in phonological processing, including posterior inferior frontal gyrus/operculum, precentral gyrus, insula, superior temporal gyrus/sulcus, and supramarginal gyrus (Alexander, Friedman, Loverso, & Fischer, 1992; Henry, Beeson, Stark, & Rapcsak, 2007; Rapcsak et al., 2009; Roeltgen, Sevush, & Heilman, 1983). Collectively, these functionally linked perisylvian regions constitute the dorsal language pathway that plays a critical role in mapping phonological representations onto articulatory networks during speech production and also provides

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the neural substrate of phonological short-term memory and phonological awareness (Hickok & Poeppel, 2007).

More recently, functional imaging studies have been used to isolate the neural systems that support lexical-semantic and sublexical processing during reading and spelling in healthy individuals. Regarding the lexical-semantic pathway, these investigations have confirmed the critical role of the VWFA in gaining access to word-specific orthographic representations during reading and the recruitment of perisylvian phonological and extrasylvian semantic networks when reading familiar words (Binder, Medler, Desai, Conant, & Liebenthal, 2005; Graves, Desai, Humphries, Seidenberg, & Binder, 2010; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Taylor, Rastle, & Davis, 2013). Functional imaging studies of reading nonwords relative to real words show greater activation in left perisylvian cortical areas involved in phonological processing (IFG/operculum, PCG, insula, STG/STS, and SMG) (Graves et al., 2010; Jobard et al., 2003; Mechelli, Gorno-Tempini, & Price, 2003; Taylor et al., 2013), overlapping with regions recruited during speech production, phonological short-term memory, and phonological awareness (Acheson, Hamidi, Binder, & Postle, 2011; Buchsbaum et al., 2011; Burton, Locasto, Krebs-Noble, & Gullapalli, 2005; Jobard et al., 2003; Katzir, Misra, & Poldrack, 2005; Price, 2012; Vigneau et al., 2006). Reading nonwords also produced greater activation in the VWFA relative to real words, presumably reflecting the increased processing demands associated with mapping unfamiliar combinations of letters onto the corresponding phonological representations (Price & Mechelli, 2005; Taylor et al., 2013). In addition to increased activation within domain-specific components of the language network implicated in phonological and orthographic processing, the greater task difficulty and cognitive effort associated with reading novel nonwords is also reflected by the engagement of domain-general frontoparietal networks involved in selective attention and executive control (Binder et al., 2005; Graves et al., 2010; Ihnen, Petersen, & Schlaggar, 2015). Components of this (bilateral) multi-demand frontoparietal system include regions within dorsal and ventrolateral prefrontal cortex (e.g., inferior frontal junction), intraparietal sulcus (IPS), and anterior cingulate gyrus (Fedorenko, 2014; Fedorenko, Duncan, & Kanwisher, 2013; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008).

The vast majority of imaging studies of written language processing have focused on reading, and empirical data regarding the neural substrates of spelling is relatively modest. Nevertheless, recent meta-analyses of functional imaging studies of written language production have revealed that the cortical regions involved in spelling show considerable overlap with those implicated in reading (Planton, Jucla, Roux, & Démonet, 2013; Purcell, Turkeltaub, Eden, & Rapp, 2011). Specifically, these studies have confirmed the central role of lvOT/VWFA for gaining access to orthographic lexical representations during both reading and spelling (Planton et al., 2013; Purcell et al., 2011; Tsapkini & Rapp, 2010). In addition, similar to reading, written language production has been associated with activation in several perisylvian cortical areas implicated in phonological processing, including IFG/operculum, PCG, insula, STG/STS, and SMG (Beeson et al., 2003; Planton et al., 2013; Purcell et al., 2011; Rapcsak & Beeson, 2015). It is important to note, however, that although these imaging studies have provided important information about the neural correlates of lexical-semantic processing associated with spelling familiar words, conclusions about the sublexical spelling pathway were limited by the fact that these studies did not specifically investigate spelling nonwords. An exception is the recent study by Ludersdorfer, Kronbichler, and Wimmer (2015) that attempted to identify the neural systems that support lexical-semantic versus sublexical processing by directly contrasting real word and nonword spelling in German speakers. These investigators reported that the lvOT/VWFA, left IFG (pars triangularis, pars opercularis), and superior frontal gyrus/paracingulate gyrus were activated to a greater extent during real word than nonword spelling, whereas the superior temporal gyrus (STG) showed the opposite response pattern. As acknowledged by the authors, these results were somewhat surprising because studies of reading have consistently demonstrated increased activation to novel nonwords relative to familiar real words in cortical regions implicated in orthographic and phonological processing, including the VWFA and posterior IFG/operculum.

The aim of the present investigation was to elucidate the cortical regions recruited during sublexical spelling using fMRI data collected in healthy English speakers while they spelled irregular words and nonwords to dictation[1]. A control task of drawing geometric shapes to dictation was employed to enable us to remove peripheral components of the experimental task relating to motor planning and implementation. Based on the results of neuroimaging studies of reading, we hypothesized that spelling irregular words and nonwords would produce overlapping patterns of activation in left-hemisphere regions specialized for phonological and orthographic processing, including perisylvian cortical areas comprising the dorsal language pathway and the lvOT/VWFA. Given the greater computational difficulty/cognitive effort associated with spelling novel nonwords compared to familiar real words, we anticipated that the nonword/irregular word contrast would reveal evidence of increased neural activation within components of the language network critical for sublexical phonology-to-orthography translations as well as the recruitment of domain-general frontoparietal networks involved in selective attention and executive control.

2. Material and methods

2.1. Participants

Thirteen healthy right-handed English-speaking adults (5 male, 8 female) participated in this study. The mean age for the group was 29.5 years (20–53 years) with an average of 15 years of education (12–18 years). Right handedness was confirmed in all participants using the Edinburgh Handedness Inventory (Oldfield, 1971), yielding a mean laterality quotient of 83.5 (64–100). The participants had no history of neurological impairment or learning disability. The study was approved by the University of Arizona Human Subjects Protection Program and informed consent was obtained from each individual prior to participating.

2.2. Design and materials

A functional MRI experiment was implemented to examine and isolate the relevant processes that support sublexical spelling using a blocked design with the following conditions: (a) writing real words with irregular spellings, (b) writing nonwords, and (c) drawing common geometric shapes. Participants were instructed to write or draw each item on a pad of paper that rested on their lap during scanning. The stimuli were presented auditorily as a writing-to dictation or drawing-to-dictation task, as appropriate, via MR compatible headphones (Resonance Technologies) during 30-s blocks. Each block was initiated by a 3-s spoken instruction, followed by spoken presentation of five items presented at 6-s intervals over the course of the 30-s block (see Fig. 1). For the nonword condition, the participant heard, "Write this nonword, "followed by a verbal prompt for each item and six seconds to respond, for example, "'boke,' ... 'herm,' ... 'feen,' ... 'dewt,' ...

[1] The data for this study were previously presented in abstract form (Beeson & Rapcsak, 2003).