The Neurocognitive Basis of Reading Single Words As Seen Through Early Latency ERPs: A Model of Converging Pathways

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ABSTRACT

This paper first provides a brief review of the functional neuroanatomy of reading single words, focusing on the lexical and phonological routes. Next, early (defined as peaking prior to 350 ms) reading event-related potential components are summarized. A comprehensive effort is made to organize existing observations into a coherent scheme and commentary is made on terminology. Proposals are made regarding the cognitive function reflected by each ERP component and the associated generator sites. The overall framework constitutes a neurocognitive model of reading and demonstrates how the high temporal resolution of event-related potentials can provide additional insights into the reading process beyond those available from behavioral and neuroimaging studies, with a special focus on how the two pathways implied in reading are coordinated. The present model suggests that there are two such coordinating operations, Convergence processes during an initial information burst and Resonance processes during an extended harmonization process that follows.

Key Words: ERPs, Language, Visual Word Form Area, Neuroimaging

Despite the importance of language to the understanding of current issues of education and ultimate questions of the nature of human thought, the study of reading processes persists in a contentious state. While there is broad agreement on some aspects of reading, such as the presence of both orthographic (the letter sequence) and phonological (the sound sequence corresponding to the letter sequence) codes, basic questions regarding their implementation, relative importance, and time course remain under debate. The development of neuroimaging techniques has provided some helpful insights into the architecture of language processing that have helped guide and constrain cognitive models but they lack crucial information on the time course of the observed neural activity.

Event related potentials (ERPs) have the promise of helping resolve some of these issues by providing timing information. This relatively new literature provides a rich source of information but thus far is fragmented, with numerous ERP components reported in a bewildering array. This review will seek to provide a systematic overview of these findings and consideration of their implications for cognitive models. The ultimate goal is to seek to develop a neurally based model of language comprehension that is informed by the event-related potential literature. This effort will differ from a previous such effort (Barber & Kutas, 2007) in that it will focus on cataloging ERP components and assessing what they reveal about the time course of putative neurocognitive functions whereas the prior review focused on the time course of psycholinguistic variables and their implications for the architecture of connectionist models.

In order to simplify the task, this effort will focus on reading comprehension as opposed to speech comprehension. Also, although some sentence studies will be cited, this review will not address sentence-specific processing such as syntax or discourse. It will also set aside the magnetoencephalography (MEG) literature (e.g., Simos et al., 2002) for a future treatise for space reasons and because it would distract from the focus of this special issue, which is on ERP studies. First a base neural model of reading comprehension will be outlined and then the ERP literature will be reviewed in an effort to develop a neurocognitive timeline of reading comprehension (Table 1). Finally, there will be some speculations on implications of these findings for theoretical models, with a special focus on how the two pathways are coordinated.

A NEUROCOGNITIVE MODEL OF EARLY READING COMPREHENSION

The literature on reading comprehension in both the cognitive and neuroimaging literatures is quite complex and therefore a full treatment of this topic lies outside the scope of the present review. Instead, this section will describe one version of a neurocognitive reading architecture that is able to provide a framework for the succeeding ERP review.

To start with, the most relevant cognitive model of reading is the influential dual route cascaded (DRC) model of visual word recognition (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001). In this model, there are essentially two major pathways from the printed word to semantic access. After initial low-level perceptual analysis and identification of the letters, the information is passed along to the lexical and phonological pathways. The lexical pathway begins with orthographic analysis of the percept, and then the orthographic code is identified in the orthographic input lexicon. The result is then passed on to the semantic system. If the word is not present in the orthographic input lexicon, a less efficient pathway is available that first involves a grapheme-phoneme rule system to generate a phonological representation which is then passed on to a response buffer. From there it can be passed to a phonological output lexicon where the word can be identified. From there it can be passed on to the semantic system. Reciprocal connections between the orthographic input lexicon and the phonological output lexicon allow for the two pathways to interact. An important characteristic of this model is that although it highlights discrete stages of the reading process, it explicitly acknowledges that partial information is output from each stage, resulting in a cascaded or continuous flow dynamic (see also Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Eriksen & Schultz, 1979).

Turning to neural models of reading comprehension (Fiez & Petersen, 1998; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Joseph, Noble, & Eden, 2001; Price, 2000; Price & Mechelli, 2005; Vigneau et al., 2006), findings thus far are largely compatible with the DRC but require some elaborations on it.

Lexical Pathway

Evidence suggests the existence of a lexical pathway running along the inferior surface of the temporal lobe. One model suggests that along this pathway the visual percept of the word is increasingly abstracted (Dehaene, Cohen, Sigman, & Vinckier, 2005; Vinckier et al., 2007). The ultimate form of this representation would be a lexical-level representation that is independent of physical stimulus characteristics like case, of a sort that has been inferred by behavioral studies (Reicher, 1969; Wheeler, 1970).

Three areas in this region have received special attention. The first is the inferior occipital cortex (IOC) encompassing the inferior occipital gyrus and lingual gyrus. The laterality of this word sensitive area has varied between left-lateralized (Madden et al., 2002; Petersen, Fox, Snyder, & Raichle, 1990; Puce, Allison, Asgari, Gore, & McCarthy, 1996), right-lateralized (Dehaene et al., 2001), or bilateral (Indefrey et al., 1997). While an initial report (Petersen et al., 1990) suggested that it contained a lexical-level visual word form area (being more active to orthographically regular letter strings than consonant strings), subsequent studies have not supported this conclusion. For example, one study (Tagamets, Novick, Chalmers, & Friedman, 2000) actually reported the opposite pattern, namely that the consonant strings produced more activation than words. It is likely that this region is instead responding to global word shape (Indefrey et al., 1997; Mechelli, Humphreys, Mayall, Olson, & Price, 2000) and is therefore responsive to changes in perceptual characteristics such as case (Dehaene et al., 2001) and letter length (Valdois et al., 2006). Functionally, the IOC is therefore more likely to be part of the initial feature and/or letter analysis prior to the two pathways than to be part of the lexical pathway as initially thought.

The second area has been dubbed the visual word form area (VWFA). It is located midway along the fusiform gyrus, anterior to the IOC, and is strongly left-lateralized to the extent that its laterality is independent of visual field presentation (Cohen et al., 2002). The VWFA appears to mediate orthographic analysis at the bigram level as part of a series of processing steps (Dehaene et al., 2005). Striking evidence for its role in the reading process has been provided by a case study of brain surgery case before and after this area was removed (Gaillard et al., 2006). Support for the bigram hypothesis comes from the finding (Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006) that VWFA activity is correlated with bigram frequency and that this is the case even for non-orthographic non-words. Further evidence that the VWFA mediates (sub)lexical-level analysis is that the VWFA has been shown to be case-insensitive in repetition priming, as one would expect for a representation that has been abstracted from the original percept (Dehaene et al., 2001; Dehaene et al., 2004). The VWFA also showed evidence of abstraction in that it was not affected by retinal position (Dehaene et al., 2004) and in that it was more responsive to orthographic regularity than to whether the stimuli were presented in perceptually unfamiliar mixed-case format (Polk & Farah, 2002). Further information can be found elsewhere in a review of lateralized orthographic processing (Dien, submitted).

The third area is located anterior to the VWFA, along the anterior fusiform gyrus, and is one of three areas cited (Jobard et al., 2003) as displaying evidence of responding to semantics, both for words and for object pictures (Moore & Price, 1999). Furthermore, it shows greater activation to the lexical kanji script than to the phonological kana script (Nakamura, Dehaene, Jobert, Le Bihan, & Kouider, 2005). The term fusiform semantic area or FSA has been suggested to facilitate discussion of this area (Dien et al., in press). A study of semantic priming (Gold et al., 2006) reported that it responded to automatic spreading activation (ASA) effects, providing further evidence of its sensitivity to this level of processing. Despite the sensitivity to semantic manipulations (e.g., Moore & Price, 1999), it is suggested here that it may correspond best with the DRC's orthographic input lexicon. This suggestion is made based on the reasoning that given the apparent hierarchic gradient of processing along the inferior temporal lobe (e.g., Vinckier et al., 2007), one would expect a whole-word level of lexical analysis to follow the sub-lexical level of the VWFA. Furthermore, ascribing the complexities of semantic knowledge to such a small patch of cortex seems implausible. The ASA effects (Gold et al., 2006) could be explained more parsimoniously as being the result of lexical-level associations rather than semantic-level. Although one might therefore argue for a name like Fusiform Lexical Area, such a name would have a possibly unsupportable implication that it only responds to words whereas the term FSA is not restricted to one stimulus class and it reflects the empirical observation that this area responds to semantic manipulations. This sensitivity to semantic manipulation in turn is suggested to reflect top-down influences from semantic systems and not that the FSA is narrowly concerned with semantics per se.

Phonological Pathway

There is also widespread evidence of a phonological pathway, although some of its details have been subject to controversies that will not be considered in this review. It is suggested that the phonological pathway begins with a projection, whose details are still being elucidated, from the extrastriate cortex to the frontal cortex. In particular, the posterior portion of the inferior frontal gyrus, part of the classical Broca's area, is thought to be implicated in phonological processing in general (Fiez, 1997; McDermott, Petersen, Watson, & Ojemann, 2003; Paulesu, Frith, & Frackowiak, 1993; Poldrack et al., 1999). One possibility is that this motor region is responsible for helping translate visual letter codes into motor codes (Vigneau et al., 2006), consistent with models implicating motor codes in speech representation (Hickok & Poeppel, 2004; Liberman & Whalen, 2000).

Studies of phonology have further implicated the inferior parietal cortex, notably the angular gyrus and the supramarginal gyrus. Lesions to both these areas disrupt both reading and writing (Philipose et al., 2007). One possible view is that the angular gyrus mediates a translation of the motor code conveyed from Broca's Area into phonology, a view not incompatible with the original hypothesis (Dejerine, 1891; Dejerine, 1892) that it stores visual word codes. From there, the phonological code could then be conveyed to the supramarginal gyrus for temporary storage. Both lesion (Saffran & Marin, 1975; Warrington, Logue, & Pratt, 1971) and neuroimaging (Jonides et al., 1998; Logie, Venneri, Sala, Redpath, & Marshall, 2003; Paulesu et al., 1993) data have suggested that this area serves as a phonological store. Such a buffer may be needed due to the temporally extended nature of phonological representations.

From this buffer the phonological code could then be transferred to the same regions responsible for decoding auditory speech. Studies (summarized in Hickok &

Poeppel, 2004) have especially implicated the lateral temporal lobe, notably the auditory association cortex in the superior temporal sulcus and the superior temporal gyrus. A particularly relevant part of this region is the posterior middle temporal gyrus or pMTG, which has been proposed to be involved in phonological code retrieval (Hickok & Poeppel, 2004; Indefrey & Levelt, 2004) and could correspond to the lexical pathway's FSA. Thus, the posterior inferior frontal gyrus and the angular gyrus could serve as the DRC's grapheme-phoneme rule system, the supramarginal gyrus could serve as the response buffer, and the pMTG could correspond to the phonological output lexicon.

Pathway Interactions

Something not addressed thus far is how the representations in the two routes might be coordinated at an automatic level. In the DRC model reciprocal inhibitory connections mediate competition between different outputs (Coltheart et al., 2001). When translated to neural systems, however, it becomes evident that the association of phonology with orthography can be quite complex and might require a specialized region to mediate this process. It is an explicit postulate of the present model that lexical and phonological processing are initially separate and only begin to influence each other after their activation paths converge, aside from top-down expectancy influences (Ashby, Sanders, & Kingston, in press). It has been suggested (Dien et al., in press) that a poorly understood region, the Language Formulation Area or LFA (Nielsen, 1946) located in the posterior inferior temporal gyrus, might serve such a function. This suggestion was made based on the observation (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Nielsen, 1946) that lesions in this region can lead to anomia (an inability to name recognized items, presumably due to a disconnection between phonology and the ventral object recognition pathways that include word recognition) and the observation that it lies midway between the FSA of the lexical pathway and the pMTG of the phonology pathway. Such a function would also be consistent with the proposal (Damasio & Damasio, 1994; Damasio et al., 1996) that the inferior lateral temporal region, of which the LFA is a part, is a convergence zone where information from other cortical regions is coordinated. In this study (Dien et al., in press), activation of the LFA was inversely correlated with the cloze probability of a sentence ending (the proportion of a norming group that spontaneously generated the ending word given the sentence stem). Such a response could reflect the need to adjudicate amongst a range of possible congruent endings as the effort to bridge the two pathways proceeds.

An important challenge to this dual-route view has been posed in the neural literature on two grounds. The first is the argument that the areas in the putative orthographic route are also involved in general object recognition (Devlin, Jamison, Gonnerman, & Matthews, 2006). For the purposes of this article, it is not relevant whether these cortical functions are specific to language or have a more general role in object recognition. The second is the argument that the orthographic areas also respond to auditory and tactile stimuli and are therefore not specific to visual orthographic analysis (Price & Devlin, 2003; Price & Devlin, 2004; Price, Winterburn, Giraud, Moore, & Noppeney, 2003). A countering study reported that the VWFA does not necessarily respond to auditory stimuli (Dehaene, Le, Poline, Le Bihan, & Cohen, 2002) and that such reports may therefore be due to top-down influences as these stimuli activate representations of associated visual word forms (Cohen & Dehaene, 2004; Dehaene et al., 2002). A key obstacle to resolving these issues is the limited temporal resolution of neuroimaging techniques. This review will therefore turn next to the event-related potential literature, which may help clarify these and other issues.

READING COMPREHENSION EVENT-RELATED POTENTIALS

The view of reading comprehension from the event-related potential literature has been evolving steadily. In what might be termed the standard model of reading comprehension, orthographic analysis first peaks at about 200 ms (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999), phonological analysis at about 300 ms (Bentin et al., 1999), semantic analysis at about 400 ms (Kutas & Hillyard, 1980), and syntactic analysis at about 600 ms (Osterhout & Holcomb, 1992). An increasingly accepted modification to this simple linear model is the addition of an initial first pass at syntactic analysis at 200 ms (Friederici, 1995). More recently, this timeline has been challenged, motivated by evidence from the eye tracking literature that substantial semantic processing is completed by 250 ms (Sereno, Rayner, & Posner, 1998). Contributions to this special issue represent some of the current efforts to better elucidate the nature of early latency language comprehension.

One issue that arises for the enterprise of relating ERP findings to PET and fMRI findings is to what extent it is reasonable to expect them to correspond. Studies in animal models indicate that they do both reflect the same aspect of neural activity, namely that of dendritic potentials, as opposed to action potentials (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Raichle & Mintun, 2006). Although their relationship is not entirely linear (Devor et al., 2003), linearity is a reasonable approximation (Arthurs & Boniface, 2003; Sheth et al., 2004). Nonetheless, there are indications that the measures may sometimes diverge for various reasons (Fell, 2007; Huettel et al., 2004; Puce, Allison, Spencer, Spencer, & McCarthy, 1997). An issue that will be especially relevant at a later point is that ERPs appear to be more sensitive to brief strong ("phasic") activations whereas fMRI and PET are more sensitive to gradual prolonged ("tonic") activations (see Martinez et al., 1999; Puce et al., 1997). Thus, the approach that will be adopted is to look for potential correspondences but to acknowledge that they will require rigorous verification.

Another issue is the difficulty of comparing the results of different studies. Many studies have cautiously avoided attributing effects to specific components whereas other studies have done so but with conflicting terminologies. This review will therefore seek to provide a coherent ordering of these findings in an effort to highlight commonalities and to provide a useful framework. ERP components will be defined primarily according to their scalp topography and peak latencies. Ultimately, the attribution of different experimental effects to the same ERP component requires verification within the confines of a single experiment and hence this current classification effort should be understood as being preliminary.

In trying to make sense of the ERP literature, an ongoing problem is that of terminology. In the conventional naming scheme, ERP components are referred to according to their polarity at the peak electrodes (i.e., “N” for negative and “P” for positive) followed by a number indicating either the general peak latency in milliseconds or the general order of the peaks (e.g., “P300” for positivity at about 300 milliseconds or “P3” for third positivity). It eventually became necessary to supplement this scheme with subscripts (e.g., “P3a” versus “P3b”) to distinguish between components that would otherwise share the same label. Unfortunately, the rapidly multiplying population of ERP components is making this approach increasingly unwieldy and, as will be apparent, has led to some confusion.

It is suggested that it may be helpful to adopt an extension to the current naming scheme in which the peak channel is included as part of the label for ERP components (e.g., “N2-PO7). Scalp topography has traditionally been an important distinguishing feature (see Fabiani, Gratton, Karis, & Donchin, 1987; Sutton & Ruchkin, 1984). Scalp topography is a reflection of the neural generator site and so should remain relatively fixed, in contrast with latency, which can be quite variable for some components (e.g., the P300). Although the sparse recording montages of early studies made latency a more useful distinguishing feature, it may be argued that with modern montages scalp topography is a more reliable characteristic. Also, scalp topography should be largely independent of reference site (see Dien, 1998). As with peak latency, it is accepted that the peak channel may vary somewhat between datasets and so the choice of the channel can be representative (as in a well-known 10-20 site) rather than necessarily the precise peak channel, just as one might term an ERP component an “N200” when in fact the latency is actually at 208 ms. This proposed nomenclature will be used where peak channel information is available.

Visual Feature and Letter Analysis

P100-PO8

The P100 peaks at about 100 ms and is maximal over posterior regions. It appears to reflect a very low-level perceptual analysis. It is larger for longer words (Hauk & Pulvermuller, 2004) and this effect was reported to center on PO8. It was reported (Hauk et al., 2006c) that atypical words (as operationalized by positional bigram and trigram values) produced more positive (apparent trend towards left-lateralized) P100 amplitudes than typical words. Furthermore, a paper in this special issue (Hauk, Pulvermüller, Ford, Marslen-Wilson, & Davis, in press) reports that it also correlates with orthographic neighborhood size and that its topography varies with lexicality. By 158 ms this effect shifted to being specific to words as opposed to non-words. Although the scalp topography appears similar (and hence will be categorized under the P100), source analyses suggested that it was due to a different component. In a sentence reading paradigm (Penolazzi, Hauk, & Pulvermuller, 2007), effects of cloze probability was reported for short words only (apparent trend towards right-lateralized). There was also an effect of word frequency in this time window that may have also been attributable to the P100. Finally, a paper (Segalowitz & Zheng, in press) in this special issue presents some evidence for word versus non-word effects in the P100.

Studies of ERP activity in the P100 range have implicated low-level perceptual areas (Heinze et al., 1994; Martinez et al., 1999; Martinez et al., 2001). If these word effects prove to be replicable, it is likely that they reflect perceptual fluency for features prior to parsing of individual letters.

P150-Cz

The P150-Cz peaks at about 150 ms and is maximal near the vertex. It appears to reflect an early level of perceptual analysis. An initial study (Schendan, Ganis, & Kutas, 1998) reported that this component was more positive to words compared to object pictures (but not faces). It has also been reported to words and pseudo-words versus symbol strings (Maurer, Brandeis, & McCandliss, 2005), although not identified as a P150-Cz.

Another study (Sereno et al., 1998) reported that it could also distinguish between different types of verbal stimuli when they found an increased P150-Cz (which they termed a P1) to consonant strings versus words and pseudo-words that started as early as 100 ms and reported no effect of either word frequency or regularity. A similar effect, but in the opposite direction, was subsequently reported (Proverbio, Vecchi, & Zani, 2004) with letter strings eliciting a smaller P150-Cz than words and pseudo-words. Another study (Hauk, Davis, Ford, Pulvermuller, & Marslen-Wilson, 2006a) showed what appears (Figure 5 of their report) to be a larger P150-Cz to pseudo-words than to words.

Additionally, a study (Proverbio et al., 2004) reported a P150-Cz frequency effect, with high-frequency words producing a larger response than low-frequency words. It was suggested that the frequency effect could be due to sublexical effects rather than semantic access. A further study (Hauk et al., 2006a) reported what appears (Figure 5 of their report) to be a P150-Cz effect that responded to a synthetic variable composed of both word length and orthographic neighborhood size but that did not distinguish between words and pseudo-words. Additionally, there also appears (Figure 4 of their report) to be a P150-Cz effect in which greater semantic coherence, the extent to which morphologically similar words share similar meanings (Ford, Marslen-Wilson, & Davis, 2003), increased its amplitude. There is also some possibility that it displayed a response to cloze probability in a sentence paradigm (Penolazzi et al., 2007) but the scalp topography and latency information was unclear.

Some uncertainty about the P150-Cz has been introduced by the face recognition literature. The scalp topography of the word P150-Cz is quite similar to the face P150-Cz effect (Schendan et al., 1998). It has been argued that the face P150-Cz, also known as the face-specific vertex positive potential (VPP), is just the positive pole of the N170-PO7 (Joyce & Rossion, 2005). Whether or not this is the case for face recognition, data for word recognition (e.g., Maurer et al., 2005) suggests that the word P150-Cz is indeed distinct from the word N170-PO7.

Although information on the P150-Cz is still sparse, it is suggested that it reflects activity in the IOC and hence reflects word shape effects. Aside from the possible cloze effect, the P150-Cz effects can be understood as reflecting perceptual fluency for more common letter forms. If there is indeed a cloze effect (not at all certain), it could reflect a top-down expectancy effect. A study consistent with this line of reasoning (Pickering & Schweinberger, 2003) reported what they termed to be an N200, but appears to be a

P150-Cz effect, that responded to case-specific repetition priming of names. This finding is consistent with those of an fMRI study (Dehaene et al., 2001) that reported case-specific repetition priming in the IOC, which the present paper suggests is the source of the P150.

Further evidence for this line of reasoning comes from an ERP study (Holcomb & Grainger, 2006) of masked repetition priming which reported an enhanced P150-Cz for unrelated words relative to repetitions. This P150 differed from the other P150-Cz reports in that it was strongly right-lateralized. Intriguingly, the one neuroimaging study (Dehaene et al., 2001) with a strongly right-lateralized IOC effect also used masked primes. It therefore seems likely that the masking procedure was responsible for the right-lateralization and the similar lateralization effect seen for both the ERP and the fMRI studies further solidify the case that they reflect the same neural activity. Although the ERP study showed the effect for cross-case priming whereas the neuroimaging study showed it only for same-case priming, the authors (Holcomb & Grainger, 2006) suggested that it may be that the ERP methodology was simply more sensitive overall (and hence able to detect a weak cross-case priming effect) and that it would have shown an even larger same-case priming effect (consistent with the fMRI study) had this condition been present in the ERP study.

Lexical Pathway

N170-PO7

The N170-PO7 is a posterior negativity that peaks around 170 ms and is considered to be a contributor to the overall N1. It is also sometimes termed the N150 (Mondini et al., 2008; Spironelli & Angrilli, 2007) but the N170 term seems to predate the N150 term (e.g., Bentin et al., 1999). This difference in terminology appears to reflect a general tendency for this component to have an earlier latency in studies by this group (as early as 116 ms in one study, Spironelli & Angrilli, 2007), perhaps due to the differences between processing Italian and English.

Although best studied with respect to a right-lateralized face recognition potential, it has also been observed to occur as a left-lateralized negativity to words (Bentin et al., 1999; Rossion, Joyce, Cottrell, & Tarr, 2003). It would be best to term it a "word N170-PO7" to distinguish it from the face N170, which is likely to have a different cortical source (for a review of the relevant neural areas, see Dien, submitted). In general, the word N170-PO7 is thought to reflect sub-lexical processing.

The earliest report that appears to be about the word N170-PO7 (Compton, Grossenbacher, Posner, & Tucker, 1991) was tentative about whether their effect was part of the P1 or part of the N1. They found an increased negativity to consonant strings compared to words starting at 125 ms. This effect, this time termed an N1, was replicated in a later study by the same group (McCandliss, Posner, & Givon, 1997). Two studies (Bentin et al., 1999; Simon, Bernard, Largy, Lalonde, & Rebai, 2004) found it to not distinguish between consonant strings, pseudo-words, and words but to be larger for all three letter stimuli types than to non-letter stimuli (shapes, symbols, and pseudo-letters). A later study did report that it was stronger to words than pseudo-words (Maurer et al., 2005). On the other hand, another study reported data that seem to indicate that it was non-significantly stronger to pseudo-words (Hauk et al., 2006a). To the extent that there are effects of lexicality on the word N170-PO7, they could be due to either visual familiarity or semantics.

Efforts to evaluate the effects of visual familiarity have yielded conflicting results. It has been reported (Hauk & Pulvermuller, 2004; Sereno et al., 1998) that the word N170-PO7 component was more negative to low versus high frequency words, even when controlling for bigram and trigram frequencies (Hauk & Pulvermuller, 2004), especially in short words (Penolazzi et al., 2007), perhaps because it was overall stronger for shorter words (Hauk & Pulvermuller, 2004). On the other hand, it has been reported (Hauk et al., 2006c) to be more negative to typical rather than atypical words (according to bigram and trigram measures). Furthermore, with intensive practice, the word N170-PO7 to symbol strings increased in amplitude until it came to approximate that to words (Brem et al., 2005).

One possibility is that these conflicting results reflect the influence of top-down expectancy processes, as there are several reports of such effects. For example, one study (Gros, Doyon, Rioual, & Celsis, 2002) presented a stimulus series with either letters or shapes but with an occasional stimulus of the other type. The same ambiguous stimulus "o" had the same left hemisphere N170 as letters when presented in the letter context and the same right hemisphere N170 as figures when presented in the figure context. In a sentence study (Sereno, Brewer, & O'Donnell, 2003) that built on the previous observation that the N170-PO7 is stronger for low frequency words (Hauk & Pulvermuller, 2004; Sereno et al., 1998), it was demonstrated that, for ambiguous ending words, the N170-PO7 was stronger when the sentence context biased its meaning towards the low frequency meaning than when it was biased towards the high frequency meaning. Also, in a paper (Segalowitz & Zheng, in press) in this special issue, a task effect is reported in the N170-PO7. In contrast, in a follow-up study (Scott, O'Donnell, Leuthold, & Sereno, in press) also presented in this special issue, this group reports that emotion valence interacts with this frequency effect, suggestive of a bottom-up process.

As for the source of the word N170-PO7, a leading proposal (Brem et al., 2006; Schlaggar & McCandliss, 2007) is the visual word form area (VWFA), although others have suggested that the VWFA is instead associated with longer-latency N2s (Dehaene et al., 2001; Dien, Frishkoff, Cerbone, & Tucker, 2003; Martín-Loeches, 2007). An fMRI version (Gros, Boulanouar, Viallard, Cassol, & Celsis, 2001) of the N170-PO7 study (Gros et al., 2002) using the ambiguous “o” stimulus in series of letters and shapes did report a similar (although not identical) pattern of effects in a region whose furthest anterior extent includes the VWFA. Furthermore, intracranial ERP studies (Nobre, Allison, & McCarthy, 1994; Nobre, Allison, & McCarthy, 1998) have reported negativities to words in the period of 150-200 ms in this mid-fusiform region, although the nature of intracranial recordings (electrode placement dictated by medical needs) left systematic information about the latencies and the exact locations unclear (so it is possible that at least some of these negativities reflected the negative dipole complement to the P150-Cz instead). Also, if the N170-PO7 reflects VWFA activity then the question arises as to why some studies (Bentin et al., 1999; Simon et al., 2004) have reported that it does not distinguish between consonant strings and orthographically regular letter strings. The bigram hypothesis of the VWFA (Binder et al., 2006; Dehaene et al., 2005) would suggest that these results are due to uncontrolled bigram parameters; indeed, at least one report (Hauk et al., 2006c) did find that the N170-PO7 responded to bigram/trigram parameters.

Although the report (Spironelli & Angrilli, 2007) that the N170-PO7 (here termed an N150) is enhanced in a case-matching task, versus phonology and semantic matching tasks, could be taken as evidence against a case-independent (Dehaene et al., 2001) VWFA source, it is possible that this enhancement just reflects a generalized increase in attention to the lexical pathway. A follow-up study (Angrilli & Spironelli, in press) in this special issue did not replicate the task effect, further suggesting that it reflects a special circumstance.

N2-P3

A later N2 effect with a left parietal scalp topography seems to reflect a further level of processing. In a sentence reading study (Dien et al., 2003) an N2-P3 peaking at 208 ms was reported to be correlated with unexpectedness (as rated by a separate norming group) of incongruent sentence endings. Although originally identified as an instance of the Recognition Potential (Martín-Loeches, Hinojosa, Gómez-Jarabo, & Rubia, 1999; Rudell, 1991), a subsequent sentence study of the Recognition Potential (Martín-Loeches, Hinojosa, Casado, Munoz, & Fernandez-Frias, 2004) revealed that it differed in terms of latency, topography, and direction of incongruity effect, and is therefore likely to be a different component. A report (Ruz & Nobre, in press) of an N2 effect of attention to orthography might reflect the presence of the N2-P3, although the topography information is not clear enough to be certain.

An fMRI replication (Dien & O'Hare, submitted) co-localized the N2-P3 ERP effect with a similar effect in the FSA. Further support for this link between this N2-P3 and the FSA is provided by intracranial recording studies (Halgren et al., 2006; Nobre et al., 1994) that have reported that the initial peak activation in the FSA vicinity has a latency of about 200 ms. Since all the incongruent sentence endings were odd and unpredictable, it was further suggested (Dien & O'Hare, submitted) that the unexpectedness ratings reflect subtle distinctions in the automatic spreading activation of these words by the sentence context, consistent with the FSA's sensitivity to automatic priming (Gold et al., 2006). There is, however, a need for further studies of the N2-P3 effect to better characterize it and to confirm that it does not arise from some type of confound. Note that it was not detectable as a main effect for incongruity, although the correlation with the unexpectedness parameter was quite strong (r=.50).

N2-T6

Another N2 effect of potential theoretical significance was also reported in the same sentence reading study (Dien et al., 2003) and was termed a meaningfulness recognition potential or MRP. In retrospect, it seems better to just term it by a more neutral term of an N2-T6. It was reported to be correlated with the meaningfulness (as rated by a separate norming group) of incongruent sentence endings. Although peaking at roughly the same time as the N2-P3, its scalp topography suggested a right hemisphere source. This hemispheric pattern was suggested to be consistent with studies of humor appreciation in which the left hemisphere is more involved in the recognition that a punch line is unexpected and the right hemisphere is more important for the recognition that the punch line nonetheless makes sense (Bihrle, Brownell, Powelson, & Gardner, 1986; Brownell, Michel, Powelson, & Gardner, 1983). This question is to be discussed elsewhere (Dien, in preparation) in further depth in the context of the Janus model of laterality (Dien, in press), wherein it is hypothesized that the left hemisphere has the forward-oriented role of generating predictions whereas the right hemisphere has the backward-oriented role of detecting and making sense of unexpected events. It is not currently clear what the role of the right hemisphere might be in the dual-route context so no more will be said at this point.

Phonological Pathway

Turning to the phonological pathway, the picture is much less clear than that for the lexical pathway. It may be that phonological processing is less amenable to the precise time-locking required for the ERP trial-averaging procedure. In any case, the first component that clearly reflects phonology is the subject of some confusion. As described elsewhere (O'Hare, Dien, Waterson, & Savage, 2008), there are a number of ERP effects that have a similar frontal topography (usually somewhat left-lateralized) and a similar time course running from about 200-450 ms. The extended time course obscures the peak latency, rendering it ambiguous. Furthermore, their effects are sufficiently similar that although they have been ascribed to different cognitive processes, they could plausibly account for the other sets of effects. Moreover, although some are described as being negativities and others are described as being positivities, their true polarity is generally not self-evident and their nomenclature therefore a matter of convention. Thus, this set of ERP observations could reflect the influence of a single ERP component or it could reflect that of multiple components. They can be divided into three groups of observations based on the nature of the experimental designs, although the underlying componentry is unclear at this point. To simplify discussion they will be termed the semantic, phonological, and auditory groups. Since the componentry is unclear, they will named according to the terms used by the reports. A fourth group, the N300-T3, can be readily distinguished from the prior three based on scalp topography.

Semantic

A number of visual word semantic studies (Franklin, Dien, Neely, Waterson, & Huber, 2007; Frishkoff, Tucker, Davey, & Scherg, 2004; Frishkoff, 2007; Hill, Ott, & Weisbrod, 2005; Hill, Strube, Roesch-Ely, & Weisbrod, 2002; Nobre & McCarthy, 1994) have reported a frontal effect to words that is relatively more negative to incongruent endings and tends to be somewhat left-lateralized. It has been termed a word N300 (Franklin et al., 2007) in order to highlight its similarity to a frontal effect termed the N300 seen for pictures that mismatch with the current semantic context (Barrett & Rugg, 1990; Hamm, Johnson, & Kirk, 2002; McPherson & Holcomb, 1999); if the word N300 and the picture N300 are the same, they may therefore reflect some sort of amodal semantic process. By the proposed nomenclature, this would be termed a word N300-Fz. An fMRI replication (O'Hare et al., 2008) found strong evidence that it emanated from the posterior cingulate and that therefore it reflected a process with some role in stimulus-response matching. In this report it was suggested that this word N300-Fz might actually be a P2 due to the direction of the fMRI effect but further consideration suggests that since the fMRI signal can reflect both inhibitory as well as excitatory dendritic activity, it does not provide clear guidance as to the appropriate polarity of the component.

Other names of components that fall into this group include N310 (Hill et al., 2005; Hill et al., 2002), the frontal part of a broader N330 (Nobre & McCarthy, 1994), and mid-frontal negativity or MFN (Frishkoff et al., 2004; Frishkoff, 2007). Although these studies interpreted the findings in terms of semantics, they could also be mediated by associated phonological codes. Finally, an intriguing, but puzzling, pair of studies (Federmeier, Mai, & Kutas, 2005; Wlotko & Federmeier, 2007) with visual sentence presentation has reported P2 effects that were higher for high constraint sentence stems, with no effect of congruency (Wlotko & Federmeier, 2007). Again, it is unclear how many ERP components underlie these various reports.

Phonological

Another line of research (Barnea & Breznitz, 1998; Carreiras, Vergara, & Barber, 2005; Landi & Perfetti, 2007; Liu, Perfetti, & Hart, 2003) has reported a P2 effect that is more clearly phonological in nature, namely an enhancement for phonological mismatches to visual word stimuli (termed an N2 in one study: Niznikiewicz & Squires, 1996). For example, one of them (Carreiras et al., 2005) reported P2 effects in a lexical decision experiment depending on whether the color boundary in a two-color word coincided with the syllable boundary or not. Another study (Sereno et al., 1998) reported that the P2 was enhanced for low frequency regular versus exception words, in participants showing a behavioral effect for regularity in a lexical decision task. The boundary between the semantic and phonological studies has been blurred, however, by a report (Landi & Perfetti, 2007) of P2 effects in a semantic task as well, although it made the unsupported observation that the P2 effect was not as frontal as the MFN. There have also been reports (Angrilli & Spironelli, in press; Spironelli & Angrilli, 2007) of a frontal N350 that seems to respond to phonological tasks and may be another instance of the word N300, although it is difficult to be sure since these studies did not manipulate congruency. In another paper in this special issue (Proverbio, Adorni, & Zani, in press), the left frontal effect distinguishing between L1 versus L2 languages in the 260-320 ms range is likely to be another instance of this effect.

Auditory

A third line of research on a similar appearing ERP component concerns the Phonological Mismatch Negativity or PMN (now renamed Phonological Mapping Negativity by the main group investigating it). Although usually observed in studies using auditory stimuli (Connolly, Stewart, & Phillips, 1990; Connolly, Phillips, Stewart, & Brake, 1992; Connolly & Phillips, 1994; Connolly, Service, D'Arcy, Kujala, & Alho, 2001; Phillips, Klein, Mercier, & de Boysson, 2006; Newman, Connolly, Service, & McIvor, 2003; Phillips et al., 2006; Revonsuo, Portin, Juottonen, & Rinne, 1998), it has been reported to be evoked by visual stimuli as well (Connolly, Phillips, & Forbes, 1995). In the key studies using auditory sentences (Connolly & Phillips, 1994) it was demonstrated that the PMN to the terminal word was responsive to the distinction between an incongruent ending with the same phoneme as the expected word and an incongruent ending with a different phoneme as the expected word whereas the N400 responded only to semantic congruency. It was therefore suggested that the PMN reflected expectations for the stimulus identity maintained at the phonological level. The boundary between the PMN studies and the other three groups has been blurred by the report (Connolly et al., 1995) that the PMN is also found for visual word stimuli.

Systematic studies will be required to determine whether these three sets of studies do indeed concern three different ERP components or whether some or all of them overlap with each other (or even whether they in turn are comprised of multiple components, as in the word N300 versus the MFN). Source localization results could be helpful in this regard but thus far are inconclusive. MEG studies of the PMN have reported either no PMN (Helenius et al., 2002) or a PMN anterior to that of the N400 (Kujala, Alho, Service, Ilmoniemi, & Connolly, 2004). The latter suggested a left hemisphere anterior temporal source but the inconsistent findings underscore the ambiguities of source localization results, even with MEG. A current source density study (Connolly et al., 2001) of the PMN also suggested a left anterior source but the results would allow for other sources as well. Another PMN source analysis study (D'Arcy, Connolly, Service, Hawco, & Houlihan, 2004) suggested both left inferior frontal and inferior parietal sources. The P2 has been localized to right hemisphere BA 6 and 8 using LORETA (Liu et al., 2003). The picture N300 has been localized to bilateral frontal areas and bilateral occipital/parietal areas (Hamm et al., 2002). The MFN has been localized to a number of sources of which the anterior cingulate seems to be a prominent contributor (Frishkoff et al., 2004; Frishkoff, 2007). Most recently, an fMRI replication (O'Hare et al., 2008) of the word N300 study (Franklin et al., 2007) reported strong co-localization with a posterior cingulate activation that was suggested to be involved in stimulus-response mapping.

Further studies will be required to determine if these differences in source analyses are due to the presence of differing ERP components or due to differences in source localization methodology, although it should be noted that co-localization of ERP and fMRI results (e.g., O'Hare et al., 2008) may be considered to be especially persuasive when obtained. Although the posterior cingulate is not considered to be part of the phonological pathway, it could be an indirect index of phonological processing occurring elsewhere in the cortex.

N300-T3

Another set of components that appear to be phonological in nature has not been given a consistent name. As it has more coherent characteristics than the other three groups, it will simply be termed the N300-T3 component. It was first reported (Neville, Kutas, & Schmidt, 1982) as an N410 and being left-lateralized regardless of visual-field of presentation and was then reported as being more negative to semantically congruent words (Neville, Kutas, Chesney, & Schmidt, 1986), a finding that was echoed in a latter report by Nobre and McCarthy (1994) who termed it part of an N330. It was later linked specifically to phonology as an N320 and an N350 (apparently the same component) that was more negative to pronounceable letter strings (Bentin et al., 1999; Simon et al., 2004). Furthermore, when the task was to make a phonological decision, an N350 was reported to be enhanced (Ruz & Nobre, in press). It has also been reported in sentence studies (Dien et al., 2003; Frishkoff, 2007) where it was termed an N3 and has again been more negative for congruent words. An N3 in a report (Frishkoff, Perfetti, & Westbury, in press) in this special issue has also been suggested to be another instance of this component.

Neuroimaging data also support a link between the N300-T3 and the phonological pathway. In an fMRI replication (Dien & O'Hare, submitted) of an N300-T3 study (Dien et al., 2003), it was reported in a reanalysis of the ERP data that the N300-T3 correlated strongly with word familiarity. Familiarity correlates highly with age-of-acquisition (AoA) measures (Brown & Watson, 1987; Gerhand & Barry, 1999; Gilhooly &

Logie, 1980). It has been hypothesized that the AoA ratings, and thus familiarity ratings, reflect the coding of words in the output phonological lexicon that is used in post-lexical verification of word identification (Brown & Watson, 1987; Morrison & Ellis, 1995). It is therefore of interest that the familiarity effect in the fMRI data (Dien & O'Hare, submitted) was in the left supramarginal gyrus region.

Pathway Interactions

Although all the ERP components described thus may very well reflect input from both pathways (the degree to which they are encapsulated is unclear at this point), only one ERP component has been specifically proposed as reflecting a neurocognitive function with an explicit role in coordinating the two pathways. It should also be noted that 'interaction' is being used in the sense of automatic processes activated when the bursts of information passing down the two pathways collide and is therefore separate from the issue of top-down modulation.

Recognition Potential

The Recognition Potential or RP (Rudell, 1991) is a negativity usually peaking at about 250-270 ms (but as early as 200 ms), centered over the left posterior scalp at about PO7. With single word presentations, it was largest for words, smaller for orthographic non-words, and smallest non-orthographic non-words (Martín-Loeches et al., 1999). In three studies (Hinojosa, Martin-Loeches, Munoz, Casado, & Pozo, 2004; Mari-Beffa, Valdes, Cullen, Catena, & Houghton, 2005; Martín-Loeches, Hinojosa, Gómez-Jarabo, & Rubia, 2001) it has been reported to be larger to the target category of living versus non-living things; this observation further supports the contention that it responds to semantic content, although the possibility of confounds remains since none of the studies counterbalanced the stimuli. Further support for its semantic nature is provided by a sentence study (Martín-Loeches et al., 2004) where it was reported that the RP was larger for congruent endings. It has therefore been suggested to reflect lexical selection (Hinojosa, Martín-Loeches, & Rubia, 2001) as part of an integration function for different types of information including the lexical and phonological routes (Martín-Loeches et al., 2001; Martín-Loeches, 2007). The left posterior effect distinguishing between L2 and L3 languages in the 260-320 ms range in another paper in this special issue (Proverbio et al., in press) is likely to be another instance of this RP. Interestingly, another paper in this special issue (Kissler, Herbert, Winkler, & Junghofer, in press) notes that the RP may also be responsible for an emotional word effect reported in this and another study (Scott et al., in press).

While it was originally suggested (Dien et al., 2003; Martín-Loeches, 2007) that the RP emanates from the VWFA based on a source analysis (Martín-Loeches et al., 2001), the sensitivity of the RP to semantic parameters is not consistent with what is known of the VWFA. Furthermore, the peak latency of about 250 ms is too late. The N170-PO7, as summarized earlier, seems to be a better candidate for the electrophysiological correlate of the VWFA. One possibility for accounting for the late peak latency is that RP studies typically use a rapid stream stimulation or RSS technique (Martín-Loeches, 2007; Rudell, 1992) that may alter the normal time course of activity, especially given the latency variability seen in this component. The one RP report (Mari-Beffa et al., 2005) that did not use the RSS technique obtained a posterior negative ERP component with a roughly 200 ms latency that is therefore not incompatible with N170-PO7 reports. Finally, the scalp topography for the N170-PO7 and the RP appear to be quite similar (see Figure 1).

On the other hand, other studies not using RSS have also reported effects that appear to be instances of the RP. For example, one report (Dehaene, 1995) found both what appears to be an N170-PO7 that distinguished consonant strings from words and an N304 with the RP scalp topography that distinguished between different semantic categories. Another apparent instance of the RP in a non-RSS paradigm occurred in an experiment (Friedrich & Kotz, 2007) that primed a word with an auditory sentence stem and then presented a visual ending word; an N250 (although it was termed a P250, it had the RP scalp topography and the polarity was ambiguous) distinguished between ending words that shared the initial syllable with the expected final word and ones that did not. This paradigm would be well-suited for activating competing phonological and lexical pathway representations and thus triggering the hypothesized LFA coordination function. As with the RP sentence study (Martín-Loeches et al., 2004), this N250 was larger for congruent endings. There are also other reports not using RSS of ERP components in the 250 ms range that may or may not also be RPs (Grainger, Kiyonaga, & Holcomb, 2006; Holcomb & Grainger, 2006; Martin, Nazir, Thierry, Paulignan, & Demonet, 2006; Newman & Connolly, 2004; Penolazzi et al., 2007; Pickering & Schweinberger, 2003; Simon et al., 2004).

It is therefore suggested here that an alternative location that would be consistent with the RP with respect to timing, source analysis, and experimental manipulations is the LFA. With respect to source analysis, dipole analyses provide the inferred source location only by making the assumption that the source is a dimensionless point (Scherg, 1990). Such a solution therefore corresponds to a set of solutions that are increasingly more diffuse and superficial. Following this logic, an alternative source solution is the lateral inferior temporal region in the vicinity of the LFA. Such a location would also be consistent with the timeline thus far described in this review (Table 1). The junction between the two pathways would also be a logical point at which to start resolving the competing lexical alternatives as part of the lexical selection process, as proposed for the RP (Hinojosa et al., 2001). The reason why the RP seems to be larger, rather than smaller, for congruent sentence endings could be the differential sensitivities of ERP and fMRI methods (with the ERP measure being more sensitive to the discrete burst of activity evoked by a match between the two pathways and the fMRI measure being more sensitive to the extended activity evoked by efforts to resolve a mismatch between the pathways). Although it is not clear if phonological processing for a current word is completed by 250 ms, as evident in this review, it seems plausible that expected words might be activated in the phonological pathway via subvocalizations, especially in paradigms where extended inter-stimulus periods favor the use of the phonological loop component of working memory.

There are also some suggestive parallels between the LFA and the RP. Not only does the LFA also respond to semantics (Dien et al., in press), both the RP (Rudell & Hua, 1997) and the LFA (Shaywitz et al., 2002) have been reported to correlate with reading ability (see also Frishkoff et al., in press). In general, the proposed integration function indexed by the RP (Martín-Loeches, 2007) would correspond well with the proposed convergence function of the LFA (Damasio et al., 1996; Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Dien et al., in press).

IMPLICATIONS

Thus far event-related potential findings have largely not been assimilated into the broader literature on the neurocognitive underpinnings of reading comprehension, with some notable exceptions (e.g., Friederici, 2002). This review suggests that sufficient progress has been made that it is time to start doing so. For example, as noted earlier, there has been a vigorous debate regarding whether the language-sensitive portions of the inferior temporal lobe region are dedicated to visual lexical analysis or have a broader multi-sensory role (Cohen & Dehaene, 2004; Dehaene et al., 2002; Price & Devlin, 2003; Price & Devlin, 2004; Price et al., 2003). ERP components appear to provide a view into the activity of several portions of the lexical pathway. From this view, it would seem that immediately following a visual presentation of a word, a fast sequence of activations (presumably cascaded in nature) occurs within 250 ms (Table 1). Inspection of ERP reports of speech perception (for example, see in this issue: Friedrich & Schild, submitted; Newman & Connolly, in press) indicates that the activity in these first 250 ms is quite different from that for visual stimuli (for a review, see Hagoort, 2007).

It may be that neural processing occurs in two phases. In the first phase, a cascaded sequence of activations progresses through the various pathways in order to establish an initial analysis (with the LFA seeking to establish an immediate orthography-phonology linkage based on just local information). It is self-evident that such sequences will often not arrive immediately at a conclusive identification (oftentimes percepts remain ambiguous even after extended inspections). It is therefore suggested that a second phase occurs in which the activity spread across this distributed network interacts in order to resolve itself into a single coherent representation, perhaps via a resonance process (see Stone & Van Orden, 1989; Van Orden & Goldinger, 1994; Van Orden, Pennington, & Stone, 1990). The first phase might be termed the Estimation Phase to denote its role in computing a fast estimate and the second phase might be termed the Resonance Phase to denote its role in seeking a more accurate solution by coordinating information across the entire representational network. Such a second phase would be consistent with the reentrant processes proposed in the Neural Darwinism model (Edelman, 1987) and the oscillatory dynamics visible in frequency-domain analyses of electroencephalographic signals (Klimesch, Sauseng, Hanslmayr, Gruber, & Freunberger, 2007; Makeig, Debener, Onton, & Delorme, 2004; Nunez, 2000; Nunez & Srinivasan, 2006), as opposed to the time-domain analyses represented by

ERPs. With regards to semantics, one might consider the first phase to provide mostly implicit semantic information (as in associations between related word forms), which is then elaborated during the Resonance phase.

From this point of view, the position that the inferior temporal region responds primarily to visual information and the position that it is multimodal in nature are both correct - the first applies to the initial phase and the second applies to the latter phase. Given the different characteristics of ERP and fMRI methodologies noted earlier (see Martinez et al., 1999; Puce et al., 1997), it would be reasonable to suppose that ERPs are most sensitive to this first phase and fMRI is most sensitive to the second phase. The first phase would be an initial short burst of largely synchronized activity as the initial information reached the cortex, favorable for ERP recordings, and the second phase would involve coordination over the entire brain and hence would be expected to be both less synchronized and more temporally extended, more favorable for fMRI recordings. While areas most active in the first phase would presumably often be the area most active in the second phase, this would not necessarily be the case, accounting for divergences between the measures.

Likewise, this distinction between an initial Estimation Phase and a succeeding Resonance Phase could help clarify ongoing disputes in the cognitive literature. Stagewise theories like the DRC could be characterized as focusing more on the initial information burst during the Estimation Phase and connectionist models like the Complex Systems Framework (Van Orden & Goldinger, 1994; Van Orden et al., 1990) seem more focused on the Resonance Phase during which information is being coordinated in parallel across the neural network.

In closing, this review has sought to make the case that there is a need for a systematic framework to make sense of findings as the literature becomes increasingly more complicated to avoid, for example, the situation of multiple ERP components being attributed to the same VWFA area. Furthermore, it has sought to establish that it is now possible to construct a detailed timeline of the neurocognitive stages in reading comprehension. Finally, it is suggested that both stagewise cognitive and neural models of reading could benefit from a deeper consideration of how different representations are coordinated. The present model suggests that there are two such operations, Convergence processes during the initial information burst and Resonance processes during an extended harmonization process that follows.

TABLES

Peak Latency	ERP	Anatomy	Function
100	P100	Extrastriate Occipital	Low-Level Perception
150	P150-Cz	Inferior Occipital Cortex	Word Shape
150-180	N170-PO7	Visual Word Form Area	Bigram Analysis
200	N2-P3	Fusiform Semantic Area	Lexical Access
250	Recognition Potential	Language Formulation Area?	Lexical Selection and Orthographic-Phonological Mapping
250-350	MFN/N300/P2/PMN	?	Phonological Analysis?
300-350	N300-T3	Left Supramarginal Gyrus	Phonological Store

Table 1. Summary Table of Early Latency Reading Comprehension Event-Related Potentials.

FIGURE LEGENDS

Figure 1. Neurocognitive Model and ERP Components. The figure presents the brain areas discussed in the present manuscript as being possible generator sites of the ERP components. The abbreviations are: dPCC - dorsal posterior cingulate cortex; FSA - fusiform semantic area; LFA - language formulation area; SMG - supramarginal gyrus; VWFA - visual word form area. Sample data are also provided that are associated with each putative ERP generator site. The citations for the ERP data are: N170-PO7 (Spironelli & Angrilli, 2007); N2-P3 (Dien et al., 2003); RP (Martin-Loeches, Sommer, & Hinojosa, 2005); N300-T3 (Dien et al., 2003); N300-Fz (Franklin et al., 2007).

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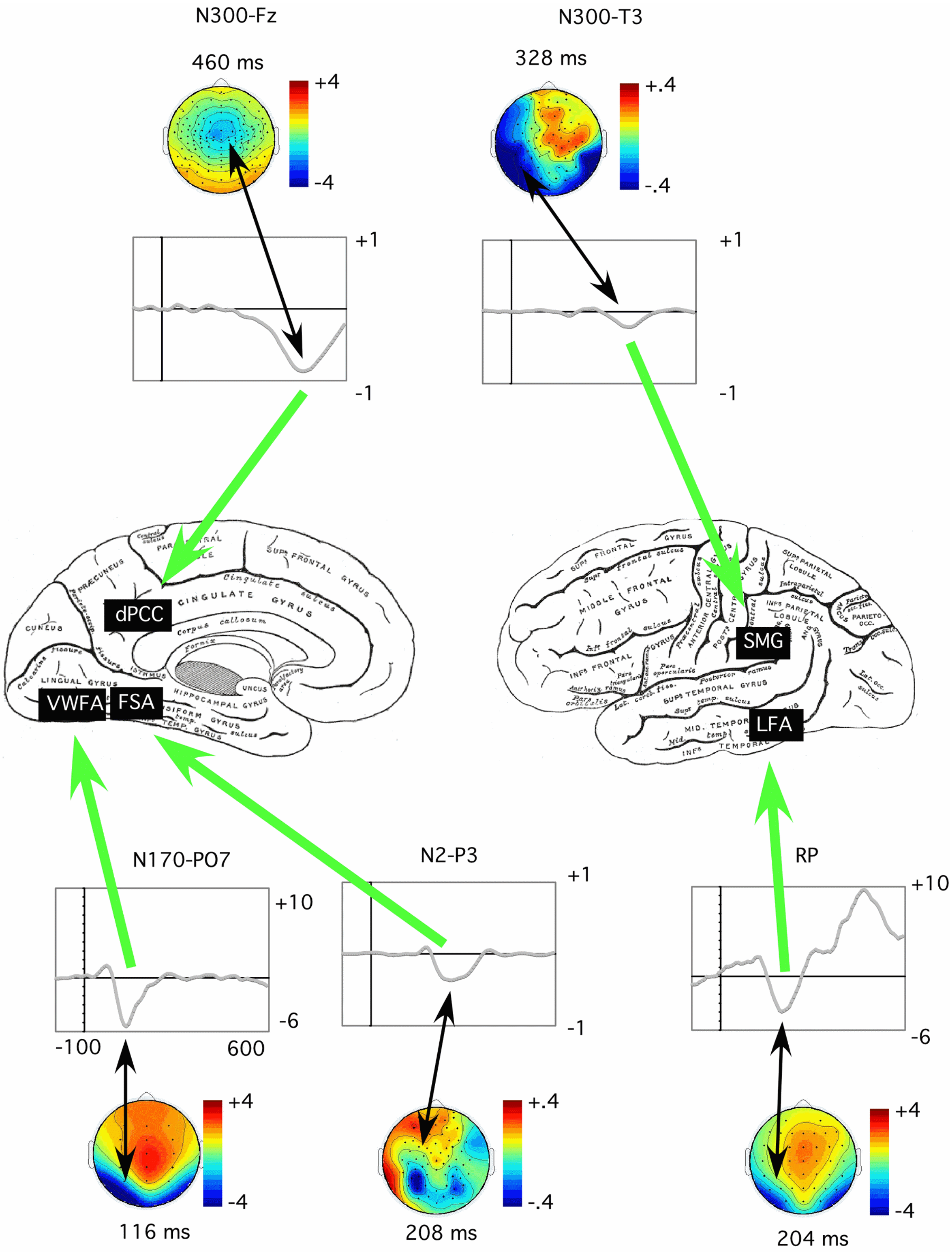
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