Neuropsychologia 64 (2014) 230–239

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Hemispheric differences in orthographic and semantic processing as revealed by event-related potentials

Danielle S. Dickson [a,*], Kara D. Federmeier [a,b,c]

[a] Department of Psychology, University of Illinois at Urbana-Champaign, 603 East Daniel St., Champaign, IL 61820, USA
[b] Program in Neuroscience, University of Illinois at Urbana-Champaign, 505 South Goodwin Ave, Urbana, IL 61801, USA
[c] Beckman Institute for Advanced Science and Technology, University of Illinois at Urbana-Champaign, 405 North Mathews Ave, Urbana, IL 61801, USA

ARTICLE INFO

Article history:
Received 6 June 2014
Received in revised form
1 September 2014
Accepted 22 September 2014
Available online 30 September 2014

Keywords:
ERPs
N400
Orthographic neighborhood
Cerebral hemispheres
Visual word recognition

ABSTRACT

Differences in how the right and left hemispheres (RH, LH) apprehend visual words were examined using event-related potentials (ERPs) in a repetition paradigm with visual half-field (VF) presentation. In both hemispheres (RH/LVF, LH/RVF), initial presentation of items elicited similar and typical effects of orthographic neighborhood size, with larger N400s for orthographically regular items (words and pseudowords) than for irregular items (acronyms and meaningless illegal strings). However, hemispheric differences emerged on repetition effects. When items were repeated in the LH/RVF, orthographically regular items, relative to irregular items, elicited larger repetition effects on both the N250, a component reflecting processing at the level of visual form (orthography), and on the N400, which has been linked to semantic access. In contrast, in the RH/LVF, repetition effects were biased toward irregular items on the N250 and were similar in size across item types for the N400. The results suggest that processing in the LH is more strongly affected by wordform regularity than in the RH, either due to enhanced processing of familiar orthographic patterns or due to the fact that regular forms can be more readily mapped onto phonology.

1. Introduction

Most skilled readers have the perception that they are not performing a particularly impressive feat by extracting meaningful information from letters strung together on a page, but decades of research and the prevalence of reading disorders suggests that this undertaking is actually quite challenging for the brain to accomplish. Part of the challenge comes from the fact that reading is a multifaceted process, involving the recognition of visual patterns that make up letters, letter combinations, and words, and linking these both to phonological information (important for reading aloud) and to meaning. Across languages, and across different types of inputs within a language, wordforms differ in the extent to which they are regular (follow the orthographic patterns of that language), phonologically transparent (pronounceable using conventional spelling-to-sound "rules"), and familiar. Electrophysiological studies have pointed to important similarities in when and how these types of inputs are linked to meaning (Laszlo and Federmeier, 2008, 2009, 2011; Kutas and Federmeier, 2011; Maurer et al., 2008; Fischer-Baum et al., 2014). Yet, the underlying neural mechanisms that support reading – and, especially, how these might differ for various types of inputs and task situations – remain unclear.

Studies examining the neurobiology of reading (and of language processing more generally) have described a network of areas in the left cerebral hemisphere (LH) that seem to be critical for various aspects of word recognition (for a review, see, e.g., Price, 2012). Most commonly, the process of decoding letter strings to map their orthographic (and/or phonological) representations onto appropriate semantic information has been associated with the left occipito-temporal region (including what is sometimes called the "Visual Word Form Area" or VWFA, McCandliss et al., 2003), which has been proposed to be a hub along the ventral visual pathway that integrates lower-level visual features from posterior, occipital regions with higher-level lexico-semantic properties of stimuli from more anterior regions (Twomey et al., 2011; see Wandell et al., 2012 for a discussion of the challenges facing this research line). Although activation of the right hemisphere (RH) homologs of these areas is typical in early stages of normal reading development (e.g., Waldie and Mosley, 2000), studies of adults with reading disorders have described abnormal lateralization patterns including hypoactivation and disturbances in LH areas, interpreted as a possible causal factor in dyslexia (Shaywitz and Shaywitz, 2008), and increased bilateral recruitment,

* Corresponding author. Tel.: +1 858 699 5455.
E-mail addresses: ddicksn2@illinois.edu (D.S. Dickson), kfederme@illinois.edu (K.D. Federmeier).

http://dx.doi.org/10.1016/j.neuropsychologia.2014.09.037
0028-3932/

interpreted as a co-occurring indicator of specific language impairment (e.g., Whitehouse and Bishop, 2008; De Guibert et al., 2011).

Interestingly, however, when typically developing readers are examined, bilaterality and/or RH dominance is not linked to lowered reading outcomes and is sometimes connected to better reading skills (Bishop, 2013). Moreover, there is evidence from studies of commissurotomized patients (e.g., Zaidel and Peters, 1981; Zaidel, 1983), as well as electrophysiological and fMRI data from neurally intact readers (e.g., Seghier and Price, 2011; Mei et al., 2013; Federmeier et al., 2008), indicating that the RH is not only able to map word forms to meaning but contributes to normal language comprehension, through the use of processing mechanisms that are importantly different from those used by the LH. This suggests that when the brain is otherwise typically functioning, the participation of the RH is not necessarily a hindrance and that accounts of reading exclusively focusing on the LH may be underestimating RH contributions. The question then becomes what specific contributions each hemisphere might be making to the decoding of words.

Behavioral assessments of hemispheric processing differences in populations without neural damage often employ the visual half-field method, in which presentation of items is lateralized to fall into either right or left visual field. Due to the anatomy of the visual system, this results in preferential processing by the hemisphere contralateral to the visual field of presentation (see Banich, 2002 for a review of this method). Studies of this nature usually find that perceptual accuracy is greater and that readers perform more quickly and accurately on lexical decision tasks (i.e., discriminating between words and non-words) when items are presented in the right visual field (RVF) than in the left visual field (LVF). This bias has been attributed to the more efficient processing of verbal information in the LH (e.g., Jordan et al., 2003a; see also Bradshaw and Nettleton, 1983, for a review), but the nature of this efficiency is a matter of debate. Ellis (2004) has claimed that RVF/LH advantages are the result of parallel processing of whole strings, versus more sequential RH processing mechanisms. In contrast to this view, Jordan et al. (2000) have reported that attention is allocated over strings similarly in both hemispheres, suggesting that mechanisms other than simple text decoding (i.e., other than letter processing) differ across the hemispheres.

One source for a LH advantage in word recognition may be that the LH is more sensitive to regularities in orthographic structure and/or to the mapping between orthographic and phonological features of words. For example, Jordan et al. (2003a) found RVF/LH processing advantages for words and pseudowords but no advantage for nonword strings, suggesting a bias for processing orthographically regular inputs, independent of their meaningfulness (see also Jordan et al., 2003b; Young et al., 1984). This sensitivity to orthographic regularity may be related to the LH's superior abilities at mapping orthographically transparent (i.e., alphabetic) text onto phonological information. Behavioral and neuropsychological evidence from commissurotomized and deep dyslexic patients suggests that phonological processing is dependent on an intact LH (Zaidel and Peters, 1981; Rapcsak et al., 2009; see Peleg and Eviatar, 2012, for a review of behavioral work in support of this view). In healthy controls, after participants were trained to read an unfamiliar script (modified Korean) in an orthographically transparent manner, designed to mimic the reading of alphabetic languages, activations became more left-lateralized in the posterior section of the previously-described occipito-temporal ("VWFA") region than prior to training. Conversely, activations became less left-lateralized when a matched group of participants were taught to read the same scripts in a logographic/"holistic" manner, designed to mimic the reading of Chinese and more opaque languages (Mei et al., 2013). This suggests an important role for the LH in the decoding of scripts whose words comprise decomposable patterns that map predictably onto phonological representations, as opposed to the processing of scripts containing individual logographs, whose mapping to phonology is indirect. For English, these findings suggest that the reading of orthographically regular items, which can be pronounced using well-learned spelling-to-sound patterns, may be more dependent on LH function.

Despite these LH advantages, the RH has been found to be more sensitive to some aspects of the written form of text (Lindell, 2006; Beeman and Chiarello, 1998; Ellis, 2004; c.f. Jordan et al., 2003b). For example, there are LVF/RH advantages for encoding letter strings veridically (Marsolek, 2004; Tzeng et al., 1979) and retaining that information over time (Federmeier and Benjamin, 2005; Evans and Federmeier, 2007). These findings are consistent with fMRI object recognition work showing that right occipito-temporal cortex priming is more form-specific than that seen in the homologous left regions that are typically involved in word processing (Koutstaal et al., 2001). Furthermore, similar to the pattern in the Mei et al. (2013) study described above, more bilateral or RH-biased activations are also observed when participants read orthographically opaque Chinese characters relative to when they read English words (Peng and Wang, 2011; Tan et al., 2000; in these studies, however, visual complexity is necessarily confounded across scripts). Thus, the RH may be important for decoding orthographically irregular items in English – including, for example, acronyms – that are not pronounceable using conventional spelling to sound rules

Taken together, the existing word recognition literature suggests that the processes used to link wordforms to meaning and other higher-level information are different across the hemispheres, with a notable lack of phonological processing and an emphasis on retention of holistic physical form in the RH. Although there are important similarities in how the full range of string types – meaningful and novel, regular and irregular – access meaning (Laszlo and Federmeier, 2007, 2008, 2011), these asymmetries suggest that both hemispheres may be contributing to normal word recognition, but doing so differently and, in particular, making contributions that vary in their import for different types of inputs. The current study, therefore, was designed to examine how the hemispheres process the full range of types of strings, crossing orthographic regularity and meaningfulness by looking at words (meaningful and regular), pseudowords (regular but not meaningful), acronyms (meaningful but not regular), and illegal nonwords (neither regular nor meaningful).

A limitation of the current literature is that it mostly derives from end state behavioral data, which sums across multiple perceptual and cognitive processes whose individual influences can be difficult to disentangle, or from fMRI data, which provides some functional specificity through localization but with a temporal resolution that is not well suited to tracking word recognition on its native millisecond-level timescale. Therefore, we collected event-related potential (ERP) data, which comprise functionally specific responses that can reveal how word recognition unfolds with high temporal resolution. In particular, we examine two components, the N250 and the N400. The N250 is a visually-evoked component, beginning around 150 ms and peaking around 250 ms with a wide-spread, slightly left-lateralized scalp distribution, which has been shown to be responsive to orthography properties of stimuli (Holcomb and Grainger, 2006; Grainger and Holcomb, 2009). To date, the N250 has been characterized only in the context of masked repetition priming, wherein amplitude reductions have been observed for strings (words and pseudowords) with orthographic overlap. Ours is the first study to examine and characterize N250 effects in the absence of masking, and in a lateralized design. Our primary focus, however, is on the N400, a negative-going waveform with a stable timecourse that onsets around 250 ms and