The development of visual expertise for words: the contribution of electrophysiology

Urs Maurer and Bruce D. McCandliss

Skilled readers are able to process written text at a remarkable speed that surpasses the rate of typical speech. A significant part of this fluent processing of connected writing involves computations applied to individual words. Individual words are processed in order to activate corresponding information about word meaning and pronunciation in the reader's mental lexicon. The current chapter in this book on single word processes focuses on the contribution of electrophysiology for understanding single word processes, especially processes associated with accessing the visual forms of written words. Although some processes applied to single words in isolation have been demonstrated to interact with other processes related to text (for review see Balota, 1994), investigations of mental processes at the single word level represent a critical component process within reading, and also provides scientifically pragmatic paradigms for examining sub-processes involved, from processing the visual forms of words to accessing linguistic representations of phonology and semantics.

The process of rapidly processing visual word forms to access linguistic representations may be understood as a form of perceptual expertise (Gauthier & Nelson, 2001) that develops with reading experience (McCandliss, Cohen, & Dehaene, 2003). Aspects of this fast perceptual process for visual words that is inherent in our ability to rapidly process text have been isolated by several cognitive paradigms (reviewed in this book, chapter x), and such processes have been localized to a network of brain regions (also reviewed in this book, chapter y). This chapter investigates the contribution of electrophysiology to understand the neural basis of this skill, as well as its development. Specifically, we examine early perceptual responses related to visual words as well as responses to speech sounds that may be critical to the foundation of reading skills, and have been implicated in both typical and atypical development of reading ability.

Behavioral evidence for rapid perceptual processing of visual words

Naturally, when focusing on fast visual perceptual expertise for reading, issues of time-course of perception of visual words become critical. Eye-tracking studies of reading provide insights into the time-course of information processing for visual words, and have shown that readers typically fixate a word for a short period of time (typically between about 200 and 300 ms) before moving to fixate the next (Rayner, 1998). During this brief fixation, information about the currently fixated word, such as its lexical frequency, influences the amount of time the eye remains on that word, thus providing a lower limit for the estimation of the 'eye-mind' lag in lexical access, suggesting that some information regarding the word being viewed is accessed within the first 200 milliseconds (Reichle, Rayner, & Pollatsek, 2003). Such research, examining single word processing in the context of connected text, converges nicely with a large body of cognitive research conducted using eye tracking, naming, and lexical decision tasks applied in paradigms that present single words in isolation. For example, converging evidence from studies of brief, masked presentation of visual words suggests that the rapid perceptual processes we apply to letter strings are facilitated by common patterns of combining letters into word forms – the word superiority effect (Reicher, 1969) demonstrates that subjects are more accurate in detecting brief exposures to letters presented within words than letters presented alone or within random consonant strings. Such perceptual facilitation even occurs for letters embedded in pronouncable nonwords (pseudoword superiority effect, for a recent study see Grainger, Bouttevin, Truc, Bastien, & Ziegler, 2003). Such studies provide additional information into the nature of processes that occur within early perceptual processes applied to visual words. While these behavioral studies allow inference about fast cognitive processes during reading, such evidence is open to questions about the time-course of processing, as they potentially reflect post-perceptual strategies. Electrophysiology research provides direct means of examining early components of visual word perception through the analysis of electrical signals of brain activity recorded on the human scalp.

A brief introduction to event-related potentials in electrophysiology

Basic concepts

The electroencephalogram (EEG) is the recording of fluctuating voltage differences between electrodes placed on the scalp, and is measured with millisecond precision. The event-related potential (ERP) represents the electrophysiological response in the EEG that is time- and phase-locked to a particular event. An ERP is extracted by averaging many time-locked EEG epochs suppressing the background activity in the EEG that is unrelated to the particular event.

Traditionally, ERPs are depicted as waveforms at particular electrodes, and the peaks and troughs in the waveforms are thought to reflect components, which are typically labeled according to their polarity and timing. For example components may be labeled as P1, N1, N170, P300, N400, with the letter depicting whether the component was a positive or negative deviation from baseline, and the component number representing the timing, either in cardinal order (as in P1, N1, P2, N2) or the millisecond latency of the peak (e.g. P300: a positive-going component peaking at about 300 ms after stimulus onset). Additional labels, such as “visual” or “occipital”, are often added to the component name, because polarity and timing can vary with stimulus modality and electrode site.

To account for varying head sizes and head forms in interindividual comparisons, electrodes are placed in relation to landmarks (inion, nasion, left and right preauricular points) that can be found on each head. By dividing the distance between these landmarks into equidistant parts of 10% each, one of the commonly used electrode placement system - the 10-10 system - creates a grid on the scalp to place the electrodes (Chatrian, Lettich, & Nelson, 1985). The labels of the grid points (e.g. Oz, P1, C2, F3, Fpz) indicate their anterior-posterior locations on the scalp (Fp: frontopolar, F: frontal, C: central, P: parietal, O: occipital) and their relations to the midline (z: central, odd numbers: left; even numbers: right) with increasing numbers indicating increasing excentricity.

ERP mapping approach

In traditional ERP analyses, topographic effects such as laterality are often limited by examination of a few channels on the scalp, but modern EEG systems allow recordings from many channels (commonly as many as 128) providing additional topographic information. One approach to topographic analysis of multi-channel ERP data, termed a "mapping" approach, has been developed that looks at the data primarily as a sequence of topographic ERP maps changing in topography and global strength over time (Lehmann & Skrandies, 1980). Within this approach, analysis methods have been developed that take full advantage of the additional topographic information while preserving the high time-resolution benefits of ERP data (e.g. Brandeis & Lehmann, 1986; Lehmann & Skrandies, 1980; Michel et al., 2004; Pascual-Marqui, Michel, & Lehmann, 1995).

ERP map strength can be described by Global Field Power (GFP; Lehmann & Skrandies, 1980), which is computed as the root mean square of the values at each electrode in an average-referenced map. ERP map topography can be described by map features, such as the locations of the positive and negative maxima (Brandeis & Lehmann, 1986) or the locations of the positive and negative centroids (centers of gravity; Brandeis, Vitacco, & Steinhausen, 1994).

The use of topographic information for ERP analysis is important, because it can resolve ambiguities that result from the fact that amplitude differences between two conditions recorded at a single electrode can result from identical topographies which are stronger in one condition compared to the other or they can result from different topographies which may or may not differ in global strength. This distinction is important because topographic information allows a characterization of the underlying neural processes: Different topographies are produced by different neural networks, and identical topographies are likely to reflect the same neural networks.

In an additional step, ERP topographies can be used to estimate location and orientation of the underlying cortical sources, provided that a number of assumptions can be validly adopted. Assumptions are necessary to mathematically solve the "the inverse problem" which captures the fact that one can model the scalp topography given a set of neural sources of known location, orientation, and strength, but given a known scalp topography, many potential combinations of number, location, orientation, and strength of neural sources are equally plausible as solutions. Thus, different assumptions about the sources of electrical activity and its propagation to the scalp, as implemented in different source estimation models, have an influence on the nature of the results (for a recent review see Michel 2004).

Topographic 3D centroid analysis

The large number of electrodes used in modern EEG systems results in a vast amount of topographic information. Selecting only a subset of these channels for analysis can lead to results that are biased by the pre-selection of the channels. The use of map centroids offers an un-biased means for topographic ERP analysis (see Figure 1). The positive and negative 3D centroids are the centers of gravity of the positive and negative fields in 3D space (e.g. Talairach coordinate system, Talairach & Tournoux, 1988) and are computed as the voltage-weighted locations of all electrodes showing positive or negative values, respectively. Accordingly, an ERP map consisting of 129 electrodes can be reduced to 2 centroids, each defined by 3 values representing the x-, y-, and z-coordinates of the 3D space. Subsequent statistical analyses can be computed for the x-, y-, and z-coordinates of the centroids resulting in topographic differences in 3 spatial dimensions “left-right”, “posterior-anterior”, and “inferior-superior”. Importantly, although the centroids are located within the head space - which is typical for centers of gravity of scalp measures, they are by no means estimations of the underlying sources. The advantage of the centroid measure vs. source estimation is that the centroids are features of the measured topography, whereas source estimations depend on additional assumptions that may or may not apply.

Overview of electrophysiology of visual word processing

Visual word processing has been extensively investigated with ERP measurements, and various aspects of psychological processes involved in reading have been linked to several different ERP components. Perhaps the most studied language component in response to visual words is the N400, a component linked to semantic processes. The N400 component is a negative deflection which is significantly enhanced when a word is presented as semantically anomalous within a sentence (Friederici, Gunter, Hahne, & Mauth, 2004; Kutas & Federmeier, 2000). Studies on syntactic violations in sentence processing have revealed a rather different component, the P600. Differences in topography of the N400 and P600 suggest that distinct processes are involved in processing semantic and syntactic violations, even in cases when manipulations of syntactic expectations produce ERP responses to syntactic violations within 400 ms (Friederici et al., 2004). N400-like effects have also been used to investigate phonological processes in visual word tasks (Rugg, 1984), although some aspects of phonological processing may occur between about 200 and 350 ms, earlier than semantic N400 effects (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999). For the purposes of the current chapter, each of these effects appear to implicate processes that occur much later than the time-course of specialized word perception, which other cognitive research suggests occurs within the first 200 ms of word perception. Reading-related effects, however, have also been reported in earlier components, especially in the N170 component.

Perceptual expertise N170 effects

The visual N170 (or N1) component of the ERP peaks between 150 and 200 ms and shows a topography with posterior negativity and anterior positivity. Although elicited by visual stimuli in general, the N170 is strongly elicited by certain classes of visual stimuli, such as faces (Bentin et al., 1999; Rossion, Joyce, Cottrell, & Tarr, 2003), compared to control stimuli.

The psychological principles that lead to a larger N170 for one stimulus category compared to another may lie in perceptual expertise with the stimulus category at hand. Increased N170 responses were elicited in bird-experts looking at birds (Tanaka & Curran, 2001), and in car-experts looking at cars (Gauthier, Curran, Curby, & Collins, 2003). An increase of the N170 could even be induced by expertise-training with novel objects (e.g. “greebles”, Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002). These results suggest that extensive visual experience with an object category leads to fast, specialized processing within the first 200 ms.

This perceptual expertise framework for evaluating N170 effects may also account for increased N170 responses that skilled readers show for visual words. A robust reading-related N170 specialization in electric fields (as well as a similar component in magnetic fields of magnetoencephalography) is found for contrasts between categories of stimulus classes including words versus other low-level visual control stimuli such as strings of meaningless symbols, forms, shapes, or dots (Bentin et al., 1999; Brem et al., 2005; Eulitz et al., 2000; Maurer, Brandeis, & McCandliss, 2005; Maurer, Brem, Bucher, & Brandeis, in press; Schendan, Ganis, & Kutas, 1998; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Zhang, Begleiter, Porjesz, & Litke, 1997). Such overall reading-related N170 specialization appears to be automatic, as it is also detected in tasks that do not require the words to be read (Bentin et al., 1999; Brem et al., 2005; Eulitz et al., 2000; Maurer et al., 2005; Maurer et al., in press; Schendan et al., 1998; Tarkiainen et al., 1999).

Examination of the pattern of stimuli that elicit an N170 response provides support for a form of similarity gradient in these implicit tasks, such that the more the stimuli resemble letter-strings, the larger their N170 component, as found e.g. in a larger N170 for word-like pseudofonts compared to control stimuli (Eulitz et al., 2000; Schendan et al., 1998; Tarkiainen et al., 1999). On the other hand, words, pseudowords, and even consonant strings have been shown to produce similar N170 responses, which differed from that elicited by symbol strings and other visual forms (Bentin et al., 1999; Maurer et al., in press).

Although specialization for words appears to be one example out of a broader class of perceptual expertise stimuli that affect the N170, there is also evidence that visual words represent a special case of perceptual expertise, as N170 responses to words are typically left-lateralized (for review see Maurer et al., 2005).

Left-lateralization of the N170

Several studies have shown that overall reading-related N170 specialization is left-lateralized (Bentin et al., 1999; Maurer et al., 2005; Maurer et al., in press; Tarkiainen et al., 1999), with larger amplitudes over the left hemisphere for words than for low-level visual control stimuli. This left-lateralized N170 topography elicited by visual words stands in contrast to N170 responses for other forms of perceptual expertise related to faces or objects of expertise, which are typically bilateral or right-lateralized (Rossion et al., 2003; Tanaka & Curran, 2001). The degree of left-lateralization in the N170, however, varies across studies and seems to depend on additional factors, which are not yet fully understood. In pursuit of a suitable explanation we propose below factors that may help explain this variability.

Source localization estimates for the N170 elicited by words found left-lateralized sources in inferior occipitotemporal cortex (Maurer et al., in press; Michel et al., 2001; Rossion et al., 2003). This is in agreement with intracranial recordings finding a negative component around 200 ms in basal occipitotemporal cortex (Nobre, Allison, & McCarthy, 1998) and with source localization of the word-specific M170, the N170 analogue recorded with MEG (Tarkiainen et al., 1999).

The characteristic trend towards a left-lateralized N170 topography for words might be linked to similarly left-lateralized hemodynamic activation during visual word tasks. Functional neuroimaging studies reported reading-related activation in many areas of the extrastriate visual cortex, especially in the left hemisphere (Petersen, Fox, Posner, Mintun, & Raichle, 1988; Price, Wise, & Frackowiak, 1996; Tagamets, Novick, Chalmers, & Friedman, 2000). In particular, an area in the left fusiform gyrus, located in the inferior part of the occipito-temporal cortex, may constitute a Visual Word Form Area, because it shows sensitivity for visual word forms at a highly abstract level (for a review see McCandliss et al., 2003).

Similar sensitivity for abstract properties of visual words may also already occur during the N170 component.

Sensitivity of the N170 for higher language functions

Several studies have also examined the nature of cognitive processing indexed by the N170 word effect by investigating additional stimulus category contrasts. Comparing consonant strings with pseudowords or words serves to control letter expertise while contrasting information on the structure of a word form. One set of results demonstrated that consonant strings have larger N170 amplitudes than words (Compton, Grossenbacher, Posner, & Tucker, 1991; McCandliss, Posner, & Givon, 1997), and orthographically irregular pseudowords were in between (McCandliss et al., 1997). Such results provide support for the notion that perceptual expertise for words indexed by the N170 reflects not just expertise for letter recognition, but also expertise associated with recognition of familiar patterns of letters within visual word forms. Other studies, however, failed to show N170 sensitivity to the contrast between words and pseudowords (Bentin et al., 1999; Wydell, Vuorinen, Helenius, & Salmelin, 2003), and differences between consonant strings and words were found only during explicit lexical and semantic tasks, not during implicit reading (Bentin et al., 1999).

In contrast to such studies that make inferences based on comparisons of different stimulus categories (i.e. words, pseudowords, consonant string), studies that compared different levels of word frequency provide more consistent results regarding the role of lexical information in modulating the N170. Low frequency words typically elicit larger N170 amplitudes than high frequency words in lexical or semantic decision tasks (Assadollahi & Pulvermuller, 2003; Hauk & Pulvermuller, 2004; Neville, Mills, & Lawson, 1992; Sereno, Brewer, & O'Donnell, 2003; Sereno, Rayner, & Posner, 1998, but see also Proverbio, Vecchi, & Zani, 2004), providing evidence of perceptual expertise at the level of accessing specific words. Thus, different approaches to the question of whether N170 responses are sensitive to specific word representations, such as categorical distinctions between words and pseudowords vs. within category parametric manipulations of word frequency) provide contrasting answers, and raise new potential questions regarding the nature of processing applied to pseudowords.

As these studies based their analyses mostly on a few channels, an ERP mapping approach, which takes full advantage of the topographic information available, may be able to better characterize the processes involved and to resolve some ambiguities.

N170 ERP mapping studies in German and English

Reading-related N170 specialization was investigated in two separate studies with the same paradigm in Zurich, Switzerland (Maurer et al., in press), and subsequently at the Sackler Institute in New York (Maurer et al., 2005).

In both studies, literate adult subjects looked at blocks of serially presented stimuli that contained runs of either words, pseudowords, symbol strings, or pictures. For each class of stimuli the subjects remained motionless in response to the majority of stimuli, but pressed a button whenever they detected an occasional immediate stimulus repetition. This 'one-back' paradigm allowed ERPs to be calculated for each word on its initial presentation without any reaction on the part of the subject, and behavioral responses to be collected on occasional repeated stimuli, thus ensuring that subjects engaged in the task. Moreover, as repeated words could be detected even without reading, this implicit reading task could potentially be applied with illiterate children, thus allowing the investigation of changes due to learning to read.

In the Zurich study, German-speaking adults viewed German stimuli, and EEG was recorded from 43 electrodes. Data were analyzed with an ERP mapping strategy, i.e. differences in N170 maps were measured according to global strength (GFP) and topography (3D centroids).

Statistical t-maps showed that among ERP responses to stimuli that required no manual response, larger N170 amplitudes were found for words than symbols particularly over left occipitotemporal electrodes consistent with earlier studies analyzing waveforms at selected channels (Bentin et al., 1999). The mapping analyses showed that GFP was stronger for words than for symbols and that N170 topography differed between words and symbols, implicating different neural networks involved in word and symbol processing within the first 200 milliseconds. The most prominent topographic feature that differed between word and symbol maps was found in the distribution of the centroids along the inferior-superior z coordinate axis. These centroid differences reflected that the negative fields over the posterior part of the scalp were most pronounced at inferior sites for words and at superior sites for symbols, whereas over the anterior part the positive fields were most pronounced at inferior sites for symbols and at superior sites for words. The centroid differences also reflected that the largest negative differences occurred at left inferior occipito-temporal electrodes at the edge of the electrode montage.

For the word-pseudoword contrast, however, there were no N170 differences in response to German words and pseudowords, suggesting that reading-related N170 specialization generalized from words to pseudowords, and thus may reflect perceptual expertise for letters or well-ordered letter strings.

For the pseudoword-symbol contrast, similar prominent topographic differences in the centroid distribution were found as for the word-symbol contrast. In addition the centroids were more left-lateralized for pseudowords than for symbols. This reflected that the negative fields of the N170 were more left-lateralized for pseudowords than for symbols, which was also apparent in the word-symbol comparison, where it reached significance in the last two thirds of the N170.

The topographic analysis of the Zurich study extended earlier studies by showing that reading-related N170 specialization is characterized not only by more left-lateralized fields but by more inferior negative fields over the posterior part of the head and more superior positive fields over the anterior part of the head. This suggests that the differences arose because different neural networks were activated in an early phase of word processing compared to symbol processing, rather than the same network being more strongly activated.

In the New York study we investigated whether the effects from the Zurich study could be replicated with the same paradigm (after adaptations for language) in a sample of English speaking participants (Maurer et al., 2005). An additional aim of the study was to apply a high-density EEG recording system, because this system samples more densely and extends the coverage on the scalp to more inferior locations than traditional EEG systems do. The traditional 10-20 electrode placement system covers only regions as much inferior as the Oz and Fpz electrodes, thus – roughly speaking – electrodes are only placed about above the ears. For signals that presumably originate in inferior brain regions, a more inferior sampling may provide a better characterization of the resulting scalp topography. For this reason the 10-20 system has been extended to more inferior regions in some studies (e.g. Bentin et al., 1999; Maurer et al., in press). However, high-density recordings sample from sites that are located even more inferior than those in these previous studies (Luu & Ferree, 2000). As the maximal effect in the Zurich study was found at the edge of the montage at posterior inferior channels, more inferior sampling may provide better characterization of the effects.

The central contrast for the replication study was the most robust contrast of words versus unfamiliar symbol strings in the N170. The statistical t-maps in the New York study showed that words elicited larger N170 amplitudes than symbols at left inferior occipitotemporal electrodes similar to the Zurich results. The mapping analyses revealed that GFP was not larger for words than for symbols, but as in the Zurich study the N170 topographies differed between words and symbols, confirming that specialized neural networks are active within the first 200ms of word presentation. These topographic differences showed very similar characteristics to the results of the Zurich study with a different centroid distribution along the inferior-superior z coordinate axis between word and symbol responses, suggesting that similar neural networks are specialized for reading across languages.

In addition, a topographic effect was also found in the left-right axis, suggesting a larger involvement of the left hemisphere in word processing and the right hemisphere in symbol processing. A similar difference in left-lateralization was also present in the Zurich data, where it reached significance in the last two thirds of the N170.

These results suggested that overall reading-related N170 specialization can be detected across different languages and EEG systems and that the maximal effect is inferior to the coverage of traditional EEG montages. Because the topographic effects where consistent while the GFP effects varied across studies, it can be inferred that similar neural networks are activated across languages, whereas the relative strength of the engagement of these networks may depend on additional factors. Finally, contrasts between results in German and English may provide additional insights into how differences in these writing systems may lead to different forms of perceptual expertise for reading.

One difference that emerged between the English and German studies involved the responses to pseudowords. While the Zurich study revealed comparable N170 effects for words and pseudowords, in English, N170 topographic effects for pseudowords were not identical to words. Words and pseudowords, when compared to symbol strings, both demonstrated similar topographic effects in the inferior-superior z-axis in both English and German, yet words were more strongly left-lateralized than pseudowords in English.

These findings may suggest that inferior-superior topographic effects may be indexing some form of processing which is constant across these two languages, but that the left-lateralized topographic effect reflects a form of processing that is more language-specific. We suggest that the inferior-superior N170 modulation indicates visual expertise for letters or well-ordered letter strings, and may reflect more general visual perceptual expertise effects that are also found with stimuli outside of reading.

Considering that pseudowords elicit a left-hemisphere modulation of the N170 in German, but not in English, may reflect differences between these writing systems that impact the processing of novel visual word forms. In fact a prominent difference between the two languages involves the degree of consistency with which letters map onto word sounds. As a result, pseudowords are more ambiguous for English speakers to pronounce than for German speakers. Thus the left-lateralized subtype of perceptual expertise may specifically relate to processes involved in mapping letters onto word sounds. The lack of such a left-lateralization for English pseudowords may suggest that such processes are less automatic in English (Zevin & Balota, 2000), and are engaged to a lesser degree while detecting pseudoword repetitions, because repetition detection does not require explicit pronunciation of the stimuli.

Although direct comparisons of these studies with English and German subjects may be limited by the use different words, pseudowords, and EEG systems, the results suggest that left-lateralization may be related to spelling-to-sound mapping, which leads to formulation of a more general hypothesis about learning to read and left-lateralized specialization of the N170 word effect — the phonological mapping hypothesis.

The phonological mapping hypothesis

Converging evidence from electrophysiological and hemodynamic studies suggests that left-lateralized activation is a characteristic of visual word processing in the brain. As the left hemisphere has long been known to be dominantly involved in speech perception and speech production, one straightforward hypothesis is that during reading acquisition the left-lateralized characteristic of the visual language system is induced by the pre-existing left-lateralization of the auditory language system.

More specifically, the left-lateralization might be driven by a particular aspect of auditory language processing, namely phonological processing, which leads to the phonological mapping hypothesis (McCandliss & Noble, 2003). The essence of this hypothesis is that given that phonological processes are typically left-lateralized (Price, Moore, Humphreys, & Wise, 1997; Rumsey et al., 1997), specialized processing of visual words in visual brain areas also becomes left-lateralized.

The results of the Zurich and the New York ERP mapping studies suggest that the phonological mapping hypothesis also accounts for fast reading-related expertise in the N170 component. Accordingly, the characteristic left-hemispheric modulation of the N170 may be specifically related to the influence of grapheme-phoneme conversion established during learning to read. This left-hemispheric modulation may add up to the inferior-superior modulation thought to reflect visual expertise for letters or well-ordered letter strings, and which may also develop during learning to read. This inferior-superior modulation of the N170 might be more generally related to visual discrimination learning and thus might be less language-specific. However, it cannot be ruled out that this modulation could nonetheless be shaped by grapheme-phoneme conversion or other language-specific aspects during learning to read.

In its simplest form the phonological mapping hypothesis for the left-lateralized N170 component has several implications for reading-related N170 specialization:

1) The left-lateralization of the N170 responses to visual words should be more pronounced in scripts using grapheme-phoneme conversion rules, but less pronounced in logographic scripts which are based on lexical morphemes. Furthermore, the phonological mapping hypothesis is specific to the left-lateralized modulation of the N170, thus the inferior-superior N170 modulation should not be influenced by scripts that differ in their phonological properties.
2) Reading-related N170 specialization, with inferior-superior and left-lateralized modulations, should develop in children when they learn to read, as well as in laboratory experiments that simulate this process.

3) Reading-related N170 specialization in dyslexic readers should show a smaller degree of left-lateralization, because of the phonological core deficit that has been associated with dyslexia, although such disorders could also affect the inferior-superior modulation.
4) Early phonological ability should predict the degree of N170 specialization with reading acquisition, especially with respect to its left-lateralization. Remediation of the phonological core deficit through intervention should specifically increase left-lateralization of the N170 specialization.

We consider the implications of these facets of the phonological mapping hypothesis in a broader consideration of the literature on reading-related N170 specialization.

N170 specialization in scripts of different language systems

Comparisons between fundamentally different writing systems may allow conclusions about processes involved during early visual word processing. For example a study with Koreans who were educated in both Chinese characters and written English, reported a left-lateralized N170 for both English words and Korean words, but a bilateral N170 for Chinese characters and pictures (Kim, Yoon, & Park, 2004). Both English and Korean writing systems map characters onto phonemes, whereas Chinese uses a logographic script, in which graphic symbols represent lexical morphemes. Thus, left-lateralization in the N170 was confined to language systems that use spelling-to-sound mapping that can be described at the grapheme-phoneme level, which suggests that the left-lateralization, developed during reading acquisition, is mediated by phonological processing related to grapheme-phoneme conversion.

Such cross-cultural and cross-linguistic differences, although confounded by many challenges of between-group, between-lab, and between-culture factors, nonetheless provide support for the phonological mapping hypothesis for the left-lateralization of the N170.

One such confound in cross-linguistic studies is the possibility of a difference in lateralization between first and second languages. For example, Proverbio et al. (2002) reported N170 responses for bilinguals that suggested a left-lateralization for the first language (Slovenian), but not for the second language

(Italian; Proverbio et al., 2002), a result which was also found in Italian-English interpreters (Proverbio et al., 2004), suggesting that reading skill for languages acquired later in life may be organized somewhat differently than for languages acquired early in life. Contrasts between first and second languages, however, may be complicated by differences in perceptual expertise across the two languages, and thus further studies are needed to clarify whether this lateralization effect is related to differences in spelling-to-sound mapping between first and second languages, differences in the strength of specialization, or whether it represents an additional factor driving left-lateralized N170 specialization.

Learning to read and development of N170 specialization

The predictions of the phonological mapping hypothesis on reading acquisition can be tested with developmental studies in children learning to read, as well as within laboratory experiments with adults in which aspects of reading acquisition are simulated.

The most direct evidence for specialization due to learning to read can be obtained by studying the same children before and after the start of reading acquisition. Within the context of the Zurich study, described above, children's N170 responses to words and symbol strings were recorded before and after learning to read. EEG was recorded from pre-literate children in kindergarten, in the same paradigm as described above, as they detected occasional immediate repetitions of words, and pseudowords, (a task which they could perform even without reading skills), as well as immediate repetitions of symbols and pictures. As reported above, adult readers in this paradigm had shown a large difference in the N170 between words and symbol strings, with a bilateral occipito-temporal topography, which was slightly stronger on the left. In contrast, the kindergarten children did not show a reliable difference in the N170 elicited by words and symbols (Maurer et al., in press). This result demonstrates that reading-related N170 specialization develops between kindergarten and adulthood. It also suggests that rudimentary levels of visual familiarity with print and letter knowledge are not sufficient to produce the typical reading-related N170 response, as the children could tell whether a stimulus string consisted of letters or other symbols, and could name about half of the letters in the alphabet. A further analysis which examined subsets of children with high and low letter knowledge confirmed that the children with low letter knowledge did not show a N170 specialization at all, but revealed that the children with high letter knowledge showed a weak specialization. The topography of this difference, however, was right-lateralized and strikingly different from the adult N170 effect, which suggested that the children's difference indicated a precursor to the mature fast specialization in adults. This precursor in non-reading children is presumably due to their letter knowledge or visual familiarity with print (Maurer et al., in press).

The absence of reading-related N170 specialization in pre-literate Swiss kindergartners, and especially the lack of a left-lateralized N170 modulation, lends some support to the phonological mapping hypothesis, which suggests that N170 responses develop as a result of increased mapping from letters to sounds. In addition, these same children have recently participated in the same paradigm during the middle of the 2nd grade, after they had mastered initial reading training. Forthcoming analyses of the longitudinal data will reveal whether reading-related N170 specialization emerges quickly with the initial reading training or whether it develops rather slowly, and may also provide additional subset analyses between children who differ in their initial phonological skills (Maurer et al., submitted).

One cross-sectional developmental study also provides a similar developmental account of N170 specialization. Posner and McCandliss (2000) reported a study looking at four-, seven-, and ten-year-old children, using a contrast between words and consonant strings previously reported to demonstrate visual N170 effects in adults (Compton et al., 1991; McCandliss et al., 1997), modified to ensure that the words used were familiar to both the seven- and ten-year-olds in the study. Using an implicit reading task, they reported that no N170 specialization for words over consonant strings emerged with initial learning to read (between age 4 and 7), but showed that 10-year olds began to demonstrate some evidence of differential N170 responses to words versus consonant strings (Posner & McCandliss, 2000). These results suggest that familiarity with words alone is unlikely to account for such N170 expertise effects, as the 7 year olds demonstrate familiarity but no N170 effect, and suggest instead that such effects may arise gradually over development of extensive expertise with fluent visual word recognition, a process that is emerging in 10-year-olds.

Developmental studies with children provide crucial data on learning to read that is ecologically valid, and provide insights into the nature of the processes that create the adult specialization, yet such studies raise questions about whether observed changes are specifically linked to learning-based increases in reading expertise or to maturation processes that play out over this same age range. Developmental studies can be usefully complemented by training studies with skilled adult readers to address these very issues. McCandliss and colleagues (McCandliss et al., 1997) introduced a novel way of investigating the impact of visual familiarity and lexical status of visual stimuli, by holding the exact stimulus set constant across a series of repeated testing sessions, but manipulating subjects' experience with a subset of the stimuli. With repeated measures this study investigated potential changes in the N170 induced over the course of 5 weeks as students spent 50 hours learning to read 60 words of a 120-word artificial pseudoword-language called "Keki" (the other 60 were reserved for testing purposes only). All pseudowords were comprised of familiar Roman letters, yet followed a visual word form structure generated by an algorithm that was designed to deviate from English in subtle but identifiable ways (e.g. all words ended in a vowel). N170 responses to several classes of stimuli were collected over the course of the five week learning experiment, and overall results demonstrated a significant effect of stimulus class, such that consonant strings elicited larger N170 responses than words, and responses to the Keki pseudowords fell in between. The central finding from the training study was that fifty hours of training, which increased both the visual familiarity and the associated meanings for the trained Keki words, did not change the stimulus-class effects on the N170 (i.e. no training-by-stimulus-type interaction was present for the N170 component). Even after training, the N170 for trained and untrained Keki words were not significantly different, and responses to the entire class of Keki items were still significantly more negative than for words, and significantly less negative than for consonant strings. In contrast, a component subsequent to the N170 demonstrated a significant and systematic training effect for the trained Keki items in relation to the other stimuli, from approximately 280 to 360 ms, revealing the sensitivity of the electrophysiological technique to training effects. From these results, the authors concluded that the N170 likely reflects orthographic structure, as letter familiarity was held constant across stimuli, and lexical familiarity was manipulated over 50 hours to no effect, and yet robust differences persisted across the three classes of stimuli (well structured English words, slightly atypically structured Keki words, and strongly atypically structured consonant strings). Furthermore, they suggested that, since the N170 was unresponsive to 50 hours of studying the novel structure of Keki word forms relative to consonant strings, such processes may change very slowly over time. Considering this pattern of results in the context of the phonological mapping hypothesis draws focus to the fact that the Keki words could be decoded via grapheme-phoneme associations related to reading English both before training and throughout training, and thus a lack of N170 training-related changes for the specifically trained Keki items might be predicted. In order to address this implication, future research in training studies should employ novel graphical features that lie outside the ability to generalize based on already existing grapheme-phoneme decoding abilities, and to directly contrast training methods that encourage learning via associations between graphic features and phonemes versus training that encourages associations between entire visual characters and auditory words.

N170 specialization in dyslexia

The phonological mapping hypothesis of the left-lateralized N170 expertise effect has important implications for dyslexia because it provides a developmental pathway account for how well-documented core phonological deficits present in early childhood and other precursors of dyslexia (for a review see Shaywitz, 2004) impact the developing neural mechanisms underlying fluent visual word recognition. Furthermore, individual differences in phonological mapping ability may also relate to the degree of reading-related N170 specialization in dyslexic children and adults, especially with respect to its left-lateralization.

Evidence for reduced reading-related N170 specialization in dyslexia has come from magnetoencephalographic studies. Helenius and colleagues (1999) presented words and symbol strings to dyslexic adults who attended to the stimuli and were prepared to report them if prompted. In normally reading adults, sources in the inferior occipito-temporal cortex, predominantely in the left hemisphere, differed between words and symbols around 150ms (Tarkiainen et al., 1999). In dyslexic subjects, however, such word-specific sources were undetectable in the same time range (Helenius et al., 1999). This pattern of results is corroborated by another MEG study which found that words and pseudowords activate sources in the left occipito-temporal cortex in normal readers between 100 and 200 ms, but less so in dyslexic readers (Salmelin, Service, Kiesila, Uutela, & Salonen, 1996). Such results are at least consistent with the phonological mapping hypothesis, in that they present further evidence on the link between adult expertise in reading and the left-lateralized N170, and are consistent with the notion that phonological core deficit in dyslexia may impact the process of progressively increasing left-lateralized recruitment of visual regions that are the hallmark of reading-related expertise in the form of the N170. However, such developmental claims about the late emergence of left-lateralized N170 responses for skilled readers, and not dyslexics, require developmental data. Interestingly, two studies that directly compared dyslexic children to age-matched controls did not find group differences in visual word processing in the N170 time range (Brandeis et al., 1994; Simos, Breier, Fletcher, Bergman, & Papanicolaou, 2000). This contrast between the adult and child literature may suggest that differences between normal and dyslexic reading develop only late during childhood and become manifest in adulthood only with the emergence of visual expertise in skilled adult readers.

Future developmental work on the cognitive and neural basis of the N170 effect in dyslexia will need to include longitudinal designs that examine early manifestations of phonological deficits, and relate such deficits directly to the emergence of behavioral and neurophysiological indexes of perceptual expertise in reading. Such developmental work on early phonological deficits may also be enhanced by the inclusion of electrophysiological measures of phonological processes, as behavioral assays of phonological deficits may reflect not only deficiencies in phonological processing, but also deficiencies in other processes such as executive attention functions (for a review see Noble, McCandliss, & Farah, submitted). Such electrophysiological studies of phonological processing have tried to directly measure brain processes related to the phonological core deficit, thus aiming to improve prediction of dyslexia.

One candidate for a neurophysiological measure of phonological processing deficits in dyslexia is the mismatch negativity (MMN), a component of the auditory ERP. The MMN is regarded as a measure of the auditory memory or the central sound representation (Naatanen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001). MMN responses are also elicited by deviant phonemes and thus may represent a measure for phoneme representations in the brain (Naatanen, 2001). The MMN is also very suited to be used with children, as it measures automatic discrimination, i.e. the participants are given a distracting task, such as reading a book or watching a silent video. The MMN is also regarded as developmentally stable as it has been elicited in young children and even in infants (Cheour, Leppanen, & Kraus, 2000), although in children it can change its topography under certain conditions (Maurer, Bucher, Brem, & Brandeis, 2003a).

Currently, several longitudinal studies with children from families with risk for dyslexia are being conducted that have obtained MMN measures before the start of reading acquisition.

In the Zurich study (described above) that looked at development of reading-related N170 specialization in children before and after learning to read, a subgroup of children came from families with one or more parents demonstrating symptoms of dyslexia. The kindergarten children were tested with two auditory oddball paradigms containing tone stimuli (standard: 1000Hz, deviants: 1030 Hz, 1060 Hz) and phoneme stimuli (standard: ba, deviants: da, ta). Between approximately 300 and 700 ms the children showed a frontally negative mismatch response to the deviant stimulus compared to the standard. This late-MMN differed between children at risk and control children (Maurer, Bucher, Brem, & Brandeis, 2003b). Children at risk for dyslexia demonstrated an attenuated late-MMN response following deviant tone stimuli, and demonstrated an atypical topography of the late-MMN in response to deviant phoneme stimuli. This topographic difference following deviant phonemes was potentially informative, as the control children showed one major positive pole, which was strongly left-lateralized, indicating left-lateralized mismatch processing, whereas the children at risk showed two positive poles of the MMN, indicating bilateral mismatch processing.

These results suggest deviant automatic phoneme perception in children at risk for dyslexia. The attenuated MMN to tones may suggest that the deviant phoneme processing is related to a more low-level auditory processing deficit. Pending longitudinal results may reveal whether such effects are early predictive markers of specific dyslexia-risk for these individual children, or merely markers of familial risk. Moreover, such longitudinal designs provide the framework to test whether these measures of speech perception can predict the degree of reading-related N170 specialization and its left-hemispheric modulation.

Evidence for predictive values of ERP measures of early speech perception for later reading ability comes from studies that have followed children from early perception of speech through development of early reading skills. The Jyvaskyla longitudinal study in Finland, followed the development of children at familial risk for dyslexia in contrast to typically developing children. Testing, including ERP recordings, started in the first days after birth, and will continue intermittently until the 3rd grade. The ERP data, assessing basic speech processing and automatic mismatch response to speech stimuli, showed that the at-risk infants already differed from the control group during their first days and months of infancy (Lyytinen et al., 2004; Lyytinen et al., 2004). Comparison of the ERP data from the first days of life with later language development showed correlations with receptive language skills and verbal memory (Guttorm et al., 2005). Preliminary data also indicates correlations with initial reading and spelling skills (Lyytinen et al., 2004). The results from this longitudinal study are generally consistent with earlier reports that ERP responses to speech sounds recorded within hours after birth are strongly correlated with reading ability at 8 years of age (Molfese, 2000). In this study, some selected indexes derived from the ERP results collected in infancy were able to support discrimination among children into three different groups of reading and IQ impairments with an overall accuracy of 81%.

Such longitudinal studies provide evidence for the role of early speech processing in later language development and reading acquisition. These studies, however, did not investigate reading-related N170 specialization and thus do not allow for a test of the phonological mapping hypothesis with regard to the role of phonological processing for specialized visual word recognition. Based on our review of current findings, such developmental studies would need to include children beyond age seven to characterize the rise of perceptual expertise and N170 responses to visual words.

Conclusions.

Behavioral studies have indicated that word-specific information is processed within the first 200ms of stimulus presentation. Such fast visual word processing ability in skilled adults may rely on left-lateralized visual expertise effects linked to the N170 component. Converging evidence shows larger N170 amplitudes, especially over the left hemisphere, for words compared to visual control stimuli such as symbol strings, but results regarding specialization among different types of letter strings and the degree of the left-lateralization of the word N170 suggest large variation due to additional factors involved. An ERP mapping approach that takes advantage of modern multi-channel EEG recordings in participants with different language backgrounds suggested two overlapping processes in the N170, leading to the formulation of the phonological mapping hypothesis for the development of reading-related N170 specialization. A left-lateralized modulation may develop under the influence of grapheme-phoneme conversion during learning to read and reflects the involvement of spelling-to-sound mapping during visual word processing. Furthermore, a more domain-general inferior-superior modulation may develop through visual discrimination learning during reading acquisition. This hypothesis frames a set of specific predictions regarding reading-related N170 specialization in language systems using different scripts, in learning to read, and in dyslexia, that can be tested in specific studies. Results that allow such tests are just emerging and seem to support the predictions of the phonological mapping hypothesis for N170 specialization. Emerging and future results that directly examine the developmental and learning changes that link phonological processes to the emergence of expertise in fluent visual word recognition via development and training studies will provide more direct evidence that bear on such predictions, and will likely provide further neural-circuitry-level insights into the developmental and learning pathways that give rise to fluent visual word recognition.

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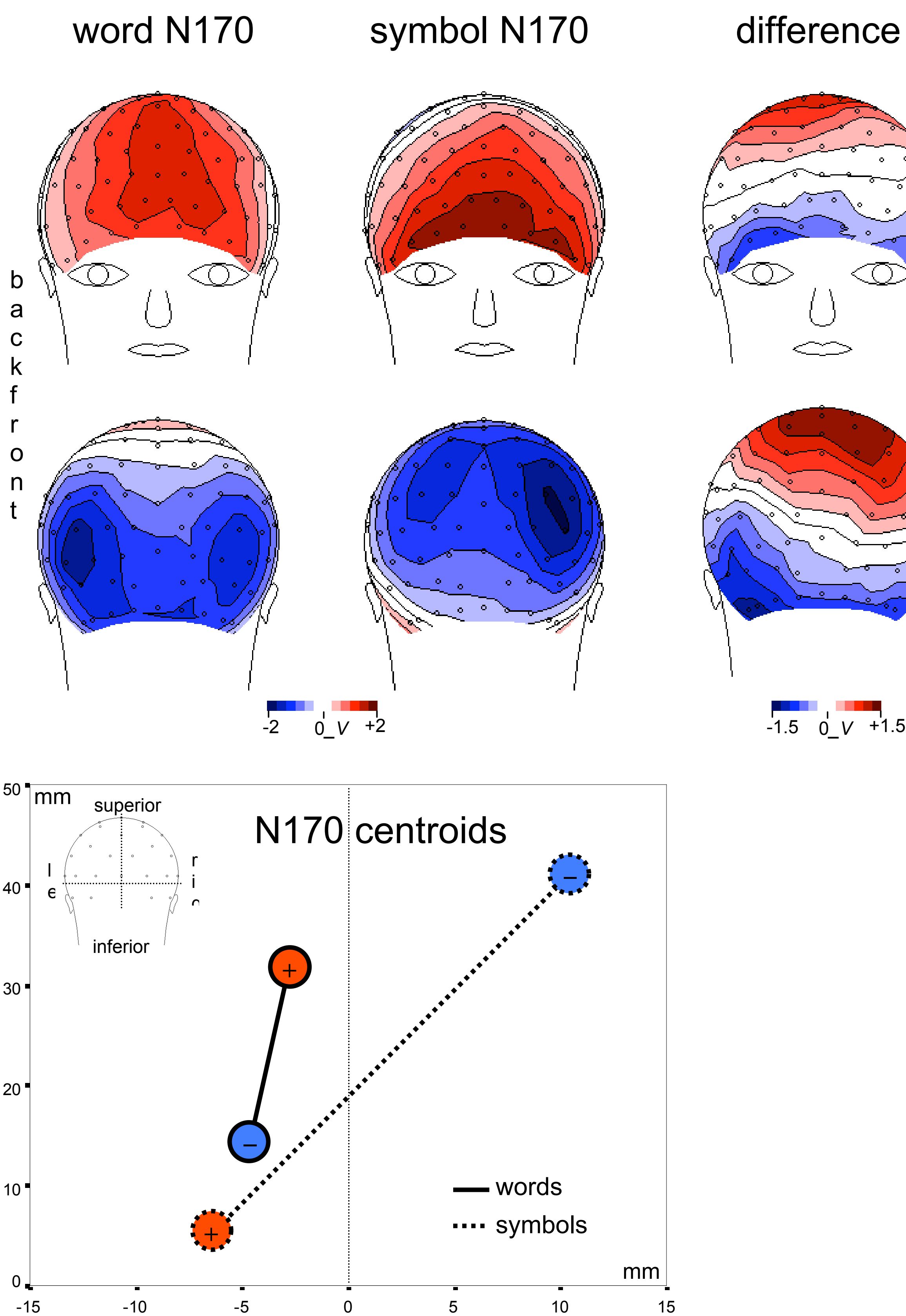
Figure legends

Figure 1. ERP maps and centroids.

The different distribution of the positive (indicated by a "+") and negative (indicated by a "-") fields in the N170 between words and symbols is illustrated in maps seen from the front and from the back (upper figure, left and middle). The difference maps show that the maximal negative difference appears at the left occipito-temporal electrodes at the edge of the montage (upper figure, right). The different distribution of the positive and negative fields between word and symbol N170 in the 129-channel maps are summarized by the centroid locations in Talairach space (lower figure), which can be used for further statistics. The centroids are shown from the back with their x- and z-coordinates. The additional posterior-anterior y-axis is not depicted here.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