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Neural Correlates of Letter-String Length and Lexicality during Reading in a Regular Orthography

T. N. Wydell[1], T. Vuorinen[2], P. Helenius[2], and R. Salmelin[2]

Abstract

■ Behavioral studies have shown that short letter strings are read faster than long letter-strings and words are read faster than nonwords. Here, we describe the dynamics of letter-string length and lexicality effects at the cortical level, using magnetoencephalography, during a reading task in Finnish with long (eight-letter) and short (four-letter) word/nonword stimuli. Length effects were observed in two spatially and temporally distinct cortical activations: (1) in the occipital cortex at about 100 msec by the strength of activation, regardless of the lexical status of the stimuli, and (2) in the left superior temporal cortex between 200 and 600 msec by the duration of activation, with words showing a smaller effect than nonwords. A significant lexicality effect was also evident in this later activation, with stronger activation and longer duration for nonwords than words. There seem to be no distinct cortical areas for reading words and nonwords. The early length effect is likely to be due to the low-level visual analysis common to all stimulus letter-strings. The later lexicality and length effects apparently reflect converging lexico-semantic and phonological influences, and are discussed in terms of dual-route and single-route connectionist models of reading. ■

INTRODUCTION

Cognitive behavioral research into reading has shown that in alphabetic languages, the letter-string length affects the naming latencies of words and nonwords: As string length gets longer, so do the naming latencies (e.g., Balota & Chumbley, 1985; Henderson, 1982; Frederiksen & Kroll, 1976 for a review; Rastle & Coltheart, 1998; Weekes, 1997). For real words, this length effect is modulated by word frequency: Low-frequency words show a larger length effect than high-frequency words (Content & Peereman, 1992), and often high-frequency words show no length effect (Weekes, 1997). Further, the length effect is also modulated by lexical status: The size of the length effect is much larger for nonwords than words (Weekes, 1997). These string-length effects have been taken as strong evidence of sequential processing in reading aloud (e.g., Coltheart & Rastle, 1994).

There are two main kinds of reading models that account for the observed phenomena of the cognitive processes involved in reading—a dual-route reading model (e.g., Zorzi, 2000; Coltheart, Curtis, Atkins, & Haller, 1993; Coltheart & Rastle, 1994) and a single-route parallel distributed connectionist model (e.g., Plaut, McClelland, Seidenberg, & Patterson, 1996; Seidenberg & McClelland, 1989). The dual-route models typically assume that transcoding from orthography to phonology is achieved by two procedures: a lexical (whole-word level) procedure,[1] which operates in parallel across the input string, and a sublexical (subword level) procedure, which operates serially from left to right across the string. The sublexical-assembled (as opposed to lexical addressed) phonology is achieved by applying a fairly concise set of grapheme-to-phoneme correspondence rules (see Patterson & Coltheart, 1987 for a review on assembled vs. addressed phonology). Not only do these rules enable the generation of accurate pronunciations of regular or consistent words, but they also provide a plausible account of how skilled readers can read nonwords.

Thus, length effects on naming latency in these models simply reflect the serial operation of the sublexical route, and the size of the length effect for any stimulus is determined by the extent to which sublexical processing is involved. Because the lexical route(s) processes high-frequency words very quickly, the sublexical route makes little or no contribution to pronouncing these words. However, for a low-frequency word, lexical processing is slow enough to allow a substantial contribution from the sublexical route. For a nonword, the sublexical route must be the major determinant of pronunciation (Rastle & Coltheart, 1998), because nonwords cannot be pronounced correctly via the lexical route(s). It follows, therefore, from the dual-route account of reading aloud that the length effect on naming latency should be modulated by word frequency as well as lexicality. Rastle and Coltheart's (1998) dual-route cascade (DRC) model thus can give a reasonable account

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of the length effects as well as the interactions with word frequency or lexicality.

In contrast, distributed connectionist models assume that orthographic, phonological, and semantic information is represented in terms of distributed patterns of activation over groups of simple units. Similar words are represented by similar patterns of activation within each orthographic, phonological, or semantic domain (e.g., Plaut et al., 1996; Seidenberg & McClelland, 1989). Reading aloud, for example, requires the orthographic pattern for a word to generate the appropriate phonological pattern. Such transcoding is thought to be achieved by the co-operative and competitive interactions among units, including additional hidden units that mediate between the orthographic, phonological, and semantic units, and both words and nonwords are processed via a single interactive process. However, because these single-route connectionist models do not include sequential processing at any level, length effects are not readily accounted for.

In order to account for length effects using connectionist models, Plaut (1998) presented a simulation model, which uses position-specific letter units and a re-fixation mechanism. The network model is trained to produce the appropriate sequence of phonemes for a letter string, but at the same time, it is also trained to maintain a representation of its current position within the string. The network uses this position signal to re-fixate a portion of input when it finds it difficult to pronounce. The length effect in Plaut's model is thus shown (in accuracy rather than latency) by the number of fixations that the model made to produce correct pronunciations for different types of stimuli. For example, low-frequency words or nonwords require a greater number of fixations in order to produce correct pronunciations than high-frequency words, because the model has less or no exposure to letter-string sequence for these letter strings. Another major difference between Plaut's model and previous single-route connectionist models is the way in which phonological output is generated. The previous models generated a representation of the pronunciation of an entire word, while Plaut's model generates a pronunciation phoneme-by-phoneme. The model, thus, incorporated two distinct sequential processes—a re-fixation mechanism with position-specific letter units at the input level, and phoneme-by-phoneme generation of a pronunciation at the output level—which are outside of central processes relating to orthography, phonology, and semantics. Plaut's model accounted well for experimentally observed length effects.

If one takes the perspective of a dual-route reading model, it follows that for reading alphabetic and even nonalphabetic languages, both lexical whole-word reading and sublexical grapheme-to-phoneme translations are involved. Which strategy is emphasized depends on the regularity/consistency of orthography-to-phonology mapping of the particular writing system (e.g., Wydell, Butterworth, & Patterson, 1995; Baulch & Besner, 1991; Frost, Katz & Bentin, 1987). For regular orthographies such as Italian, Serbo-Croatian, or Dutch, the emphasis is more likely to be placed on the sublexical strategy (e.g., Hudson & Bergman, 1985; Turvey, Feldman & Lukatela, 1984), because this strategy is fast and efficient. Hudson and Bergman (1985) further revealed that in Dutch length effects had a significantly larger impact than word frequency on naming latency. This suggests that the length effects on naming latency are more pronounced in regular orthographies than in quasi-regular or deep orthographies such as English. Finnish is another very regular language represented by 21 phonemes (cf. 40 phonemes in English), and the transparency of the Finnish language makes correspondence between phonemes and graphemes practically one-to-one (Niemi, Laine, & Tuominen, 1994). Finnish is also an agglutinating language with many different forms/cases [e.g., talo (house), talossa (in the house), taloissa (in the houses)] with each form representing a single word. Hence, the preferred and perhaps optimal reading strategy is thought to be the sublexical grapheme-to-phoneme conversion (Leinonen et al., 2001; see also Paulesu et al., 2000 for Italian). Length effects should thus be evident for both high- and low-frequency Finnish words. Of course, this does not preclude whole-word level contribution during reading in Finnish.

Some imaging studies have also addressed the question of reading routes and/or length effects, and their manifestations in the human brain (e.g., Paulesu et al., 2000; Hagoort et al., 1999; Indefrey et al., 1997; Price, 1997; Rumsey et al., 1997; Pugh et al., 1996; Petersen, Fox, Snyder, & Raichle, 1990). Paulesu et al. (2000), using positron emission tomography (PET), for example, compared the regular (shallow) Italian and quasi-regular (deep) English orthographies during reading words and nonwords. Their Italian participants showed greater activation in the left superior temporal regions (associated with phoneme processing), while their English participants showed greater activation in the left posterior inferior temporal gyrus and anterior inferior frontal gyrus (both of which were associated with word retrieval). Paulesu et al.'s study thus revealed that the cortical network activated during reading appears to depend on the regularity/consistency of the orthography.

PET and functional magnetic resonance imaging (fMRI) give excellent spatial information but lack the temporal information necessary to follow the progression of activation during word processing. Studies utilizing magnetoencephalography (MEG) have provided information on cortical activation sequences during reading (e.g., Salmelin, Service, Kiesilä, Uutela, Salonen, 1996; Salmelin, Helenius, & Service, 2000; Helenius, Salmelin, Service, & Connolly, 1998). MEG measures the neuromagnetic fields generated by synchronous macroscopic activation in cortical pyramidal cells (Lounasmaa, Hämäläinen, Hari, & Salmelin, 1996; Hämäläinen, Hari,

Ilmoniemi, Knuutila, & Lounasmaa, 1993; Hari & Lounasmaa, 1989). Salmelin et al. (1996), for example, showed that during passive viewing of words/nonwords, activation of up to 200 msec after stimulus presentation concentrated in the posterior parts of the brain, and then the activation spread to the temporal and frontal lobes in both hemispheres. However, between 200 and 400 msec, greater activation was observed in the left temporal lobe including Wernicke's area.

In the present study, whole-head MEG was used to investigate the neural correlates of letter-string length and lexicality effects in a covert reading task in Finnish, a regular orthography. Four experimental conditions were used: short (four-letter) and long (eight-letter) letter strings; words and nonwords. In this study, an attempt was also made to interpret the data in terms of both the DRC and Plaut's single-route connectionist models, although these models are computer simulation models of word naming derived from the theoretical cognitive models, which were developed in order to explain the normal and neurologically impaired cognitive behaviors. The dual-route reading models would predict different spatio-temporal cortical patterns for reading words and nonwords, whereas in the connectionist model no such dissociation would be expected. Length and lexicality effects should be observed according to both models, but manifested at different processing levels. Here we explore the cortical dynamics of the behaviorally and theoretically predicted length and lexicality effects.

RESULTS

Figure 1 displays the whole-head MEG record of one subject (S2), with the responses to the short words (SW) and long nonwords (LNW) overlaid. The sensors above the posterior visual areas showed short-lasting changes of magnetic field, with clear peaks. Later in time, the sensors above the left temporal cortex, in particular, showed signals of longer duration which differentiated between the stimulus categories.

The location of the active cortical patches (source areas) and the time behavior of activation were determined from the distribution of magnetic field (Figure 1, see Methods). Figure 2 illustrates the result of this source modeling procedure in the same subject (S2). For all stimulus conditions, the sequence of cortical activation was essentially similar. However, potentially interesting differences in activation strength were evident in some of the source areas, for example, in the left superior temporal cortex (source 5).

Although there was considerable interindividual variability in the exact spatio-temporal sequence of activa-

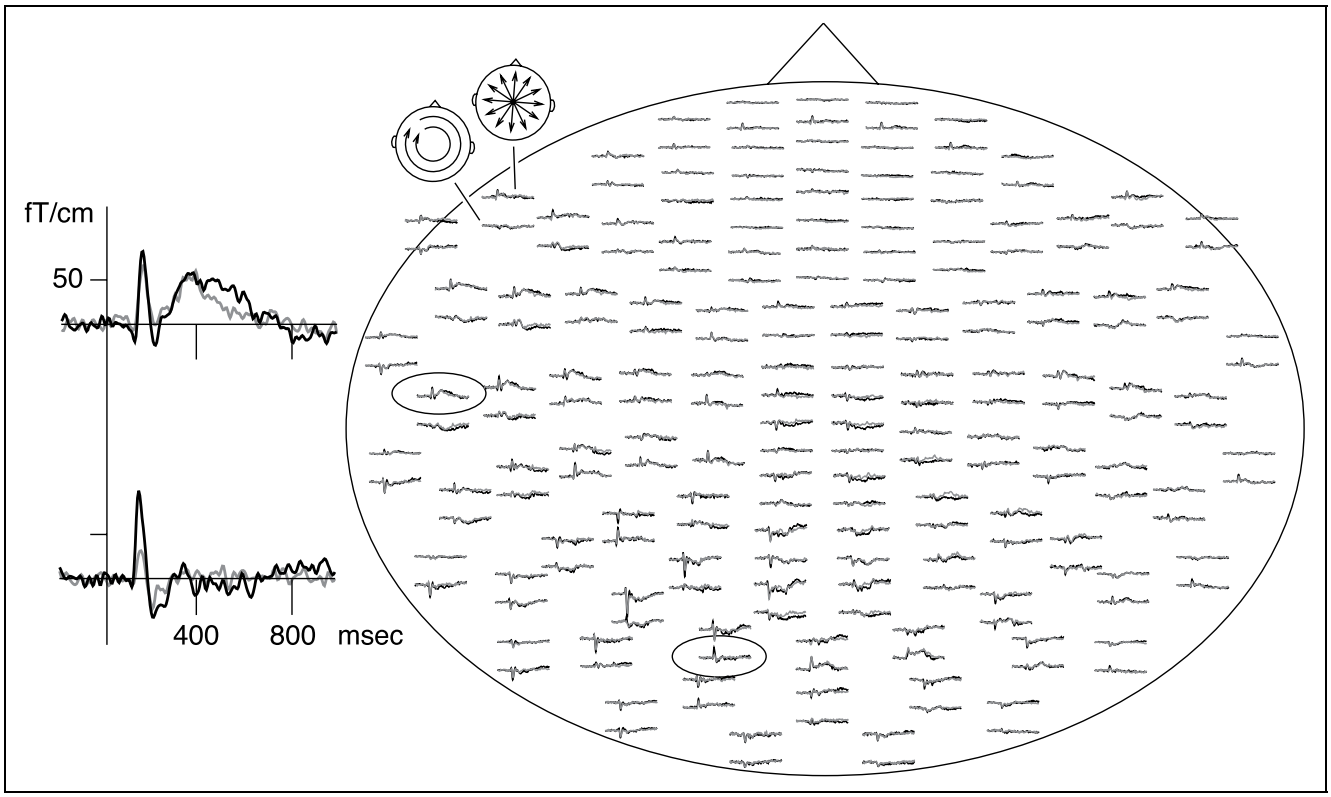

Figure 1. MEG responses of subject S1 to SW (gray) and LNW (black), averaged from −200 to +1000 msec with respect to the stimulus onset. The measurement helmet is viewed from above, flattened onto a plane, with the nose pointing upwards. Time runs along the horizontal axis and the variation of the magnetic field is shown on the vertical axis. The 204 planar gradiometers of the Vectorview system are arranged in 102 locations along the helmet. At each location, there are two orthogonally oriented sensors, with the upper and lower curve depicting the output of the gradiometer most sensitive to longitudinally and latitudinally oriented currents, respectively (schematic heads in the upper left corner). Two sensor signals (ovals) are shown enlarged on the left.

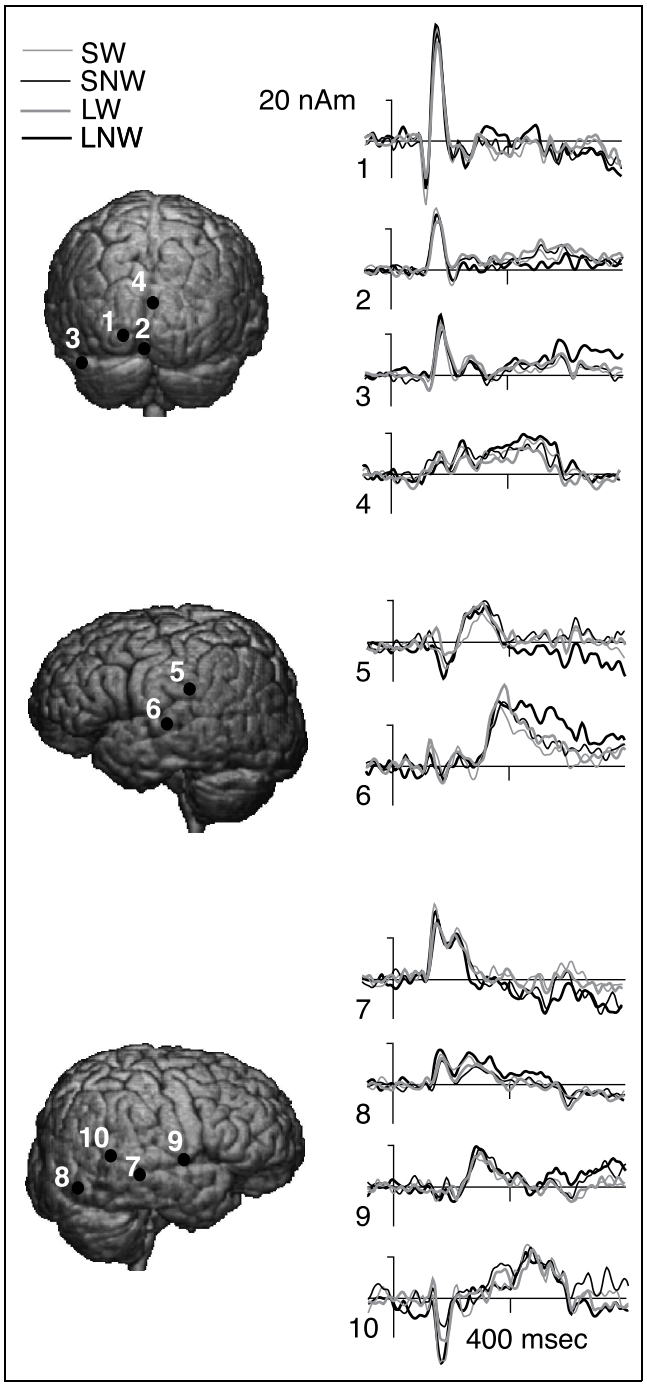

Figure 2. Left: The active brain areas of one subject (S2), modeled as 10 ECDs and displayed on her MRI. Each dot indicates the center of an active cortical patch. Right: The activation strength in these source areas (in nAm, nanoamperemeter) as a function of time for the four different stimulus conditions. The different stimulus types are indicated with different lines.

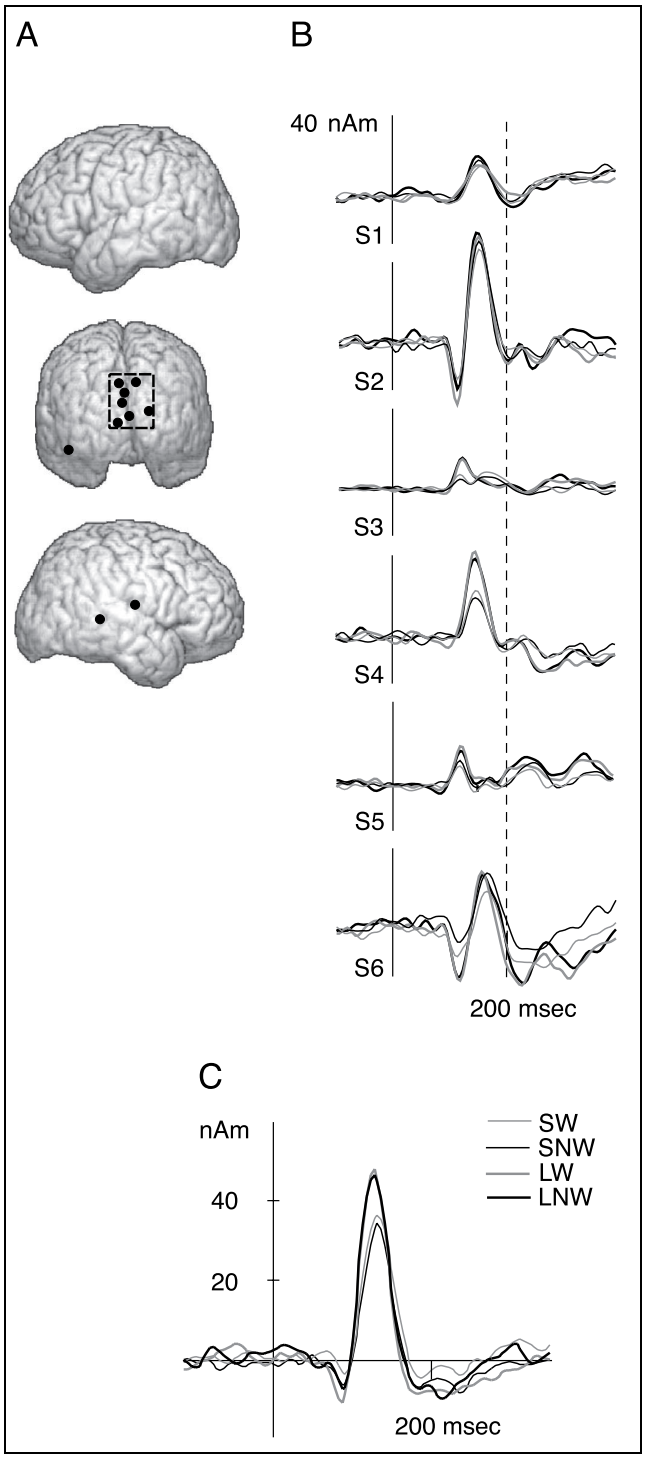

Figure 3. (A) Sources showing a significantly stronger peak amplitude to LNW than SW stimuli within 200 msec after stimulus onset. The rectangular box depicts a cluster of these sources in the occipital lobe (from six subjects, S1 to S6). (B) The time course of activation of the sources in the occipital cluster. In one subject (S6) with two sources, only the earlier one is shown. (C) The mean time course of activation across the six subjects.

tion, the bilateral posterior–anterior progression of cortical processing was consistent across the participants as described by Salmelin et al. (1996, 2000). Within the first 200 msec, the source waveforms showed temporally well-defined peaks. After 200 msec the activity was more sustained.

As the active source areas were similar for all four stimulus categories within each individual, it was possible to compare directly activation strengths and latencies

across the different stimulus conditions. As the focus of this experiment was to identify the cortical effects of letter-string length and lexicality, and their possible interaction, we isolated those source areas where the activation was affected by any one of these variables. To achieve this in the most general way, we compared the extreme cases (i.e., SW and LNW). The significance test SW versus LNW (see Methods) was performed separately for each source of each participant. Within the first 200 msec, where the signals were short-lasting with clear peaks, the test was performed on peak amplitudes. For the more sustained activations after 200 msec, the significant difference between activation strengths was required to last for at least 100 msec to indicate a stable, reliable difference in activation.

Figure 3A shows the distribution of source areas where peak activation within 200 msec after stimulus onset was significantly stronger to LNW than SW stimuli. Stronger activation to SW than LNW stimuli was not detected. A cluster of sources (six of eight subjects) was formed around the occipital midline (rectangle in Figure 3A). The individual time courses of activation of these sources (Figure 3B) and their mean time behavior (Figure 3C) show that the onset and peak latencies were identical for words and nonwords, but the peak amplitude was greater for long letter strings than for short letter strings, regardless of the lexical status.

After 200 msec, significantly stronger sustained activation to LNW than SW stimuli was detected in both hemispheres (black spheres in Figure 4A) and also a few source areas with stronger activation to SW than LNW stimuli (gray spheres in Figure 4A). Again, one clear cluster of sources (six of eight subjects) was found, now in the left superior temporal cortex (rectangle in Figure 4A). The individual time courses of activation for the LNW > SW sources in this cluster (Figure 4B) and their mean time behavior (Figure 4C) show that the onset and peak latencies were comparable for all the stimulus conditions, but the duration of the sustained activation was longer and the amplitude was stronger for LNW than for the other stimulus categories.

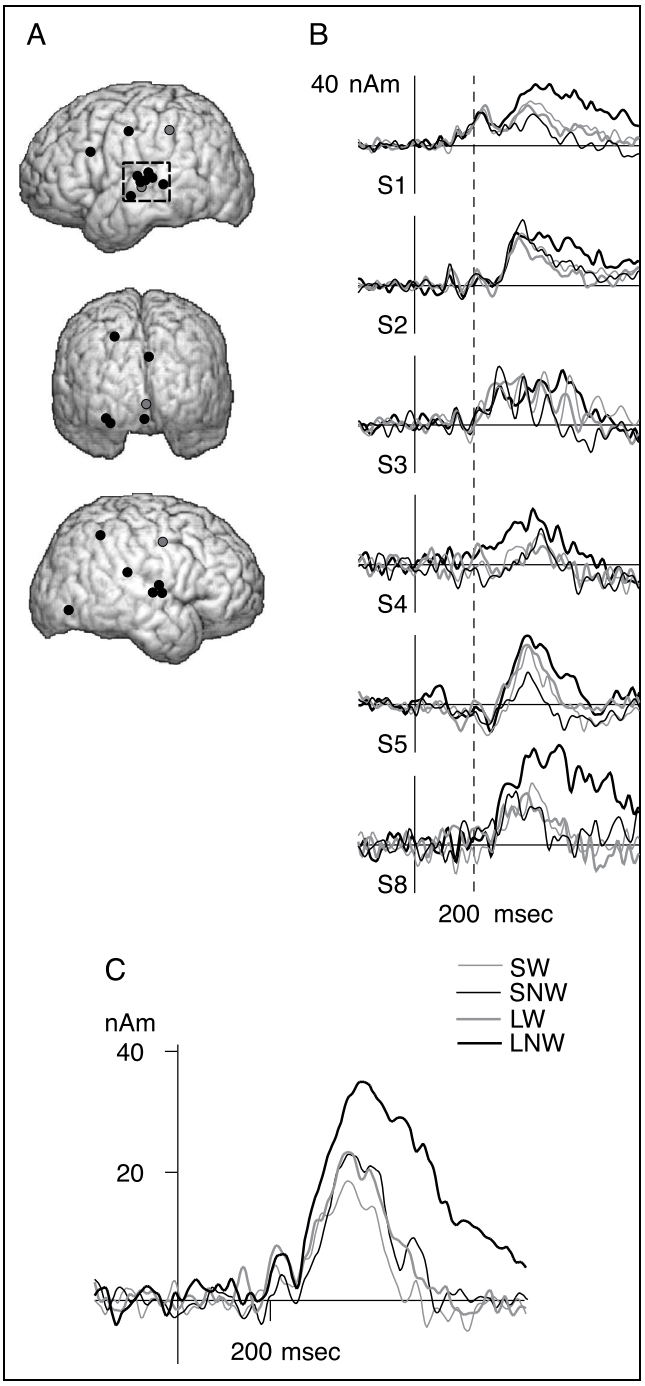

Figure 4. (A) Sources showing a significant difference in amplitude for SW and LNW stimuli after 200 msec after stimulus onset, lasting for at least 100 msec. The rectangular box depicts a cluster of these sources in the left temporal lobe (from six subjects, S1 to S5 and S8). The sources represented by black dots indicate significantly stronger responses to LNW than to SW, and the gray dots indicate significantly stronger responses to SW than to LNW. (B) The time course of activation of the sources (LNW > SW) in the left temporal cluster. In one subject (S6) with two sources, only the earlier one is shown. (C) The mean time course of activation across the six subjects.

Statistical Analysis

A repeated-measures analysis of variance (ANOVA) with string length (four- or eight-letter strings) and lexicality (words or nonwords) as independent variables was carried out for peak activation strengths and peak latencies of the early occipital sources in Figure 3B. The mean (±SEM) peak amplitudes are shown in Figure 5A. The peak activation (SW: $x = 25 \pm 8$ nAm; LW: $x = 34 \pm 9$ nAm; SNW: $x = 24 \pm 8$ nAm; LNW: $x = 34 \pm 9$ nAm) showed only a main effect of length, $F = 11.95$, $p < .02$. The amplitude of the occipital activation increased as the string length increased, regardless of the lexical status of the stimuli. For the peak latency, neither significant main effects nor interaction emerged.

Similarly, for the activation of the left superior temporal sources (Figure 4B), a repeated-measures ANOVA was performed on the maximum amplitude, the duration of

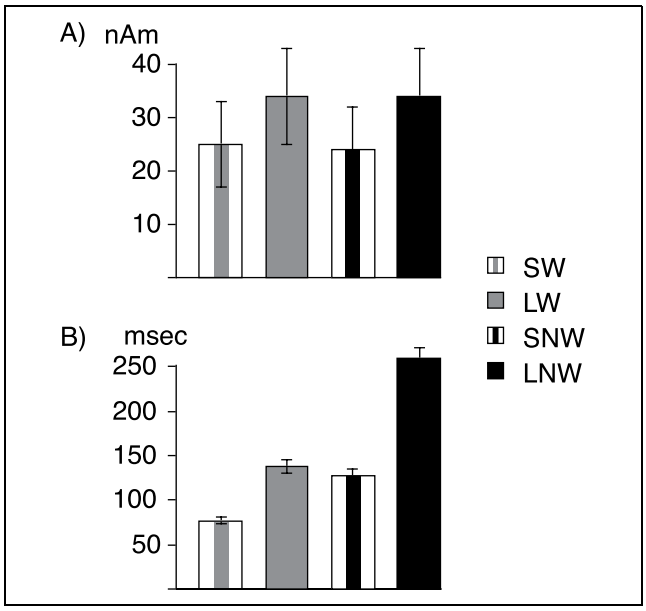

Figure 5. (A) Mean (±SEM) peak amplitude (nAm) for the four stimulus types—SW and LW, and SNW and LNW—for the early source cluster in the occipital lobe. (B) Mean (±SEM) duration of activation (msec) for the four stimulus types in the left superior temporal lobe.

activation defined as the full width of the activation at half the maximum amplitude, and the mean activation strength across the duration of the sustained activation. The mean (±SEM) duration of activation for each stimulus condition is shown in Figure 5B. The duration (SW: $x = 77 \pm 14$ msec; LW: $x = 138 \pm 16$ msec; SNW: $x = 128 \pm 11$ msec; LNW: $x = 259 \pm 35$ msec) revealed significant main effects of lexicality, $F = 23.14$, $p < .005$ and length, $F = 35.51$, $p < .002$. The interaction between them approached significance, $F = 5.23$, $p = .07$. A priori means comparisons revealed that the duration of activation was significantly longer for LW than for SW, $F = 8.24$, $p < .04$, and significantly longer for LNW than for SNW, $F = 37.29$, $p < .002$. Thus, the duration of activation for eight-letter strings was significantly longer than that for four-letter strings for both words and nonwords. However, the length effect for words was attenuated compared with that for nonwords. The results of an ANOVA on the mean activation strengths showed a very similar pattern of the results, while those on the maximum amplitudes revealed only the main effect of lexicality, $F = 14.78$, $p < .02$.

DISCUSSION

Clear differences in the amplitude or duration of activation were observed between the stimulus letter-string types, that is, SW or long words (LW) or nonwords (SNW, LNW) in two distinct cortical areas and in two different time windows: the occipital midline, with clear transient activation at 100 msec, and the left superior temporal cortex, with strong sustained activation between 200 and 600 msec. The amplitude of activation in the occipital lobes for long letter strings was significantly greater than that for short letter strings, regardless of the lexical status of the stimuli. In contrast, the later sustained activation in the left superior temporal cortex persisted significantly longer when subjects read longer letter strings than short letter strings. This later length effect was particularly pronounced for nonwords. A lexicality effect was only evident in this later time window, similar to earlier observations of Salmelin et al. (1996). To our knowledge, this is the first neuroimaging study which specifically addresses combined letter-string length and lexicality effects during reading (i.e., both length and lexicality were systematically manipulated). For example, Petersen et al. (1990) investigated the lexicality effect with PET using words, wordlike nonwords, consonant strings, and false fonts. Similarly, Hagoort et al. (1999) compared the neural correlates of reading German words and pseudowords with PET, equating the number of letters and syllables between the words and the pseudowords. Indefrey et al. (1997), on the other hand, investigated the length effect with fMRI using pseudowords, single false fonts, and strings of the same false fonts.

Early Length Effect in the Occipital Cortex

The strength of activation (i.e., peak amplitudes) for short letter strings was significantly less (by 30%) than that for long letter strings regardless of the lexical status of the stimuli, with both stimuli peaking at the same time. This indicates that the physical length/size of the stimuli matters, and that possibly a larger population of neurons are coherently activated for longer letter strings. It also indicates that in these early sources there is no apparent language-related processing involved, and instead these sources may reflect only low-level visual analysis that is common to all stimulus letter strings. Indefrey et al.'s (1997) PET study also revealed that activation of visual occipital areas increased with string length. Similarly, Tarkiainen, Helenius, Hansen, Cornelissen, and Salmelin (1999), in their MEG study of letter-string perception in Finnish, showed that under zero noise (i.e., no visual degradation) the increase in the number of visual targets was directly related to the increase in the peak amplitude in the occipital lobe close to the midline, at about 100 msec after stimulus onset. Also this increase did not show object specificity (analogous to lexical status of the stimuli) as there was no difference between language-related visual stimuli (i.e., one-letter, two-letter syllables, and four-letter words) and letterlike symbols (i.e., one, two, and four symbols). The current MEG data revealed no consistent modulation in the subsequent activation of the left inferior occipito-temporal cortex at around 150–200 msec, which has been associated with letter-string specific analysis (Tarkiainen et al., 1999).

Later Length and Lexicality Effect in the Left Superior Temporal Cortex

It is generally agreed in the cognitive behavioral literature that the letter-string length effects during reading indicate some kind of sequential processing (Plaut, 1998; Rastle & Coltheart, 1998; Weekes, 1997; Howard, 1991). The size of length effects, however, varies according to the experimental tasks employed. For example, length effects for lexical decision tasks are generally smaller than those for reading-aloud tasks (e.g., Balota & Chumbley, 1985; Bub & Lewine, 1988). The size of length effects also varies according to the lexical status of the stimuli, as well as word frequency. Nonwords tend to show much greater length effects than real words, and often there is no length effect for high-frequency words (e.g., Weekes, 1997). The present experiment employed a covert reading task. The participants were requested to prepare for articulation at every trial, but only a few trials (about 4% of all trials) required actual articulation. The experimental design falls short of reading aloud, but allowed tracking the spatio-temporal sequence of reading up to the point of articulation.

How do the existing cognitive models of reading account for the current data? As discussed in the Introduction, it has been claimed that both Plaut's (1998) single-route connectionist model and Rastle and Coltheart's (1998) DRC model can give a reasonable account of the length and lexicality effects. An attempt was thus made to interpret the present MEG data in terms of these two models of reading.

DRC Model of Reading (Rastle & Coltheart, 1998)

As outlined in the Introduction, dual-route models of reading typically assume that reading involves both a lexical reading route, which operates in parallel across the input string, and a sublexical reading strategy, which requires sequential decoding of the string (e.g., Coltheart et al., 1993). It is also assumed that for a regular orthography such as Finnish, the emphasis is more likely to be placed on the sublexical reading strategy (e.g., Hudson & Bergman, 1985; Turvey et al., 1984). Length effects on naming latency therefore reflect the sequential sublexical reading strategy, and the size of the effects is determined by the extent to which sublexical processing is involved (Rastle & Coltheart, 1998). The late length and lexicality effects in the present MEG study could therefore result from the net neural activity of both lexical and sublexical reading routes. The length effect could be interpreted as on-line sequential phonological processing, which includes grapheme-to-phoneme mapping, subsequent blending, and articulatory programming. The sequential nature of the sublexical processing can account for the linearity of the length effects for both words and nonwords. The interpretation of the left superior temporal activation reflecting phonological processing is in keeping with several imaging studies of word processing (e.g., Paulesu et al., 2000; Fiez & Petersen, 1998; Price, Wise, & Frakowiak, 1996; Price, 1997; Rumsey et al., 1997; Pugh et al., 1996; Bookheimer, Zeffiro, Blaxton, Gaillard, & Theodore, 1995).

The reduced length effect for the real words is likely to reflect the influence of lexical/semantic processing.[2] Again, imaging data lend some support to the left superior temporal activation playing a role in lexico-semantic processing (e.g., Bavelier et al., 1997; Price, 1997; Just, Carpenter, Keller, Eddy, & Thulborn, 1996), particularly in this time window (Helenius et al., 1998; Osterhout & Holcomb, 1995; Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994). According to Pugh et al. (1996), phonological and semantic processing together make greater demands on the superior temporal gyrus than phonological processing alone, suggesting multifunctionality.

However, dual-route models would also assume that the lexical and sublexical routes, which require qualitatively different processes, could be subserved by two distinct cortical networks. This interpretation is not supported by the present data. Given that the onset latencies in the temporal cluster are more or less the same between words and nonwords, it seems plausible to suggest that processing of words and nonwords itself might be the same. We did not find spatially distinct areas involved in word and nonword reading, in agreement with a previous PET study by Rumsey et al. (1997), which was specifically designed to contrast lexical and sublexical routes in reading. In principle, it is possible that such specific neuronal populations could be located in the left superior temporal cortex, close to each other, or partly overlapping. If this were the case, then localization of these two possible cortical loci would be beyond the resolution available with MEG.

Plaut's (1998) Single-Route Connectionist Model of Reading

In connectionist models, both words and nonwords are processed via a single interactive process and the amount of exposure to the stimuli affects the processing times (i.e., real words are processed faster than nonwords), thus accounting for the lexicality effect (e.g., Plaut et al., 1996; Seidenberg & McClelland, 1989). Also, Plaut (1998) developed a particular single-route connectionist model where serial processing mechanisms were implemented at two loci—at the visual input and at the articulate output levels. The model assumes that when pronouncing a letter string, the sequence of phonemes corresponding to its pronunciation is activated, while the position of the grapheme is tracked at the same time. If all the phonemes and their positions are generated correctly, the activations over the letter units remain fixed. Otherwise, the model refixates the input string and tries again, often producing a length

effect. Accordingly, the model generates a pronunciation phoneme-by-phoneme, and hence produces a length effect. Alternatively, a representation of an entire word is generated, and then this representation is used as input to generate sequential articulatory output (Plaut & Kello, 1998). Seidenberg & Plaut (1998) thus argued that length effects on naming latency are due largely to peripheral mechanisms including visual and articulatory factors outside the central processes relating to orthography, phonology, and semantics.

At the cortical level, words and nonwords activated the same network, in agreement with the theoretical account. However, the current MEG data imply that the later length effect was due to central rather than peripheral processes. The combined length and lexicality effect in the left superior temporal cortex is likely to reflect both lexico-semantic and phonological manipulation at the central level.

Conclusion

In conclusion, the current MEG study showed significant lexicality and letter-string length effects in the cortical activation during the reading of a shallow orthography, which were qualitatively akin to behavioral RT data (e.g., Frost et al., 1987). A pure length effect was observed in the occipital cortex at about 100 msec after stimulus onset. A combined length and lexicality effect was detected in the left superior temporal cortex between 200 and 600 msec. There were no separate cortical areas activated for words and nonwords. It appears that neither dual-route models nor single-route connectionist models of reading can satisfactorily explain the current MEG data. An apparent way forward would be increasing the interaction between theoretically driven imaging paradigms (e.g., testing of specific effects such as word frequency or neighborhood size) and computational models of reading which would make more direct use of the types of neural processing suggested by neuroimaging.

METHODS

Participants

MEG signals were recorded from eight normal healthy participants: 4 women and 4 men (aged between 22 and 32; mean 27 years). All subjects gave their informed consent to participate in this study. They were right-handed, and their native language was Finnish. They had no history of reading disorders. All had normal or corrected-to-normal vision.

Materials and Procedure

The stimuli consisted of 400 letter strings. Half the stimuli were high-frequency Finnish words in base form, and the other half, pronounceable nonwords. The stimuli were further divided into long (eight letters) and short (four letters) strings, hence we had four conditions with 100 stimulus letter strings in each (i.e., SW, LW, SNW, and LNW).

The real words were high-frequency words from the WordMill Lexical Search Program (Laine & Virtanen, 1999). The mean word frequency (occurrence per one million) was 926 for the 100 SW and 237 for the 100 LW. It was not possible to fully match the frequencies as SW tend to have somewhat higher frequency than LW. High-frequency words, rather than low-frequency words, were chosen as they should provide the maximal contrast against nonwords (frequency 0) in testing for length and lexicality effects. Furthermore, it was practically impossible to find 100 four-letter words which would be so uncommon as to be regarded as low-frequency items.

All the nonwords had the syllabic structure of a legal Finnish word but had no known meaning. The four-letter nonwords were composed of the syllables/letters in the real four-letter words. The eight-letter nonwords were based on a selection of ancient seven- to eight-letter Finnish words which are no longer in use. In the seven-letter ''old words'', one letter was added, while retaining the syllabic structure typical to Finnish language.

All the stimulus strings were mixed randomly and divided into three blocks. Each stimulus was presented for 400 msec, and the interstimulus interval was 2600 msec. Participants were instructed to read each stimulus silently, and when prompted by ''?'' (4% of the trials), they were required to read aloud the stimulus that they had just seen. The overt responses and the covert responses immediately after the overt responses were not included in the analysis. The prompt was used to make the subjects prepare for the pronunciation of each stimulus (i.e., up to zarticulatory programming), and also to maintain concentration. The covert task was chosen to avoid the noise fields caused by muscle movement during articulation, and to focus on the processes involved in reading rather than speech production.

Magnetoencephalography

MEG is a noninvasive method, which is based on measuring the weak magnetic fields generated by synchronous activation of thousands of nerve cells. MEG has excellent temporal (1 msec) and good spatial resolution (0.1–1 cm). The measurement is performed outside of the head using highly sensitive superconducting quantum interference device (SQUID) sensors (Ahonen et al., 1993). The properties of the underlying neural currents can be estimated from the distribution of the measured magnetic field (for a thorough review of MEG, see Hämäläinen et al., 1993). The magnetic activity was measured using a Vectorview system (Neuromag, Helsinki, Finland), which contains

306 sensors arranged in 102 locations on a helmet-shaped array.

Data Analysis

The MEG signals were sampled at 600 Hz, pass-band filtered at 0.03–200 Hz, and averaged for a time interval from −200 to +1000 sec with respect to stimulus onset. Epochs contaminated by eye movements were rejected from the average. A minimum of 90 artifact-free epochs was collected for all subjects for each condition. The averaged MEG signals were digitally low-pass filtered at 40 Hz. The baseline for signal value was computed from the 200-msec time window preceding the stimulus presentation. The magnetic field patterns were analyzed individually for each subject employing the 204 gradiometers of the Vectorview system. These planar gradiometers detect the maximum signal directly above an active cortical area. The conductivity profile of the brain was approximated by a sphere, fitted to the anatomical magnetic resonance images of each subject's brain.

All subjects' data were analyzed individually, separately for each condition (SW, LW, SNW, LNW). The active cortical areas were modeled as equivalent current dipoles (ECDs; cf. Hämäläinen et al., 1993). The ECDs' location, orientation, and amplitude represent the center of gravity of the active cortical patch and the direction and mean strength of current flow therein. The whole-head MEG patterns were scanned for dipolar field distributions, signaling local coherent brain activation, up to 800 msec after stimulus presentation. The ECDs were identified one by one, at time points where each specific field pattern was clearest. The ECDs were determined from subsets of 16 to 32 sensors, covering the local dipolar patterns: the goodness-of-fit value, which described how much of the measured field is accounted for by the ECD, typically exceeded 85%. The identified ECDs were then simultaneously introduced into a multi-dipole model, keeping their location and orientation fixed, while the strengths were allowed to vary to achieve the optimal explanation of the data measured by all the MEG sensors. The final set of ECDs accounted for above 80% of the total magnetic field variance. The number of active source areas (ECDs) varied from 8 to 12 between the participants.

In each subject, a single set a source areas accounted for MEG signal variation in all four experimental conditions. However, activation strength in some areas varied by stimulus condition. The significance of differences between two conditions was tested against standard deviation (SD) of the signal in that source area during the baseline interval. Differences between source waveforms were considered significant when they exceeded 2.58 times SD, corresponding to $p < .01$ (cf. Tarkiainen et al., 1999). In addition, at least in one of the conditions to be compared the activation had to be clearly nonzero (i.e., exceeding 5 nAm, twice the typical noise level) when the activity was sustained, or exceeding 10 nAm when the main component of the signal was a short-lasting peak of activation.

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Notes

1. The lexical, whole-word route is further divided into two—the direct route bypassing the semantics and the semantically mediated route.
2. Reviewers of this manuscript rightly pointed out that the later ''word'' length effect—reduced but nevertheless significant—might be confounded by either the word frequency or neighborhood size (or possibly both). It is often the case that short words tend to have higher word frequency counts than long words, and the present study is no exception. Although both the short and long words were high-frequency words, there is a clear frequency difference between them. Behavioral studies show that naming latency for high-frequency words is shorter than that for low-frequency words (e.g., Frost et al. 1987). Similarly, neighborhood size is often correlated with the number of letters (e.g., Weekes, 1997). When the neighborhood size was controlled, no length effect even with low-frequency words was observed especially in a lexical decision task (Lavidor & Ellis, 2002).

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