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Parafoveal-on-foveal and foveal word priming are different processes: Behavioral and neurophysiological evidence

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Parafoveal-on-foveal priming refers to the presentation of an item (the prime) in parafoveal vision followed by the presentation of an item (the target) in foveal vision. In natural reading, the 'parafoveal preview benefit' subserves fluent reading as, e.g., reading times increase when such information is not available. Yet, the neural correlates of reading are mostly studied with foveally presented stimuli and little is known of this parafoveal influence. Here, we used complementary information from a behavioral study and a magnetoencephalography experiment to clarify the relationship between parafoveal-on-foveal and foveal priming. Unlike foveal priming, parafoveal-on-foveal priming was present only at short prime-to-target delay (< 100 ms). Behaviorally, the parafoveal priming effect was influenced by the prime visual field (left/right) and target lexical type (word/non-word), suggesting emphasis on perceptual analysis for LVF primes and on conceptual analysis for RVF primes. At the neural level, the overall sequence of activation was similar for foveal and parafoveal primes followed by foveal word targets, but the priming effects were bilateral for foveal primes versus left-lateralized for RVF primes. No neural effects of priming appeared for LVF primes, in line with the RVF preference imposed by the Western writing system. These results highlight the role of the left hemisphere in linguistic analysis and point out possible limitations of foveal stimulus presentation for drawing conclusions about natural reading.

Keywords: Lexical decision; Reaction times; MEG; Parafoveal-on-foveal priming; Reading

Introduction

Priming refers to the influence of the prior presentation of a stimulus (the prime) on the processing of a subsequent stimulus (the target). Behavioral and neuroimaging experiments on visual word processing most often use foveal presentation of both primes and targets. The use of parafoveal primes, in contrast, has been limited mainly to behavioral studies focusing on reading. There are two types of approaches: In parafoveal-on-foveal priming, a prime is displayed parafoveally in the left or right visual field, followed by a foveal target. Parafoveal preview benefit, in contrast, refers to the influence of the prime on the target during 'natural' reading, i.e., after a saccade is performed toward the prime (which then becomes the target). In natural reading the primes are always located on the same side (e.g., on the right side for Western reading systems), which affects attention orientation. Importantly, parafoveal-on-foveal word priming, regardless of the exact paradigm used, seems to differ from foveal priming in a number of interesting ways.

Visual priming studies using foveally presented primes and targets typically distinguish between perceptual and conceptual priming effects. In perceptual priming, the prime bears a perceptual relation to the target (Schacter, 1987) whereas in conceptual priming, the prime bears an "elaborative encoding" relationship to the target (Schacter and Buckner, 1998), such as lexical, semantic or phonological similarity. Foveal word priming studies also advocate two different mechanisms subserving word vs. pseudo-word priming (e.g., Bowers, 1996). In addition, data from word priming experiments in which the test stimuli have been presented in one hemi-field suggest that the right hemisphere (that initially receives information from the left visual field, LVF) processes perceptual ('form-specific') information (Marsolek et al., 1992) whereas the left hemisphere (with earliest input from the right visual field, RVF) processes abstract, conceptual ('categorical') information (Marsolek, 2004). Interestingly, studies focusing on the parafoveal preview benefit have shown little evidence of perceptual priming and mainly reported conceptual effects (note that during natural reading primes appear in the RVF and are, thus, initially led to the left hemisphere). Although there is a debate on which kind of information is extracted from the parafoveal word and when, it is generally agreed that the parafoveal preview benefit relies on at least orthographic and phonological processes (Balota et al., 1985; Pollatsek et al., 1992; Henderson et al., 1995; Lesch and Pollatsek, 1998; Binder et al., 1999; Sereno and Rayner, 2000; Miellet and Sparrow, 2004, Kennedy and Pynte, 2005). One could thus expect that foveally presented words would induce both perceptual and conceptual priming effects as they address both

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hemispheres whereas words presented in the LVF (right hemisphere) would show *primarily* perceptual effects and words presented in the RVF (left hemisphere) would show *primarily* conceptual ones.

Another potentially interesting difference relates to the delay from prime to target, or the time allowed for processing the prime. The parafoveal preview benefit occurs with relatively short delays (tens of milliseconds) between primes and targets. In natural reading, priming occurs during fixations, and the delay, indeed, corresponds to saccade duration (Rayner, 1998). By contrast, foveal priming effects have been reported for delays ranging from milliseconds to hours, days or months (see, e.g., Schacter and Buckner, 1998). Apparently, the encoding level of foveally presented primes varies according to their processing time and influences the duration of the priming effect on targets (Versace and Nevers, 2003). While the main objective of this type of studies has typically been to distinguish between short-term vs. long-term priming effects, they additionally suggest that the time allotted for processing the prime influences the level at which primes are processed (perceptual, conceptual). For foveally presented primes, one would thus expect only perceptual priming effects with short prime-to-target delays and both perceptual and conceptual priming effects with longer prime-to-target delays. For primes presented in the RVF, however, this logic apparently does not hold as mainly conceptual priming effects are reported in ‘parafoveal preview benefit’ studies. The effect of prime duration or prime-to-target delay may thus be an important distinguishing factor between foveal and parafoveal priming.

At the neural level, foveal and parafoveal stimuli initially activate different parts of the visual cortex. The central visual field is the ‘preferred’ area as it carries detailed information coded by thalamic parvocellular neurons. By contrast, in parafoveal vision, the magnocellular pathway is involved as well, and the quality of the visual information (acuity) decreases with the eccentricity (Dacey, 1994). Therefore, foveal vs. parafoveal word primes should show some differences in early cortical processing. Beyond the early visual responses, reading is accompanied by strongly lateralized cortical activation, independent of the stimulus position in the visual field. According to magnetoencephalography (MEG) studies, visual stimuli are identified specifically as letter-strings by about 150 ms after stimulus presentation, with left-lateralized activation in the inferior occipitotemporal cortex (Tarkiainen et al., 1999; Tarkiainen et al., 2002). Using functional magnetic resonance imaging (fMRI) an area in the left middle fusiform gyrus (slightly anterior to the electrophysiologically identified letter-string area, Cornelissen et al., 2003), has been suggested to code the visual form of words (Cohen et al., 2000). This region is activated more by words than non-words (consonant strings), regardless of the hemi-field of presentation (Cohen et al., 2000). Neurophysiological recordings with MEG and electroencephalography (EEG) show the most salient priming effects from about 250 ms onwards, in activation that reflect semantic and probably also phonological analysis of written words (Helenius et al., 1998; Wydell et al., 2003), with the active areas concentrated to the left superior temporal cortex and possibly extending to the left anterior temporal and prefrontal cortex (Marinkovic et al., 2003). It is, however, unclear whether those effects, observed with foveal word presentations, would also appear with parafoveal-on-foveal priming. This question is particularly relevant if one wishes to draw conclusions on neural mechanisms of natural reading based on studies using foveal single-word reading.

It is, therefore, essential to establish the similarities and differences between foveal and parafoveal priming. The present study aims, for the first time, to compare these effects at both the behavioral and neurophysiological level. The behavioral experiment was the more extensive, including words and non-words both as primes and targets. Effect of the time allowed for processing the prime was tested with 50-ms and 100-ms prime-to-target delays. The reaction times and number of correct responses were measured when the subjects performed a lexical decision task. The MEG experiment sought to identify the neural correlates of the priming effects, focusing on word targets only. Both the behavioral and neurophysiological results point to clear differences between foveal-on-foveal and parafoveal-on-foveal priming. Parafoveal priming effects were detected only for a very short time delay between prime and target (50 ms) whereas foveal priming was not influenced by the delay duration. At the neural level, the timing and activated areas were overall similar between the different conditions. The priming effects, however, were bilateral for foveal presentation, left-lateralized when primes were presented in the right visual field and essentially non-existent when they were presented in the left visual field. The observed asymmetry between visual fields seems to agree with the preference to right visual field imposed by the Western writing system.

Method

Participants

Ten subjects participated in this experiment (8 males, 2 females, mean age ± S.D. 25 ± 3 years). The subjects were right-handed, native Finnish-speaking university students, with normal or corrected-to-normal acuity.

Behavioral experiment

Stimuli and paradigm

Two five-letter strings (the prime and the target) were presented serially, and subjects performed a lexical decision task on the target, i.e., decided whether it was a word or a non-word. The design (Fig. 1) followed a forward masking procedure. A fixation cross, flanked by X’s was first displayed foveally for 1300 ms, 1453 ms or 1595 ms (randomized), together with strings of four X’s on both sides, centered at ±3°. Next, a word or a consonant string (prime) was shown for 187 ms in one of these three locations: foveally, in the LVF, or in the RVF. After a delay of 50 ms or 100 ms (randomized) a word or a consonant string (target) was presented foveally.[1] There were thus 4 types of stimulus pairs (word/word, non-word/non-word, word/non-word and non-word/word), each with 3 prime visual field locations. The participants were shown altogether 240 prime–target pairs (10 pairs per priming condition * 3 prime visual field locations * 4 priming conditions * 2 delay durations), divided into two sessions. The different mask durations were equally assigned to the different priming conditions. For each condition, items were randomly selected from a set of 52 five-letter Finnish words (mean ± S.D. frequency 7930 ± 2297 per million, Laine and Virtanen, 1999) and from another set of

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[1] The choice of these two delays was motivated by pilot data, the results of which revealed that 50/100 ms was the critical time window for observing parafoveal-on-foveal priming effects (pilot data as online supplementary text).

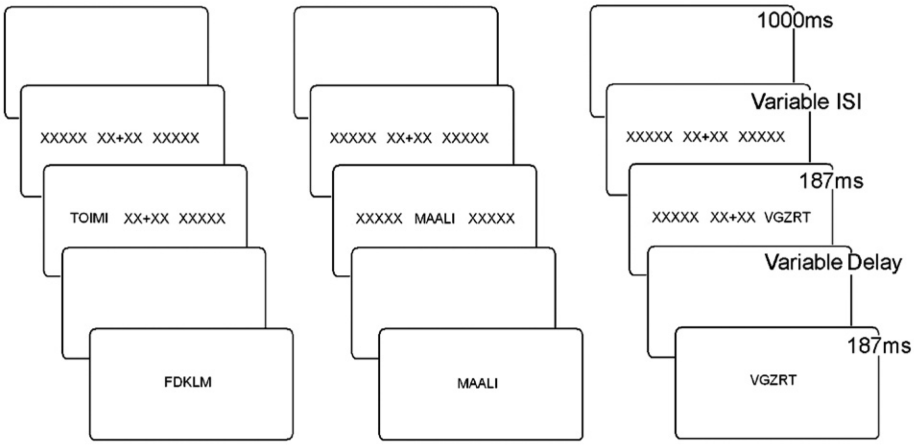

Fig. 1. Examples of stimuli used in the behavioral experiment. Primes appeared after a variable fixation period (1300 ms, 1453 ms or 1595 ms) and targets after a delay (50 ms or 100 ms); from left to right, incongruent non-word, congruent word, and congruent non-word conditions.

five-letter consonant strings. The response was given by a right-hand button press (Cedrus® response box RB620), with the right button corresponding to words and the left button to non-words in one session and the reverse assignment in the other session. RTs were measured post target onset. The order of sessions and the order of items within sessions were counterbalanced across subjects.

Statistical analysis

Reaction times (RTs) for the correct answers were analyzed using an ANOVA with *Delay* (50 ms, 100 ms), *Prime visual field location* (LVF, RVF, foveal), and *Priming condition* (word/word, non-word/non-word, non-word/word, word/non-word) as repeated measures. The four different types of prime–target pairs were all considered on an equal footing (factor *Priming condition*), instead of splitting them by the nature of the prime (word/non-word) or target (congruent/incongruent), because the cognitive processes underlying lexical decision differ for words and non-words (Ratcliff et al., 2004) and because this approach made the behavioral data more directly comparable with the MEG data which was focused specifically on word targets. The analysis was performed within the general linear model framework that allows non-equivalent groups[2] because data for the foveal prime condition were not available for two subjects due to technical problems. Sphericity was tested with a Mauchley test and a Greenhouse–Geisser correction was applied when necessary. Post-hoc tests were performed using a Fisher LSD test (alpha = 5%). Central vs. parafoveal priming conditions were also tested in planned contrasts $(\text{incongruent–congruent})_{\text{foveal}}$ vs. $(\text{incongruent–congruent})_{\text{RVF+LVF}}$, separately for word and nonword targets and for 50-ms and 100-ms prime-to-target delays. The percentage of errors, not normally distributed, was tested with a Friedman non-parametric ANOVA that examines whether one condition differs from the others.

In addition to these analyses, an ANOVA with *Delay* (50 ms, 100 ms), *Prime visual field location* (LVF, RVF, foveal) and *Type of targets* (words, non-words) was performed to investigate the lexical decision task *per se*.

MEG experiment

Stimuli and paradigm

The MEG experiment focused on the neural correlates of foveal vs. left/right parafoveal priming when processing real words. The paradigm was essentially the same as in the behavioral experiment, with the exception that the stimulus set was composed mostly of word targets (83.3%, word/word and non-word/word prime/target pairs). This choice was made in order to ensure a high signal-to-noise ratio in the neuroimaging experiment which requires a considerably higher number of trials per condition than the behavioral experiment. Neural activity associated with preparation for movement, uninteresting and unwanted as regards the present research question, was minimized by requiring manual response (button press) to rarely occurring (16.7%) non-word targets only. Only the 50-ms prime-to-target delay was used because, based on a pilot study (see Supplementary material, pilot study), it was expected to capture differences in foveal vs. parafoveal processing (see also current behavioral results). The experiment included a total of 864 prime/target pairs divided into five sessions: 120 items for each of the six conditions of interest (word/word and non-word/word pairs with foveal, LVF or RVF prime presentation), and 24 items for each of the six other conditions (word/non-word and non-word/non-word pairs with foveal, LVF or RVF prime presentation). For half of the participants, the MEG experiment was performed before the behavioral session, and in the reverse order for the other half. The order of sessions and the order of items within sessions were counterbalanced across subjects.

Recording and data preprocessing

MEG data were recorded with a Vectorview whole-head system (Elekta Neuromag Ltd., Helsinki, Finland). The device contains 102 triple sensor elements composed of two orthogonal planar gradiometers and one magnetometer. The planar gradiometers detect the maximum signal directly above an active cortical area. The signals were band-pass filtered at 0.03–200 Hz and digitized at 600 Hz. Horizontal and vertical eye movements were monitored (electro-oculogram, EOG). Trials with MEG amplitude exceeding 3000 fT/cm were discarded automatically.

The MEG data were averaged across trials from −0.2 s to 1.5 s relative to the stimulus onset. The averaged MEG responses were

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[2] Analyses were computed using the unique sum square method (effective hypothesis; Hocking, 1996).

baseline corrected to the 100-ms interval immediately preceding the prime onset, and low-pass filtered at 40 Hz. Only MEG signals related to the word/word (congruent) and non-word/word (incongruent) pairs were analyzed. Because subjects did not produce a response to these stimuli, signals were not corrupted by motor-related activity. The rare trials in which the subject erroneously responded to a word target (1.4%) were excluded from the analysis. Artifacts due to eye movements were removed from the data by rejecting trials during which the subject blinked (EOG > 150 μV) or a horizontal eye movement (saccade toward the prime) occurred. Two subjects were excluded from the MEG analysis because of excessive eye movements. For the remaining eight subjects, 80–110 artifact-free trials were obtained for each stimulus type (but one subject with ∼60 artifact-free trials).

Areal mean signal (AMS) analysis

Areal mean signals (AMS) provide an overview of the time behavior of neural activation and rough spatial information without actual source localization. The AMS were calculated over six areas of interest: left and right fronto-temporal, temporal, and occipito-temporal areas (Supplementary Fig. S1). Vector sums of each gradiometer pair were obtained by squaring the MEG signals, summing them together, and calculating the square root of this sum. The AMS were computed by averaging these vector sums for each area of interest, individually for each subject. Finally, the AMS were averaged across subjects. Because of the way the sensor-level areal mean signals are calculated (square root of sum of squared signals) they always have a positive value (>0).

Equivalent current dipole (ECD) analysis

In order to extend the analysis to the source level, activated brain areas were modeled as Equivalent Current Dipoles (ECDs) that represent the mean location of an active cortical patch and the activation strength and direction of current flow in that area (Hämäläinen et al., 1993). The location of the ECDs was defined in the head coordinate system that was set by the nasion and two reference points anterior to the ear canals. Prior to the MEG recording, four Head Position Indicator (HPI) coils were attached to the subject's head and their locations were measured with a 3D digitizer (Polhemus, Colchester, VT, USA). At the beginning of the recording, the HPI coils were briefly energized to determine their location with respect to the MEG helmet. The head was approximated with a homogeneous conducting sphere that best fitted the individual anatomy, as determined from the structural MR images. Separately for each subject, the magnetic field patterns were visually inspected to identify local dipolar fields, and sensors covering each of these patterns were chosen to determine isolated ECDs. These ECDs were incorporated into a multidipole model in which the locations and orientations of the dipoles were fixed but their strengths were allowed to vary in time to best explain the signals recorded by all MEG sensors over the entire analysis interval. The number of ECDs in the multidipole model was 9 to 11 per subject (Supplementary Fig. S2). A separate multidipole model was constructed for each of the prime visual field locations (LVF, RVF, and foveal). In each individual, the same set of ECDs accounted for the activation elicited by the congruent (word/word) and incongruent (non-word/word) conditions within the same prime visual field location. The final multidipole models typically accounted for above 85% of the total magnetic field variance at the signal maxima in each condition. For visualization and comparison of the sources between subjects the ECDs were transformed to a standard brain (Roland and Zilles, 1996) using elastic transformation (Schormann et al., 1996; Woods et al., 1998).

Statistical analysis

The AMS curves showed a number of salient maxima at different time points. The mean signal strength was computed across four time windows which typically contained these local maxima in the individual subjects: 80–200 ms, 200–300 ms, 300–400 ms, and 400–700 ms after the stimulus onset. ANOVAs were conducted separately in these time windows and separately for the fronto-temporal, temporal and occipito-temporal areas with the *Priming condition* (congruent = word/word pairs, incongruent = non-word/word pairs), *Prime visual field location* (foveal, LVF, RVF) and *Hemisphere* (left, right) as repeated measures. ANOVAs were performed within the general linear framework and sphericity was estimated using a Mauchley test. Post-hoc tests on the priming effects were performed using a Fisher LSD test (alpha = 5%).

Source-level effects of priming (from 450 to 650 ms) were evaluated in each source (ECD) of each individual subject, and separately for the foveal, LVF, and RVF conditions. The difference between the time courses of activation to incongruent vs. congruent prime–target pairs was compared to the standard deviation of the neural signal during the pre-stimulus baseline interval (Tarkiainen et al., 1999). A difference larger than 2.58 times the baseline standard deviation (corresponding to $p < .01$) between two signals of the same polarity for 50 ms or longer was considered significant.

The distribution of the percentage of correct responses and the RT distribution (RTs obtained to the non-word targets only) were compared with those recorded in the separate behavioral experiment using a Chi square test. In the MEG experiment, no response to word targets was considered a correct response whereas no response to the non-word targets was considered an error. An ANOVA with *Priming condition* and *Prime visual field location* as repeated measured was also conducted on these non-word target RTs, and a Fisher LSD test (alpha = 5%) was used as a post-hoc analysis.

Results

Behavioral experiment

Analysis of the RTs to correct answers revealed main effects of *Priming condition* ($F(3,21) = 16.83$ $p < .0001$) and *Prime visual field location* ($F(2, 14) = 4.02$ $p < .05$) and interactions *Priming condition × Prime visual field location* ($F(6,42) = 8.84$ $p < .0001$) and *Priming condition × Prime visual field location × Delay* ($F(6,42) = 3.82$ $p < .004$ GG correction $\varepsilon = 0.43$ $p < .04$); see Table 1 and Fig. 2 for detailed results. The error patterns did not differ between conditions (χ^2 (9,11)=18.4 $p = .8$ mean 3.5%, S.D. 6.6%).

Post-hoc analyses revealed a priming effect (congruent faster than incongruent) for both word and non-word foveal primes at both the 50-ms ($p = 8.9 \times 10^{-7}$ for words; $p = 1.5 \times 10^{-7}$ for non-words) and 100-ms prime-to-target delay ($p = 1.5 \times 10^{-9}$ for words; $p = 1.9 \times 10^{-8}$ for non-words). In contrast, for parafoveal primes the priming effect was present at the 50-ms prime-to-target delay only (Fig. 2). Priming was observed for word primes presented in either LVF ($p = .0004$) or RVF ($p = .00004$) but for non-word primes only when they were presented in the LVF (LVF $p = .006$, RVF $p = .3$) Planned comparisons confirmed that the foveal priming effect was greater than the parafoveal one both at the 50-ms ($F(1,7) = 5.9$ $p = .04$) and 100-ms prime-to-target delay ($F(1,7) = 26.8$ $p = .001$).

Table 1
RTs (in ms) and standard deviations for each experimental condition

Prime	Target	50 ms			100 ms		
		LVF	Foveal	RVF	LVF	Foveal	RVF
Words	Words	402±51	366±93	393±88	421±76	339±95	424±98
Non-words	Words	468±79	476±113	455±109	426±96	495±123	446±114
Non-Words	Non-words	435±95	360±102	441±74	478±106	337±100	435±88
Words	Non-words	493±91	484±113	460±99	448±76	480±100	457±107

The prime-to-target delays are listed on top (50 ms, 100 ms), together with the prime locations (LVF, foveal, RVF). Congruent and incongruent conditions are presented separately for word and non-word targets.

An additional finding was that RTs did not systematically vary as a function of eccentricity: For instance, there was no difference between LVF, foveal and RVF prime presentation for incongruent non-word/word pairs or word/non-word pairs. In some conditions, RTs were even longer for foveal than parafoveal priming (100-ms prime-to-target delay, incongruent conditions, $p<.05$; Fig. 2).

Comparison of RTs for words vs. non-words revealed a main effect of *Type of targets* (words 421 ms vs. non-words 444 ms; $F(1,8)=7.4$ $p=.02$) and an interaction *Prime visual field location*×*Type of targets* ($F(2,16)=4.3$ $p=.03$). Post-hoc analysis revealed that this word superiority effect (Ratcliff et al., 2004) was present when primes were displayed in parafoveal vision only (LVF $p=.006$, RT difference −41 ms; foveal $p=.7$ difference +4 ms; RVF $p=.02$, difference −33 ms; Supplementary Fig. S3). In fact, subjects processed target words at the same speed regardless of the *Prime visual field location* (LVF 423 ms, foveal 419 ms, RVF 420 ms; $p_{\min}=.8$) whereas a significant difference was observed for non-words (LVF 464 ms, foveal=415 ms, RVF 453 ms; LVF vs. foveal $p=.006$, RVF vs. foveal $p=.03$). Importantly, these lexical effects did not interact with the priming effects (Supplementary behavioral analysis Table S1).

MEG experiment

AMS analysis

The grand average areal mean signals (Fig. 3) showed transient peaks at 0–400 ms after the stimulus onset and a more sustained response from 400 ms onwards. A salient peak was typically

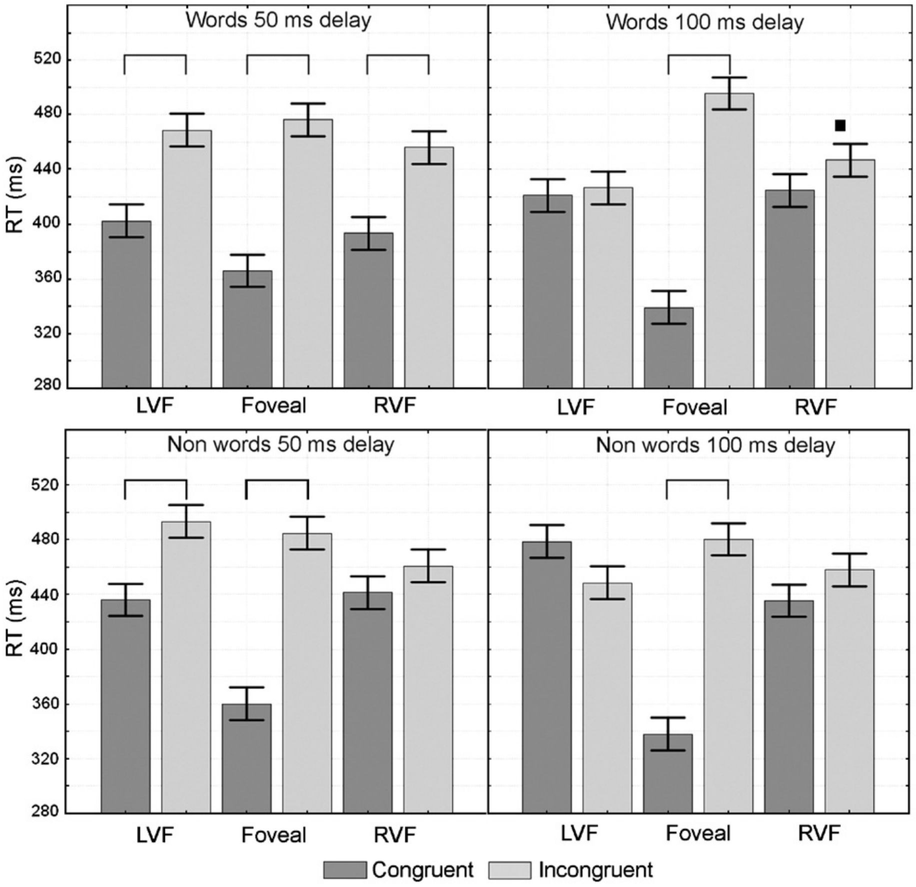

Fig. 2. Priming effect (congruent vs. incongruent items) depicted for word targets (top) and non-word targets (bottom) for 50-ms (left) and 100-ms delay (right). The bars are grouped according to the prime location (LVF, foveal, RVF). Error bars represent 95% confidence intervals for pooled within-subject errors (CI=11.9 ms; Loftus and Masson, 1994).

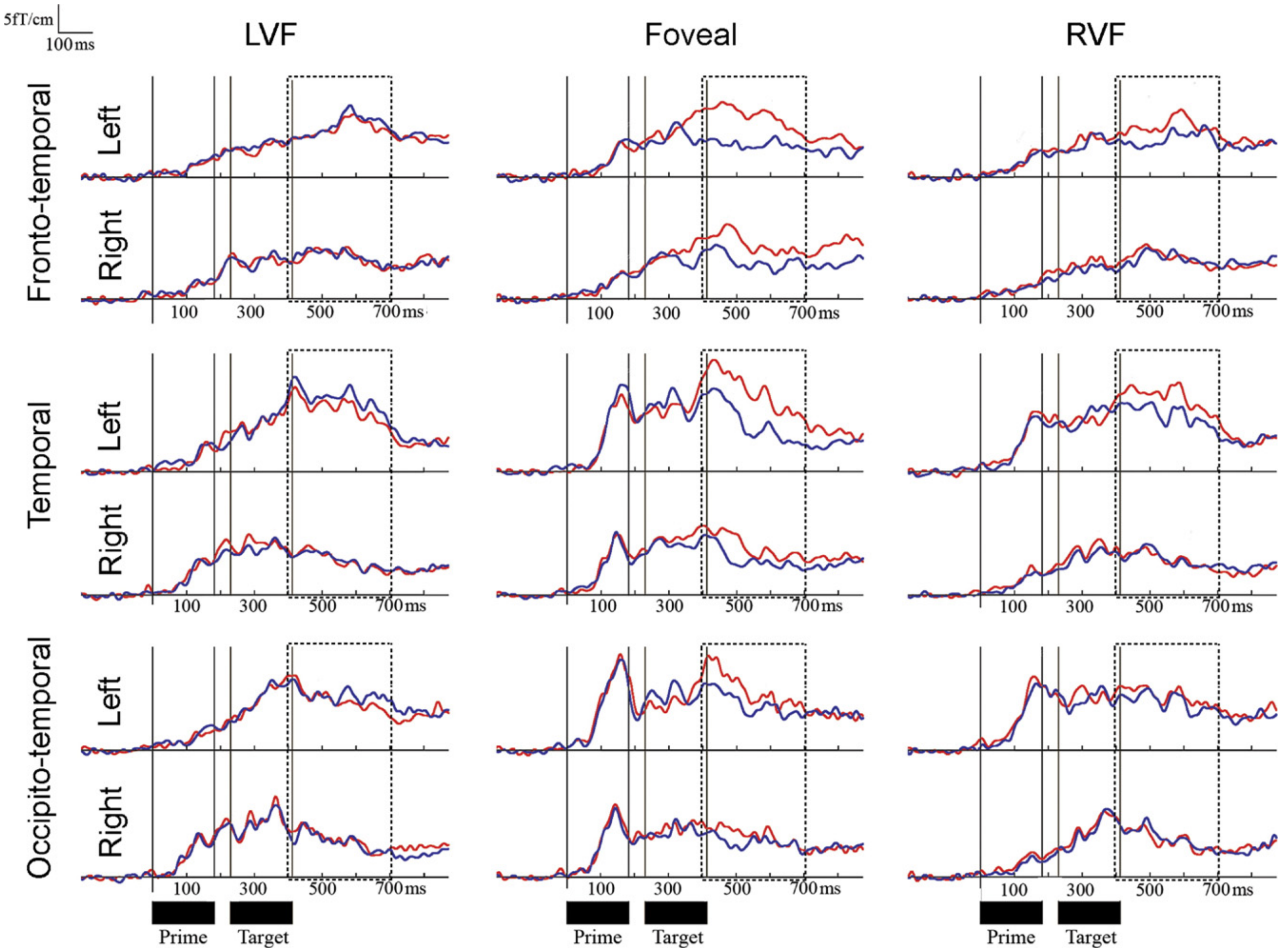

Fig. 3. Sensor-level AMS waveforms for the congruent (blue) and incongruent (red) conditions, averaged across all subjects. The curves are organized according to the prime visual field location (columns) and the sensor region of interest (rows). Vertical lines mark the prime and target onset/offset and dashed rectangles indicate the temporal window in which a priming effect was observed.

detected in individual data within 80–200 ms post stimulus which was followed by separate transient maxima within 200–300 ms and/or 300–400 ms in some subjects. These components were detected over all regions of interest, however, with signs of hemispheric lateralization (e.g., stronger signals in the left-hemisphere sensors for RVF than LVF primes). A more sustained response was typically detected at 400–700 ms, particularly over the temporal and fronto-temporal regions. The target appeared at 237 ms after the prime onset (prime duration 187 ms plus 50-ms prime-to-target delay). Therefore, components observed within 350 ms after prime onset (i.e., until ~100 ms after target onset) could have only reflected the effect of the prime itself independently of its subsequent effect on the target processing.

Effects of letter-string location as such were evident within the first 300 ms after the prime onset. Interaction *Hemisphere × Prime visual field location* was significant over the occipito-temporal, temporal and fronto-temporal regions (occipito-temporal: $F(2,14)=7.5$ $p=.006$ for the 80–200 ms time window and $F(2,14)=4.2$ $p=.03$ for the 200–300 ms time window; temporal: $F(2,14)=8.7$ $p=.003$ for the 80–200 ms time window and $F(2,14)=3.7$ $p=.04$ for the 200–300 ms time window; fronto-temporal: $F(2,14)=6.5$ $p=.01$ for the 80–200 ms time window). Post-hoc tests revealed that for the 80–200 ms time window activity was always lowest for ipsilateral primes. For example, over the left occipito-temporal region, LVF primes elicited significantly less activity than RVF ($p=.004$) and foveal ($p=.00008$) primes; in contrast, over the right occipito-temporal region, RVF primes elicited less activity than LVF primes ($p=.003$). Moreover, from 80 ms to 200 ms, foveal and RVF primes evoked stronger activity over the left than right hemisphere (occipito-temporal $p=.06$ and $p=.004$, temporal $p=.02$ and $p=.002$, fronto-temporal $p=.01$ and $p=.004$); from 200 ms to 300 ms this effect was detected for RVF primes only (occipito-temporal $p=.03$, temporal $p=.04$).

Priming effects emerged in the fourth time window (400–700 ms after the prime onset, ~160–460 ms after target onset). The interaction *Prime visual field location × Priming condition* was significant over the fronto-temporal region ($F(2,14)=5.69$ $p=.01$) and the interaction *Prime visual field location × Priming condition × Hemisphere* over the temporal region ($F(2,14)=18.5$, $p<.01$). For foveal primes, incongruent targets elicited a stronger response than congruent targets bilaterally over the fronto-temporal ($p=.0003$) and temporal (left hemisphere $p=.0001$; right hemisphere $p=.01$) regions. For RVF primes, priming effects were detected over fronto-temporal regions bilaterally ($p=.005$) but over the temporal region only on the left (left hemisphere $p=.002$; right hemisphere $p=.8$). Foveal priming was stronger than RVF priming

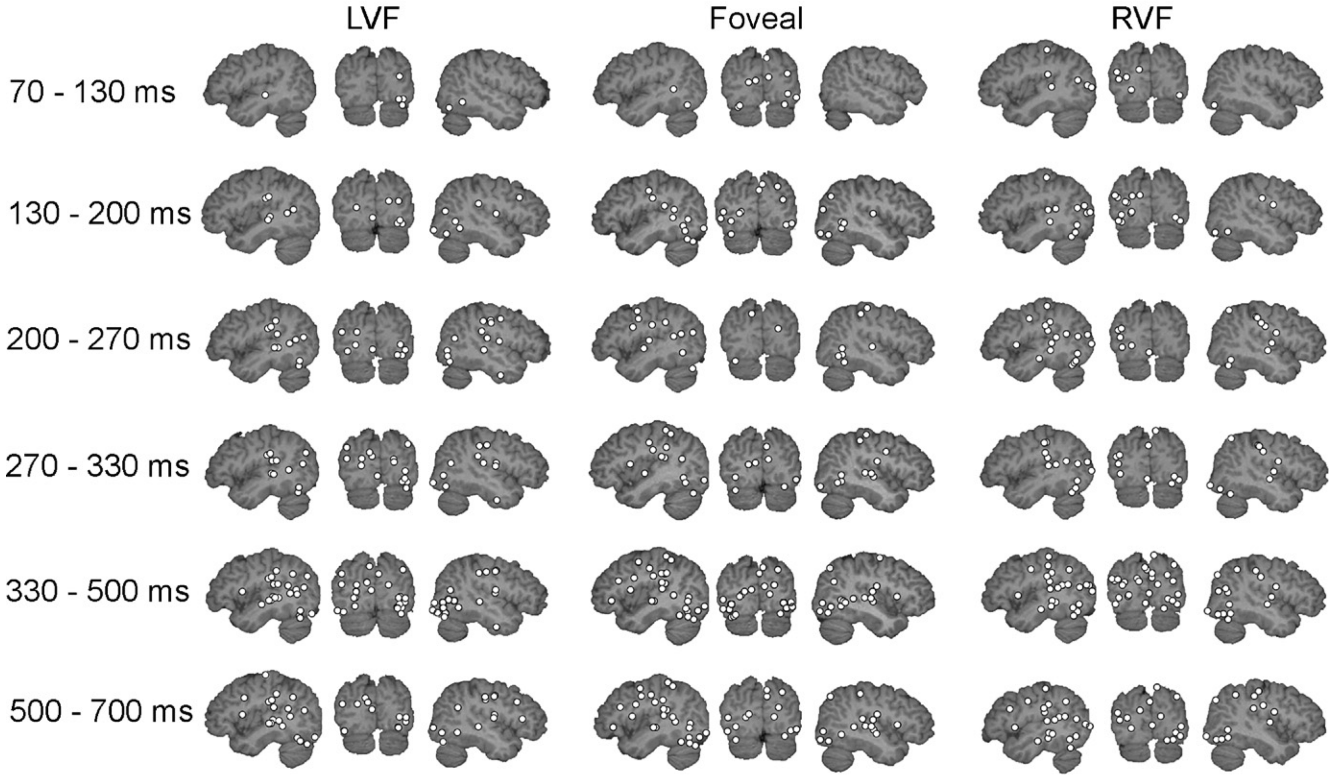

Fig. 4. Sequence of cortical activation, starting from prime onset (0 ms). The dots indicate centers of active cortical patches, collected from all participants. From left to right, cortical areas activated when primes were presented in the left visual field, foveally and in the right visual field. For each prime location, the source areas were the same in the congruent and incongruent conditions.

over both fronto-temporal (left hemisphere $F(1,7)=7.14$ $p=.03$; right hemisphere $F(1,7)=6.91$ $p=.03$) and temporal region (left hemisphere $F(1,7)=2.13$ $p=.18$; right hemisphere $F(1,7)=5.93$ $p=.04$). No priming effect was observed for LVF primes.

Source-level effects

ECD models (Fig. 4) revealed a typical sequence of activation for written word processing (Salmelin, 2007). At about 100 ms, occipital areas were activated either unilaterally for parafoveal primes (e.g., left occipital activation for RVF primes) or bilaterally for foveal primes. Next, from about 130 ms to 270 ms, activation spread to the posterior inferior and middle temporal cortex bilaterally for all three conditions. After the target appearance (at about 270 ms, i.e., 30 ms after target onset), in addition to the ongoing inferior temporal and superior temporal activity, precuneus/posterior parietal activations were observed. On the whole, very similar source locations were observed for LVF, foveal and RVF conditions (Fig. 4).

Comparison of source-level time courses of activation revealed priming effects (incongruent > congruent) mainly for the foveal and RVF primes (Fig. 5). Differences congruent > incongruent were occasionally observed as well but only in a few ECDs of a few subjects. For the foveal primes, the priming effect was bilateral (8 out of 8 subjects; left hemisphere 24 ECDs, right hemisphere 16 ECDs), in agreement with the AMS (cf. Fig. 3). For the RVF primes, the effect was mostly concentrated to the left hemisphere (7 out of 8 subjects; left hemisphere 10 ECDs, right hemisphere 3 ECDs) which again agrees with the AMS. For the foveal primes,

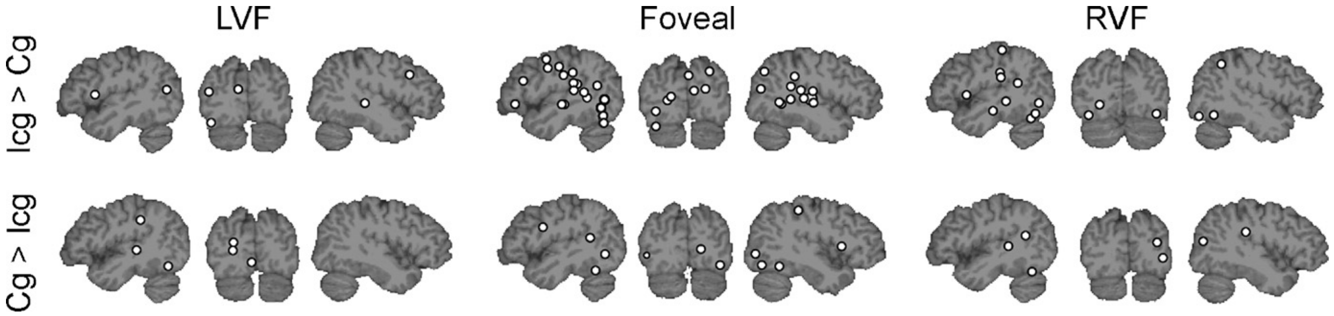

Fig. 5. Source areas showing stronger activation to incongruent than congruent stimuli (Icg > Cg, i.e., priming effect, top) and stronger activation to congruent than incongruent stimuli (bottom) at 450–650 ms.

ECDs showing a priming effect were located mainly in and around the left and right superior temporal sulcus, the left central sulcus and the left occipito-temporal cortex. For the RVF primes, ECDs were located mainly in the left superior temporal and occipito-temporal cortex.

Behavioral data in the MEG experiment

Subjects generally detected word targets equally accurately in the MEG and in the behavioral experiment ($p_{\min}=.3$, Supplementary Table S2). They made slightly more errors in the MEG experiment for the word/non-word pairs (percentage of correct responses to LVF, foveal and RVF were, respectively, 85.9%, 90% and 91.4% in the MEG experiment, and 94.4%, 93.3% and 98.4% in the behavioral experiment; MEG vs. behavioral $p=.00001$ for LVF, $p=.006$ for foveal and $p=.01$ for RVF). This difference was probably due to the fact that in the MEG experiment subjects only responded to the (rare) non-word targets whereas in the behavioral experiment they responded to all stimuli.

The analysis of reaction times collected for the rare non-word targets (16.7%) revealed that subjects were overall slower in the MEG experiment than in the behavioral experiment (700 ± 109 ms vs. 449 ± 74 ms, $\chi(7)=122$ $p<.001$—Supplementary Table S3, and a significant interaction *Priming condition* × *Prime visual field location* was observed ($F(2,14)=4.45$ $p<.03$). Post-hoc tests revealed a clear priming effect for non-word targets when the primes were presented foveally (RT difference −107 ms; $p=.03$) but not when they were presented parafoveally (LVF $p=.9$ RVF $p=.7$).

Discussion

Foveal and parafoveal priming are two distinct paradigms used to study word recognition and reading. Because natural reading relies on parafoveal perception and its' interaction with the subsequent foveal word processing (Rayner, 1998) it is important to evaluate differences between these approaches if one wishes to draw conclusions on reading from studies on foveal word recognition.

Behaviorally, foveal and parafoveal-on-foveal effects were distinguished (i) by the strength of the effects, i.e., the foveal effect was stronger than the parafoveal one and (ii) by the enduring vs. transient nature of foveal vs. parafoveal priming, i.e., foveal priming was present for both 50-ms and 100-ms prime-to-target delays whereas parafoveal-on-foveal priming was observed with the 50-ms prime-to-target delay only. A possible explanation for these differences is that, because the central field is the preferred area for detailed visual analysis (Dacey, 1994) and the information flows in both hemispheres, analysis of foveal inputs may be supported by well-formed and efficient bilateral feedforward–feedback loops, thus resulting in a strong and sustained priming effect for subsequent information (target) presented at the fovea. In contrast, for parafoveal primes (followed by foveal targets), the visual input initially reaches the contralateral hemisphere only, unable to launch a recurrent loop of activation. The priming effect would likely be of a one-shot type and, therefore, only effective for a very short time. The observed differences between foveal and parafoveal priming cannot be accounted for by differences in visual acuity as the reaction times, overall, did not vary systematically with stimulus eccentricity (Fig. 2). One could also argue that the parafoveal vs. foveal priming effects differ for the two delays because the 50-ms delay was too short for the subjects to distinguish between foveal primes and foveal targets, thus resulting in the perception of a single stimulus of long duration instead of two successive stimuli. However, several arguments support the interpretation that subjects perceived two separate stimuli also at the 50-ms prime-to-target delay. First, all subjects were able to perform the task, and their manual responses were detected from 150 to 180 ms after target offset for the 50-ms as well as 100-ms delay. Second, the RTs to word targets remained the same regardless of whether the word primes were presented foveally or parafoveally. Finally, electrophysiological data displayed salient visual responses in the occipital cortex first to the prime and then to the target, indicating perception of two separate stimuli at the brain level.

Interestingly, LVF and RVF priming effects varied according to the target type (word or non-word). For real words, parafoveal-on-foveal priming effects emerged for both LVF and RVF primes. However, parafoveal-on-foveal priming on non-words was detected for LVF primes only, suggesting different processes in the two hemispheres. The analysis of non-words can only make use of perceptual priming whereas real words can, *a priori*, benefit from both perceptual and conceptual cues. Therefore, our behavioral results can be understood if one assumes that the right hemisphere, which initially processes primes displayed in the LVF, performs mainly perceptual analysis (hence priming effects for words and non-words alike; Marsolek et al., 1992) whereas the left hemisphere, which initially processes primes displayed in the RVF, would perform predominantly conceptual analysis (hence priming effects for words only; Marsolek, 2004). In natural reading, the perceptual span is oriented toward the RVF (Rayner, 1998), with little or no influence from the LVF, resulting in emphasis on conceptual priming effects. In a more artificial experimental setup, such as the one used here, both LVF and RVF priming occurs, likely reflecting a general neural mechanism that differs from foveal priming, and with the exact nature (perceptual or conceptual) related to hemispheric specialization. In the present LVF parafoveal-on-foveal priming condition, lexical decision on both words and non-words would have been speeded up because of facilitated visual analysis (perceptual effect) whereas for the RVF parafoveal-on-foveal priming, which was observed for words only, the lexical decision would have been speeded up because of enhanced pre-lexical or lexical processing (or more generally on 'wordness' analysis (see, e.g., Ratcliff et al., 2004)) for a detailed discussion on lexical decision).

In the MEG data, early visual processing of the parafoveal primes was strongest in the contralateral occipital cortex, and more balanced between hemispheres for the foveal primes, reflecting the gross anatomical organization of the visual cortex (Bear et al., 1995; Tootell et al., 1998). Effect of priming was observed from about 160 ms to 460 ms after target onset. When primes were displayed in the RVF, facilitated processing of the foveal target word (priming) was localized to the left occipito-temporal cortex and superior temporal cortex. According to literature, activation in those areas in that time window corresponds to orthographic/lexical and phonological processes (Tarkiainen et al., 1999; Garrett et al., 2000, Gros et al., 2001; Joseph et al., 2003; Pernet et al., 2005; Cohen et al., 2000, 2002, Price et al., 1994; Beauregard et al., 1997; Helenius et al., 1998; Tagamets et al., 2000; Mechelli et al., 2003; Pylkkänen and Marantz, 2003; Wydell et al., 2003). For LVF primes, no facilitation was detected either in the neural activation (to word targets) or in the simultaneously recorded behavioral data (to non-word targets). As all experimental conditions activated a similar set of cortical areas, the absence of an LVF priming effect at the neural level could not be accounted for by differences in the spatial pattern of activation. It is possible that the large proportion of word targets (83.3%) in the MEG study, as compared with their proportion in the separate behavioral experiment (50%), resulted in a top-down predisposition for conceptual analysis and a lack of LVF-driven perceptual priming effects. Finally, foveal primes had a facilitatory effect on the processing of the foveal target words that occurred in the same time window as for RVF primes but was bilateral and significantly stronger than for the RVF primes. The pronounced neural effects may well reflect recruitment of a feedforward–feedback loop that supports the sustained foveal priming effects observed in the behavioral experiment. The findings of the MEG study are in general agreement with our behavioral results: both experiments indicate a distinction between foveal and parafoveal-on-foveal priming effects.

Methodological considerations

The parafoveal preview benefit occurs during natural reading and is thus difficult to study using event-related potentials (or event-related fields) which require accurate timing of prime and target onsets and well-defined baseline intervals between trials. Here, we used a parafoveal-on-foveal paradigm which, to a degree, simulates the movement of the prime on the retina. Previous studies have demonstrated – and the present study confirms – that this paradigm shows similar, although not as strong, priming effects as those detected in natural reading (Rayner, 1998). An important point to consider is the time-to-target delay: In natural reading, this delay is very brief (tens of milliseconds) and corresponds to the time between two fixations. In the present study, the goal was to directly compare foveal and parafoveal-on-foveal priming effects and, therefore, the delay could not be reduced below 50 ms. At shorter intervals (that would have been closer to those in natural reading), subjects were no longer able to differentiate foveal primes from foveal targets. Finally, a large number of repetitions is required to achieve a good signal-to-noise ratio in MEG/EEG evoked responses and stimulus repetition may reduce the influence of priming. Nevertheless, we observed clear priming effects, which could probably be further increased by using a larger set of different stimuli.

Conclusion

Neuroimaging literature typically uses foveal word presentation to investigate reading processes. However, as demonstrated by eye-tracking studies, fluent reading relies on the parafoveal preview benefit, i.e., on the integration of parafoveal word information with the subsequent foveal analysis. Here, we show that integration of the parafoveal input, i.e., parafoveal-on-foveal priming, does not rely on the same neural processes as foveal word priming. Foveal priming affects both hemispheres, relying on both perceptual and conceptual processes. Parafoveal priming effects, however, are left-lateralized, rely largely on conceptual processes and appear for word targets preceded by primes presented in the right visual field, in line with the direction of attention that is most efficient for coping with the Western reading system.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2007.07.035.

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