

Neural processing of spoken words in specific language impairment and dyslexia

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Young adults with a history of specific language impairment (SLI) differ from reading-impaired (dyslexic) individuals in terms of limited vocabulary and poor verbal short-term memory. Phonological short-term memory has been shown to play a significant role in learning new words. We investigated the neural signatures of auditory word recognition and word repetition in young adults with SLI, dyslexia and normal language development using magnetoencephalography. The stimuli were 7-8 letter spoken real words and pseudo-words. They evoked a transient peak at 100 ms (N100m) followed by longer-lasting activation peaking around 400 ms (N400m) in the left and right superior temporal cortex. Both word repetition (first vs. immediately following second presentation) and lexicality (words vs. pseudowords) modulated the N400m response. An effect of lexicality was detected about 400 ms onwards as activation culminated for words but continued for pseudo-words. This effect was more pronounced in the left than right hemisphere in the control subjects. The left hemisphere lexicality effect was also present in the dyslexic adults, but it was non-significant in the subjects with SLI, possibly reflecting their limited vocabulary. The N400m activation between 200 and 700 ms was attenuated by the immediate repetition of words and pseudo-words in both hemispheres. In SLI adults the repetition effect evaluated at 200–400 ms was abnormally weak. This finding suggests impaired short-term maintenance of linguistic activation that underlies word recognition. Furthermore, the size of the repetition effect decreased from control subjects through dyslexics to SLIs, i.e. when advancing from milder to more severe language impairment. The unusually rapid decay of speech-evoked activation could have a detrimental role on vocabulary growth in children with SLI.

Keywords: dyslexia; specific language impairment; speech perception; N400m; MEG

Abbreviations: ERP = event-related potential; MEG = Magnetoencephalography; SLI = specific language impairment

Introduction

Children with specific language impairment (SLI) have delayed language development, which is typically reflected as difficulties in both understanding and producing spoken language. The impairment is manifested from 2 to 3 years onwards, at the age when most children show rapid progress in the mastery of receptive and expressive language skills. As specific language impaired

children grow older, their expressive language tends to be aberrant, containing phonologically incomplete words, missing inflections, incorrect word orders and missing or incorrect words. Receptive vocabulary is also poor in the majority of these children throughout childhood (Bishop, 1997). If the language problems do not resolve by the age of five, significant difficulties in all aspects of language functioning persist into adolescence (Stothard *et al.*, 1998). The nature of the impairments seen in SLI is still debated.

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They have sometimes been suggested to reflect impaired innate grammatical capacity, but an alternative account views the condition as an information-processing deficit (verbal memory, phonological processing, auditory processing) that interferes with language learning (reviewed by Joanisse and Seidenberg, 1998).

Vocabulary learning builds on setting up long-term phonological representations in a mental store, i.e. mental lexicon. This process could be hampered by poor phonological memory (Bishop, 1997). An effect of reduced verbal working memory capacity on vocabulary growth was first reported by Baddeley *et al.* (1988). As a result of a large lesion in the left hemisphere, their patient had severely impaired short-term verbal memory performance but was nonetheless able to comprehend complex speech and had no obvious speech production difficulties. However, working memory deficits had a particularly detrimental effect on learning words of a foreign language. It has been proposed that adequate temporary storage of phonological structures is an important prerequisite for learning new vocabulary in young children as well. Children's performances on tests of phonological short-term memory (digit span and non-word repetition tasks) are predictive of their future vocabulary size (Gathercole and Baddeley, 1989; Baddeley *et al.*, 1998). Furthermore, children with SLI have profound difficulties on non-word repetition tasks (Gathercole and Baddeley, 1990).

Inaccuracy in the perception and extraction of phoneme sequences of spoken words could also hamper vocabulary learning and word understanding (Bishop, 1997). SLI has sometimes been associated with phonological deficits that could have a more general auditory basis (Tallal and Piercy, 1973; Tallal *et al.*, 1993). Importantly, accurate phonological representations are essential during reading acquisition (Lundberg *et al.*, 1980). When a child is learning to read he or she must be able to pay attention to sub-word level units of spoken language such as syllables and phonemes in order to learn that speech is related to print via a set of rules. Phonological processing deficits are the only reliably identified causal correlates of the developmental reading impairment, dyslexia (Bradley and Bryant, 1983). Reading problems appear frequently in SLI children (Snowling *et al.*, 2000).

Syntactic information is used to aid online speech comprehension (Mitchell, 1994), e.g. in deducing word meaning. Longitudinal follow-up studies suggest that in children with SLI, learning of grammar may be more delayed than language acquisition in general (Rice *et al.*, 2000). Ullman and Pierpont (2005) have suggested that SLI is the consequence of a deficit in the procedural fronto-basal circuitry that is involved in rule learning (grammar), learning of skills and also in working memory processes. The other, declarative, memory system is dependent on medial temporal lobe regions and temporal and parietal neocortical regions, and it is thought to be more involved in the acquisition and representation of facts and vocabulary. According to Ullman and Pierpont (2005), this latter system would be impaired in dyslexia but not in SLI. Their view thus seems to depart markedly from behavioural evidence showing a pronounced impairment of vocabulary growth in SLI that extends into adolescence (Stothard *et al.*, 1998). It appears that we are

lacking a neurocognitive model of SLI that would optimally assimilate behavioural and neural findings of this impairment.

There is a sizeable amount of electroencephalography (EEG) literature on the event-related potentials (ERPs) measured from scalp electrodes that are strongly modulated by the presentation of words. These studies suggest that a negative ERP component, the N400, is a sensitive marker of cognitive processes underlying word recognition. An N400 response seems to be evoked by all potentially meaningful word-like auditory and visual stimuli, and its strength is sensitive to semantic priming, i.e. the N400 is attenuated to words that follow a semantically related word (Bentin *et al.*, 1985; Rugg, 1985) or to a word that is expected on the basis of the preceding sentence context (Kutas and Hillyard, 1980). In the auditory domain, it has also been shown that the N400 activation is longer-lasting and stronger to pseudo-words than real words (O'Rourke and Holcomb, 2002; Friedrich *et al.*, 2006).

The N400 component is also attenuated by stimulus repetition both in auditory and in visual domains (Rugg, 1995). The attenuation is larger when the word is repeated immediately than when the repetition occurs after several intervening items (Nagy and Rugg, 1989; Bentin and Peled, 1990). The short-delay repetition effect is equally strong for familiar and unfamiliar stimuli and may be viewed as a consequence of a short-lasting change in perceptual operations necessary for recognition of the repeated item (Bentin and Moscovitch, 1988). The long-delay repetition effect has been suggested to derive from a change in the long-term representation of the stimulus.

In the current study we investigated the neuromagnetic signatures of auditory word recognition and repetition in adults with dyslexia or SLI and in adults with no history of language impairment using magnetoencephalography (MEG). MEG is based on detecting weak magnetic fields associated with neural activation. MEG tracks both the spatial and temporal patterns of cortical activation and thus, for instance, the left- and right-hemisphere N400m responses, the magnetic counterparts of the electric N400, can be readily separated (see, e.g. Helenius *et al.*, 1998; Helenius *et al.*, 2002b). A previous auditory repetition study on normal adult subjects by Marinkovic *et al.* (2003) demonstrated that novel auditory real words elicited stronger activation than repeated words around bilateral perisylvian areas between 225 and 500 ms after word presentation. Similar results have been reported in MEG studies of visual word processing as well (Sekiguchi *et al.*, 2001; Marinkovic *et al.*, 2003).

We measured neuromagnetic signals to the first presentation of auditory words and pseudo-words and to their repetition about 2 s later. A number of studies have looked at sentence-level N400m responses in dyslexic adults using MEG (Helenius *et al.*, 2002b) and the N400-response in dyslexic children (Sabisch *et al.*, 2006a) and SLI children (Sabisch *et al.*, 2006b) using ERPs, but the effects of repetition or lexicality on speech-evoked N400 or N400m responses have not been investigated in dyslexia and SLI. Sabisch *et al.* (2006a, b) recorded ERP responses to correct sentences and semantically incorrect sentences and discovered that the SLI children lacked an N400 effect whereas children with dyslexia had an N400 effect similar to that observed in the control children. The absence of the effect in children with SLI

seemed to result from an unusually large N400 amplitude to the correct sentences. The authors suggested that the relatively stronger N400 could reflect weaker lexical–semantic representations in SLI, although sentence level explanations, such as abnormally weak contextual priming during online speech comprehension, can not be ruled out. We used MEG to further clarify the spatial and temporal pattern of auditory lexical activation in language-learning impairments. If the stored spoken word forms are poorly established in SLI or dyslexia, group differences in activation evoked by words vs. pseudo-words should be detected already at the first presentation of the stimuli. If there are problems in neural short-term maintenance of auditory linguistic information, differences should appear in stimulus repetition.

Methods

Participants

We recorded data from 10 young adults with a history of SLI (three females) recruited from special vocational institutions and through SLI organizations. They were 18–25 years of age (mean 20.3 years) at the time of the MEG measurement, and all right-handed. All spoke Finnish as their first language although two of the subjects had been exposed to a bilingual environment. Seven of the SLI subjects had been studying in special classes or institutions during the elementary school years and only three individuals were in normal classes with special support. Ten dyslexic participants (five females) had an early history of reading difficulties and had been tested by a psychologist, a speech therapist, or a special education teacher. They were 18–25 years (mean 21.7 years). Two individuals were left-handed and one ambidextrous. The 13 control subjects (six females) were 18–21 years of age at the time of the MEG measurement (mean 20.0 years). All control subjects were

right-handed according to their own report and spoke Finnish as their first language. There were no university students among the control subjects. Informed consent was obtained from all subjects, in agreement with the prior approval of the Helsinki and Uusimaa Ethics Committee.

Behavioural testing

All subjects were tested on a concise neuropsychological test battery tapping linguistic and non-linguistic reasoning, reading related skills and auditory short-term memory. A shortened version of the Wechsler Adult Intelligence Scale-Revised (WAIS-R; Wechsler, 1981) including two Verbal (Vocabulary, Similarities) and two Performance Scale subtests (Block design, Object Assembly), was used to estimate linguistic and non-linguistic performance profile of the subjects. Verbal short-term memory was tested using digit span forward (Wechsler, 1981) and pseudoword span (modified from Numminen *et al.*, 2002). The Finnish Token test (modified from Spreen and Benton, 1977) and Repetition of words, phrases, and sentences (from the Western Aphasia Battery) were also used to further evaluate the linguistic functions. Furthermore, several measures sensitive to dyslexia were included. A measure of oral reading speed was obtained from reading aloud a narrative passage. Naming speed was estimated as a time to name colour squares (RAN; Denckla and Rudel, 1976) or colour squares, letters and digits in a 5 × 10 matrix (RAS; Wolf, 1986). Spelling to dictation of ten words and pseudowords, and phonological processing (phoneme deletion, syllable reversal) were also tested (Leinonen *et al.*, 2001).

Table 1 summarizes the behavioural profiles of the three subject groups. The control and SLI groups did not differ in non-verbal reasoning whereas dyslexic subjects were slightly inferior to control subjects in the WAIS-R Block design task. In the dyslexic group 3 of 10 individuals had 5 normal scaled scores or less (reference group mean 10 ± SD 3) indicating that they may have compromised

Table 1 Cognitive profile of the three subject groups

	Control Ss	Dyslexic Ss	SLI Ss	
N	13	10	10	
Mean age (year)	20.0 (1.1)	21.7 (2.3)	20.3 (2.5)	
Age range	18–21	18–25	18–25	
Percent male	54	50	70	
Behavioural testing				significant <i>P</i>
Vocabulary ^a	11.0 (1.8)	8.6 (2.7)	4.8 (2.2)	C > D > SLI
Similarities ^a	11.3 (2.5)	9.5 (4.2)	7.4 (4.0)	C > SLI
Block design ^a	12.5 (2.7)	8.0 (4.1)	11.3 (2.9)	C > D
Object assembly ^a	11.4 (3.2)	9.1 (3.0)	11.4 (2.1)	NS
Digit span	5.9 (1.1)	5.0 (0.7)	4.0 (0.9)	C > D > SLI
Pseudoword span	3.7 (0.9)	3.2 (0.4)	2.8 (0.4)	C & D > SLI
Token test	162.5 (1.0)	161.5 (1.6)	158.8 (5.1)	C > SLI
WAB (repetition)	98.8 (1.7)	95.5 (3.0)	89.4 (5.5)	C > D > SLI
Reading (words/min)	145 (16)	111 (13)	79 (27)	C > D > SLI
Naming speed (ms/item)	502 (87)	578 (111)	690 (206)	C > SLI
Spelling (correct/20)	18.5 (1.1)	15.4 (2.3)	8.4 (4.5)	C > D > SLI
Phoneme deletion	15.5 (0.5)	12.8 (1.9)	10.2 (2.5)	C > D > SLI
Syllable reversal	18.2 (0.9)	13.2 (3.0)	9.9 (4.7)	C > D & SLI

^a Normal scaled scores in WAIS-R; Standard deviations in parentheses; C = control subjects, D = dyslexic subjects, SLI = SLI subjects; WAB = Western Aphasia Battery (repetition of words, phrases and sentences).

visuo-spatial processing skills (see Eden *et al.*, 1995, for visuo-spatial difficulties in a sub-population of dyslexic individuals). In both linguistic tasks the SLI group performed clearly worse than the control subjects. The results of WAIS-R Vocabulary subtest fell at or below 5 normal scaled scores in 6 of 10 SLI individuals whereas equally poor performance was seen in only one dyslexic subject. Thus, although the vocabulary scores of the dyslexic group were inferior to those of the control group they mostly performed within normal range, unlike the individuals with SLI. In verbal short-term memory tasks the performance of the SLI group was clearly inferior to either of the two other groups. The short-term memory problem was also reflected in the repetition of words, phrases, and sentences (WAB) as the SLI subjects performed poorly in repetition of the longest sentences. The dyslexic subjects also had slightly compromised verbal short-term memory. Verbal comprehension of commands measured by the Token Test was additionally slightly impaired in the adults with SLI, as compared with the control group. However, only three SLI individuals performed below the 157 score that has been considered a lower cut-off in the normal adult population (Spreen and Strauss, 1998). These results, together with the clinical interview and observations during the behavioural and MEG measurements, confirmed that while the comprehension and vocabulary scores were below the expected normal level in the SLI individuals, their comprehension skills were mostly adequate for everyday interaction. In the measures sensitive to dyslexia the SLI individuals performed as poorly as the dyslexic subjects: they had very slow reading and naming speed and error prone spelling. Phonological processing was compromised even more than in dyslexic individuals, partly due to short-term memory requirements in these tasks.

The young SLI adults had been included in this study on the basis of an earlier diagnosis of SLI. The present behavioural tests confirmed a pervasive impairment of language-related functions, especially as regards vocabulary and verbal short-term memory, in accordance with earlier studies (Tomblin *et al.*, 1992; Stothard *et al.*, 1998), whereas non-linguistic reasoning, as a group, was within normal limits.

Stimuli and procedure in the MEG recordings

Our stimuli were 7-to-8 letter real words and pseudowords spoken by a male speaker. Stimuli were either repeated immediately following the first presentation (75 target words/pseudowords) or presented only once (150 filler items; 125 words and 25 pseudowords). The mean duration of the 75 target words (552 ± 59 ms; mean \pm SD) and 75 target pseudowords (562 ± 52 ms) was comparable. The stimuli were presented once every 2.5 s (mean interstimulus interval was 1953 ms). The mean frequency of the target words was 122 per million (\pm SD 130, range 1–735 per million; Language Bank of Finland, CSC—Scientific Computing Ltd.). For comparison, in the WAIS-R Vocabulary subtest the mean word frequency of all items was 12 per million (\pm SD 14). Of the 75 target words, 16% had frequency overlapping (within 1 SD) with the Vocabulary subtest words and could thus be thought to be less familiar for the SLI subjects. The pseudowords followed Finnish phonotactic rules (sounded like real Finnish words but had no meaning, e.g. haikuli). All subjects performed almost error free in behavioural testing when they were asked to repeat these 7-to-8-letter pseudowords out loud, one at a time (one error out of 10 pseudowords in 2 SLI and 2 dyslexic subjects).

During measurement the participants were seated in a magnetically shielded room, with the head covered by the MEG helmet.

The participants were instructed to listen to the stimuli and press a button upon hearing a proper name (10 common first names, each presented twice during the measurement). They were instructed to avoid excessive blinking and to this end they could also intermittently keep their eyes shut. Stimuli were controlled with the program Presentation (Neurobehavioural Systems Inc., San Francisco, CA) running on a PC. The experiment included two approximately 10-min sessions with a short break in between them.

MEG recording and analysis

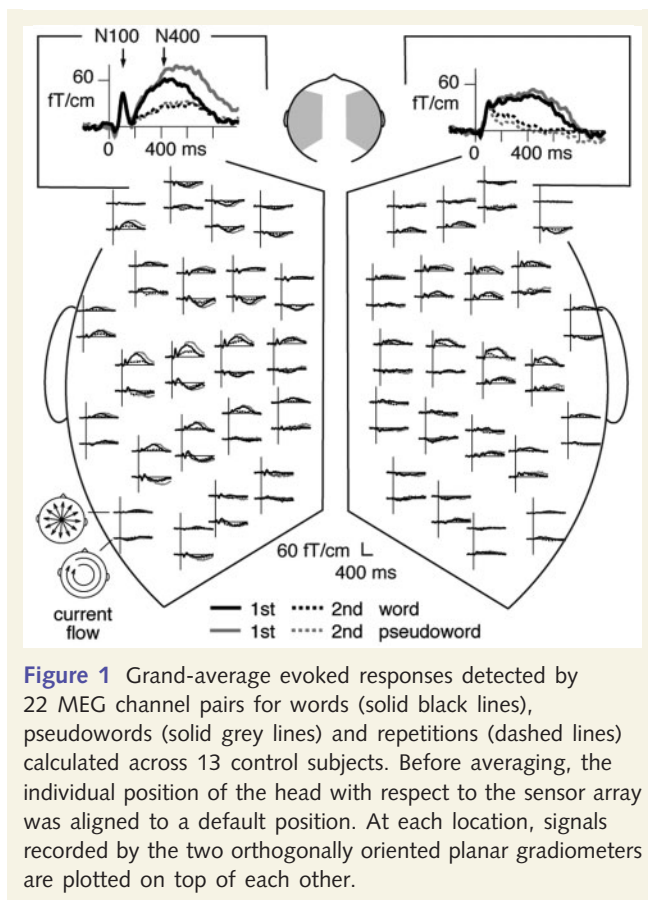
Brain responses were recorded using a 306-channel Elekta Neuromag neuromagnetometer (Elekta Neuromag Ltd., Helsinki, Finland) that measures magnetic field strength in 102 locations over the scalp, with a sensor triplet (two planar gradiometers and one magnetometer) at each location. The gradiometers detect the maximum signal directly above an active cortical area. Four head-position indicator coils were attached to the scalp and their locations were determined with respect to anatomical landmarks (pre-auricular points and nasion) with a 3D digitizer. At the beginning of the experimental session, an electric current was fed to the coils and their locations with respect to the MEG helmet were measured. The MEG signals were band-pass filtered at 0.1–200 Hz and sampled at 600 Hz. Responses were averaged online across trials from 200 ms before to 1000 ms after the stimulus onset. Vertical and horizontal eye movements were continuously recorded and epochs contaminated by ocular signals were rejected.

We localized the active source areas in the individual subjects using Equivalent Current Dipole analysis (Hämäläinen *et al.*, 1993). ECD analysis reduces the signals detected by the MEG sensors into the time behaviour of distinct cortical areas. Each ECD represents the centre of an active cortical patch and the strength and direction of electric current in that area. Individually in each subject, for each distinct dipolar field pattern, a subset of sensors (typically 22 planar sensor pairs) was selected that optimally covered the pattern, and the location of the neural population generating that response was determined. Thereafter, time courses of activation in those brain areas (represented by the ECDs) were obtained by including the ECDs simultaneously in a multi-dipole model: the locations and orientations of the ECDs were fixed while their amplitudes were allowed to vary to achieve maximal explanation of the recorded whole-head data. Structural MR images were not available for the subjects. Therefore, the sources of each individual are displayed on an average brain, with the N400m sources aligned with reference to the location of the robust 100 ms response (N100m) evoked by the speech sounds (cf. Helenius *et al.*, 2002b).

Results

Evoked responses on MEG sensors

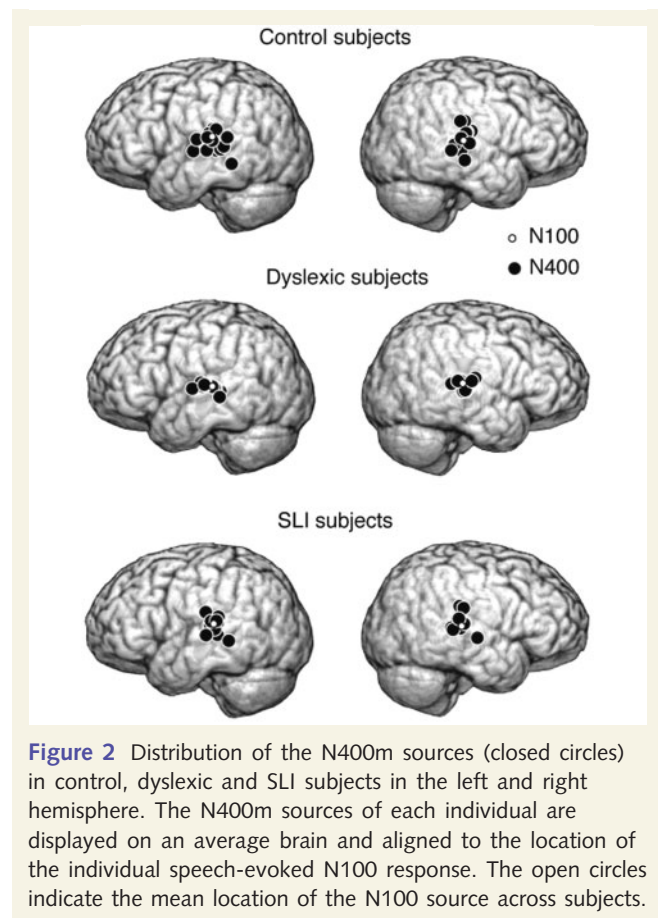
Figure 1 shows the mean evoked responses recorded by planar gradiometer MEG sensors and calculated across 13 control subjects to words and pseudo-words presented for the first time and to their immediate repetitions. The responses are displayed for those 22 channel pairs centred above the temporal areas that typically show the maximum signal in auditory experiments (see, e.g. Marinkovic *et al.*, 2003; Bonte *et al.*, 2006). The speech stimuli evoked a transient peak at 100 ms (N100m) followed by a longer-lasting response that reached the maximum at about



400 ms (N400m), over both temporal lobes. The effect of lexicity (words vs. pseudo-words) was detected about 400 ms onwards as activation culminated for words but continued for pseudo-words. This effect seemed especially pronounced over the left hemisphere of control subjects. The N400m response between 200 and 700 ms was attenuated by the immediate repetition of words and pseudo-words, in both hemispheres. A detailed analysis of the effects of stimulus manipulations on the N100m and N400m responses was conducted after the signals detected by the MEG sensors had been reduced into time behaviour of distinct cortical areas.

Equivalent current dipole analysis

The location of the neural population generating the N400m response in each hemisphere was computed from the mean response to the first presentation of words and pseudowords. In about 60% of the cases this robust salient response could be modelled in the 400–500 ms time window (around the response maximum) using a standard set of 22 planar gradiometer channel pairs covering the temporal area (Fig. 1). In a minority of the cases, the magnetic field pattern was more optimally covered by a slightly smaller, individually adjusted channel selection. Figure 2 depicts the spatial distribution of the N400m responses in all three subject groups, with the source of the N100m response serving as an individual reference point. No statistically significant differences



were detected between the subject groups in the N400m source locations.

Figure 3 depicts the mean time course of left and right hemisphere activation after the first and second presentation of words and pseudo-words in all three subject groups. The left- and right-hemisphere N400m sources of each subject were used to account for the measured activation. The typical sustained downward-oriented current flow associated with the N400m response (see, e.g. Helenius *et al.*, 2002b; Uusvuori *et al.*, 2008) was reliably detected in all subjects and both hemispheres, except for the right hemisphere of one SLI subject; in this one case, the N100m source was used, instead. As the spatial location and orientation of the current flow of the N100 and N400m responses are very similar (see, e.g. Helenius *et al.*, 2002b; Bonte *et al.*, 2006), the N400m source accounted for the measured signal in the N100m time window as well. To estimate the time points at which the effects of stimulus lexicity and repetition emerge in normally functioning linguistic network, we measured the strength of activation for each category in each control subject from the source waveforms. We used *t*-tests ($P < 0.05$) to compare the signal strengths every 10 ms. In control subjects, the source waveforms for words versus pseudo-words (lexicity) showed stable statistically significant difference at every timepoint from 400 ms onwards in the left hemisphere and from 570 ms onwards in the right hemisphere. A stable statistically significant effect of word/pseudo-word repetition started at 230 ms after stimulus

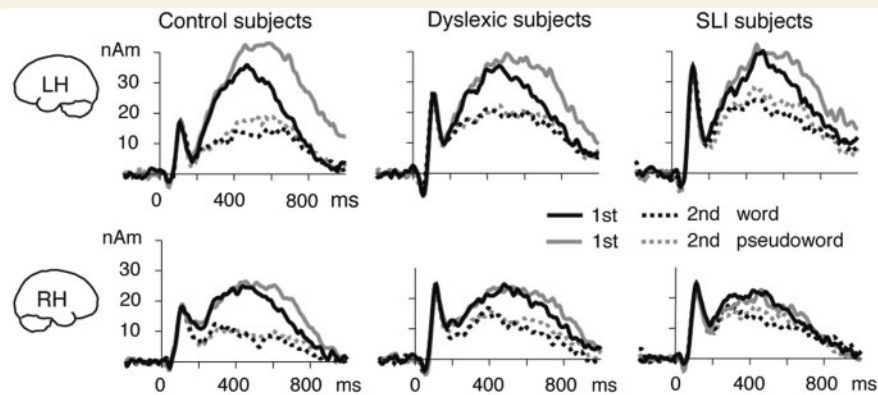


Figure 3 Mean time course of activation in the left (above) and right (below) temporal area in control, dyslexic and SLI subjects. Activation elicited by words is depicted with solid black line, pseudowords with a solid grey line and repetitions with dashed lines.

onset in the left hemisphere and at 160ms in the right hemisphere. For words, the effect lasted over the entire N400m response up to 650–700 ms.

Repetition effect (200–400 ms)

The magnitude of the repetition priming effect was evaluated during the 200–400 ms time window, when the lexical status of the word did not yet influence the activation, by computing the mean strength of activation to the first and second presentation of words/pseudo-words (average) in each individual subject (Fig. 4A). In a 2 (first/second presentation) \times 2 (hemisphere) \times 3 (subject group) mixed ANOVA, a significant main effect of word presentation was detected [$F(1,30)=42.2$; $P<0.001$; effect size estimated as partial $\eta^2=0.59$]. Words/pseudo-words evoked a stronger response when they were presented for the first time than when they were repeated 2.5 s later. This repetition effect was stronger in the left than right hemisphere indicated by a significant presentation by hemisphere interaction [$F(1,30)=4.4$; $P<0.04$; $\eta^2=0.13$]. The presentation by subject group interaction approached significance [$F(2,30)=2.9$; $P<0.07$; $\eta^2=0.16$]. When the SLI group was separately contrasted to control subjects in a 2 (first/second presentation) \times 2 (hemisphere) \times 2 (subject group) ANOVA a significant subject group by presentation interaction was detected [$F(1,21)=4.5$; $P<0.05$; $\eta^2=0.18$]. When dyslexic subjects were similarly contrasted to control subjects the subject group by presentation interaction was non-significant [$F(1,21)=2.0$; $P<0.17$]. In the left hemisphere, all three subject groups showed significant repetition priming (separate t -tests, $P<0.001$ in control and dyslexic subjects and $P<0.05$ in SLI subjects). In the right hemisphere, the control subjects showed significant priming ($P<0.01$) whereas in dyslexic and SLI subjects the difference between the first and second presentation of the stimuli only approached significance ($P<0.057$ in dyslexic and $P<0.08$ in SLI subjects). It is worth noting that the responses elicited by the first presentation of words/pseudo-words were very similar between the three subject groups in both hemispheres (hemisphere \times subject group ANOVA, $P=0.99$).

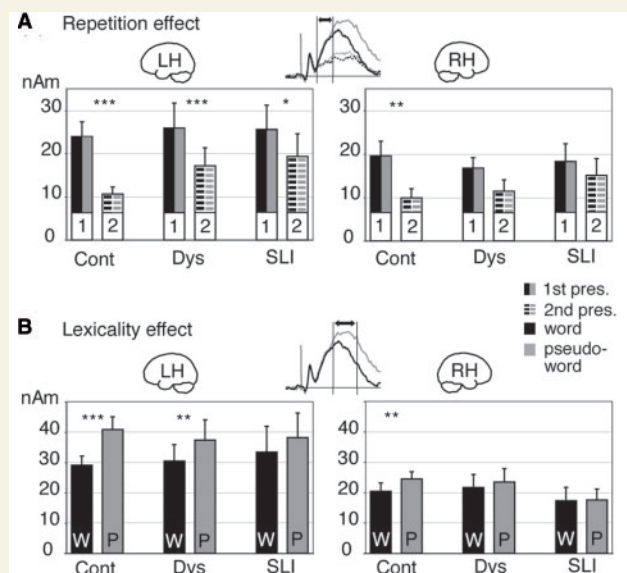


Figure 4 (A) Repetition effect. Mean strength (+SEM) of activation to the first (1) and second (2) presentation of words and pseudo-words calculated over 200–400 ms for the three subject groups. (B) Lexicality effect. Mean strength (+SEM) of activation to words (W) and to pseudo-words (P) calculated over 400–700 ms for the three subject groups. The significance level of *** $P<0.001$, ** $P<0.01$ and * $P<0.05$.

To statistically test the apparent linearity of the repetition effect magnitude across the three subject groups we calculated in each subject the difference in activation between the first and second presentation divided by the strength of activation to the first presentation. A significant linear trend of the magnitude of the repetition suppression was detected across the three subject groups in the left [$F(1,30)=4.7$; $P<0.04$] and right hemisphere [$F(1,30)=5.2$; $P<0.03$].

In SLI adults the repetition effect was thus abnormally weak between 200 and 400 ms after word and pseudoword onset, and the dyslexic subjects fell between the SLIs and control subjects with respect to the magnitude of the repetition effect.

Lexicality effect (400–700 ms)

To quantify the lexicality effect we computed the mean strength of activation at 400–700 ms to the first presentation of words and pseudowords in each subject. Figure 4B shows the mean strength of activation to words and pseudo-words for the three subject groups in both hemispheres. In a 2 (lexicality) \times 2 (hemisphere) \times 3 (subject group) mixed ANOVA, a significant main effect of lexicality was detected [$F(1,30)=19.8$; $P<0.001$; $\eta^2=0.40$] as pseudo-words evoked stronger response than real words. Overall, responses were also stronger in the left than right hemisphere [$F(1,30) = 25.4$; $P<0.001$; $\eta^2=0.46$]. The hemisphere by lexicality effect was significant due to a larger effect of lexicality in the left than right hemisphere [$F(1,30)=28.6$; $P<0.001$; $\eta^2=0.49$]. When the SLI and dyslexic groups were again separately contrasted to control subjects in a 2 \times 2 \times 2 ANOVA, the SLI versus control group comparison showed a tendency for subject group by lexicality interaction [$F(1,21)=3.5$; $P<0.07$; $\eta^2=0.14$]. In the left hemisphere, the control and dyslexic subjects showed a significant effect of lexicality (separate *t*-tests, $P<0.001$ in the control subjects, $P<0.01$ in the dyslexic subjects and $P>0.1$ in the SLI subjects), while in the right hemisphere the lexicality effect was significant only in control subjects ($P<0.01$ in the control subjects, in dyslexic and SLI subjects $P>0.1$). Again, it is worth noting that the mean strength of activation at 400–700 ms elicited by the words did not show statistically significant differences between the three subject groups in either hemisphere (hemisphere \times subject group ANOVA, $P=0.98$). Both in the control subjects and in the SLI subjects the responses elicited by the words were stronger in the left than in the right hemisphere (separate *t*-tests, $P<0.01$ in control subjects, $P<0.01$ in SLI subjects; in dyslexic subjects $P>0.1$).

To statistically test the apparent linearity of the magnitude of the left-hemisphere lexicality effect across the three subject groups we calculated in each subject the difference between activation to pseudowords and words divided by the strength of activation to the first presentation. The linear trend of the lexicality effect across the three subject groups only approached significance [$F(1,30)=3.3$; $P<0.08$].

In SLI adults the lexicality effect in the left hemisphere was thus abnormally weak between 400 and 700 ms and the dyslexic subjects fell between the SLIs and control subjects with respect to the lexicality effect magnitude.

The N100m response

The main interest in the current study was effects of repetition and lexicality that emerged from about 200 ms onwards. However, the N100m response seemed stronger in the language-learning-impaired adults than in the control subjects, particularly in the left hemisphere (Fig. 3). Such an effect would be in accordance with our previous studies using natural spoken words and syllables (Helenius *et al.*, 2002a, b; but see also negative findings by Parviainen *et al.*, 2005, using synthetic speech sounds). The peak strength of the N100m response of each individual was measured from source waveforms that were generated by including only the N100m sources in the multidipole model

(Helenius *et al.*, 2002b). Statistical tests did not, however, yield any significant group effects, even when testing only for the control vs. SLI subjects in the left hemisphere [$F(1,21)=3.0$, $P<0.10$; $\eta^2=0.13$]. A large variance of the response strengths across individuals contributed to the low level of significance: the mean left-hemisphere N100m peak amplitude was 17.3 nAm in control subjects and 27.1 nAm in SLI subjects and standard deviations were 14.8 and 11.6 nAm, respectively.

Discussion

We tracked cortical processing of spoken words and pseudowords in young adults with SLI, dyslexia and normal language development using MEG. We compared the responses in the left and right temporal cortices elicited by the first presentation of spoken real words and pseudo-words and their immediate repetitions. The spoken words evoked a transient peak at 100 ms (N100m) followed by a longer-lasting activation peaking at around 400 ms (N400m) in the left and right temporal cortex. These left- and right-hemisphere responses elicited by spoken words presented for the first time did not reveal differences between the control, dyslexic or SLI adults. However, differences between subject groups were detected in terms of repetition and lexicality. In the controls, repetition dampened the N400m activation between 200 and 700 ms, and an effect of lexicality (words vs. pseudo-words) was detected about 400 ms onwards as the activation persisted longer for pseudowords than words, in both hemispheres. In our adult SLI subjects, the bilateral repetition effect was abnormally weak between 200 and 400 ms after word and pseudo-word onset, and the lexicality effect was non-significant in both hemispheres. In both measures, the dyslexic subjects fell between the SLIs and control subjects. The behavioural tests of verbal short-term memory and vocabulary showed a similar differentiation; the SLI group performed clearly inferior to both the dyslexic and the control group, and the dyslexic group performed inferior to the control group.

Psycholinguistic models of spoken word processing characterize word recognition in terms of activation of stored representations within the lexicon. The long-term phonological representations of spoken words are being activated online as speech unfolds over time. The spoken input activates a cohort of lexical candidates based on the speech segments so that new candidates are activated and those candidates not matching the input are deactivated until a single candidate for a word is selected. (e.g. Marslen-Wilson and Tyler, 1980; Luce, 1986; McClelland and Elman, 1986; Marslen-Wilson, 1987). While the form-based phonological–lexical activation proceeds, the meaning, i.e. the semantic representations of these word candidates are activated in parallel (Marslen-Wilson, 1987; Gaskell and Marslen-Wilson, 1997). Thus, no single meaning is accessed during the auditory word processing but instead multiple candidates are activated online based on the speech stream (see also Moss and Gaskell, 1999).

In the current study, we assume that the parallel activation of phonological–lexical and semantic representations is reflected in the onset phase of the N400m activation, starting around 200 ms,

and lexical selection in the later phase at around 400 ms when the N400m response culminates for words but continues for pseudo-words. This timeline is also in agreement with earlier MEG studies (Helenius *et al.*, 2002b; Bonte *et al.*, 2006). Lexical selection thus took place about 150 ms before the words used in the current study ended, reflecting the fact that the uniqueness point of a word is reached well before the whole word has been heard, particularly in the case of long words (Luce, 1986). For pseudo-words the lexical and semantic candidates continued to be activated until the very end of word presentation. Previous ERP studies report this same general trend: a longer-lasting and stronger activation for spoken pseudo-words than real words (O'Rourke and Holcomb, 2002; Friedrich *et al.*, 2006).

Immediate repetition of a word or a pseudo-word dampened the N400m activation from about 200 ms onwards, indicating suppressed lexical–semantic activation. During the course of auditory word processing lexical candidates most strongly resembling the speech input receive the highest activation level while mismatching information deactivates unsuccessful lexical candidates (Marslen-Wilson, 1987). Various models have been proposed to account for repetition-related changes in neural activity (Grill-Spector *et al.*, 2006). They have been developed, for the most part, to consider mechanisms of repetition suppression in early visual processing. According to the sharpening model (Desimone, 1996), neurons coding features irrelevant for stimulus identification are most strongly suppressed, i.e. they fire less when a stimulus is repeated. Assuming that there is some degree of correspondence between the theoretical linguistic concept of deactivation and neural-level deactivation, as measured by MEG, the sharpening model could be interpreted to suggest that deactivation of mismatching phonological–lexical and semantic candidates after the first stimulus presentation would mostly account for a decreased level of the population response on stimulus repetition.

It has been suggested that developmental language disabilities can arise as a consequence of a difficulty in establishing long-term representations, activating these representations or maintaining such activation (see, e.g. Bishop and Snowling, 2004; Bishop, 1997). In the current study, the activation of phonological–lexical and semantic representations was interpreted to be reflected in the onset phase of the N400m activation, which did not differ between the three subject groups. Thus, despite their impaired performance on clinical tests of vocabulary and comprehension, these young adults with a history of SLI had succeeded in establishing a mental lexicon broad enough to support superficially normal neurophysiological activation of phonological–lexical and semantic representations. This finding is in line with their good everyday comprehension skills. However, the current study showed that in SLI, for a repeated stimulus, the bilateral dampening of the ascending slope of the N400m response (200–400 ms) was abnormally weak, pointing to impaired short-term maintenance of linguistic activation—or perhaps, in terms of the sharpening theory, unusually rapid release of irrelevant, recently deactivated, representations. Interestingly, Wernicke's aphasics, suffering from unilateral lesions of the dominant posterior-superior temporal gyrus, were not facilitated by immediate word repetition in a behavioural auditory task, unlike control subjects (Blumstein

et al., 2000). In the present study, the size of the repetition suppression also displayed a linear trend from controls through dyslexic individuals to SLI subjects. Thus, in terms of neural short-term maintenance of linguistic activation (maintaining the activated or deactivated state of the representations) in the temporal cortex, the individuals with language learning impairments seemed to form a continuum from milder to more severe difficulties.

The subject groups also differed in terms of the lexicality effect. In the control subjects, the lexicality effect was detected in both hemispheres, whereas in the dyslexic individuals the effect reached significance only in the left hemisphere, and in the SLI subjects even the left-hemisphere lexicality effect remained non-significant. The left-lateralized lexicality effect in dyslexic individuals is in accordance with our previous findings of stronger left- than right-hemisphere sentence-level auditory N400m responses in dyslexia (Helenius *et al.*, 2002b). Although the lexicality effect was non-significant in the SLI subjects, the responses elicited 400–700 ms after word onset were stronger in the left than right hemisphere, as in the control subjects. Thus, in the current study the lateralization of speech perception did not show marked differences between the control and language-impaired individuals. As this is the first MEG study conducted on SLI adults, it is impossible to determine whether the fairly normal lateralization detected in the current experiment might be specific to this subject groups or task. For instance, in a recent study by Whitehouse and Bishop (2008), persistent SLI was associated with reduced or reversed cerebral dominance in the majority of adults when the experimental measure was blood flow through the middle cerebral arteries serving the left and right hemispheres during speech production.

The non-significant lexicality effect in SLI subjects could derive from their abnormally limited vocabulary. It is evident from their behavioural profile that many of the real Finnish words have failed to establish long-term lexical representations in these individuals. Thus, if some real words evoke a long-lasting activation similar to that elicited by pseudo-words, the lexicality effect will be less clear. Another possibility would be that activation evoked by all words lasts longer due to impaired deactivation of inappropriate lexical candidates. Such a process has been suggested to underlie atypical behavioural response patterns to spoken words in Wernicke's aphasics (McNellis and Blumstein, 2001; Janse, 2008).

In the current experiment, the subject's task was to press a button upon hearing a proper name. Thus, we do not have behavioural data on word and pseudo-word detection speed and repetition effects on our subjects. Such data will be essential in order to further clarify the relationship between word recognition speed and neural repetition priming, and their relationship with short-term memory and vocabulary. In behavioural tasks, short-term priming effects are coupled with long-term priming effects which have been suggested to result from changes in long-term representation (Janse, 2008). Thus, if the short-term maintenance of the linguistic activation is impaired, establishing and updating of long-term lexical representations could also be disrupted. According to this view the unusually rapid decay of activation may thus contribute to impaired vocabulary growth in children with SLIs.

The aim of the study was to investigate the activation of auditory lexical representations in adults with a history of language-learning disorder. Such studies, particularly in the case of SLI, have been scarce (Sabisch *et al.*, 2006b). Robust modulation of the N400m response was detected in the MEG signals by contrasting (i) words and pseudo-words and (ii) the first presentation to the immediate repetition. The current experiment demonstrates that MEG is a valuable tool for understanding speech perception and its disorders and provides novel complementary information to behavioural measures. The interpretations that were proposed regarding theoretical linguistic concepts and neural activation will need to be verified or complemented by future studies using experimental manipulations with increasing sophistication and detail.

The current data accentuate the point that speech perception deficits, at least in terms of defective short-term maintenance of linguistic neural activation, must be assimilated in any theory that seeks to fully explain the pattern of difficulties associated with SLI. Furthermore, SLI and dyslexia seem to form a continuum from a milder to a more severe expression of difficulties in terms of subtle defects of linguistic activation that underlies successful word recognition. Importantly, however, as the behavioural manifestation of these impairments can vary considerably, particularly in children, it is unlikely that a similar continuum from dyslexia to SLI is seen in all areas of linguistic function. Future imaging studies will need to clarify the nature of speech perception, speech production and grammatical processing deficits in the full manifestation of SLI and dyslexia.

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