

■ Special Lecture

MEG Studies of Higher Cortical Functions: Language Function and Dysfunction

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Sharing abstract ideas by means of a highly developed language is a uniquely human capability. The sophistication of this skill is reflected in the many years of continuous training required to advance from the state of only listening to speech to producing names of concrete objects ('flower'), to expressing wishes ('I want') and, finally, to formulating meaningful and logical sentences. Several more years are still needed for learning to read, where specific visual objects must be efficiently recognized and conveyed to the linguistic network, and for learning to write, requiring also developed motor skills and visuomotor integration.

Once mastered, language governs and directs our thinking — we tend to verbalize all events and experiences. Virtually all cognitive functions, such as memory, learning, and imagery unavoidably contain a strong linguistic component. Similarly, language function depends heavily on other cognitive processes, in particular on long-term memory for storing the vocabulary and word meanings, and on working memory for production and comprehension of continuous spoken or written language.

Language, as we know it, can only be studied in humans and, therefore, the measurement techniques need to be non-invasive. Optimally, the technique should be safe enough to allow

repeated testing of the same subjects in various experimental conditions. The representation of language shows considerable interindividual variability (Ojemann et al, 1989), unlike the fairly robust brain activations associated with simple auditory, visual, and somatosensory stimulation, or finger movements. For this reason, relevant information is more likely to be gained from analysis of brain activations in each individual subject than from activations averaged over groups of subjects. Finally, the relative timing is essential in deducing the possible roles of the different activated brain areas. Language function, in particular, necessarily involves several levels of processing from sensory input to memory which can only be satisfactorily characterized and understood using combined spatial and temporal information.

FUNCTIONAL IMAGING OF THE HUMAN BRAIN

Positron emission tomography (PET) and, more recently, functional magnetic resonance imaging (fMRI) have provided extensive information on brain areas involved in language-related tasks (Posner et al, 1994 ; Frackowiak et al, 1997) and proposed improvements to models of language processing (Petersen et al, 1988). As suggested by lesion studies, which have set

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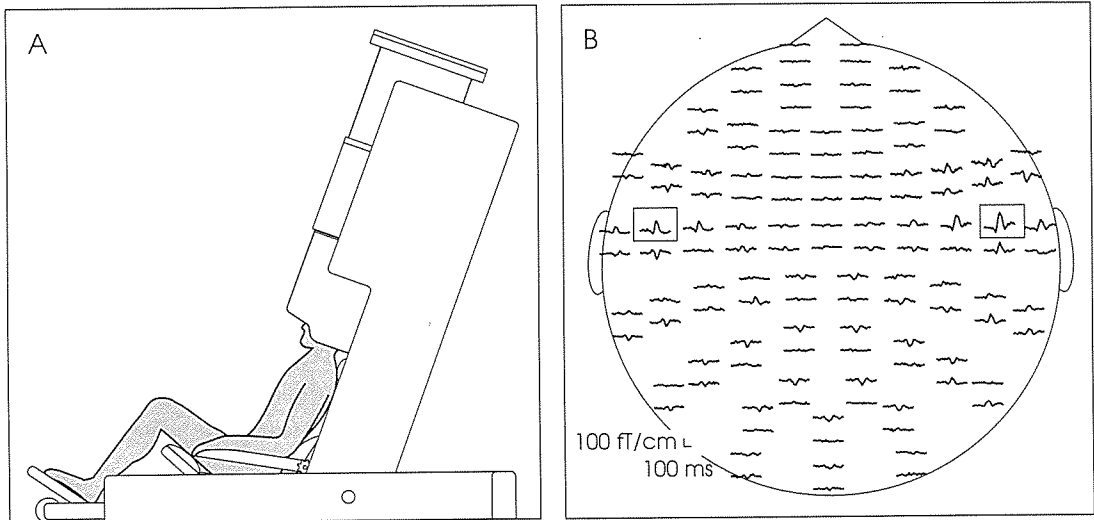


Fig. 1.

Schematic drawing of the Neuromag-122™ whole-head magnetometer. The subject rests his head against the helmet-shaped bottom part of the large thermos bottle containing 122 superconducting SQUID sensors (Superconducting QUantum Interference Device) for detection of the extremely weak magnetic fields of the brain (a). When brain activity is recorded during about 100 repetitions of a brief tone given to the left ear and averaged with respect to tone onset, we obtain the variation of magnetic field as a function of time at each sensor (b). The sensor array is viewed from above, flattened into a plane. The horizontal axis represents the time and the vertical axis the magnetic field. The sharp deflections at about 100 ms after tone onset, concentrating over the left and right temporal lobes, are associated with transient current flow in the left and right auditory cortices.

the basis for our current understanding of the representation of language function in the brain, the frontal and posterior temporal structures typically show strongest activation in such experiments. However, the interpretation of the functional roles of the distinct subregions varies, depending on the task employed. The activation patterns are certainly partly confounded by the variable contributions of sensory, motor, and cognitive (*e.g.*, memory, attention) components in the different experimental conditions. This is where time information, by adding one relevant dimension, becomes invaluable.

The electric activity of the brain is a direct real-time signature of signal transmission between neurons. The tiny currents in the brain can be measured via the electric and magnetic fields they create. The spatial accuracy of the electroencephalogram (EEG) is handicapped because of the poorly conducting skull and the

high-conductivity scalp which create a layered structure around the brain tissue, blurring the electric potential recorded by electrodes placed on the scalp. The concentric structures around the brain are, however, transparent to magnetic signals. MEG is recorded outside of the head with sensors arranged in a helmet-shaped holder and brought close to the head (Hämäläinen et al, 1993). Figure 1 illustrates such a measurement system and, as an example, MEG signals recorded during auditory stimulation.

The macroscopic EEG and MEG signals arise mainly from coincident postsynaptic potentials in about 10^6 nearby pyramidal cells in the cortex. MEG is most sensitive to currents tangential to the surface of the head, *i.e.*, it detects predominantly activity in the fissures. About 2/3 of the cortex lies in the fissures and thus most of the cortex is readily accessible to MEG. Ultimately, combined whole-head MEG and EEG may, in some cases, be needed for a

complete description of the electric activation pattern. The by far most successful approach for localizing the source areas is the dipole model: a local active area recorded from a distance can be reasonably modelled as a current dipole, *i.e.*, a point-like region representing the center of the active cortical area, where the current is flowing in a certain direction. With this approximation, a solution can be found to the otherwise non-unique problem of determining the distribution of source currents from the measured magnetic field pattern. In many cases, the localization of active cortical areas with about 5-mm resolution is straightforward because of the distinct spatiotemporal distributions of the signals. However, studies of cognition often set a challenge to the experimenter because of the considerable spatiotemporal overlap of the activations.

MEG records the normally occurring electric activity of the brain, with no need for radioactive substances or high magnetic fields and, therefore, the same subjects can be safely studied as many times as necessary. The highest sensitivity of MEG to cortical activation is optimal for language studies as the role of the cortical (as compared to subcortical) structures seems to be emphasized in higher cognitive processing. MEG data are always analyzed individually, not as group averages.

None of the available techniques alone gives the ultimate answer to solving how the human brain works: MEG, EEG, fMRI, and PET all have their advantages and limitations. In fact, the hemodynamic and electrophysiological measures may not necessarily give the same information: MEG and EEG typically show strong transient response to intermittent synchronous activation of large neuronal populations, whereas fMRI and PET activations are most prominent to continuous stimulation of the neurons, with no requirements for syn-

chrony. Thus, studying similar questions with more than one technique may give both supporting and complementing information.

PICTURE NAMING

Detection of language-related MEG activation

It is not intuitively obvious that linguistic processes are associated with sufficiently reproducible, time-locked, and synchronous electric activation as to reach an acceptable signal-to-noise ratio over several stimulus repetitions, nor that such MEG activations are localizable. We assessed this question by recording cortical dynamics during picture naming (Salmelin et al, 1994), one of the most thoroughly characterized tasks in language production research (Glaser, 1992). It involves essentially all stages of language production which are, moreover, expected to occur in a fairly sequential order, an optimal choice for a time-sensitive imaging technique.

To distinguish between cortical areas concentrating on visual analysis *per se* and on ideation and oral production of the appropriate word the subjects performed three tasks: The experiment started with a passive viewing task, where the subjects, thinking they were participating in a study on the visual system, were shown black-and-white line drawings of everyday objects (*silent condition*). Thereafter, the subjects were shown the same set of pictures but this time instructed to name them aloud (*overt*). In the final run, the instruction was to name the pictures mentally only, without overt vocalization (*covert*). There were altogether more than 100 different pictures, so each picture was shown only once during each session. The subjects saw the pictures for the first time in the MEG experiment so they had to think what they saw and name it accordingly.

Figure 2 illustrates the sequence of cortical

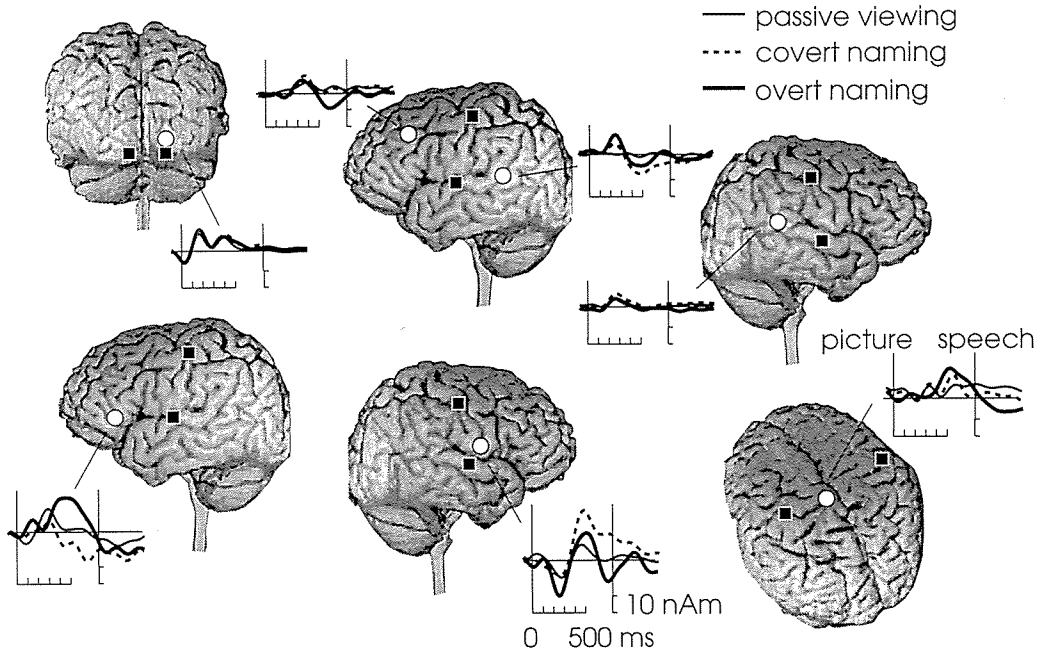


Fig. 2.

Cortical activations in one subject during passive viewing (thin curves), covert naming (thick dashed curves), and overt naming (thick solid curves). The black squares indicate the visual, auditory, and hand somatosensory cortices for reference. The white dots show the active cortical sites identified during the overt naming condition. The curves depict the temporal variation of the source activity over a period of about 1 s. The picture was shown at the first vertical line and vocalization started at the other vertical line.

activation in one subject and the variation of activation strengths in the different tasks. The occipital visual cortex was activated first. During the next 200 ms, the temporo-parieto-occipital junctions in both hemispheres became active. These regions are believed to be involved in visual-to-auditory transformations. The early frontal source presumably indicates motor preparation for mouth movements. About 500 ms after picture onset, signals were recorded from the inferior parts of the frontal lobes; the region in the left likely represents Broca's area — it was most active when vocalization was required. A site close to the vertex, slightly frontal to the foot area, then became active, apparently reflecting involvement of the supplementary motor area in coordination of vocalization.

As expected, the early visual response was the same for all tasks. This was also true for

the signal in the right temporo-parieto-occipital junction. All the other sources showed naming-specific activation, most strongly those in the left hemisphere. Signal processing during picture naming thus advanced from the posterior visual to temporal and frontal vocalization-related areas, symmetrically in both hemispheres, although the left-hemisphere activation was usually slightly earlier and appeared to be more sensitive to the actual task. Thus, it was possible to record language-related neuro-magnetic responses and identify their cortical source areas. Although there was considerable interindividual variability, the bilateral posterior-anterior progression of cortical processing was consistent across subjects. The activation of both hemispheres was clearly a counter-intuitive finding in light of the usual left-hemisphere dominance of language function (in 96% of right-handed population), shown unequivocally

cally by the dramatic effect of injuries to the left side of the brain. Objects, their names, and their other non-verbal attributes are so intimately intertwined that picture naming is likely to be a highly global task for the brain, with the purely linguistic component playing only a minor role. As will be shown below, hemispheric lateralization is strongly affected by the task: *e.g.* reading results in a clear left-hemisphere dominance of cortical activation.

Correlating behavioural and MEG results

Picture naming appears to be composed of the following stages: object recognition, finding the lexical concept (object's name in the communicative situation, *e.g.*, vehicle, car, a Mercedes), lemma selection (syntax, *e.g.*, gender), phonological encoding (what the word sounds like), phonetic encoding (finding the right syllables and associated gestures), articulation and, finally, self-monitoring of the overt speech. Measurement of reaction times to decide whether one has heard a word or a non-word, whether the word contained a certain phoneme (*e.g.*, /l/), and other related behavioural experiments provide time limits for the theoretically postulated stages. Picture naming and MEG are thus an optimal combination for trying to identify possible neuroanatomical correlates of distinct cognitive processes (Levelt et al, 1997).

A selection of 42 pictures with monosyllabic names was employed to maximize the reproducibility of the brain activations. Prior to the measurement, the subjects were also trained to use the correct name for each picture. They were instructed to name the objects as quickly and accurately as possible. Behavioural studies have shown that a high-frequency (common) name is given about 30 ms faster than a low-frequency (rare) name. According to theory, such a difference should arise in the stage of phonological encoding. Assuming that there

was a one-to-one correspondence between the postulated processing stages and a certain site and time window of cortical activation, a systematic difference in timing or strength of MEG responses to low- and high-frequency pictures would allow identification of the putative cortical correlate of phonological encoding. To test this hypothesis, half of the pictures had high-frequency and the others low-frequency names.

It turned out that the 30-ms difference in reaction times was not reproducible in the MEG measurement and the cortical responses to the low- and high-frequency names were indistinguishable. In fact, the subjects were naming all pictures faster than in the prior behavioural experiment, possibly because they were somewhat nervous of the experimental situation and trying their utmost to give a perfect performance. Whatever the reason, the lesson is important: The human brain is flexible and adjusts its whole behaviour according to the demands of the current situation. Even the apparently most robust behavioural paradigms may not be directly transferrable to functional neuroimaging environment.

Figure 3a combines the activated brain areas of 8 subjects in the estimated time windows for the distinct stages of picture naming. The posterior occipital activation 0-150 ms after picture onset should correspond to visual processing and access of the lexical concept. Thereafter, during the proposed stage of lemma selection at 150-275 ms, the right posterior parietal cortex was consistently active. Since this region has mostly been reported to be involved in visual working memory and in visual attention (Ungerleider, 1995), it is far more likely that the observed activation reflects a strong attention component enhancing the process of lemma selection than lemma selection *per se*. In fact, the high attentional effort, or readiness to

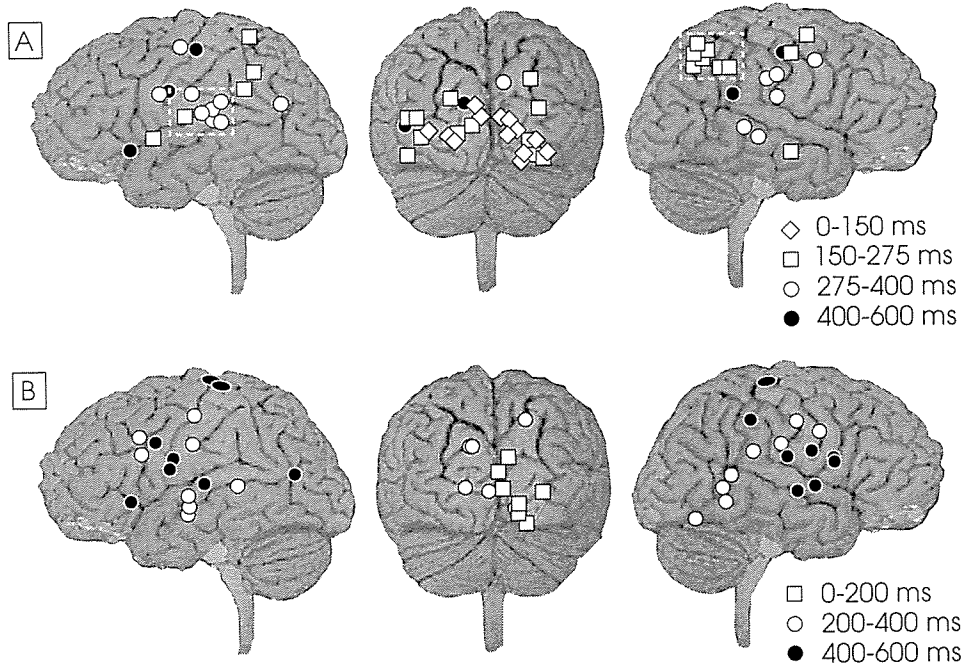


Fig. 3.

Source areas identified during the two picture naming experiments. (a) Well-practiced set of 42 pictures with high- and low-frequency names, strict speed instructions given. (b) Unpracticed sets of over 100 pictures, no speed instructions. The activation sequence was collapsed into selected time windows, indicated by the different symbols.

quickly disengage from the picture in order to be ready for the next one may have contributed to the short naming latencies observed in the MEG measurement. During the postulated stage of phonological encoding (sounding out the name) at 275-400 ms active areas clustered in the posterior end of the superior temporal lobe in the left hemisphere, agreeing with the site of Wernicke's area. The left temporal lobe showed long-lasting activation, from about 200 ms until about 500 ms after word onset and could thus reflect, to some extent, also the stages of lemma selection and self-monitoring.

Figure 3b illustrates, for comparison, the source areas identified in the first study on picture naming, described above. The activation patterns are dramatically different, indicating that the experimental situation has a strong effect on the strategies and allocation of resources chosen by the brain. The strong em-

phasis on motor activation in the first study likely reflects the novelty of the stimuli: for each picture, the subject had to think of the name and produce the accurate motor program. However, in the latter study where the names were familiar and practiced and the motor program well established, the emphasis of cortical activation was on attentional and phonological components for rapid and accurate retrieval of the correct name, with essentially no motor cortical activation and thus, apparently, less need to concentrate on the articulation. Such global optimization of resources is most probably a fundamental aspect of brain function, warranting further studies.

READING AND UNDERSTANDING

For reading and understanding of written text, several perceptual and cognitive processes must be mobilised: The basic visual features

must first be extracted and combined to form an image of a letter. Several letters must be processed as a whole to perceive a word. Successful lexical access based on or accompanied by phonological activation then opens the way for identifying the meaning of the word and, finally, for evaluating the word meaning in a particular context. On the basis of experimental psychology and specific deficits known to result from brain lesions, the analysis of written words is thought to consist of distinct subprocesses, such as orthographic/lexical (written form), phonological (spoken form), syntactic (grammar), and semantic (meaning) analysis.

In visualizing the cortical processes of reading, our approach is to routinely parallel dyslexics and normal fluent readers. Developmental dyslexia is a specific disability in learning to read despite conventional instruction, adequate intelligence, and sociocultural opportunity. Dyslexia persists into adulthood although with adequate tutoring and the development of compensatory strategies reading ability may be markedly improved. The prevalence of dyslexia ranges from 3 to 15% of population; about 4% are seriously affected. The little evidence for anatomical differences between normal and dyslexic readers has been found in the structure of the left *vs.* right planum temporale in the upper surface of the sylvian fissure. Behavioural and functional neuroimaging studies have also shown deficits of auditory perceptual and phonological processing in dyslexics (Tallal, 1980; Rumsey et al, 1992). But these findings do not provide a direct explanation for the persistent difficulties in reading and writing, *i.e.*, with visual language.

So far, we have concentrated on dyslexic adults. The possible deficits in the functional neuroanatomy of reading should have reached a stable level in them. Also, the brain activity of children is very different from that of adults,

and we have currently far better knowledge of adult brain function.

Recognition of isolated words

To track the cortical activation sequences during visual word recognition, dyslexic and normal subjects were shown Finnish words and nonwords. The words were chosen to be long enough to enforce actual reading instead of quick impression-like recognition. To keep the subjects alert, they were instructed to say aloud the rarely occurring word "kirahvi" (giraffe) which was not included in the analysis (Salmelin et al, 1996).

Figure 4 compiles the activation sequences following the first visual responses in normal and dyslexic subjects. The early source distributions (Fig. 4a), showing activation in the inferior temporo-occipital junctions (L1, R1), were significantly different for the two groups in the left but not in the right hemisphere. In controls, signals in this area peaked within a very narrow time window about 180 ms after word presentation. In the dyslexics, however, this area became active only much later, if at all. Direct recordings of neuronal activity during brain surgery have shown letter-string specific responses in this region, peaking about 200 ms after word presentation (Nobre et al, 1994). Thus, it appears that, in the dyslexics, the coherent response to letter strings was missing or delayed in the language-dominant left hemisphere.

After 200 ms, activity spread to the temporal and frontal areas (Fig. 4b). In controls, there was a strongly lateralized left temporal lobe activation between 200 and 400 ms (L2) but, in dyslexics, this area was practically silent. This time window would reasonably correspond to the stage of phonological processing, or sounding out, of the word. Interestingly, instead of the left temporal lobe, dyslexics activated the left inferior frontal cortex (L3), approximately

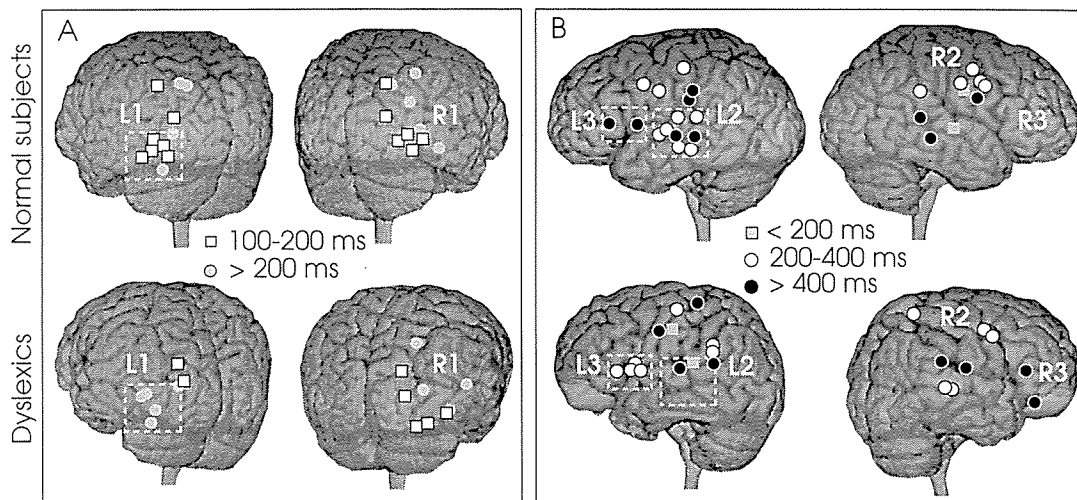


Fig. 4.

Source areas of all control subjects are shown on top and source areas of all dyslexics below. (a) Posterior parts of the brain, predominantly active during the first 200 ms. The brains are viewed slightly from the left and slightly from the right. (b) Left and right views. The anterior parts of the brain were most active after 200 ms. Rectangles indicate areas showing significant differences between dyslexics and normal subjects.

Broca's area, within this same time window. These quite early signals raise the possibility that the dyslexics, in order to compensate for the deficits in the automatic visual word recognition, in fact tried to guess the words, thus adopting a top-down rather than a bottom-up approach in this task.

Normal readers and dyslexics thus showed distinct spatiotemporal patterns of cortical activation, particularly in the left hemisphere. Our data agree with the suggested dysfunction of phonological processing in the left temporal lobe of dyslexics. However, the impaired visual word form perception may well be the immediate reason for the manifest difficulties with written words: We first learn to listen to words and only much later make the connection between the symbolic written words and the original phonological code. If the phonological analysis itself is slow and incomplete, the tight reciprocity of visual letter strings and spoken entities is difficult to build. A visual word recognition unit which would automatically set letters apart from other objects and facilitate

normal, fast reading might thus fail to develop. If this is the case, early training in the parsing of auditory language (Merzenich et al, 1996; Tallal et al, 1996) might help to reduce later problems with reading and writing.

Reading and comprehension: connected text

Dyslexics seem to rely heavily on guessing words, based on a limited set of cues, like the first few letters. Could we then make dyslexic brains look more like normal brains when reading sentences instead of isolated words? A powerful tool for characterizing the temporal aspects of language comprehension was developed in EEG research: When subjects are shown sentences which create a very high expectation for a certain final word but a semantically inappropriate word is shown, instead, a strong activation is recorded 300-500 ms after the final word onset (Kutas et al, 1980). MEG allows accurate characterization of both the activated brain areas and their time behaviour (Helenius et al, submitted).

Dyslexic and normal subjects were shown

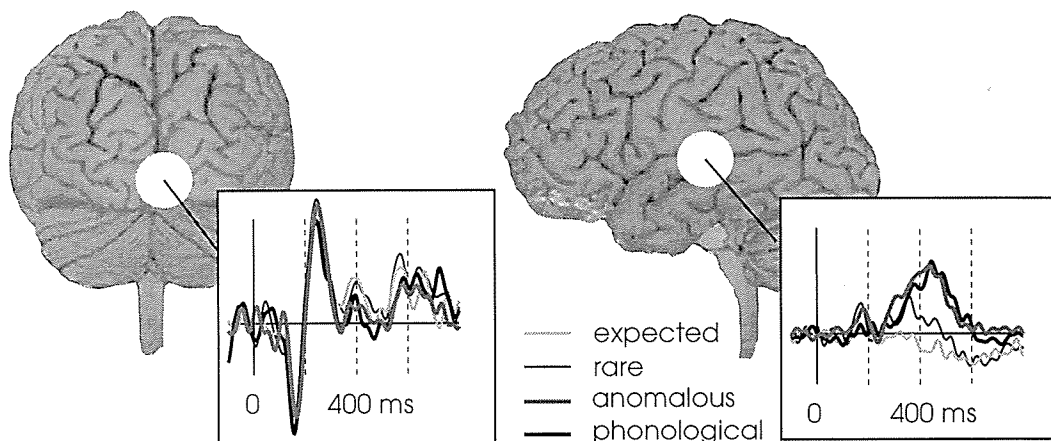


Fig. 5.

MEG responses to the different types of final words in the occipital and left temporal regions in one normal subject.

400 Finnish sentences, one word at a time. The last word of the sentence was either expected, like in *The piano was out of tune*, rare but reasonable, like in *When the power went out the house became quiet*, when most people would expect dark — or the sentence could end with a totally anomalous word, like *The pizza was too hot to sing*. In addition, we had so-called phonological sentences, where the first letters both looked and sounded correct but the word was semantically wrong, like in *The gambler had a streak of bad luggage* instead of *luck*, aimed at visualizing the possible guessing-by-first-letters approach in dyslexics.

As illustrated in Fig. 5 for one normal subject, the posterior visual responses were the same to the four types of final words, but the systematic differences over the left temporal lobe suggested that this activation was sensitive to the meaning of the final word and its role in the sentence context: The totally wrong words (*anomalous*, *phonological*) resulted in a prominent response, peaking about 400 ms after word onset. The signal was much smaller for the *rare* but correct final words, and basically no response was recorded to the *expected* words.

When the brain areas responsible for this type of graded effects were identified in each individual and the data of all control subjects were combined, the clearest source cluster was found in the left superior temporal cortex (Fig. 6a). In two subjects, it was rather left frontal than left temporal areas that were most sensitive to semantic congruity and, in some subjects, the posterior end of the sylvian fissure was also active. This type of pattern suggests activation of the left-hemisphere perisylvian language network as a whole, with strongest emphasis on the areas in the immediate vicinity of the left auditory cortex during semantic analysis (Fig. 6a). In addition, a weaker and about 25 ms later activation in the right superior temporal cortex was found in half of the subjects. Interestingly, provided with the sentence context, the dyslexics showed a very similar concentration of source areas in the left superior temporal cortex (Helenius et al, in preparation), an activation not observed for isolated words. Based on both the number and time behaviour of identified source areas, semantic analysis appeared to be strongly lateralized to the left hemisphere in both subject groups.

Figure 7 depicts the variation of the left tem-

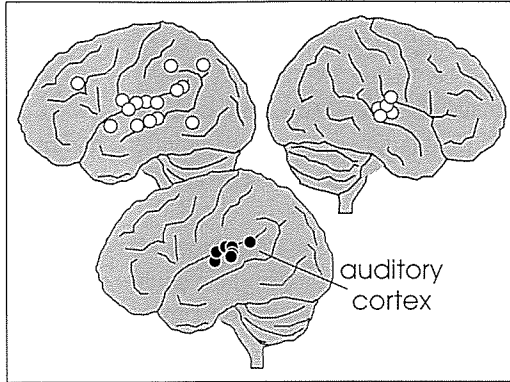


Fig. 6.

Source areas sensitive to the meaning of the word and its role in the context created by the sentence, combined in all normal subjects. For comparison, the location of the auditory cortex, activated by brief tones, is also shown in the left hemisphere.

poral lobe activation as a function of time in the normal subjects. The *expected* words elicited no activation exceeding the noise level; the brain did not react to the obvious choice. For all other types of endings, signals started to rise sharply about 200 ms after word onset. The responses to *anomalous* words and to the wrong words beginning with the correct letters (*phonological*) were equally strong, suggesting that normal subjects read a word as a whole and saw immediately if it was wrong. The turning point of the response to the *rare* words at about 350 ms suggests a transition from analysis of a single word to analysis of the meaning of the word within the sentence context, lasting up to 600 ms after word onset. The neuronal populations involved in these two processes were so closely spaced, or partly overlapping, that they could not be distinguished from each other.

Similarly, dyslexics showed a strong activation following the *anomalous* final words, and a smaller response to the *rare* but possible words. The MEG signals in dyslexics were overall smaller than in the normal subjects, likely reflecting activation of a smaller or less synchro-

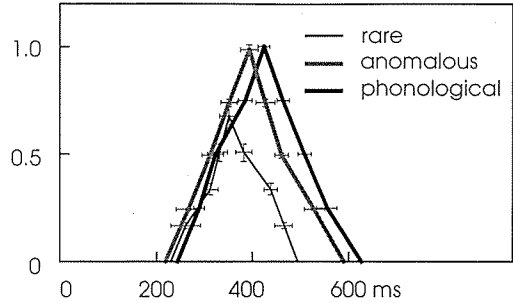


Fig. 7.

Time behaviour of the left temporal lobe response to the three unexpected sentence endings, averaged over normal subjects. To compensate for individual variability in activation strengths, the maximum response in each subject, obtained in the *phonological* condition, was set equal to 1, and response strengths in the other conditions were related to it. The onset and offset times and time points where the response reached 25%, 50%, 75%, and 100% of the maximum were determined for each word type, and averaged over subjects; the horizontal and vertical bars show the standard errors of mean.

nous neuronal population. The onset of the temporal lobe activation was delayed by about 100 ms, suggesting slowness of presemantic processing, possibly at the level of the partly dysfunctional word recognition unit (see above). Interestingly, unlike in controls, responses to the *phonological* words, *i.e.*, to semantically wrong words beginning with the correct-looking letters, was weaker than to the anomalous words. This difference suggests that the dyslexics were occasionally fooled by the correct beginnings, thinking that they saw the expected word. This again would mean that they did not take the word in as a whole but rather advanced piece by piece, in sublexical units. The data thus provide a cortical manifestation of different reading styles in dyslexic and normal readers.

CONCLUSION

We have taken the first steps in visualizing, in real time, how the brain produces and perceives language in normal subjects and where

and how these processes may go wrong. Disorders of language which are only observed at the functional level, with no clear-cut neuroanatomical correlates, are highly intriguing. Elucidating the neural correlates of, *e.g.*, dyslexia could eventually improve therapeutic techniques and, at the same time, in comparison with brain activations in fluent readers, such research gives unique insight into the cortical neurophysiology of language in the human brain.

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