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Naturalistic reading of multi-page texts elicits spatially extended modulation of oscillatory activity in the right hemisphere

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The study of the cortical basis of reading has greatly benefited from the use of naturalistic paradigms that permit eye movements. However, due to the short stimulus lengths used in most naturalistic reading studies, it remains unclear how reading of texts comprising more than isolated sentences modulates cortical processing. To address this question, we used magnetoencephalography to study the spatiospectral distribution of oscillatory activity during naturalistic reading of multi-page texts. In contrast to previous results, we found abundant activity in the right hemisphere in several frequency bands, whereas reading-related modulation of neural activity in the left hemisphere was quite limited. Our results show that the role of the right hemisphere may be importantly emphasized as the reading process extends beyond single sentences.

Reading is one of the key forms of human communication and understanding its neural basis is of utmost importance. The core of neuroscientific knowledge on reading has been gained either indirectly via eye movement measures or, if neural activity has been recorded, by using highly controlled experimental paradigms designed to avoid eye movements, as they cause confounding artifacts. This has often meant the use of rapid serial visual presentation (RSVP) where even longer text stimuli, such as sentences, are shown word-by-word. As important as the results derived with RSVP and other similar paradigms are, the obstruction of free reading makes these results deviate from the neural activity that would appear in everyday reading situations in at least three important ways[1,2]: Firstly, the presentation of words at a fixed pace may alter the timescale of visual word recognition and thus the associated neural activity[3]. Secondly, the prevention of word skipping and regressions (eye movements that are targeted backwards in the text) is assumed to affect reading comprehension[4–7]. Thirdly, parafoveal preview, referring to the processing of an upcoming word, is not possible in most RSVP-type paradigms, which appears to alter visual word processing[4,8–10].

More recently, neuroscientific reading studies have shifted from the use of these highly controlled experimental paradigms towards more naturalistic ones. This has happened via the use of paradigms in which the participants are shown several words simultaneously and allowed to read the words by moving their eyes freely, as in normal reading situations[2,11]. These paradigms have become feasible especially due to advances in techniques related to the co-registration of eye movement and brain activity recordings[11]. Due to the increased naturality of the reading situations in these experiments, these paradigms have often been referred to as natural reading.

The majority of reading studies utilizing these more natural paradigms have used electroencephalography (EEG) to measure the brain activity of the participants. The objective of the studies has been to examine the effect of given manipulations of the text features on the event-related potentials (ERP) which emerge during either a fixation on a particular word or, more rarely, during a particular saccade. The interest in neural processing associated with reading a certain word or a set of words has led to the length of the stimulus texts used in most of these studies to be rather short, such as isolated sentences[1,5,10,12–18] or word lists[8,9,19–21]. These studies have offered highly valuable insight into the cortical processing associated with individual components of reading. In particular, the studies have illuminated the effect that selected features of sentence-embedded words, such as lexical frequency or semantic content, have on neural dynamics during both the fixation and the parafoveal preview of the words[1,5,9,10,12,14–18]. The studies have also investigated how reading-associated cortical dynamics

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relate to eye movement measures[1,12,15,17,19], which has not been possible with RSVP. However, one key aspect of reading that they do not illuminate is the typical real-life situation of reading texts longer than a single sentence.

A few EEG studies have combined unconstrained eye movements with reading of paragraph-long texts. Henderson et al.[22] used this paradigm in a study that contrasted reading vs. pseudo-reading to demonstrate a technique for removing eye-movement artifacts and the potential of co-registering eye movement data and EEG ERPs. Weiss et al.[23] examined how the effect of letter spacing on EEG ERPs is influenced by reading skill. Kretzschmar et al.[24] compared the cortical activity evoked by reading slightly over two pages long texts from either a book or electronic devices, concentrating on ERPs and theta band voltage on the posterior-most EEG electrodes. Distribution and nature of neural activity characterising reading of longer texts has been addressed more directly with functional magnetic resonance imaging (fMRI). Choi et al.[25] compared brain activity measured during reading of paragraphs of normal text to pseudo-reading (moving eyes as if reading) of paragraphs of pseudowords and consonant strings. The aim of the study was to map the eye-movement network in the brain that was shared and different between the tasks, as well as the language network active during only the reading task.

The temporal resolution of fMRI, however, sets limitations on how accurately the rapid neural processes mediating reading can be captured. Fixations, during which the gaze stays locked on a part of the text to allow processing of the text, are the basic unitary functions of reading. The mean fixation duration in silent reading of English language texts is 225 ms[6], whereas the accuracy at which fMRI can measure neural processes is in the range of several seconds due to the slowness of the BOLD response[26]. In order to gain a comprehensive view on the neural correlates of reading, also measurements conducted with a higher temporal resolution are required. These can be obtained with electromagnetic methods such as EEG or magnetoencephalography (MEG). MEG is especially well suited for reading research due to its combined high temporal and good spatial resolution. Furthermore, the fundamental differences in the signals that electromagnetic methods and fMRI detect may extend to the type of activations the methods are most sensitive to. By measuring the electrical signalling of neurons directly, electromagnetic methods can yield information on the synchrony of neuronal populations, whereas with fMRI, asynchronous signals are emphasised[27]. Thus, the different method types complement each other, underlining the need for information collected with both.

Electromagnetic brain mapping of natural reading has primarily used ERPs, which reflect the wave of neural activity consistently evoked by a given event. Since ERPs are time-locked to the events, they are an excellent tool for studying the immediate neural effects. However, ERPs become less practical when the process under study is continuous and its effects unfold over time. A more natural measure for studying the neural correlates of continuous reading are the oscillatory dynamics of neural activity, since these also reflect activity that is induced, and the measure can be accumulated over time. Coherent oscillations at distinct frequency bands have been proposed to be an inherent mechanism for communication and co-operation between neuronal groups[28]. Still, oscillatory activity and the role of different frequency bands have been examined rather little in natural reading studies and the topic remains a promising future direction of study[2,11].

In general, different frequency bands have been associated with a variety of functions depending somewhat on the examined task. More traditionally, alpha oscillations have been thought to function as an inhibitory mechanism that gates the operation of task-unnecessary areas[29] but more recently they have been suggested to have a role in controlling the processing of visual information at different levels of cortical hierarchy[30]. Activity in the beta, low-gamma and high-gamma ranges have been proposed to support the comprehension of sentences with beta oscillations maintaining a neural network that reflects the currently understood meaning of the sentence and forwarding top-down predictions, low-gamma oscillations reflecting the match between top-down-predicted lexical items and bottom-up information from word perception and high-gamma oscillations mediating bottom-up prediction errors[31]. In reading, the theta band has been associated with lexical-semantic retrieval[32]. However, in practice, both the spectral and spatial distributions of rhythmic activity observed in reading experiments have been quite varied[10,16–18,21,33], depending markedly on the tasks and analysis methods utilised.

In this study, we investigated the spatial distribution of oscillatory cortical activity at different frequency bands during the naturalistic reading of multi-page texts. We aspired to unveil reading-specific neural processes by contrasting the cortical activity measured with MEG while the participants read the texts normally versus while they merely scanned the texts with reading-like eye movements. Our aim was to explore which frequency bands and cortical areas contribute to the reading process when reading is performed naturalistically and extends over the limit of individual sentences to larger textual wholes. We did not place any strict expectations on which kind of spatiospectral activity patterns would emerge as significant since, as noted above, reading and also other forms of language[34] appear to be based on a quite extensive and varied distribution of rhythmic activity. Moreover, previous literature has largely focused on time-locked transient effects and precisely limited frequency bands and locations, whereas we were interested in the broad, overall characteristics of the on-going oscillations supporting naturalistic reading. However we would expect to observe significant reading-related activation at least in the left temporal and inferior frontal cortices, since these areas have been consistently linked to the linguistic processing during reading[35–37]. In addition to the comprehension of single words, reading of connected text requires the contribution of multiple networks, devoted to functions such as memory, control and attention that serve the integration of individual semantic items into a coherent whole[38]. Consequently, the results may be expected to demonstrate the contribution of a broad array of cortical regions, possibly also including areas in the right hemisphere.

Eye movement artifacts have been a key hindrance for naturalistic reading studies due to the continuous presence of saccades as an essential part of the reading process. We removed artifacts related to both saccadic eye movements as well as blinks from our data by utilizing AMICA[39] in a pipeline intended especially for the processing of multi-page reading data[40].

Methods

Experimental design

The participants were presented with two different tasks: a reading and a scanning task. In the reading task, the participants read texts which were presented page-by-page. The participants were instructed to read in their own usual way. The texts were extracted from various novels or essays in Finnish and used in their original or a slightly edited form. In the scanning task, the participants were told to search the texts for horizontally inverted letters ”a” and ”e” by moving their eyes as if they were reading. The scanning task was designed as a control task with the motivation that the lower-level cortical processing in the two tasks would be highly similar, since this type of a scanning task has been shown to induce eye movement patterns very similar to normal reading[41,42]. The participants were asked to try to read or scan each text only once from left to right. Both tasks included eight three-page long texts, each page consisting of eight lines. There were on average 87.8 words on each page (SD 6.4), and 11.0 words on each line (SD 1.5). In the scanned texts, the location (line and position in a word) of the flipped letters were randomized for each page of text. There were three flipped letters in 25%, four in 38%, five in 23% and six in 15% of the scanned pages. Out of the flipped letters, 80% of were flipped e's and 20% flipped a's.

The participants were divided into two groups. The first group read the same texts as the second group scanned, whereas the second group read the texts that the first group scanned. The tasks were performed in blocks with a randomized order. Before each 3-page text, a page with a yellow text “read” or a blue text “scan” was presented, informing the participant of the following task. The texts were presented in black font on a white background, projected on a screen approximately 1 m in front of the participant. The visual angle formed by each pageful of text was 15.4° horizontally and 7.7° vertically. The participants changed the page of the text by lifting their right index finger.

Each text was followed by 1–2 questions (12 in total for both reading and scanning) measuring either the participants’ concentration on the scanning task by asking if there were more than a single type of flipped letters in the text or measuring the participants’ comprehension of the text on the reading task. The participants responded verbally, and their answers were written down for further analysis. The questions were answered with 87 ± 13% (mean ± SD) accuracy in the reading and 80 ± 8% accuracy in the scanning task. There was no difference between the reading and visual scanning task in the task performance, as determined using Wilcoxon signed rank test ($p = 0.195$)[43].

The whole experiment was followed by a surprise questionnaire to test how the participants had processed the semantic content in the two tasks. This surprise quiz consisted of 40 sentences in a randomized order, each beginning with the phrase “During the experiment I saw a text in which …”. The participants were asked to answer “Yes”, “No” or “I don’t know”. Ten sentences described the content of the texts presented in the reading task, 10 sentences described the content of the texts presented in the scanning task and 20 sentences were non-related to either task. The surprise questionnaire indicated that the subjects had processed the semantic content during the reading task better than during the scanning task (accuracy 87 ± 8% vs. 27 ± 20%; Wilcoxon signed rank test, $p = 0.00024$)[43].

Participants

Data from 18 right-handed Finnish speaking participants with normal or corrected-to-normal vision were measured in the study. Five of the 18 participants were left out of further analysis due to their performance on the scanning task contradicting the task instructions (significantly different eye movement patterns in the scanning and reading tasks or text being read during the scanning task). Thus, the final number of participants was 13 (7 men, 6 women; age 20–50 years, mean 25.4; SD 8.3 years). More specifically, the exclusion criteria were the following: Firstly, if the post experiment surprise questionnaire suggested that the participant had read the text during the scanning task (difference in accuracy between the reading and scanning conditions less than one standard deviation of the mean). Secondly, if the participant scanned the text from right to left or bottom to up. Thirdly, if the participant exhibited other fundamental differences in eye movement strategies between the conditions (i.e. the difference in the number of fixations or saccades between the conditions outside two standard deviations of the mean). None of the participants reported a history of neurological abnormalities or psychiatric disorders. Informed consent was obtained from all participants, in agreement with the prior approval of the Helsinki and Uusimaa Hospital District Ethics Committee. All methods were conducted in accordance with the guidelines of the Finnish National Board on Research Integrity.

Measurements and preprocessing

The participants’ brain activity was recorded with a 306-channel MEGIN VectorView MEG system (MEGIN Oy; Helsinki, Finland) at the Aalto University MEG Core, band-pass filtered at 0.03–200 Hz and sampled at 600 Hz. MEGIN VectorView records with both planar gradiometers and magnetometers but only data from the gradiometers were analysed since gradiometers are less prone to pick up signals from distant sources and external artefacts than magnetometers. The length of measured MEG data varied between 8.6 and 18.1 min per subject (mean 11.8 min) in the reading task and 5.7 to 19.2 min per subject (mean 10.2 min) in the scanning task. The MEG data were preprocessed using the temporal extension of the Signal Space Separation (SSS) method[44]. Structural magnetic resonance images (MRI) were obtained in the Aalto University Advanced Magnetic Imaging Centre with a 3 T Signa EXCITE scanner (GE Healthcare; Helsinki, Finland).

Blinks and saccades were monitored during the MEG study both by recording vertical and horizontal electro-oculogram (EOG) signals and by tracking eye movements with an Eye Link 1000 eye tracker (SR Research Ltd; Mississauga, Ontario, 195 Canada) using a sampling rate of 1000 Hz. Based on the eye-tracker data, the reading and scanning conditions showed closely matched eye-movement patterns: fixation duration 237 ± 34 ms for reading and 231 ± 31 ms for scanning ($p > 0.1$, paired-samples t-test); saccade duration 30 ± 5 ms for reading and

29 ± 3 ms for scanning ($p > 0.1$); length of forward saccades 60 ± 13 units for reading and 69 ± 17 for scanning ($p = 0.0027$); number of backward saccades 846 ± 335 for reading and 781 ± 402 for scanning ($p > 0.1$)[31,43].

Even though the eye-tracker data shows that the eye-movement patterns between the tasks match closely, small differences were detected. In order to minimise their effect on the analysis of the MEG data, blink and saccade artifacts were removed by using AMICA[39] and in-house code in a pipeline intended especially for processing full-page reading and scanning data[40]. Artifacts were removed for every participant individually by processing all the data from both tasks at the same time. This was done in order to ensure that the artifact removal affected both tasks identically, thus avoiding creation of spurious power differences. No other preprocessing steps were performed in addition to the aforementioned ones.

MEG data analysis

We estimated the spatial distribution of signal power in the contrast reading vs. scanning in six frequency bands (1–4, 5–8, 8–13, 15–25, 31–47, 60–90 Hz) using Dynamic Imaging of Coherent Sources (DICS)[45]. The estimations were performed on a surface-based grid (9-mm spacing along the surface of the cortex), first fitted on one participant's brain and then transformed into the other participants' anatomies with MNE[46], leading to spatially equivalent sampling across the subjects. Grid points which were further than 7 cm from the closest MEG sensor were excluded from the analysis. As a first step, cross-spectral density matrices for the two tasks were obtained by first estimating the cross-spectra for every individual read and scanned page with Welch's method (Hanning windows, window size 2048 time points, overlap half of the window width) and then averaging over the page-specific cross-spectra to yield single subject-specific cross-spectral density matrices for the reading and scanning tasks. Signal power was then estimated for the reading and scanning tasks at every grid point using common beamformer weights calculated with averages of the subject-specific cross-spectral density matrices from both the reading and scanning tasks. This estimation was performed separately for each frequency band. The cortical areas exhibiting significant processing differences between the tasks were estimated by first calculating the power differences between the tasks at every grid point and testing for significance with a two-sided t-test ($p = 0.001$), followed by clustering (weighted average linkage method with Euclidean distance and a maximum accepted distance of 15 mm for adding new points) of the significant t-test results and correction for multiple comparisons with clustering-based nonparametric permutation[47]. In this procedure, the sign of the power differences was randomly switched across subjects, after which new t-tests were performed, test results exceeding a given significance limit (here $p = 0.001$) clustered and the sum t-values within the clusters calculated. This permutation and testing operation was repeated 5000 times, yielding a null distribution of random cluster t-values. Finally, the cluster t-value corresponding to $p = 0.05$ on this distribution was used as a significance limit for the true, unrandomized cluster t-values.

Additionally, the effect of reading time on the level of neural activity during the reading task in the statistically significant clusters was estimated by calculating the mean activation during the reading task in every individual cluster of a participant, scaling this with his/her mean activation during the scanning task over the whole brain, and calculating the Pearson correlation between the scaled mean reading activations of the clusters and the total reading time of the participant. The correlation values were tested for statistical significance ($p = 0.05$, Bonferroni correction).

Results

Figure 1 depicts the overall view of sensor-level average power spectra above different cortical areas. These spectra show pronounced peaks in approximately the 8–13 Hz range and moderately heightened activity levels also in the 15–25 Hz range. The reading task seems to display higher activity levels than the scanning task on the central and parietal channels in the 8–13 Hz and 15–25 Hz ranges where the activity is the strongest in general. The spectra for the left and right hemispheres appear to be rather similar indicating no gross differences in overall activity levels between the two hemispheres.

Figure 2 depicts the spatial distribution of signal power in the reading vs. scanning contrast in six frequency bands (1–4, 5–8, 8–13, 15–25, 31–47, 60–90 Hz). The reading task induced more power in all statistically significant clusters, whereas no significant clusters were found where more oscillatory power would have been detected for the scanning task. The 5–8 Hz band did not yield any significant clusters in the left hemisphere and the 60–90 Hz band did not yield any significant clusters in either hemisphere. The details of all statistically significant clusters are listed in the Supplementary Information. These details include the p-values of the clusters on the permutation-based distribution and parcels according to the Desikan-Killiany atlas[48] that contain parts of the clusters.

As could be expected based on the power spectra in Fig. 1, the majority of the areas displaying significant activity differences between the tasks are concentrated on the 8–13 Hz and 15–25 Hz bands. However, Fig. 2 further indicates that there is a remarkable imbalance between the left and the right hemisphere in the statistically significant task effects. In the left hemisphere, the 8–13 Hz and 15–25 Hz bands display only isolated clusters in the posterior half of the hemisphere, on both the lateral and medial sides. In contrast, the right hemisphere is dominated by seemingly contiguous clusters, which cover most of the posterior cortex extending from the occipital to the temporal and parietal cortices. In the 15–25 Hz band, there are also solitary clusters in the right frontal cortex. The 31–47 Hz band shows three focal clusters on the lateral side of the left frontal cortex and a single cluster on the medial side of the right hemisphere. The 1–4 Hz and 5–8 Hz bands display only solitary clusters.

The mean activation level during the reading task was not significantly correlated with the reading time in any of the clusters.

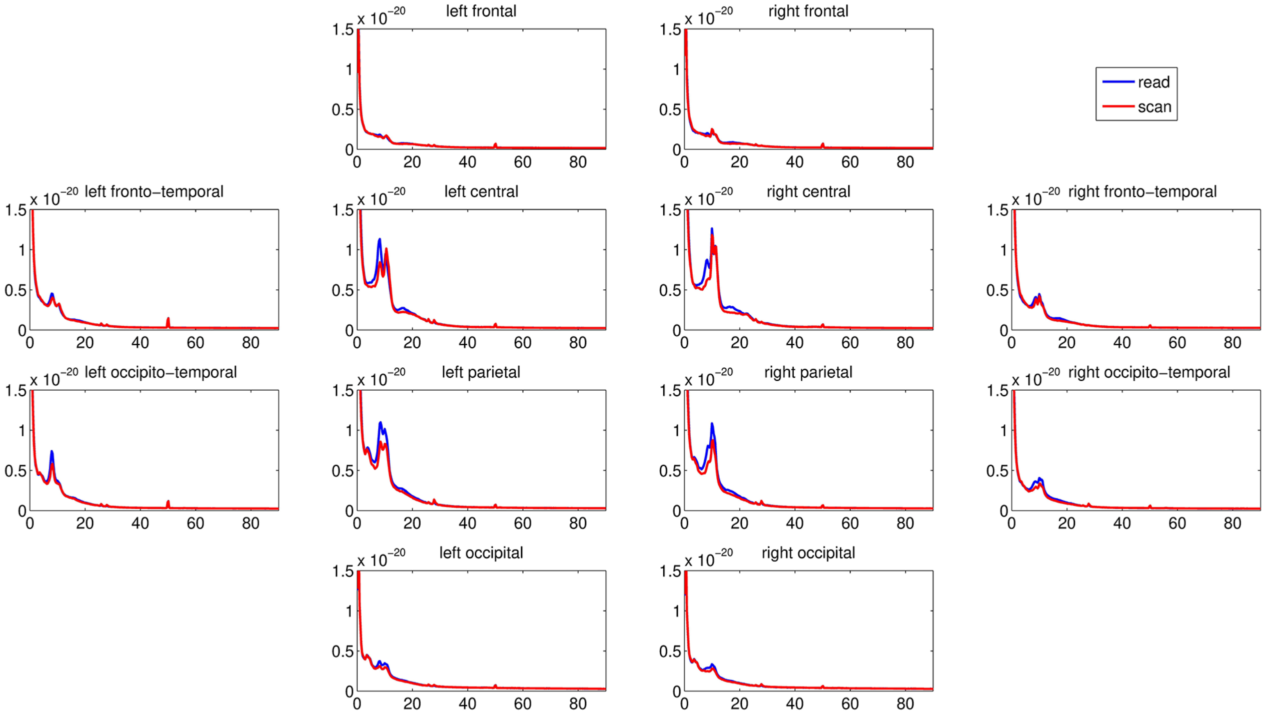

Fig. 1. Average power spectra of planar gradiometers above different cortical areas. The x-axis portrays the frequency (Hz) and the y-axis the magnitude (T^2/m^2) of the spectra. The spectra depict averages of the power spectra of individual gradiometers from 12 different sensor groups distributed across the cortex (12–20 sensors per group).

Discussion

This study expands the knowledge on the neurobiology of naturalistic reading by examining how free reading of multi-page-long texts is reflected in the spatiospectral pattern of cortical oscillatory activity. We consider this to be a crucial step forward since the study of naturalistic reading has thus far been largely limited to the use of blood-flow-based measures or short stimuli (i.e., single-sentence reading). The most significant obstacle preventing the use of electrophysiological measures in this kind of experiments has been eye-movement artifacts, which are incessant and contaminate especially the anterior-most channels close to the eyes. The fact that the significant areas in the present study were mainly concentrated on the more posterior end of the cortex implies that the AMICA-based pipeline[40] had successfully removed the artifacts and had also avoided creating spurious power differences between the contrasted conditions. As could be expected, our results showed that naturalistic reading is supported by a spectrally broad range of oscillatory activity with an emphasis on the 8–13 Hz and 15–25 Hz ranges. The centres of activity on the left hemisphere were quite isolated and focal, whereas the right hemisphere was dominated by extended activity clusters covering most of the posterior cortex. However, contrary to our expectations, we did not observe significant activity in the left temporal cortex. Conversely, the activity in the right hemisphere was substantially more abundant than anticipated. In the following, we discuss what these activity patterns may tell us about naturalistic reading and the cortical functions that have possibly produced them. We emphasise that due to the extended time span of our tasks and the lack of explicit stimulus manipulations that could have triggered a specific cognitive process, our inferences are inevitably somewhat general and speculative, but we have strived to base them on previous literature as well as possible.

Absence of left-hemispheric temporal gyrus activity in continuous rhythmic analysis

The key processes mediating reading have traditionally been considered largely left-lateralised[49], a view which has been supported also by results from MEG studies[35]. Indeed, our results did show several left-hemispheric clusters of activity, mainly in the 8–13 Hz, 15–25 Hz and 31–47 Hz bands. The posterior clusters reside in the occipital cortex, the inferior-most edges of the temporal cortex and the fusiform gyrus, the intraparietal sulcus, and various areas on the medial side which have been commonly associated with higher-level visual processing and orthographic analysis[50], functions that form the basis of the reading process. However, clusters were not observed in the occipital pole, as low-level visual processing presumably occurs rather similarly in the reading and scanning tasks.

Notably, no clusters appeared in the more superior parts of the left temporal cortex and at the junction of temporal and parietal cortices. Activity in these areas has consistently been observed in reading studies[35,36], linked, e.g., with lexico-semantic analysis and phonological activation. Based on the end-of-experiment questionnaire, the participants processed the semantic content of the text passages in the reading condition but markedly less

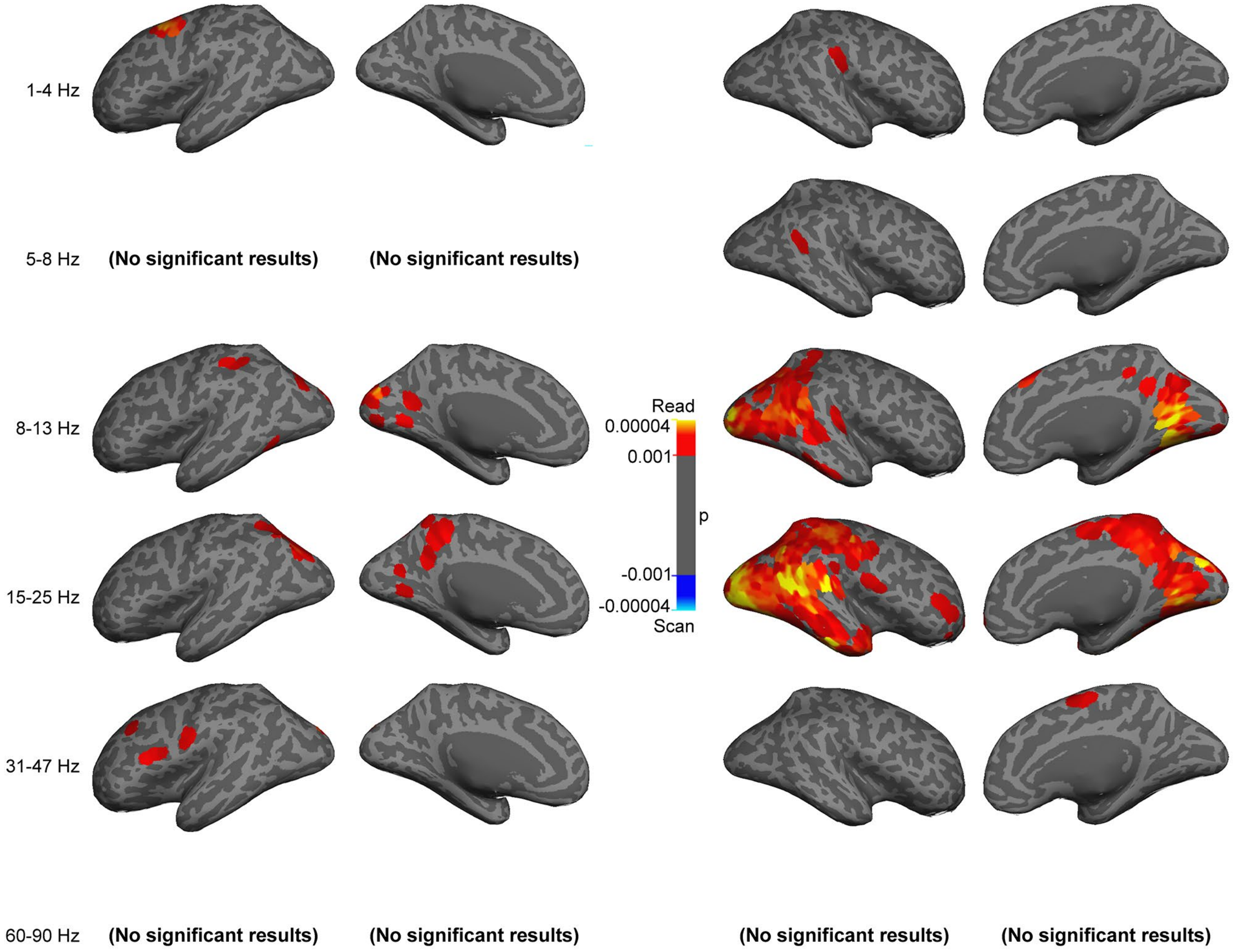

Fig. 2. Spatial distribution of statistically significant power difference clusters in the reading vs. scanning contrast. The reading task induced stronger activation than the scanning task in all coloured areas; the scanning task did not induce significantly stronger activity anywhere. No significant clusters were found in the left hemisphere in the 5–8 Hz frequency band or either hemisphere in the 60–90 Hz frequency band. The colours depict the *p*-values.

in the scanning condition, thus a left temporal cluster could have been predicted. One reason for the absence of activation in these areas may lie in the metrics we are using to track the reading process in the present study. The studies that have previously highlighted these areas have mainly used either evoked electrophysiological responses or blood-flow-based measures, such as fMRI or PET (positron emission tomography). Thus, it is possible that the electrophysiological activation is quite transient in nature and consequently is not well captured by integrating continuous oscillations over an extended time period. Additionally, it is possible that the neural signalling in those areas is spatially and spectrally narrowly defined or has high variance between individuals[51,52], making the statistical power in our experiment insufficient for capturing them.

Continuous reading promotes spatially extended right-hemispheric activity

Unlike the focal activation centres of the left hemisphere, the right hemisphere displayed remarkably extensive clusters in the 8–13 Hz and the 15–25 Hz bands. In the 8–13 Hz band, the primary cluster extended from the occipital pole to the parietal and temporal association cortices and further to the medial side. In the 15–25 Hz band, this same cluster appeared to be even broader, covering most of the occipital, temporal and parietal cortices and extending into the prefrontal cortex, with separate smaller clusters in the precentral gyrus and in the rostral-most parts of the frontal cortex. Judging by the level of significance, some of the central points of these extended clusters seemed to be the angular gyrus and the adjacent temporal cortex. The angular gyrus has been suggested to act as a cross-modal integrative hub that is highly connected and takes part in the function of several different systems[53]. Other parts of especially the 15–25 Hz cluster included areas which have been identified as parts of the dorsal and ventral attention networks[54], the frontoparietal control network[55] and the default mode network[56]. Consequently, one plausible explanation for the right-hemispheric clusters is that they reflect the type of integration or control of these networks that is essential for the comprehension of longer texts and the construction of mental models based on them[38]. The well-connected angular gyrus could have a role of a central point in this interplay, while the occipital cortex provides bottom-up visual information driving the process. Indeed, the right angular gyrus area has been identified as a key area in the integration of read information[57].

Due to the similarity of the right-hemisphere clusters in the 8–13 Hz and 15–25 Hz bands, it is difficult to determine if the two frequency bands depicted spatially similar but functionally separate networks or rather the same network operating on an exceedingly broadband range. Without taking a stand on the spectral separability of these activations, we note that the alpha (coinciding with the 8–13 Hz band) and beta (coinciding with the 15–25 Hz band) frequency bands have been hypothesized to have distinct but co-supportive functional purposes in reading tasks. As noted in the Introduction, alpha oscillations have been suggested[30] to function in naturalistic visual tasks as a pipelining mechanism which assures that visually-based information on different objects can be forwarded to and processed parallelly on hierarchically different levels of cognitive processing. Analogously to our results, alpha activity in the right posterior cortex has indeed been observed to be emphasised during reading tasks containing eye movements[17,21]. Beta oscillations have been suggested to link task-necessary cortical areas into co-active networks and serve both in maintaining the networks and in mediating top-down signals[58,59]. Specifically in the linguistic context, beta synchrony has been hypothesised to act in the construction and maintenance of sentence-level meanings of language stimuli[31]. While these theories still remain more or less at the level of hypotheses, they seem to be generally in line with our present results.

However, perhaps the most crucial question is why there was such extensive activation in the right hemisphere instead of the more traditionally language-involved left hemisphere. Paralleling our results, a previous study investigating rhythmic cortical activity associated with sentence reading observed that sentence level analysis is associated with prominent right-hemispheric activity in several frequency bands, including alpha and beta, but that for word level analysis, the activity was strongly left-lateralised[33]. The answer to this shift in lateralisation may lie in how the processing demands of naturalistic reading of multi-page texts differ from those of reading shorter stimuli. It has been proposed that the processing in the right hemisphere is coarser than that in the left hemisphere[49] and that the level of right-hemisphere involvement rises according to the integration demands placed by the text[60]. Both these aspects are likely highlighted in reading of multi-page texts. Although the evidence regarding these theories is mixed[61], it is apparent that certain language tasks do promote right-hemisphere activation. Considering that these theories concern especially semantic processing, it is noteworthy that the general areas of posterior temporal cortex and angular gyrus, which were strongly highlighted in our right-hemisphere clusters, are considered to be key hubs in the semantic system[49,62]. An additional feature of our experiment that may have contributed to the observed hemispheric imbalance is the lack of titles or context for our texts, which leads to a more effortful reading process. The reading of untitled texts has been reported to increase the activated cortical volume in the right temporal cortex and decrease it in parts of the left temporal cortex compared to the reading of titled texts[63].

Considering that our results represent the activation differences between two tasks, one possible explanation could naturally be that this rightward lateralization stems mainly from differences in how these tasks recruit the cortex instead of phenomena characterising the reading of multi-page texts. It is difficult to determine exactly which subprocesses the tasks utilise differently and to what extent, but one key difference that is evident is the amount of lexical access and semantic processing required by the tasks. This is demonstrated by both the answers to the experiment questionnaires, which indicated that the subjects had processed the text contents substantially more during the reading task than the scanning task, as well as previous studies on the eye movement patterns in these types of tasks, which have shown reduced linguistic processing in the scanning task compared to normal reading[41]. However, since lexico-semantic analysis in reading has typically been linked with left-hemispheric activity, it would be unreasonable to explain the rightward lateralization solely by task-specific differences in lexico-semantic processes.

Previous experiments[64] have shown that when reading aloud familiar words, the brains of fast readers exhibit increased activation in a visual-attentional network containing right inferior parietal areas rather than in a left-hemispheric semantic network active in the brains of slower readers. We found no significant correlation between the level of activation in the clusters during the reading task and the reading speed of the participant. Thus, although the relatively low statistical power of our study may influence these estimations, it appears that reading speed does not affect the activation in these areas at least linearly and if any effects do exist, they are of a more complex nature. Hence, the high level of right-hemispheric activity or the appearance of any other significant areas in our results do not seem to be due to the use of a more efficient reading technique in naturalistic reading.

A notable question is also to what extent the left-to-right reading direction of Finnish might affect our results. Due to this reading direction, the attention of the readers is directed more rightwards and causes the perceptual span of the reader to be much larger on the right side of the centre of fixation than the left[6]. This rightward attention bias has been suggested to be one cause for the right-lateralisation of alpha band oscillations observed during naturalistic reading[21]. Several languages, such as Hebrew and Arabian, are read from right to left and the native speakers of these languages appear to show differences with respect to natively left-to-right readers in how cognitive processing is lateralised in a number of tasks[65,66]. Thus, to understand the possible causes of the considerably right-lateralised activity patterns observed here, it would be important to conduct a similar experiment using stimuli written in a language that is read from right to left. Similarly to attention, the majority of saccades are directed rightwards while reading Finnish. Hence, although we have removed eye movement artifacts from the data, there may be other saccade-related factors that lead to a right-hemispheric bias in cortical activity. Future data concerning right-to-left reading of written text could aid in evaluating the effects of such factors on the current results.

Frontal cortical effects in the low and high frequency bands

The other frequency bands outside 8–13 Hz and 15–25 Hz showed only sporadic isolated clusters. As regards the 31–47 Hz band, some of the clusters resided in areas which have been connected to phonological processing and articulation. In the left hemisphere, such clusters appeared in the pars opercularis and the ventral central sulcus[37], with the latter region corresponding approximately to the lip and tongue area of the motor cortex. The only 31–47 Hz cluster in the right hemisphere lay in the posterior supplementary motor area which contributes to various motoric tasks, including articulation[67]. There are several possible functions these activations could reflect, but one plausible candidate is inner speech. Inner speech utilises many of the same cortical areas as covert speech[37,68] and it has been observed during several reading tasks[68].

Activity in the pars opercularis area as well as in the location of the 31–47 Hz dorsal frontal cortex cluster has also been connected with working memory tasks, including tasks of verbal working memory[69,70]. Likewise, associations with working memory have been made regarding the location of the sole 1–4 Hz band cluster in our study, and frontal cortical activity in the 1–4 Hz range, in general[69,71]. Consequently, it is highly viable that these clusters reflect the increased demands posed by the reading task on working memory or executive control generally. If these clusters indeed do result from such processes, they could be supported by the parietal activity seen in the 8–13 Hz band[70,72].

Since the questionnaires presented during the tasks consisted of very different types of questions depending on the task (questions on the content of the text for reading, questions on the number of flipped letters for scanning), it is also possible that these questionnaires could have directed the subjects to concentrate on different aspects of the stimuli, influencing also their recollection of the contents of the text during the surprise questionnaires. If this were the case, the results of the surprise questionnaire could be more an indicator of mnemonic performance than the level of semantic processing during the tasks which could mean that there might have been more semantic processing during the scanning task than presumed. This could explain the lack of activity differences in the left temporal cortex between reading and scanning. However, this factor would not provide any explanation for the abundant activity modulations between the tasks in the right hemisphere. Thus, it is highly likely that there were considerable semantic processing differences between the tasks, although the possible effect of different goals of memorising on the questionnaire results should also be noted.

Conclusions

We have shown here how the brain-level processes behind naturalistic reading of multi-page texts appear when studied via cortical oscillations. When viewed from this perspective, the contribution of the left hemisphere seems relatively limited, whereas the significance of the right hemisphere is notably emphasised. This study adds a new chapter to the discussion on the left-lateralisation of reading and linguistic tasks and demonstrates that the right hemisphere is in a key position when the reading task is demanding enough. However, we acknowledge that the general nature of the tasks as well as the rather low statistical power in our study limit the depth of the inferences that can be made on our data. We hope that future studies utilising both a higher number of participants and tasks that modulate the on-going cognitive processes in a more detailed fashion could better elucidate what exact phenomena cause the scarcity of discernible reading-related signal modulations in the left hemisphere and the emergence of right-hemisphere effects in this type of tasks.

Data availability

The MEG data cannot be made openly available, according to the ethical permission and national privacy regulations at the time of the study but are available from the corresponding author on reasonable request and with permission of the Ethics Committee of the Hospital district of Helsinki and Uusimaa.

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Author contributions

S.M.: Conceptualization, Methodology, Validation, Formal analysis, Writing – original draft, Writing – review & editing, Funding acquisition. J.K.: Conceptualization, Methodology, Validation, Formal analysis, Writing – original draft, Writing – review & editing, Supervision. P.O.: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing – review & editing; J.H.: Conceptualization, Writing – review & editing. R.S.: Conceptualization, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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