

## Interhemispheric communication influences reading behavior

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## **Abstract**

We can read words at an amazing speed, with the left hemisphere taking the burden of the processing in most readers (i.e. over 95% of right-handers and about 75% of left-handers). Yet, it is a long-standing question whether word reading in central vision is possible without information transfer between the left and the right hemisphere (LH/RH). Here we show that such communication is required by comparing word naming latencies and eye movement data of people with LH language dominance and a unique sample of healthy RH dominant people. The results reveal that individuals with LH speech dominance name words faster when they are allowed to fixate at the word beginning, whereas RH dominants are faster for fixations towards the end. In text reading the eyes of LH dominants land more to the left than the eyes of RH dominants, making more information directly available to the dominant hemisphere. We conclude that the traditional view of bilateral projections in central vision is incorrect. In contrast, interhemispheric communication is needed in central vision and eye movements are adjusted to optimize information uptake. Our findings therefore call into question the explanation of macular sparing in hemianopia based on a bilaterally projecting fovea. In addition, these results are in line with the increase of white matter in the splenium of the corpus callosum when people learn to read.

## Introduction

Reading has become an important skill in life. The human environment contains many words that must be deciphered, going from books and newspapers to billboards, text messages, and movie subtitles. Because reading is a recently acquired skill, it has to be implemented in a brain that did not evolve for this function (Dehaene, 2009). Learning to read requires years of practice and affects the anatomy of the brain by enhancing the white matter in the posterior part of the corpus callosum (Carreiras et al., 2009). The most likely reason for this change is that literacy requires a fast exchange of information between the left and the right hemisphere (LH/RH). However, little is known about the communication between the hemispheres during reading.

There is no agreement in the current literature about how written words are processed in foveal vision (approximately the central 3 degrees of visual field or 12 letters), the area of the visual field where acuity is highest and where detailed letter information is extracted from. Most recent (neuroimaging) studies do not distinguish between foveal and parafoveal vision, even though reading mainly involves foveal word identification. For example, Doron, Bassett and Gazzaniga (2012) used a dynamic network analysis in their magnetoencephalography lexical decision study in order to investigate information exchange through the corpus callosum. They presented (pseudo)words in the parafoveal left or right visual field (LVF/RVF), sending information to the RH/LH respectively due to the partial crossing of optic fibers in the optic chiasm. Results revealed an early asymmetric information transfer with most information flowing from LVF/RH to the LH, which is the dominant hemisphere for lexical processing in most readers. The increased interhemispheric coordination peaked at 100 ms (presumably reflecting visual word recognition in posterior brain areas) and at 300 ms (representing lexical

information retrieval in temporal areas). From 400 ms on, the network density for RVF presentations increased which could point to the involvement of both the LH and RH in higher-order cognitive processes. Despite these promising results that the need for interhemispheric communication can be tested in detail by noninvasive neuroimaging techniques, Doron and colleagues unfortunately presented their stimuli parafoveally so that the consequences for more frequent foveal reading remain unclear.

Knowing whether foveally presented visual information is initially split and sent to the hemisphere contralateral to the stimulated visual half field is also important for the understanding of macular sparing in hemianopia patients (i.e. the preservation of central vision on both sides of fixation despite unilateral damage to the occipital cortex). It is a long believed assumption that foveal sparing is caused by a bilateral representation of central visual information. Other researchers pointed to methodological flaws and attributed the preserved vision to spared tissue in the affected hemisphere (Lavidor & Walsh, 2004; Leff, 2004).

In the current study, we investigated whether (a) foveally and parafoveally presented words follow the same contralateral organization and central information has to be reunited, or (b) foveally presented letters have duplicated cortical representations and both hemispheres can operate independently. The best way to investigate whether central visual word recognition requires interhemispheric transfer of letters is to compare the reading behavior of typically LH and atypically RH language dominant subjects. RH speech dominance is rare (in less than 5% of right-handers and about 10-20% of left-handers; Knecht et al., 2000) but can be found with some effort in the non-clinical population (Van der Haegen, Cai, Seurinck & Brysbaert, 2011). We hypothesized that LH dominant readers would be faster at word recognition while fixating more

towards the left of a word compared to RH dominants. Most letters then fall in the RVF/LH, limiting the time cost caused by transferring letters that are projected to the non-dominant RH after an initial split. It would be more beneficial for atypically lateralized RH dominants to fixate more towards the word end. Speech dominance was assessed by comparing LH and RH neuronal activity during a functional Magnetic Resonance Imaging (fMRI) word generation task, which is often used as a standard task to measure the lateralization of word production (e.g. Cai, Paulignan, Brysbaert, Ibarrola & Nazir, 2010). Activity in the LH and RH pars opercularis and pars triangularis, known as Broca's area, was evaluated during the generation of words starting with a target letter and contrasted against a condition in which the participants silently repeated the non-word *baba*. In addition, we calculated a lateralization index (LI) for reading as different degrees of lateralization have been observed for various linguistic subprocesses (Seghier, Kherif, Josse & Price, 2011). Reading lateralization was estimated by a lexical decision task, in which brain activity for existing words was contrasted against a checkerboards condition. The region of interest now was the ventral occipito-temporal region (vOT) that is also known as the Visual Word Form Area (Cohen et al., 2000). All subjects then took part in an Optimal Viewing Position (OVP) paradigm in which they named words in isolation at different fixation positions (O'Regan & Jacobs, 1992). If words are initially split and speech lateralization influences word identification, the OVP should be more towards the word end for RH dominants compared to LH dominants. In our final task, we explored whether RH dominants fixate more towards the right than LH dominants in more natural reading, i.e. reading words in texts.

## Methods

### *Participants*

Subjects were 49 Belgian students (11 males, 38 females; mean age: 21.0 years, SD: 2.6) from universities and higher education schools. A Dutch version of the Edinburgh Handedness Inventory (Oldfield, 1971) and Porac and Coren (1981) questionnaire tested their handedness, eyedness, earedness and footedness on a scale ranging from -3 (extreme left preference) to +3 (extreme right preference; mean scores (and SDs) -2.36 (0.77)/2.68 (0.27), -1.70 (1.16)/1.98 (0.85), -1.46 (1.83)/2.05 (1.40), -1.51 (1.72)/2.37 (0.59) for left- and right-handers for the abovementioned variables respectively). Subjects reporting to at least write and draw with their left/right hand were classified as being left/right-handed. There were no restrictions applied to the remaining items of the questionnaires (e.g. using scissors) to increase chances of identifying atypically speech lateralized subjects among the left-handed sample. All subjects signed an informed consent form approved by the ethics committee of Ghent University.

### *Tasks and stimuli*

*Speech and reading lateralization assessment.* All participants completed an fMRI silent word generation task in order to determine their speech lateralization. They were asked to mentally generate as many words as possible starting with the letter presented on the screen (*b, d, k, l, m, n, p, r, s* or *t*). Each letter was shown for 15 s. In the baseline condition, the non-word *baba* was presented for 15 s and had to be repeated in silence. Experimental and baseline blocks were alternated by blocks of 15 s in which a horizontal line indicated the resting periods. A practice phase outside the scanner ensured that all subjects understood the task correctly.

Reading LIs were calculated for each individual based on an fMRI lexical decision task adopted from Cai et al. (2010). Subjects had to press the *yes* button with their left index finger if the stimulus was a word and the *no* button with the right index finger if the word was not a word. Stimuli were 4- to 7-letter high and low frequent words, consonant strings and scrambled words (created by scrambling images of word stimuli at the pixel level). We used an event-related design, in which each trial began with a central fixation cross. After a variable duration of 500-2000 ms, a stimulus was displayed for 800 ms followed by a short horizontal line for 2s until the end of the trial. All stimuli were displayed once in a random order.

Details about the tasks and procedures can be found in our previous studies (Van der Haegen et al., 2011; Van der Haegen, Cai & Brysbaert, 2012) that described the recruitment of the left-handers in the current sample.

*Optimal Viewing Position (OVP) paradigm.* Interhemispheric communication was tested for word naming in isolation by using an OVP task. Naming latencies to three-, four- and six-letter words from LH dominant left- and right-handers were compared to those from RH dominant left-handers. Words were presented with one letter between two vertically aligned fixation lines at the screen centre. The position of the fixated letter was manipulated by horizontally shifting the word. Participants were asked to name the Dutch word appearing between the fixation lines as fast and accurately as possible. They were instructed explicitly and repeatedly to carefully fixate between the lines at the centre of the screen from the moment they appeared. An eye-tracking device registered their fixation positions.

Words were all nouns and were split up in groups of 25 (three- and four-letter words) or 50 (six-letter words) items, matched independently on log frequency per million, summed type

bigram frequency, and neighbourhood size ( $ps > .23$ ). The words were presented in Courier New font, size 15. A CRT display was placed at a viewing distance of 101 cm. One letter subtended  $.27^\circ$  such that the maximum distance from the central fixation position (i.e. when fixating at the middle of an outer letter) was 1.50 degrees of visual angle. All participants named all words at all possible fixation positions in a randomized order (i.e., three times 25 words per position for the three-letter words, four times 25 words per position for the four-letter words, two times 25 words per position for the six-letter words because in the latter condition six times 25 words per position would have been too fatiguing).

*Text reading task.* Participants were asked to read two short stories, four newspaper articles and two descriptions of countries (containing information about their history, geography and population) in order to obtain reading data in a setting reflecting natural reading. Each screen contained five lines of text with a maximum of 80 characters on each line. Participants were asked to read the texts as natural as possible and to press a button with their dominant hand at the end of each screen to move on to the next trial. They had to shortly summarize each text at the end of the experiment. Texts included 6117 words in total. Analyses only included data of four- (N = 840), five- (N = 489), six- (N = 641), seven- (N = 405), and eight-letter words (N = 407). Each trial contained the following steps: 1) A fixation dot was presented one line above and one letter to the left of the first word to ensure that eye fixations started from the same position on each trial; 2) After calibration checking based on the fixation dot, the experimenter presented the next screen; The participant had to press a button when (s)he finished reading the five lines of text; 3) An intertrial interval of 1500 ms was inserted prior to the next fixation dot.

### *fMRI LI calculation*

Details about the fMRI data acquisition and preprocessing stages of the analyses can be found in (Van der Haegen et al., 2011, 2012; Cai et al., 2010). Here, we summarize the processing steps that are most relevant to the current study. The LIs reflecting the asymmetry of hemispheric activation during the word generation and lexical decision task were calculated by using the LI toolbox 1.02 of (Wilke & Lidzba, 2007). The toolbox provides reliable LIs that are insensitive to statistical outliers and arbitrarily chosen activation thresholds. In sum, 20 equally sized steps from 0 to the maximum t-value were taken as thresholds in the regions of interest (ROIs, i.e. the pars opercularis/triangularis or Broca's area during the word generation task; the vOT region in the lexical decision task was defined by the mask used in Twomey, Duncan, Price & Devlin, 2011). Hundred resamples (resample ratio  $k = 0.25$ ) in the LH and RH ROIs were acquired for each threshold using a bootstrapping mechanism. Next, the central 50% of 10 000 calculated LIs were used to compute one mean individual LI by ascribing a higher weight to the higher thresholds.

### *Eye movement data acquisition*

During the OVP and reading tasks, participants' eyes were monitored binocularly using a SR Research Eyelink 1000 eye tracking device (Ontario, Canada). Coordinates were recorded every millisecond. At the beginning of the experiment and after each break, calibration and validation were carried out with a 9-point grid.

### *Optimal Viewing Position data-analysis*

In the OVP-task, the following trials were excluded from the naming latencies analyses: (1) pronunciation errors (0.3%); (2) voice key trigger errors (1.8%); (3) RTs smaller than 200 ms or greater than 1250 ms (1.2%); (4) RTs deviating more than 2.5 standard deviations from a participant's mean (1.9%); (5) 1.5% of the data were lost due to incomplete trial transfer from the host pc to the display pc. In addition, the analysis reported below included only trials on which participants (1) made only one stable fixation throughout the 150 ms stimulus presentation, (2) fixated within the boundaries of the letter presented between the two vertical fixation lines (i.e.  $.25^\circ$ ), and (3) showed binocular disparity of less than 1 letter. In order to reject unreliable OVP curves, we decided to exclude participants that had less than ten trials left per fixation position after these strict fixation control criteria, i.e. 30 trials for three-letter words (hereafter OVP3), 40 trials for four-letter words (hereafter OVP4) and 60 trials for six-letter words (hereafter OVP6).

The OVP data were analyzed using linear mixed effects (LME) modeling with naming reaction times (RTs) as dependent variable. Fixed factors of the LME analysis included fixation position (relative to the word centre), speech dominance (2 levels: LH and RH dominant) and word length (3 levels: 3-, 4-, and 6-letter words). In addition to the random intercepts, replicated variables were also entered as random factors (Barr, Levy, Scheepers & Tily, 2013). For participants, the replicated variables were word length and fixation position. For items, the replicated variables were speech dominance and fixation position. The LME analysis additionally tested whether significant interactions between fixation position and laterality group were due to a linear trend (e.g. OVP3: -1, 0, +1) reflecting faster naming times at the word

beginning/end or quadratic trend (e.g. OVP3: +1, 0, +1) implying differences in terms of visual acuity (Brysbaert & D'Ydewalle, 1991).

### *Text reading data-analysis*

The fixation position analyses only included fixations that were longer than 80 ms and shorter than 800 ms. Analyses were further limited to fixations that did not fall on the first word of a line, initial landing fixations on a word, and fixations resulting from a forward saccade. For the initial fixation position analyses, words that were fixated more than once were excluded. This also eliminated those words that were fixated twice or more within the same fixation run, i.e. when the word was fixated more than once before moving to the next word (20.2 % of the data). These data inclusion criteria were also used for the fixation duration analyses so that both analyses were based on the same dataset. Only four- to eight- letter words were examined as these were most frequent in the texts.

The dependent variable in the main LME analysis was the initial landing position of a word. Three fixed effects variables were examined: Speech dominance (2 levels: LH and RH dominant), eye (2 levels: left eye and right eye) and word length (i.e. a centered continuous variable with a length varying from 4 to 8 letters). A random intercept and slope for word length were entered as random effects for eyes and participants. For items, a random intercept and slopes for speech dominance and eye were used.

Finally, the same data inclusion criteria as above were used for the fixation duration analyses. The fixed factors were speech dominance (2 levels: LH vs. RH), fixation position (centered around the middle of the word and modeled as a linear or a quadratic term), word length (i.e. a centered continuous variable containing 5 word lengths from 4- to 8-letter words).

As for the random effects, we added a random intercept and slope for speech dominance, eye and fixation position at the item level, and a random intercept and slope for word length and fixation position at the level of participants and eye.

The reported p-values are based on a Type III ANOVA using a  $\chi^2$ - distribution. Statistically significant main effects and interactions were further explored using generalized Wald tests on the variance/covariance matrices of the fixed effects.

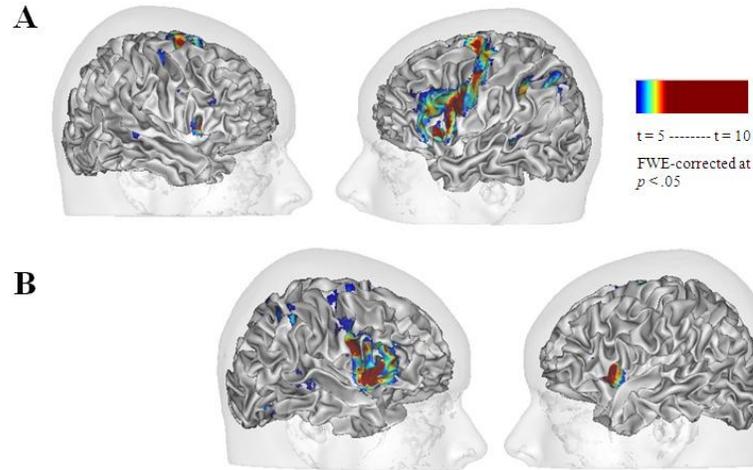
## Results

*Speech and reading lateralization indices.* A detailed description of the speech and reading dominance results can be found in our previous studies (Van der Haegen et al., 2011, 2012) where the recruitment of left-handers is discussed. Given the importance for the current study, we will briefly summarize the results here.

Lateralization indices (LIs) could range from -1.00 (complete RH lateralization) to +1.00 (complete LH lateralization). For the present study only participants with an LI lower than -.60 or higher than +.60 were retained, to have a clear distinction between the RH and the LH dominant group. The RH speech dominant group consisted of 17 left-handed participants with LIs ranging from -.62 to -.94 (mean LI = -.82, SD = .11). The LH speech dominant group contained both right-handers (N = 15, LIs ranging from .64 to .93, mean LI = .80, SD = .10) and left-handers (N = 17, LIs ranging from .62 to .94, mean LI = .79, SD = .10). Figure 1 represents the summed brain activity of both groups, illustrating the strongly diverging lateralization patterns. Lexical decision reading turned out to be more bilaterally distributed than production in the silent word generation task even though the speech and production LIs correlated

significantly ( $r = 0.57$ ,  $p < .001$  in the current sample): Most brain activity during lexical decision reading was localized in the same hemisphere as the participants' speech dominant hemisphere. We therefore classified our participants as LH or RH language dominant based on the naming task, and additionally ran OVP and text reading analyses using the continuous speech and reading LIs. Reading LIs of the participants that took part in the reading task ranged from -.78 to +.60 in the RH speech dominant group ( $N = 15$ , 1 participant did not take part in the reading study and one was excluded because he showed no significant activation in the ROI box at an uncorrected  $p < 0.01$  level, mean = -.21, SD = .41), from -.49 to +.89 in the left-handed LH speech dominant group ( $N = 13$ , four participants were excluded from the reading task as their eyes could not be calibrated accurately enough to have reliable information for the full duration of the experiment and across the entire screen, mean = .34, SD = .44), and from -.36 to +.81 in the right-handed LH speech dominant group ( $N = 11$ , two participants did not take part in the fMRI lexical decision task and two were excluded due to weak brain activity that would have lead to unreliable LI estimates, mean = .39, SD = .38).

Table 1 shows demographic data (age, gender, education type) and mean scores of the questionnaire (handedness, eyedness, earedness, footedness) for the LH and RH speech dominant subjects that took part in the OVP and/or text reading task.



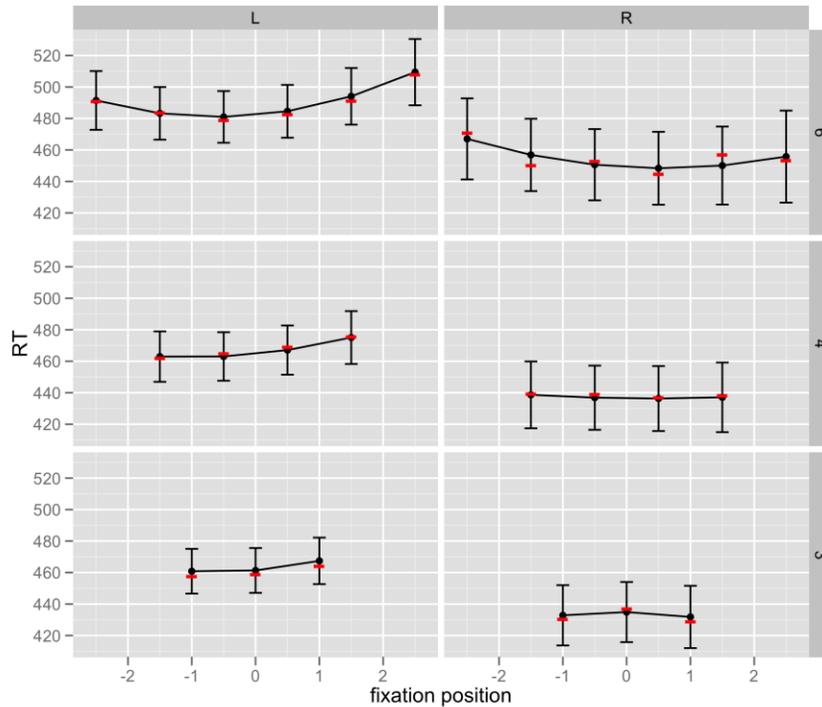
**Figure 1.** Activity observed during the silent word generation task in fMRI for the subjects participating in the behavioral naming and reading tasks. Two groups were made based on the activated voxels in Broca’s area: Panels A and B show the group activity for the left and right hemisphere dominant group respectively. Beyond the inferior frontal gyrus, activity extended to the cingulate gyrus, the precentral gyrus and the supplementary motor area, the left/right angular gyrus, bilateral putamen and thalamus, bilateral precuneus, and the right/left cerebellum at the group level.

**TABLE 1.** Demographic and questionnaire data from the three tested groups. From left to right: Mean age (and standard deviation SD), Gender proportion (male/female), Education type (University offering academic programs/Higher education schools offering professional programs), Mean scores on handedness, eyedness, earedness and footedness rated in the questionnaire. A distinction is made between the Optimal Viewing Position (OVP) and Text reading task, as a few right and left hemispheric (LH/RH) speech dominants had to be excluded from the latter task.

			Mean age (SD)	Gender (M/F)	Education (U/H)	Handedness	Eyedness	Earedness	Footedness
OVP	RH speech dominant	Left-handers (N = 17)	20,4 (2,2)	2/15	8/9	-2,22	-1,43	-1,19	-1,35
	LH speech dominant	Left-handers (N = 17) Right-handers (N = 15)	20,0 (2,0) 22,7 (2,8)	5/12 4/11	1/16 1/14	-2,49 2,68	-1,96 1,98	-1,72 2,05	-1,66 2,37
Text reading	RH speech dominant	Left-handers (N = 16)	20,5 (2,3)	2/14	7/9	-2,20	-1,42	-1,19	-1,31
	LH speech dominant	Left-handers (N = 13) Right-handers (N = 15)	20,2 (2,0) 22,7 (2,8)	4/9 4/11	1/12 1/14	-2,42 2,68	-1,83 1,98	-1,73 2,05	-1,33 2,37

*OVP results.* Figure 2 shows the 3-, 4-, and 6-letter OVP curves (hereafter OVP3, OVP4 and OVP6 respectively) for LH and RH speech dominants. Most importantly for the current issue, the linear component of fixation position interacted significantly with speech dominance [ $\chi^2(1) = 11.45, p < .001$ ] in the linear mixed effects (LME) modeling analysis, whereas the quadratic term did not [ $\chi^2(1) = 1.56, p = .21$ ]. The linear component tested whether the differences in naming latencies were due to differences at the word end/beginning, whereas the U-shaped quadratic component was used to examine the role of visual acuity (Brysbaert & D'Ydewalle, 1991). The slope of the OVP curve from the LH speech dominants increased 3.64 ms per letter fixated more towards the word end [ $\beta = 3.64, z = 4.49, p < .001$ ] whereas the slope of the RH dominants' OVP curve did not differ significantly from zero [ $\beta = -1.10, z = -0.93, p = .35$ ]. All other interactions did not reach significance ( $ps > .41$ ), including the interaction between speech dominance, the linearly defined fixation position and word length ( $\chi^2 < 1$ ). Differences in naming RTs while fixating at the word beginning versus the word end when comparing LH and RH dominants were thus found for 3-, 4-, and 6-letter words.

Main effects were found for (1) The intercept [ $\chi^2(1) = 5544.00, p < .001$ ], simply indicating that the mean naming RT was different from zero; (2) Speech dominance [ $\beta = 29.2, z = 2.41, p = .02$ ], with RH dominants being on average 29.2 ms faster at word naming than LH dominants; (3) Word length [ $\chi^2(2) = 12.37, p < .01$ ] with 3.94 ms slower naming RTs for OVP4 compared to OVP3 [ $\beta = 3.94, z = 1.09, p = .27$ ] and OVP6 being on average 22.26 ms slower than OVP3 and OVP4 [ $\beta = 22.26, z = 4.88, p < .001$ ]; and (4) The main effect of fixation position was marginally significant [ $\beta = 1.27, z = 1.76, p = .08$ ] but as described above, the fixation position factor significantly interacted with speech dominance.

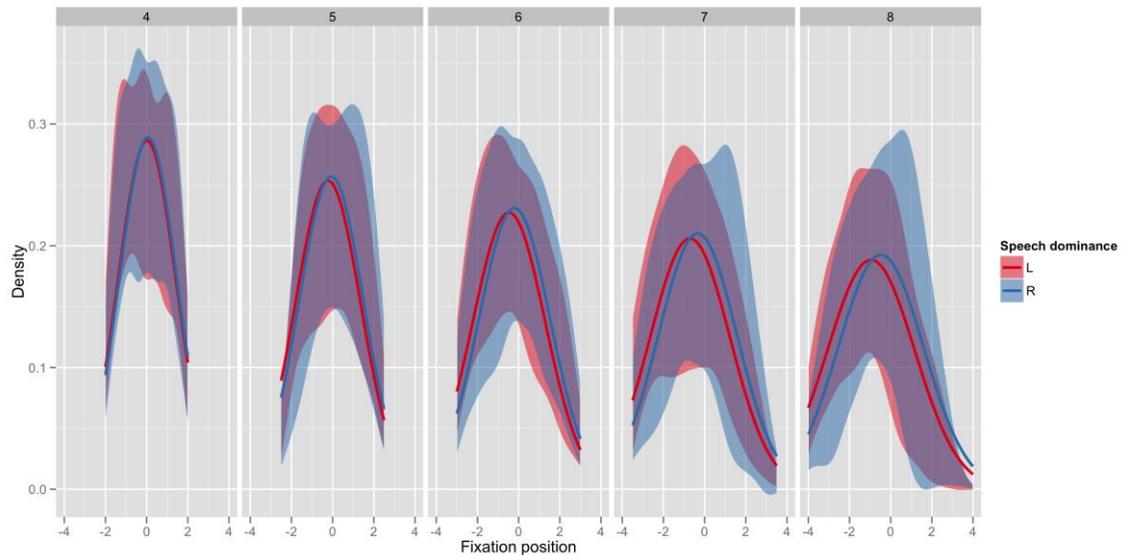


**Figure 2.** Optimal viewing position curves for left hemisphere speech dominants (L, left panel) and right hemisphere dominants (R, right panel) for 3- (lower panel), 4- (middle panel), and 6- (upper panel) letter words. The x-axis shows all possible fixation positions relative to the word centre (0); the y-axis displays the mean naming reaction times (RTs) with 95% confidence intervals (CIs) based on the regression weights (i.e. the value of the CIs) and variance-covariance matrices (i.e. length of the CIs) of the fixed effects. The black circles represent the fitted data, the red lines show the observed mean RTs.

Handedness was collapsed across the LH speech dominants in the above described results. As a control, we reran the LME analysis with 3 levels for the factor speech dominance: LH dominant left-handers, LH dominant right-handers and RH dominant left-handers. Again, the linear fixation position factor interacted with speech dominance [ $\chi^2(2) = 12.01, p < .01$ ], whereas the quadratic component did not [ $\chi^2(2) = 1.79, p = .41$ ]. The word beginning and word end naming times interacted with the speech dominance of LH dominant left-handers versus RH

dominant left-handers [ $\beta = 5.16, z = 3.24, p < .01$ ], with the speech dominance of LH dominant right-handers versus RH dominant left-handers [ $\beta = 4.35, z = 2.68, p < .01$ ], but not with the speech dominance of LH dominant left-handers versus LH dominant right-handers [ $\beta = .81, z = .51, p = .61$ ]. Similar to the above described analysis with two groups for speech dominance, the slope of the OVP-curves from LH dominants increased towards the word end [ $\beta = 4.04, z = 3.64, p < .001$  for left-handers;  $\beta = 3.23, z = 2.78, p < .01$  for right-handers], but the slope of the OVP curve from RH dominants did not reach significance [ $\beta = -1.12, z = -.96, p = .34$ ].

*Text reading results.* Figure 3 shows the initial fixation position curves for the LH and RH speech dominant group. When fixating 4- to 8- letter words in texts, the eyes of participants landed on average 0.22 letters to the left of the word centre [ $\chi^2(1) = 34.59, p < .001$ ]. Most importantly for the current research question, the mean landing position showed a main effect of speech dominance [ $\chi^2(1) = 14.13, p < .001$ ]. LH speech dominants landed 0.34 letters to the left of the word centre [ $\beta = -0.34, z = -7.92, p < .001$ ] which was significantly away from the centre, compared to 0.11 letters to the left of the word centre in the case of RH speech dominants [ $\beta = -0.11, z = -2.03, p = .04$ ]. Speech dominance also interacted with the word length factor [ $\chi^2(1) = 9.84, p < .01$ ]. Both groups showed a main effect of word length, but it was more pronounced for the LH dominants compared to the RH dominants [ $\beta = -0.18, z = -7.68, p < .001$  and  $\beta = -0.09, z = -3.36, p < .001$  respectively]. A closer look at the fixations for different word lengths revealed that LH dominants fixated significantly more to the left of the word centre for long words [ $\beta$  – values of 0.02, -0.16, -0.34, -0.51 and -0.69 for 4- to 8-letter words respectively], whereas the initial fixation positions of the RH dominants remained very much the same [ $\beta$  – values of 0.07, -0.02, -0.11, -0.20 and -0.29 for 4- to 8-letter words].



**Figure 3.** The initial landing curves for the left hemisphere (L, in red) and right hemisphere (R, in blue) speech dominant participants in the text reading task. Initial landing positions were analyzed with linear mixed effects modeling, taking into account speech dominance, word length and eyes measured as fixed effects. A random intercept and random slope for word length were entered for eyes and participants; For items, random intercepts and random slopes for speech dominance and eye were used. The analysis of text reading was limited to words from 4 to 8 letters, as these were the most common and the most interesting. The curves are based on the mean and standard deviation of a normal distribution obtained from a non-linear mixed effects model with the following specifications: Dependent variable = the frequency of landing positions relative to the word centre 0 for each participant and eye collapsed over items (i.e. the densities on the y-axis); Fixed factors = speech dominance, eye and word length. The solid lines on each panel show the fitted results, the shaded regions display the 95% confidence intervals based on the observed densities. These are larger for the right dominant group because of their smaller number.

We further observed the following significant main effects and interactions, which are mentioned for completeness: (1) A main effect of eye, with the right eye fixating on average 0.15 letters more to the left than the left eye [ $\chi^2(1) = 14.91, p < .001$ ]; (2) A main effect of word length, with fixations landing on average 0.13 letters more to the left per additional letter [ $\chi^2(1) =$

39.79,  $p < .001$ ]; (3) An interaction between eye and word length, with an increasing binocular disparity for longer words [ $\chi^2(1) = 13.29$ ,  $p < .001$ ].

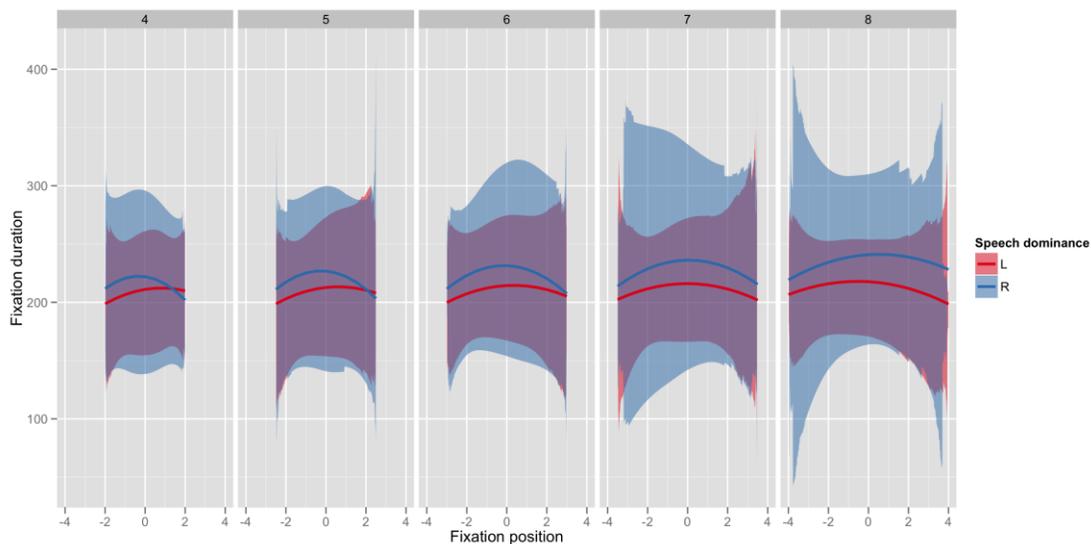
To control whether speech dominance and not handedness influenced the initial landing positions, the analysis was rerun with a three-level speech dominance factor. Exactly the same effects were found compared to the analysis with two levels. The initial fixation positions differed between the three groups [ $\chi^2(2) = 13.95$ ,  $p < .001$ ]. When contrasting the groups, the mean fixation positions of the LH dominant left-handers did not differ from those of the right-handers [ $\beta = -0.02$ ,  $z = -0.23$ ,  $p = .82$ ], but both the left-handers and the right-handers landed more towards the word beginning than the RH dominant left-handers [ $\beta = -0.24$ ,  $z = -3.35$ ,  $p < .001$  and  $\beta = -0.22$ ,  $z = -3.10$ ,  $p < .01$  respectively]<sup>1</sup>.

Third, we entered the speech dominance factor as a continuous measurement in this analysis instead of dividing the participants into two discrete groups (LH versus RH speech dominants). In addition, the LIs calculated on the basis of the fMRI lexical decision task were included. Main effects and interactions did not change compared to the pattern found when speech dominance was included as a discrete factor. Most importantly, speech dominance still had an influence on the initial fixation position [ $\chi^2(1) = 13.83$ ,  $p < .001$ ], but reading dominance could not predict the fixation pattern [ $\chi^2(1) = 2.18$ ,  $p = .14$ ]. In other words, the lexical decision LIs did not contribute to the variance of fixation positions when combined with a continuous measure of speech dominance.

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<sup>1</sup> Note that handedness is closely related to eye dominance, i.e. all right- and left-handed LH speech dominants had right/left eye dominance respectively and only three left-handed RH speech dominants had right eye dominance. When running the fixation position analysis with these three groups (excluding the three subjects with crossed hand/eye dominance), only speech dominance and not eye dominance (similar to hand preference) revealed different eye landing positions [Overall group effect:  $\chi^2(2) = 11.56$ ,  $p < .01$ ; Left vs. right eye dominant LH speech dominants:  $\beta = -0.005$ ,  $z = -0.14$ ,  $p = .89$ ; Left- and right eye dominant LH speech dominants vs. RH speech dominants:  $\beta = -0.20$ ,  $z = -3.25$ ,  $p = .001$  and  $\beta = -0.21$ ,  $z = -3.50$ ,  $p < .001$  respectively].

In the final analyses, we investigated the influence of the initial fixation positions of LH and RH dominants on fixation duration. Of most interest for the current study, we found a three-way interaction between the linear component of fixation position, speech dominance and word length [ $\chi^2(1) = 14.38, p < .001$ ]. Figure 4 shows that LH dominant subjects fixated words more shortly at the word beginning than at the word end, whereas the optimal viewing position of the RH dominant subjects was situated more towards the word end, in line with the OVP data. The interaction was however only present for the shortest word lengths, from 6-letter words on it no longer reached significance [4-letter words:  $\chi^2(1) = 10.92, p < .001$ , 5-letter words:  $\chi^2(1) = 6.77, p < .01$ , 6- to 8-letter words:  $ps > .14$ ].



**Figure 4.** The three-way interaction between Initial fixation position (on the x-axis, displayed around the word centre 0; The linear and quadratic term are combined in these curves), Speech dominance (Left (L, in red) and Right (R, in blue) hemisphere dominants) and Word length (6- and 8- letter words in the upper panel; 4- to 8- letter words from left to right in the lower panel) in the text reading task. The y-axis shows the mean fixation duration in milliseconds. The solid lines represent the fitted curves, the shaded regions display the 95% confidence intervals based on the observed fixation durations. Note that the confidence intervals expand towards the word extremes because of the smaller number of fixations at those positions.

In addition, the following main and interaction effects were significant and are mentioned for completeness: (1) A significant intercept [ $\chi^2(1) = 2246.47, p < .001$ ] with a mean fixation duration of 223 ms; (2) Fixation position modeled as a quadratic term was significant [ $\chi^2(1) = 30.81, p < .001$ ] with longer fixation durations around the word centre than at the extremes; (3) Fixations lasted on average 3.18 ms longer when the word length increased with one letter [ $\chi^2(1) = 9.37, p < .01$ ]; (4) A significant interaction between the linearly modeled fixation position variable and eye [ $\chi^2(1) = 4.10, p < .05$ ], but neither slope was significantly different from zero when tested separately for each eye [ $ps > .29$ ]; (5) The inverted U-shape of the fixation positions was more pronounced for shorter than for longer words, but reached significance for all word lengths [ $\chi^2(1) = 7.54, p < .01$ ]; (6) LH dominants did not show a word length effect [ $\beta = 1.64, z = 1.45, p = .15$ ], in contrast to the RH dominants [ $\beta = 4.71, z = 2.17, p < .001$ ], resulting in a speech dominance by word length interaction [ $\chi^2(1) = 4.05, p < .05$ ].

## Discussion

Previous studies indirectly pointed at the importance of interhemispheric communication during reading. Information exchange between the LH and RH is supported by an increase of white matter fibers in the splenium of the corpus callosum when acquiring literacy (Carreiras et al., 2009) and neuroimaging studies investigating the time course of reading indicate that information transfer is enhanced in the early stages of the visual word recognition process (e.g. Doron et al., 2012). The current study is the first to examine the need for interhemispheric communication during central word reading under strictly controlled methodological settings and in healthy subjects. We found that speech lateralization influences the naming latencies of words presented in isolation: The OVP of atypical right lateralized subjects is situated more towards the

word end compared to the optimal position for typical left lateralized readers, minimizing the time cost caused by transferring letters to the dominant hemisphere. Moreover, fixation behavior seems to be optimized according to hemispheric functional asymmetry as right dominants preferred to fixate more rightwards than left dominants.

*Speech lateralization influences word naming in isolation*

LH dominants were faster when fixating at the word beginning compared to the word end, whereas RH dominants were faster when they were fixating more towards the word end. The difference between the groups was captured by the linear component of fixation position. A difference in the quadratic trend would have meant that the two groups differ in terms of visual acuity (Brysbaert & D'Ydewalle, 1991). The effect of speech dominance was equivalent for three-, four- and six-letter words.

A closer look at Figure 2 suggests that the asymmetry in the OVP curve seems to be smaller for RH dominants than for LH dominants, in line with the facts that words are read from left to right and that word beginnings are more informative for word identification than word ends (Brysbaert & Nazir, 2005). Both factors favor fixations at the word beginning and may partially compensate for the interhemispheric transfer cost RH dominants experience when fixating there. LH dominants do not benefit from compensating factors and, therefore, show a high processing cost for fixations on the last letters.

Another remarkable finding in the data is that the RH dominant group was faster compared to the LH dominants, but there is no reason at present to assume that this would alter the conclusion that central word reading requires interhemispheric communication. Brysbaert (1994) and Hunter, Brysbaert and Knecht (2007) also found an interaction between laterality

group and fixation position, but in their OVP studies the RH dominants named the words more slowly relative to the LH dominants. Moreover, the faster naming times did not result in shorter fixation durations in the text reading task. Future research is needed to decide whether (a)typical speech dominance influences reading times. Previous studies found that the degree rather than the direction of functional asymmetries determines language performance, even though it is still unclear whether the correlation is positive or negative (see Boles & Barth, 2011 for a review). As those studies mainly used behavioral visual half field tasks as lexical asymmetry indicators instead of LIs based on neuroimaging and we only included clearly lateralized subjects, the conclusions cannot be compared directly. Additional large samples of subjects with clear or unclear (a)typical lateralization patterns are therefore needed. Note also that almost all LH speech dominant subjects studied at Ghent University aiming to obtain an academic degree, whereas about half of the RH speech dominant group was recruited from a higher education institute offering professional programs (Table 1). Education type however did not predict naming speed (e.g. mean RT university RH speech dominants = 446 ms, SD = 46 ms; mean RT higher education RH speech dominants = 441 ms, SD = 33 ms in the OVP task;  $t < 1$ ).

The influence of speech lateralization on word naming demonstrates that foveal information is initially split when it is sent to the cerebral cortex (Ellis & Brysbaert, 2010). If the entire fovea projected bilaterally, we would not have observed differences between the laterality groups for the stimulus materials we used. There remains a possibility of a two-letter overlap in central vision, as words of this length were not tested. However, the impact of such an overlap on the reading of Indo-European alphabetic languages is negligible, as two-letter words account for less than 1% of the words in these languages (Keuleers, Brysbaert & New, 2010). In addition, many of them are function words, which are typically skipped in reading.

### *Speech lateralization influences word reading in context*

Given the high processing cost for fixations on the last letters of words in LH dominants, we expected that they fixate words less on these positions in text reading to optimize information uptake and reduce interhemispheric transfer costs. To examine this issue, we asked LH and RH dominant participants to read texts while their eye movements were monitored. RH dominants indeed fixated more rightward than LH dominants. The difference was small, but very stable. The fact that RH dominants did not fixate even further into the words arguably has to do with other factors influencing eye movements in reading (such as the information distribution in words, the reading direction, and the extraction of parafoveal information; Rayner, 2009; Vitu, O'Regan & Mittau, 1990).

Further analyses ensured that speech lateralization was the critical factor and not lateralization of activity in the vOT region even though the current tasks involved silent reading. This agrees with the finding that brain activity was more lateralized in the inferior frontal gyrus than in vOT (Van der Haegen et al., 2012). It can thus be assumed that the lexical decision LIs could not differentiate the reading behavior of our participants because the cortical activation is too bilaterally distributed to have an effect on the initial fixation positions. Also note that our participants were first recruited based on the speech dominance LIs. We predict that the preferred landing positions can be explained by the reading LIs in a sample of more extremely lateralized subjects during a lexical decision task, because it can be expected that one hemisphere will also be clearly dominant for speech during a silent word generation task. The difference in hemispheric dominance between the groups would then be distinct enough to capture the shift in preferred fixation position even though our data suggest that a minority of the population will be strongly lateralized for reading.

Finally, the differences in landing distribution were not offset by differences in fixation duration. In line with the OVP findings, the RH dominants had slightly longer fixations on the first letters of words whereas the LH dominants were slower for fixations on the last letters, although the effects were small, suggesting that speech dominance primarily affects the landing position in words. In eye movement research, a distinction is made between when and where decisions (fixation durations vs. fixation positions), with the former being primarily influenced by language factors, such as word frequency and context predictability, and the latter by low-level factors such as word length and launch site (Rayner, Binder, Ashby & Pollatsek, 2001). We can now add speech dominance as a non-linguistic determinant influencing the landing position in words.

#### *Handedness cannot predict laterality consequences*

Further analyses indicated that handedness did not influence the OVP curves or the initial landing positions, as the data of both left- and right-handed LH dominant subjects differed from those of the RH dominants, whereas the optimal fixation positions were comparable for the LH dominant groups. This illustrates that consequences of lateralized cognitive functions should be investigated by comparing LH to RH (speech) dominant subjects, and not only by including left-handers as a more atypically lateralized group. This is in line with our previous study assessing the ear advantage of left- and right-handers in a dichotic listening task (Van der Haegen, Westerhausen, Hugdahl & Brysbaert, 2013). Participants were asked to report which of two consonant-vowel syllables presented in the left or right ear they heard best. Left-handers and right-handers with left-hemisphere speech dominance showed a right ear advantage, in line with the preponderance of the contralateral auditory pathways from the ear to the brain. Left-handers

with right hemisphere speech dominance favored the left ear stimuli. Similar to the speech perception or phoneme recognition asymmetries that could be related to speech dominance but not to handedness, we can conclude from the current results that differences in reading are associated with speech dominance but would not have been observed when only taking handedness into account.

### *Implications of the current results*

Our results showed that foveal information is initially split on its way to the visual cortex and needs to be reintegrated through interhemispheric communication when naming words in isolation or reading texts. This agrees with the increase of white matter in the splenium, the part of the corpus callosum involved in the transfer of visual form information, when people learn to read (Carreiras et al., 2009). However, we do not claim that the observed need for interhemispheric communication is solely driven by reading, as other visual recognition functions (e.g. object recognition) may also influence the way our hemispheres integrate left and right visual field information. The integration typically happens swiftly and does not impose major limitations. Indeed, it has been hypothesized that impairment in interhemispheric communication may be a factor involved in developmental dyslexia (Dougherty et al., 2007). Finally, our results also question the bilateral fovea explanation of macular sparing in hemianopia (i.e. the preservation of central vision on both sides of fixation despite unilateral damage to the occipital cortex). According to one view this is due to the bilateral projection of foveal information. The current findings are however in line with the alternative explanation that macular sparing is a consequence of spared tissue in the affected hemisphere (Lavidor & Walsh, 2004; Leff, 2004).

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