HEMISPHERIC DIFFERENCES IN ORTHOGRAPHIC AND SEMANTIC PROCESSING AS REVEALED BY EVENT-RELATED POTENTIALS

BY

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THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Arts in Psychology
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2014

Urbana, Illinois

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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.

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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 & Federmeier, 2008, 2009, 2011; Kutas & Federmeier, 2011; Maurer et al, 2008; Fischer-Baum et al, in press). 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, 2012 for a discussion of the challenges facing this research line). Although activation of the right hemisphere (RH) homologues of these areas is typical in early stages of normal reading development (e.g., Waldie & 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 & Shaywitz, 2008), and increased bilateral recruitment, interpreted as a co-occurring indicator of specific language impairment (e.g., Whitehouse & 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 & Peters, 1981; Zaidel, 1983), as well as electrophysiological and fMRI data from neurally intact readers (e.g., Seghier & 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 & 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 and colleagues (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 (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, 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 & Peters, 1981; Rapcsak et al, 2009; see Peleg & Eviatar, 2011, 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 & Chiarello, 1998; Ellis, 2004; c.f. Jordan, 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 & Benjamin, 2005; Evans & 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 & 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 & 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 & Grainger, 2006; Grainger & 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 peaks just prior to 400ms in healthy young adults, which constitutes part of the normal response to (potentially) meaningful stimuli. The N400 has been broadly characterized as a functionally specific marker of semantic access and has been used extensively in studies of word recognition to better understand the factors influencing the extraction of meaning from text (see Kutas & Federmeier, 2011, for a review of the N400 component).

The amplitude of the N400 to out-of-context visually-presented strings has been characterized as reflecting the general structure of the lexico-semantic network (Laszlo & Federmeier, 2011). In studies that presented strings in central vision, N400 amplitude was strongly related to orthographic neighborhood size (operationalized by Coltheart's N), such that higher N items (i.e., those that are similar to more words) elicited larger amplitude N400s than did lower N items, regardless of their lexicality (Holcomb et al, 2002; Laszlo & Federmeier, 2011). Here, therefore, we can use the N400 in response to items presented to the RVF or LVF as a probe of the overall structure of the lexico-semantic network that is contacted by information coming in through each hemisphere. Although behavioral data has suggested that only RVF/LH presentation results in sensitivity to orthographic regularity in the form of accuracy differences between words (and, in some cases, pseudowords) and illegal strings

(Jordan et al, 2000, 2003a), this was found in the context of a specific letter identification task. By measuring ERPs, we can examine effects as participants read words for comprehension, and we use a design that allows a separation of effects of familiarity/meaningfulness and regularity, which were confounded in some prior work. Moreover, we examine the effects of these factors both on the initial apprehension of words, as well as on the later-formed representation, whose nature can be probed by repetitions.

When items are encountered for a second time after a short to moderate delay, N400 amplitudes are reduced, and this is known as the “N400 repetition effect” (also reviewed in Kutas & Federmeier, 2011). This effect reveals some form of memory for the prior encounter with that item; preservation of the N400 repetition effect in patients with amnesia (Olichney, 2000) shows it does not require explicit recollection (and is not hippocampally dependent). The N400 repetition effect, therefore, can serve as a probe for the maintenance of information about wordforms. With central presentation, significant -- and equivalent -- N400 repetition effects have been found for words, pronounceable pseudowords, and meaningful acronyms (Rugg & Nagy, 1987; Laszlo & Federmeier, 2007); thus, despite baseline differences in N400 amplitude across these item types due to orthographic regularity, all are reduced (compared to that baseline) to a similar degree upon repetition. Illegal strings do not always elicit repetition effects, but can do so when task demands encourage that these items are processed deeply (Laszlo et al, 2011). These effects indicate a global similarity in the brain’s ability to retain information about meaningful and meaningless and orthographically regular and irregular stimuli. However, given the evidence just reviewed, it seems likely that the hemispheres could make different contributions to the extraction and maintenance of semantic information from text, such that the global similarity across item types is an emergent property of asymmetrically distributed processing resources -- with the LH more important for the decoding of regular items, and the RH more useful for irregular items like acronyms.

In lateralized designs using ERPs, when only the initial item or its repetition is lateralized, N400 repetition effects for real words are robust in both hemispheres, and, at long delay intervals, are larger for words originally encoded in the LVF/RH (Evans & Federmeier, 2007, 2009). This pattern, combined with the finding of enhanced potentials associated with sensory processing and attention (the P2) for LVF/RH encoded items at all retention intervals, was taken as evidence, consistent with the literature reviewed above, that the RH encodes words more veridically, allowing for processing benefits when other types of memory signals are weaker (c.f., Federmeier & Benjamin, 2005). ERP studies that lateralized both the first and the second presentation of items have found mixed results, likely because of very small sample sizes (Nowicka & Szatkowska, 2004; Nowicka et al, 2006). In one study with a larger sample size (Doyle & Rugg, 1998), repetition within either hemisphere resulted in reduction upon second presentation for pseudowords and for regular words. However, because these were immediate repetitions and a judgment was required, it is difficult to separate N400 effects from those arising on late positivities (c.f., Evans & Federmeier, 2007). In sum, the extant ERP literature suggests that N400 repetition effects can be obtained in either hemisphere, at least for words. To our knowledge, no lateralized repetition study with ERPs has examined any type of orthographically illegal items, making the present results particularly informative about how semantic information is accessed and retained in each hemisphere across levels of familiarity and orthographic regularity.

If the pattern of effects on the N400, or the earlier N250, is different for words and acronyms than for pseudowords and illegals strings, this would indicate sensitivity to the lexicality/familiarity of wordforms. A pattern in which effects are different for words and pseudowords compared to acronyms and illegal strings would suggest a regularity bias, which might emerge either as a preferential processing of regular forms (as might be expected for the LH) or a preferential processing of forms that load more heavily on visual analysis due to their irregularity (as might be expected for the RH). This study will thus allow us to reveal both the capabilities of the hemispheres and the nature of their likely contributions to normal word processing.

Methods

Participants

Data were analyzed from thirty-six young adults recruited from the University of Illinois community either for course credit or pay. All were right-handed native monolingual English speakers (18 female, 18 male) with no early exposure to a second language and had normal or corrected-to-normal vision, no history of brain trauma, and no current use of psychoactive medications. Mean age was 20, with a range spanning 20-27 years. Mean laterality quotient was 0.81 with a range spanning 0.15 to 1.0 (where 1.0 is strongly right handed; -1.0 is strongly left handed) on the Edinburgh handedness inventory (Oldfield, 1971). Nineteen participants reported having a left-handed biological family member.

Four additional participants were replaced due to inability to suppress eye movements, two participants were replaced due to stimulus code recording failures, and one participant was replaced due to failure to perform the task as instructed.

Stimuli

Items and lists were adapted from those used in previous studies (Laszlo & Federmeier, 2011; Laszlo et al 2011). There were 75 items from each of four categories: words (e.g., BUS, QUIZ), pronounceable pseudowords (e.g., VORD, KIB), orthographically illegal acronyms (e.g., CNN, NYPD) and meaningless illegal strings (e.g., CNC, TMST). Acronyms were consonant clusters of 3-5 letters, with the exception of the vowel cluster “AAA” and the strings “WWI”/”WWII”. Illegal, meaningless strings were of two subtypes: clusters of consonants found in words (e.g., GHT) and transforms of acronyms created by replacing the first and last letters of one acronym with those from another (e.g., the Q and V of QVC created an illegal string QTV by using the T present in the acronym BTW). Target stimuli were 150 common American first names (e.g., SEAN, LIZ). Stimuli were altered only in that each of the five stimulus types were divided evenly into right and left visual field conditions (counterbalanced across participants).

Quantitative values of lexical properties for each item were derived from the Medical College of Wisconsin Orthographic Wordform Database (Medler & Binder, 2005) for orthographic neighborhood size (N) and from the Wall Street Journal corpus (Marcus et al, 1993) for frequency estimates. The mean length across all item types is 3.2; the frequency of words (2.39) is on average higher than that of acronyms (0.96). Words and pseudowords have higher average N values (13.0 and 11.0, respectively) than acronyms and illegal strings (1.9 and 2.4, respectively). For all items, the lexical variables of N, length, and neighbor frequency were balanced across visual field. Word and acronyms were additionally balanced for frequency across visual field.

Familiarity with acronym items and unfamiliarity with illegal strings was measured for each participant with a pencil-and-paper questionnaire administered after the experiment. Only acronym items for which an individual participant was able to provide a meaning were included in his/her average, and illegal string items were excluded when a participant indicated that they were meaningful by providing a sensible definition (e.g., RTHS defined as “Rantoul Township High School”). On average, subjects were familiar with 66/75 (88%) of the acronym items and were unfamiliar with 72/75 (96%) of the intentionally meaningless illegal string items.

Following Lazslo & Federmeier (2011), all non-name items were repeated after lags of either 0 (immediate repetitions), or 2 or 3 (delayed repetitions) intervening items. All combinations of stimulus type (e.g., RVF words, LVF pseudowords) occurred with equal frequency within and across each of the three lag conditions. Analyses will focus on delayed repetitions, but the inclusion of immediate repetitions served to help promote attention and to prevent participants from guessing when items would repeat.

Procedure

Participants were seated 100cm from the computer monitor and instructed to respond with a button-press as fast as possible without losing accuracy to proper name targets; response hand was counterbalanced across participants. They were additionally instructed to repress lateral eye movements and to blink only during the approved interval, indicated by the presence of a white cross. A small white fixation dot was present at approximately 0.3° of visual angle below vertical center of the black screen at all times, and items in capital letters, in white Arial font, appeared laterally for 200ms (spanning 0.6° of vertical angle, with a medial edge 2° from visual center; items subtended a range of 1.6° to 3.2°) with an interstimulus interval of 2000ms. This interval consisted of 1000ms of a blank screen, 500ms of a white fixation cross, during which subjects were allowed to blink, and 500ms of a red fixation cross to serve as a warning that the next item was about to appear. The stimulus lists were broken into five blocks, between which participants were provided a short break.

EEG Recordings

Brainwaves were recorded using 26 silver/silver-chloride electrodes mounted in an elastic cap, with electrode impedances kept below 5kΩ. Electrodes were evenly distributed over the scalp (see Figure 1 for the arrangement). The vertical electrooculogram (EOG) signal was monitored with an electrode on the infraorbital ridge and horizontal EOG was monitored with electrodes placed on the outer canthus of each eye. The data were referenced on-line to the left mastoid and re-referenced offline to an average of the right and left mastoids. A separate frontocentral electrode acted as ground. EEG signal was sampled at a 250 Hz and subjected to an analog bandpass of 0.02 to 100 Hz during online amplification by Sensorium amplifiers.

Raw waveforms were assessed for inclusion on a trial-by-trial basis with artifact thresholds separately calibrated by visual inspection for each subject. Trials were excluded from averaging if they included blinks, movement artifacts, signal drift, blocking, or a horizontal eye gaze movement. Additional trials were removed if they were a repetition for which the corresponding first presentation included a horizontal saccade. Critical trials in which subjects false alarmed (reporting a name) were removed; this occurred at a rate of 4.5%, not including trials that were excluded from performance analysis due to artifacts.

For eleven subjects who had overall trial loss exceeding 20% and at least 15 blink-contaminated trials, the trials that were excluded from inclusion only due to blink artifacts were corrected and reintroduced to the average (in a procedure described by Dale, 1994). After artifact rejection, critical bins included 22 trials on average, and no individual subject had fewer than 10 critical trials in any bin.

Epochs of EEG data for each trial were taken from 100ms prior to item onset until 920ms after item onset, and the baseline acquired over the 100ms preceding the onset of each trial was subtracted prior to averaging. ERP mean amplitudes were measured after application of a digital bandpass filter of 0.2 to 20 Hz. Measurements of second presentation items collapsed across trials with either 2 or 3 intervening items in the interest of increasing trial counts and because prior use of this stimulus set in central vision had not elicited significant differences across these lag lengths (Laszlo & Federmeier, 2011).

Results

Behavior

Accuracy on the name recognition task revealed a small but significant advantage for names presented in the RVF/LH, with an average hit rate of 78% for RVF /LH and 74% for LVF/RH ($t(35) = 2.70$; $p < 0.05$). This is consistent with existing literature showing more accurate apprehension of word forms after RVF/LH exposure than LVF/RH (Jordan et al, 2000, 2003a; 2003b). A paired *t*-test assessed target detection sensitivity, operationalized through *d'* using false alarm rates to the first presentation of non-name items. This showed that participants were also more sensitive in their detection of RVF/LH than LVF/RH names ($t(35) = 3.02$; $p<.005$). Mean *d'* for RVF/LH items was 2.75, whereas for LVF/RH it was 2.48. Despite this VF-based difference, overall accuracy and sensitivity were high, showing that participants were able to apprehend the lateralized stimuli and process them for meaning.

First Presentation ERP Effects

N400 amplitude patterns for the first presentations of words have been used to probe the structure of the lexico-semantic network with which that word makes contact (see Laszlo & Federmeier, 2008, 2011, for examples with central presentation). Therefore, we measured N400 component amplitude[1] in a timewindow from 350 to 500 ms post-item-onset to capture the average latency of the peak across all conditions and channels (411ms, SE = 0.52). Mean amplitudes over all channels were submitted to an omnibus ANOVA with two levels of Visual Field (RVF/LH versus LVF/RH), two levels of Orthographic Regularity (orthographically regular/high N versus irregular/low N), two levels of Meaningfulness (meaningful/familiar versus non-meaningful/unfamiliar), and 26 levels of Electrode Site. This revealed a significant

[1] The N250 has been characterized only as an effect in the context of repetition. Given the lack of available comparison data and the fact that it is not possible to unambiguously separate the N250 and N400 based on raw component characteristics, we did not perform a targeted analysis of the N250 for the first presentation data.

main effect of Orthographic Regularity ($F(1,35) = 33.43$, $p < 0.001$). Figure 1 shows that this response followed the typical pattern (e.g., Holcomb et al, 2002; Laszlo & Federmeier, 2008, 2011) in which N400 responses were larger (more negative) to high N items (words and pseudowords, μV = -1.20, SE = 0.07) than to low N items (acronyms and illegal strings, μV = 0.01, SE = 0.07). There were no main effects of Visual Field ($F(1,35) = 0.01$, $p > 0.5$) or Meaningfulness ($F(1,35) = 1.25$, $p > 0.10$), nor were there any interactions of experimental (non-electrode) variables (all *F*'s < 1).

ERP Repetition Effects

Figure 2 shows the expected repetition effect for words across both hemispheres at a representative sample of nine channels. In both visual fields, repetitions elicited a widespread reduction in negativity, which had the typical distribution of both N250 and N400 repetition effects (largest over medial, central sites).

N250 time window: To characterize effects on the N250, mean amplitudes at all channels between 250 and 350 ms were subjected to an ANOVA with two levels of Visual Field (RVF/LH versus LVF/RH), two levels of Repetition (first presentation versus second presentation), two levels of Orthographic Regularity (regular/high N versus irregular/low N), two levels of Meaningfulness (meaningful/familiar versus nonmeaningful/unfamiliar), and 26 levels of Electrode Site. There was a main effect of Visual Field ($F(1,35) = 10.97$, $p < .01$), with RVF/LH presentation (μV = 1.27; SE = 0.04) eliciting smaller amplitude responses than LVF/RH presentation (μV = 0.71; SE = 0.04), and of Repetition ($F(1,35) = 32.76$, $p < 0.001$), with first presentation (μV = 0.63; SE = 0.04) eliciting larger (less positive) amplitude N250s than second presentation (μV = 1.35; SE = 0.04). There were also main effects of Orthographic Regularity ($F(1,35) = 6.91$; $p < 0.05$), with regular/high N items eliciting larger N250s (μV = 0.80; SE =

0.04) than irregular/low N items (μV = 1.18; SE = 0.04), and of Meaningfulness (*F*(1,35) = 8.91; p < 0.05), with meaningful/familiar items eliciting smaller N250s (μV = 1.17; SE = 0.04) than non-meaningful/unfamiliar items (μV = 0.81; SE = 0.04). None of the two-way interactions of experimental variables was significant (all *F*'s < 1.25), nor was the four-way interaction among them (*F*(1,35) = 0.08; p > 0.50). The three-way interactions of experimental variables were also non-significant (*F*'s < 1.05), except for an interaction between Visual Field, Repetition, and Orthographic Regularity (*F*(1,35) = 4.41; p < 0.05).

To follow up on this interaction, we created difference waves (first presentation minus second presentation) and performed an ANOVA with two levels of Hemisphere and two levels of Orthographic Regularity, resulting in an interaction between Visual Field and Orthographic Regularity (*F*(1,35) = 4.59, p < 0.05) and no main effects of Hemisphere or Orthography (*F*'s < 1.35). This interaction was the result of there being larger repetition effects for regular/high N items than irregular/low N items in the RVF/LH and larger repetition effects for irregular/low N items than regular/high N items in the LVF/RH. Pairwise comparisons of repetition effects within each hemisphere showed that there were N250 repetition effects for both regular/high N items (*F*(1,35) = 21.69; p < 0.001) and irregular/low N items (*F*(1,35) = 5.51; p < 0.05) with RVF/LH presentation, but with LVF/RH presentation, repetition effects only reached significance for irregular/low N items (*F*(1,35) = 17.83; p < 0.001) and not for regular/high N items (*F*(1,35) = 2.16; p > 0.10).

<u>N400 time window:</u> As in the N250 time window, to analyze repetition effects on the N400 mean amplitudes at all channels between 350 and 500 ms were subjected to an ANOVA with two levels of Visual Field (RVF/LH versus LVF/RH), two levels of Repetition (first presentation versus second presentation), two levels of Orthographic Regularity (regular/high N

versus irregular/low N), two levels of Meaningfulness (meaningful/familiar versus nonmeaningful/unfamiliar), and 26 levels of Electrode Site. There was no main effect of Visual Field ($F(1,35) = 0.65$; $p > 0.10$). The expected, typical main effect of Repetition was observed ($F(1,35) = 46.00$, $p < 0.001$), with second presentation items (μV = 0.19; SE = 0.05) eliciting smaller (more positive) N400s than first presentation items (μV = -0.60; SE = 0.05). There were also main effects of Orthographic Regularity ($F(1,35) = 21.24$, $p < 0.001$), with regular/high N items (μV = -0.67; SE = 0.05) having larger amplitude N400s than irregular/low N items (μV = 0.27; SE = 0.05), and Meaningfulness ($F(1,35) = 4.17$; $p < 0.05$), with meaningful/familiar items (μV = -0.05; SE = 0.05) having smaller amplitude N400s than nonmeaningful/unfamiliar items (μV = -0.36; SE = 0.05)[2].

The main effects were modulated by interactions between Hemisphere and Orthographic Regularity ($F(1,35) = 5.52$; $p > 0.05$) and Repetition and Orthographic Regularity ($F(1,35) = 6.53$; $p > 0.05$), as well as a three-way interaction of Hemisphere, Repetition, and Orthographic Regularity ($F(1,35) = 7.69$; $p < 0.01$). All other interactions between experimental variables, including all interactions with Meaningfulness, were non-significant (F's < 1.22). The three-way interaction between Hemisphere, Repetition and Orthographic Regularity indicates that repetition effect patterns across levels of Orthographic Regularity were different in the two VFs regardless of the item's meaningfulness/familiarity. This interaction was thus further examined within each VF condition by ANOVAs with two levels of Repetition (first, second), two levels of Orthographic Regularity (regular/high N, irregular/low N), and 26 levels of Electrode Site.

With presentation to the RVF/LH, there were main effects of both Repetition ($F(1,35) = 24.07$, $p < 0.0001$), with larger (more negative) amplitudes for first presentation (μV = -0.59; SE

[2] The direction of the effect of Meaningfulness follows the typical frequency effect wherein less frequent (ie, unfamiliar) items elicit larger amplitude N400s than do high frequency items (e.g., Van Petten & Kutas, 1990; Vergara-Martinez & Swaab, 2012).

=0.09) than second (μV = 0.32; SE = 0.09), and Orthographic Regularity ($F(1,35) = 8.02$, $p < 0.01$), with larger amplitudes for regular/high N items (μV = -0.46; SE = 0.09) than irregular/low N (μV = 0.19; SE = 0.09. Additionally, there was an interaction between Repetition and Orthographic Regularity ($F(1,35) = 15.37$, $p < 0.001$). In follow-up pairwise tests, the 1.49 μV repetition effect for regular/high N items was statistically significant ($F(1,35) = 42.22$, $p < 0.001$), whereas the 0.32 μV repetition effect for irregular/low N items was not ($F(1,35) = 1.74$, $p > 0.10$). A comparison of the size of the repetition effects (on difference waves) confirmed that regular/high N items elicited a larger difference across presentations than did repetition of irregular/low N items ($F(1,35) = 15.36$; $p < 0.001$). That is, the RVF/LH interaction between Repetition and Orthographic Regularity was due to larger and more reliable repetition effects for orthographically regular/high N items than for irregular/low N items.

With presentation to the LVF/RH, the same analysis of Hemisphere, Repetition, and Orthographic Regularity only yielded main effects of Repetition ($F(1,35) = 15.94$, $p <0.001$) and Orthographic Regularity ($F(1,35) = 23.19$, $p < 0.001$), with patterns similar to those seen in the RVF/LH. However, critically, there was no interaction between Repetition and Orthographic Regularity ($F(1,35) = 0.15$, $p > 0.50$). Indeed, pairwise tests found that both the 0.59 μV effect of repetition for regular/high N items and the 0.71 μV effect of repetition for irregular/low N items were statistically significant (regular: $F(1,35) = 7.92$, $p < 0.01$); irregular: $F(1,35) = 8.99$, $p < 0.01$), and these repetition effects were not different in size (($F(1,35) = 0.15$; $p > 0.50$). Thus, whereas repetition effects in the RVF/LH were larger for orthographically regular / high N items, repetition effects in the LVF/RH were not similarly influenced by orthographic regularity.

Discussion

When a reader encounters a string of letters, the brain attempts to link this potential word to various types of information – for example, identifying what the subpart features are, what the wordform might mean, and how it might sound or be pronounced. There are some important similarities in how all item types are processed: all have been shown to make contact with long-term memory in a timewindow around 400 ms, eliciting N400 responses and effects on this component (e.g., pseudowords, which have subpart regularity and therefore are similar to many known words but have no learned meaning, and acronyms, which are irregular but globally linked to meaning, both elicit N400 repetition effects: Laszlo & Federmeier, 2007, 2011; Laszlo et al, 2011). However, the extent to which and the ease with which different kinds of input can be linked to different types of information varies across tasks (Laszlo et al, 2011; Fischer-Baum et al, in press) as well as across types of items, and may involve different brain networks.

In particular, patterns across the literature have suggested differential involvement of the two cerebral hemispheres in extracting different types of information from visual wordforms (for reviews, see Federmeier et al, 2008; Lindell, 2006; Peleg & Eviatar, 2011; Price, 2012). The extraction of phonological information from strings, and the reading of orthographically transparent wordforms more generally, seems to especially recruit LH processing resources, whereas contributions from the RH have been found to become more important for tasks that require the extraction and maintenance of physical form information about words, as well as the reading of languages with logographic writing systems more generally (Lindell, 2006; Peleg & Eviatar, 2011; Zaidel & Peters, 1981; Mei, 2013). In the present study, we directly tested the idea that there are hemispheric biases in the ability and/or tendency to extract information from visual wordforms by using item types that varied systematically in both familiarity and regularity and measuring ERPs in a visual half-field design. We examined both the N250, a component that has been associated with orthographic processing (Grainger & Holcomb, 2009), and the N400, which has been linked to a critical transition between orthographic processing and semantic access (Kutas & Federmeier, 2011). Responses to the first presentation of each item type were assessed to look at the structure of the lexico-semantic network, and measures of repetition effects were used to ascertain what type of representation is ultimately formed and available to be accessed later in time.

Prior work has shown that responses to out-of-context words (on first presentation) are characterized by larger N400 responses to high N items than to low N items, unaffected by the lexical status of the items (i.e., they were found for both words and pseudowords), showing that the N400 reflects an initial transition between perceptual analysis and semantics, prior to the recognition/identification of a single item (Laszlo & Federmeier, 2011; 2014). Thus, N400 responses to words out of context reflect the general structure of a reader's knowledge about words (e.g., which other words they resemble and how frequent those other words are). Some have suggested that this structure might be different across the hemispheres (Lavidor & Ellis, 2001; Jordan et al, 2003b), and the field has sometimes even seemed to assume that the RH lacks a lexicon (e.g., in discussions of the LH VWFA; Cohen & Dehaene, 2003; Vicknier 2007). The N400 response to first presentation of these different item types across VF provides a new and more direct way to test these claims.

We found that first presentation of items showed the same pattern of effects across both hemispheres, in which irregular/low N items (acronyms and illegal strings) elicited lower amplitude N400s than regular/high N items (words and pseudowords) (see Fig. 1). There were no additional effects of familiarity on N400 amplitudes during initial presentation to either hemisphere. This suggests that there is general similarity in how each hemisphere links orthographic inputs to semantics, with orthographic regularity being a primary determiner of the amount of semantic activation elicited by a wordform encountered out of context (cf, Laszlo & Federmeier, 2011; Laszlo & Federmeier, 2014).

Having shown that both hemispheres have a similar basic network that maps orthography to semantics -- and, more generally, that there are not important differences in the hemispheres' baseline response to different types of letter strings -- the central question for this study was whether there are differences in the stimulus properties prioritized by each hemisphere that could influence what information is retained about a wordform. To address this question, we examined the effects of repetition after a short delay (2-3 intervening items).

As is evident in Figure 3, the morphology of the waveforms revealed a negativity preceding the N400 – the N250. This waveform has primarily been characterized in repetition paradigms that employ masking of items and short stimulus-onset-asynchronies (e.g., Holcomb & Grainger, 2006, 2007), but here we observe it in response to fully viewed/perceived items at comparatively lengthy delay intervals. Previous experiments observed that the amplitude of the N250 reduces upon repetition for both words and pseudowords and that it is sensitive to the amount of orthographic overlap shared by primes and targets (Holcomb & Grainger, 2006; Grainger et al, 2006) but not to physical changes like positional shifts and font switches (Chauncey et al, 2008; Dufau et al, 2008). Unlike the N400, the N250 is thought to be domain-specific and does not appear in cross-modal priming studies (e.g., Kiyonaga et al, 2007). Notably, despite being linked to orthographic processing, its response characteristics to illegal strings have not been previously described. Furthermore, it has never been examined in a lateralized design, so this is the first reporting of its responsivity across the hemispheres.

N250 repetition effects were obtained for all item types; thus, these data provide initial evidence that N250 repetition effects can be obtained outside of the context of masked priming and that the processes involved in the N250 apply to orthographically irregular, as well as regular, inputs. However, there were hemispheric biases in the size of the N250 repetition effect as a function of orthographic regularity. Whereas in the RVF/LH, N250 repetition effects were larger for regular than for irregular inputs, the opposite pattern arose in the LVF/RH, where regular items did not show a robust N250 effect in pairwise tests. Asymmetries based on the regularity of the input then continued into the N400 time window.

Studies using central presentation have reported N400 repetition effects that are similar in size, timing, and distribution for words, pseudowords and acronyms (Rugg & Nagy, 1987; Laszlo & Federmeier, 2007, 2011). Although irregular nonmeaningful items do not always show repetition effects, they can if readers are not able to quickly dismiss them as task irrelevant, and, in those cases, the effects are also similar in size, timing, and distribution to repetition effects seen for regular and familiar items (Laszlo et al, 2011). Thus, there are important similarities in how irregular and regular, as well as familiar and unfamiliar, items are processed for semantics. The central question of interest for this study, then, was whether these similar outcomes arise from differentiable mechanisms, distributed across the cerebral hemispheres. In fact, we found that both hemispheres manifested N400 repetition effects of overall similar magnitude, but that the pattern of these effects across stimulus type was qualitatively different.

With presentation to the RVF/LH, we found that repetition interacted with orthographic regularity, such that regular, pronounceable items elicited more robust repetition effects than did irregular items over the 2-3 item delay period. One explanation for this pattern of results is that the LH is sensitive to orthographic structure, either at a general level (e.g., the LH prioritizes the processing of items that contain mixes of consonants and vowels) or at a specific level (e.g., the LH is sensitive to the low-level statistics of words, such as the statistical frequency with which particular letter combinations are encountered). The irregular strings' lack of coherent structure might have reduced the engagement of LH processing mechanisms relative to that for the orthographically regular items. Alternatively, this pattern may have occurred because these irregular items were unpronounceable by conventional mappings from orthography to phonology (most did not even contain vowels). Thus, a possible source for the LH pattern may come from its better-developed mappings between word forms and phonology. This second interpretation in particular is consistent with literature finding greater left-lateralized activation patterns for alphabetic languages than opaque ones (Peng & Wang, 2011; Tan et al, 2000; Tzeng, 1979). That is, greater left hemisphere recruitment seems to occur for more orthographically transparent languages, wherein mappings between orthography and phonology are generally predictable and in which letters/symbols require relatively less visuospatial analysis to decode (cf, Mei et al, 2013, who also showed this pattern with wordforms that were visually matched across levels of transparency).

The finding that N400 repetition effects in the RVF/LH are biased toward regular items -- indeed, irregular items did not show a reliable N400 repetition effect at all -- builds on the pattern seen earlier on the N250, wherein repetition effects were biased towards regular items, although, in this time window, there were reliable repetition effects for irregular items as well. Thus, a bias toward regularity evident in stages of processing that have been linked to orthographic analysis (the N250) was maintained or even increased at the level of semantic processing (N400), such that activations were maintained only or primarily for regular items. This enhancement of the sensitivity to orthographic structure and regularity from the N250 to the

N400 could arise because of additional contributions from phonological mappings to related semantic representations, which would be more strongly reflected on the N400 than on a lower-level visual component like the N250. Notably, the RVF/LH pattern of repetition effects does not match any of the findings from central studies, which consistently obtain repetition effects for irregular items (at least for acronyms and sometimes also for meaningless illegal strings).

In the LVF/RH, we found a different pattern, in which N400 repetition effects were robust across stimulus type: repetition effect size was unaffected by regularity or by familiarity. This is consistent with the idea that the RH uses a more bottom-up, visually motivated strategy that operates similarly across all visual forms, including readily pronounceable and unpronounceable strings (Evans & Federmeier, 2007; Federmeier, 2007; Benjamin & Federmeier, 2005). This processing strategy could explain the RH advantage in tasks wherein the visual properties of words matter (e.g., case judgments) and its increased involvement in processing orthographies that place more demands on memory of visual form or on visuospatial analysis (e.g., Marsolek, 1999; Tan et al, 2000). Here, we see dissociations between the N250 and N400, such that although there was no reliable N250 repetition effect for regular items, by the time of the N400 these items did elicit robust repetition effects. Thus, processing at an orthographic level favored irregular items (opposite of the RVF/LH pattern, which favored regular items), whereas processing at the semantic level was equivalent across stimulus type. Interestingly, in the LVF/RH, the N400 repetition effect was observed even for illegal strings, perhaps because lateralizing them rendered them harder to read and less easy to dismiss as non-targets. These findings, combined with the lack of a repetition effect for irregular items in the LH, suggest that repetition effects in central vision for acronyms (and sometimes also for illegal strings) are likely the result of RH processing mechanisms.

In summary, this work used a within subjects design to reveal and confirm biases in how the hemispheres process different types of visual wordforms. Orthographic processing, as measured in repetition effects on the N250, seems to be skewed such that the LH favors regular items whereas the RH prioritizes irregular items. Semantic analysis, as measured in repetition effects on the N400, shows related biases, such that the LH shows a larger effect for orthographically regular items than irregular, whereas the RH seems to extract semantic information from all types of visual wordforms more uniformly, perhaps through more “direct” mappings from visual form to meaning. As only a combination of the patterns we obtained is able to account for the previous findings from central presentation, these results demonstrate that normal language processing, and extraction of meaning from wordforms in particular, is an emergent property of multiple, interacting processing mechanisms, some of which are distributed differentially across the two cerebral hemispheres. Irrespective of the precise mechanisms at work, we can conclude that the hemispheres differ when decoding text in order to access meaning, and future models of word recognition could benefit from considering the unique contributions each hemisphere makes to the process of reading.

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Figures

Figure 1: Grand average ERPs to the first presentation of each of the four item types in each visual field (LH/RVF, RH/LVF), shown at 9 representative channels (bolded in head schematic). Occipital channels (bottom) are included to display lateralized componentry (delayed N1 responses at electrode sites contralateral to the visual field of stimulation).

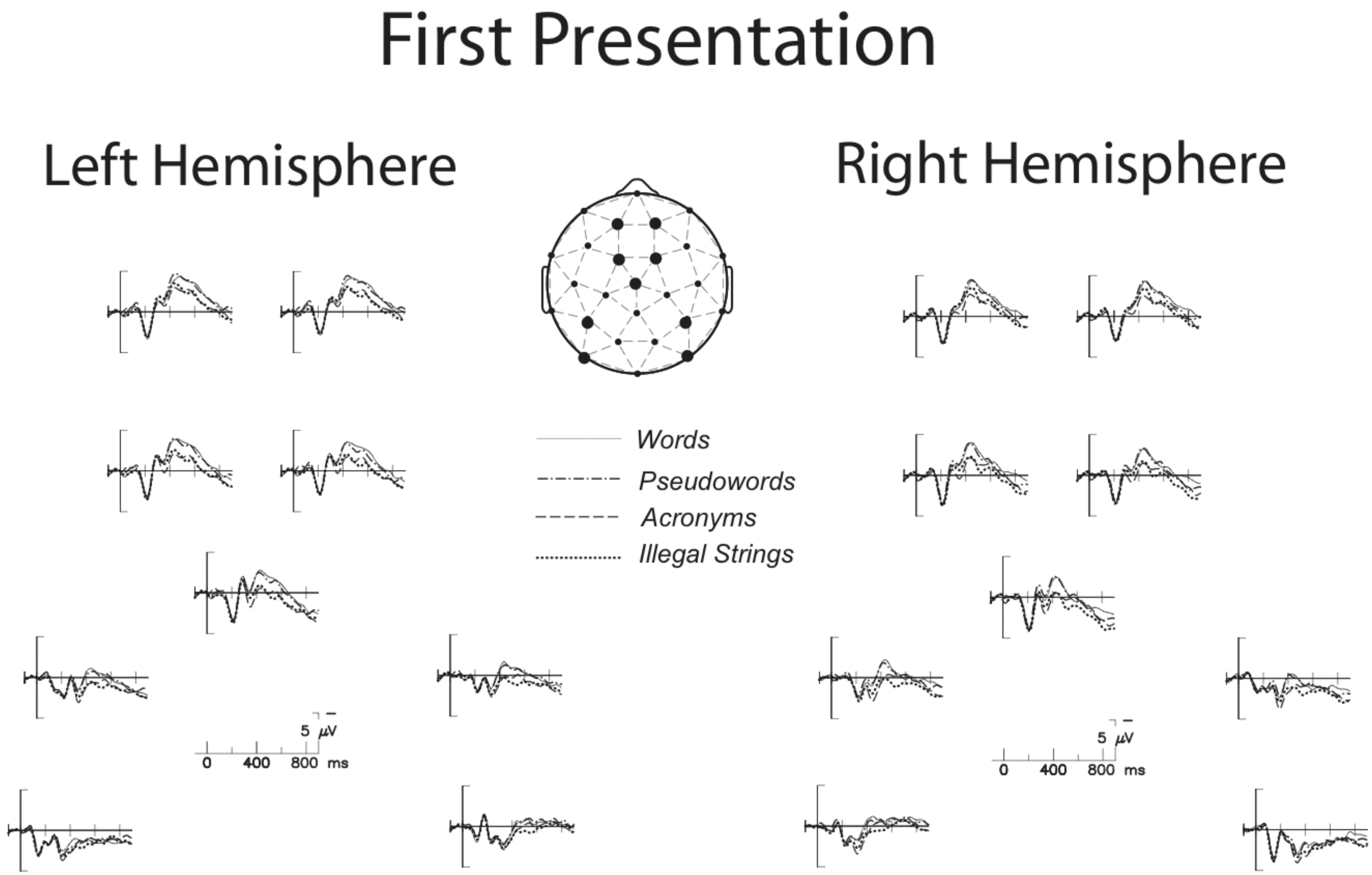

Figure 2: Grand average ERPs showing the repetition effect for real words in each hemisphere/visual field at 9 representative channels (bolded in head schematic). As in the reported analysis, second presentation includes lags of 2-3 intervening items after first presentation.

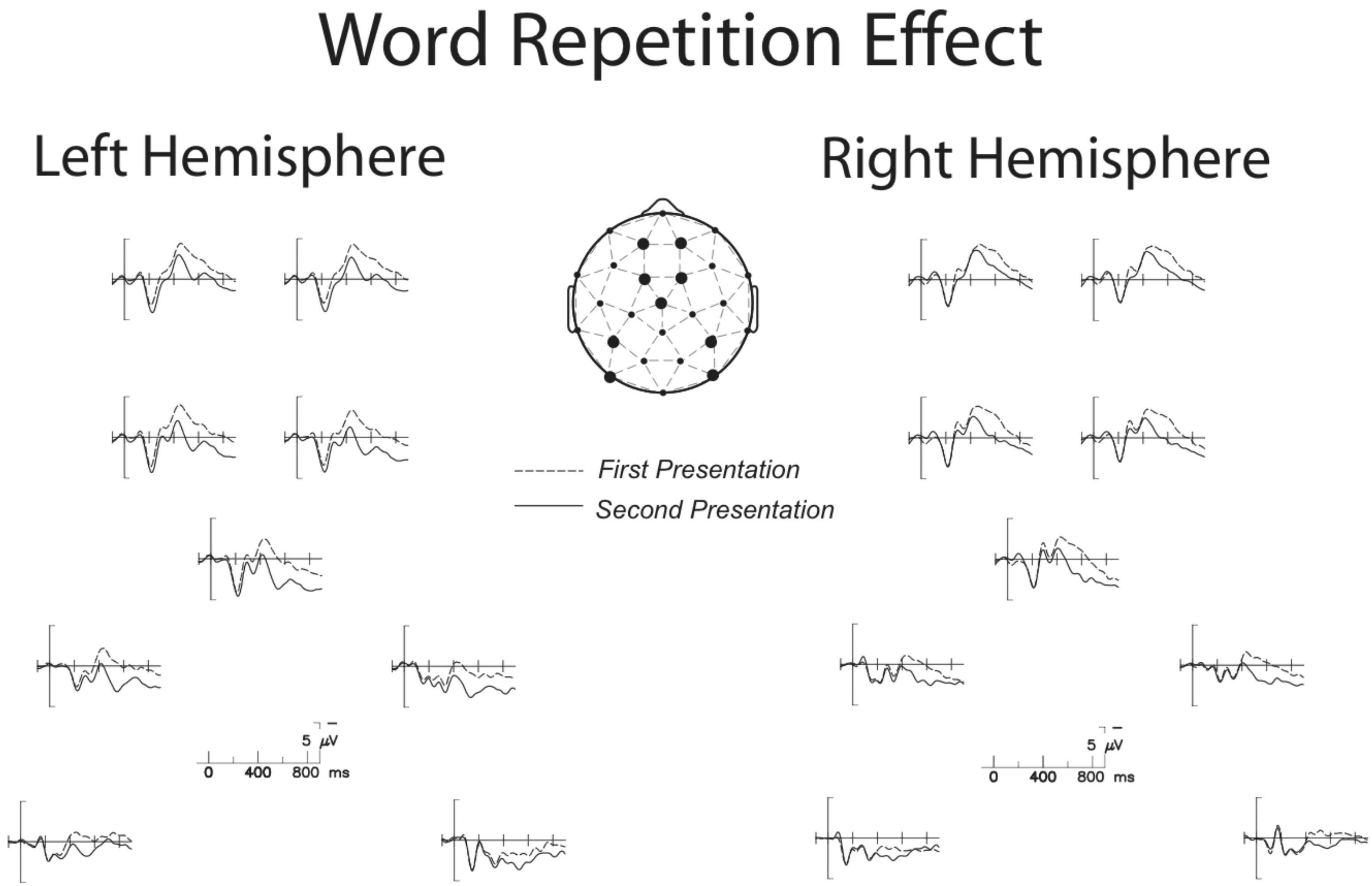

Figure 3: Grand average ERPs at three medial-central channels (bolded on head schematic) showing the repetition effects for orthographically regular/high N items (collapsed across words and pseudowords) and for orthographically irregular/low N items (collapsed across acronyms and illegal strings) with presentation either to the left hemisphere/RVF (top) or to the right hemisphere/LVF (bottom). The box surrounding the effect is divided into a dashed portion from 250-350ms (measurement of N250) and a solid portion from 350-500ms (measurement of the N400).