The mechanisms underlying the interhemispheric integration of information in foveal word recognition: Evidence for transcortical inhibition

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Abstract

Words are processed as units. This is not as evident as it seems, given the division of the human cerebral cortex in two hemispheres and the partial decussation of the optic tract. In two experiments, we investigated what underlies the unity of foveally presented words: A bilateral projection of visual input in foveal vision, or interhemispheric inhibition and integration as proposed by the SERIOL model of visual word recognition. Experiment 1 made use of pairs of words and nonwords with a length of four letters each. Participants had to name the word and ignore the nonword. The visual field in which the word was presented and the distance between the word and the nonword were manipulated. The results showed that the typical right visual field advantage was observed only when the word and the nonword were clearly separated. When the distance between them became smaller, the right visual field advantage turned into a left visual field advantage, in line with the interhemispheric inhibition mechanism postulated by the SERIOL model. Experiment 2, using five-letter stimuli, confirmed that this result was not due to the eccentricity of the word relative to the fixation location but to the distance between the word and the nonword.

Keywords: interhemispheric inhibition; laterality; split fovea theory; word recognition

Introduction

The human cerebral cortex is divided in two largely separated hemispheres. For auditory word recognition, this division is not very consequential, given that the sensory input is conveyed simultaneously to the left and the right brain half. As a result, both hemispheres receive all information and develop their own auditory word recognition capabilities (Hickok & Poeppel, 2007). In addition, the two word centers are likely to communicate with each other and to integrate their information in so-called transcortical cell assemblies (Endrass, Mohr, & Pulvermüller, 2004; Pulvermüller & Mohr, 1996). According to this view, the mental representations of spoken words consist of bilaterally integrated groups of cells encoding and storing the information related to words, possibly with a greater contribution of the hemisphere that controls the speech output than from the language non-dominant hemisphere (Shtyrov, Osswald, & Pulvermüller, 2008).

It is tempting to assume that very much the same organization evolved in the visual system as in the auditory system, so that the interhemispheric dynamics of visual word recognition are the same as those of auditory word recognition. However, such a parallel structure would only be possible if it was present already before humans started to read. Text reading is such a recent skill that we can hardly expect environmental selection to have played a major role (yet). Up to a century ago there was no need to have rapid visual word recognition skills: Only a few people could read and they did so by their own choice, not out of necessity. So, there have been very few pressures in human history to select reading-advantageous brain organizations.

One of the main differences between the visual and the auditory system is that auditory receptors can pick up information from anywhere in the environment, whereas visual receptors have a limited receptive field. As a result, many animal species have their eyes laterally, so that the largest possible visual field can be covered. In these species each eye projects to the contralateral brain half, so that stimuli in the right half of the environment are initially sent to the left cerebral hemisphere (LH) and information in the left half of the environment to the right hemisphere (RH), just like in

the somatosensory system and the motor system. In all these systems, unlike in the auditory system, receptors not only convey information about the nature of the stimulus but also about the location.

In primates and a few other species evolutionary pressures resulted in a gradual shift of the eyes towards the frontal part of the face, so that the visual fields started to overlap. It is assumed that two of the advantages of binocular overlap are increased visual acuity and depth perception (Heesy, 2009). In binocular vision, the two eyes receive slightly different information about the visual environment, from which the distance to an object can be computed, making it easier, for instance, to perceive the object against a more distant background. Overlapping visual fields, however, cause a problem when the two eyes send information to opposing cerebral hemispheres, because in that case there is no clear distinction between left and right space any more, hindering fast and efficient responding to stimuli in the surroundings. As a result, the growing overlap of the visual fields was accompanied by a decussation of the optic tract and an increasing part of the tract sending information to the ipsilateral brain half. In particular, for humans this meant that axons from the temporal hemiretina no longer crossed at the optic chiasm and all stimuli presented to the right of the fixation location (i.e. in the right visual field, RVF) were transmitted to the LH and stimuli presented in the left visual field (LVF) were transmitted to the RH (see Figure 1).
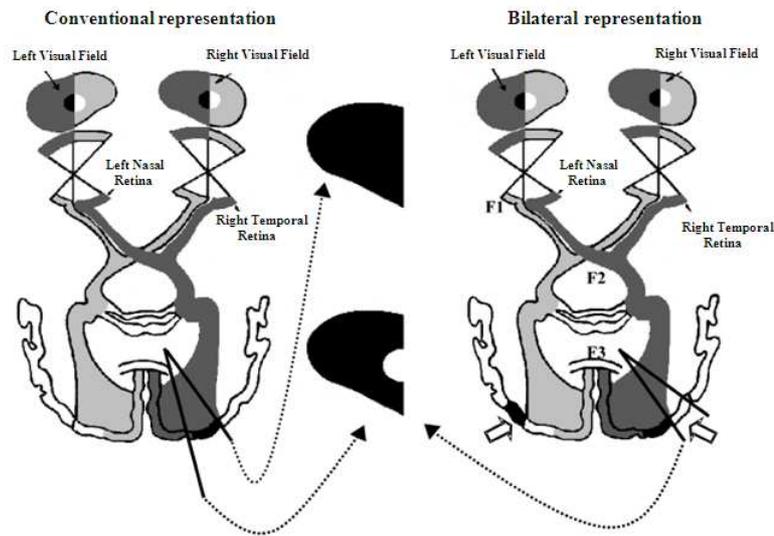
FIGURE 1. In the human visual system, information from the LVF is sent to the RH, whereas information from the RVF is projected to the LH, due to the crossing of the fibers coming from the nasal hemiretina at the optic chiasm. The axons from the temporal hemiretina do not cross. The left panel displays the split fovea theory with the left half of the fovea projecting to the right cerebral hemisphere only; the right panel shows a bilateral visual system with information from the left hemifovea sent to both the right and the left hemisphere. (Source: Leff, 2004)

The big question for reading research is whether in humans the above evolutionary changes have resulted in a sharp division between LVF and RVF, or whether there is a small part in the center of the visual field to which the partial decussation of the optic fibers does not apply or for which organisms have been selected with bilaterally projecting fibers.[1] This issue has become known as the choice between a split fovea (SF) model and a bilaterally projecting fovea (BPF) model. According to proponents of the BPF model, information presented in the region with the highest visual acuity, the fovea, is projected bilaterally (i.e., to LH and RH at the same time). Given that the fovea has a diameter of 3° of visual angle and given that under normal viewing conditions there are 3-4 letters per degree of visual angle, according to the BPF model this means that all information of centrally fixated words is immediately available to both hemispheres. The idea of a bilaterally projecting fovea is appealing, because for all reading purposes it gives the visual system the same organization as the

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[1] Remember that binocular summation is also believed to result in better visual discrimination (Heesy, 2009), so that bilateral projection of foveal vision would lead to a loss of visual acuity unless this is compensated by a higher number of receptors or by bilaterally projecting receptors.

auditory system: Information is simultaneously transmitted to both cerebral hemispheres, which can develop their own word recognition capacities and further integrate their information in transcortical cell assemblies (e.g., Pulvermüller & Mohr, 1996). This is interesting for reading because here the stimuli (words) succeed each other rapidly in time, are so detailed that they need high acuity vision to be processed, and are so rich in information that they require the correct alignment of the left and right part to be understood. However, as indicated above, these pressures are so recent that they are unlikely to have had an influence on the organization of the visual system (yet).

Indeed, a growing number of studies suggests that, certainly for the fast, fine-grained perceptual distinctions needed for letter recognition, there is little evidence for a bilaterally projecting fovea (for a recent summary, see Ellis & Brysbaert, 2010). This raises the question how visual word processing can be implemented in a visual system with a split fovea. Thus far, only two proposals have been made: one by Shillcock, Ellison, and Monaghan (2000), and one by Whitney (2001). Shillcock et al. (2000) hypothesized that both hemispheres start by independently processing the part of the word they receive and then each generating possible word candidates, which combine at a later stage to produce the correct alternative. However, previous studies found evidence against this hypothesis (McCormick, Davis & Brysbaert, in revision; Van der Haegen, Brysbaert & Davis, 2009). For instance, Van der Haegen et al. (2009) made use of the finding that high-frequency words inhibit form-related low-frequency words (Davis & Taft, 2005). A low-frequency word like "axle" is more difficult to recognize than a control word, because it has a high-frequency neighbor ("able") acting as a strong competitor in the recognition process. Van der Haegen et al. reasoned that, if Shillcock et al.'s (2000) late-integration account is true, competitors would be particularly effective if they are part of the candidates activated in one hemisphere. So, the authors selected six-letter words that did or did not have higher frequency hemifield competitors, depending on where in the word they were fixated. For example, the word *income* has the LVF competitor *indeed* and the RVF competitor *become*, when it is fixated between the second and the third letter (*in-come*). However, when the word is fixated between the fourth and the fifth letter (*inco-me*), there is no LVF competitor any more, as the letter string *inco-* is unique for English six-letter words. Contrary to the

prediction, however, Van der Haegen et al. failed to find any evidence for an influence of hemifield competitors on word processing efficiency.

An alternative explanation for reading with a split fovea was proposed by Whitney (2001) in her SERIOL model. According to this early-integration account, visual word recognition involves the integration of all the information in the language dominant LH before word processing starts.[2] This requires the temporary inhibition of the letter information presented in RVF (i.e., the end of a centrally fixated word), until the information from the LVF (the word beginning) has been transmitted to the LH. Or as Whitney (2001, p. 225) formulated it: "Feature information from the RH is […] transferred to the LH. We assume that the features from the RH inhibit the activations of the LH features, such that the feature activations of the LH's leftmost letter are lower than those of the RH's rightmost letter. As a result, an activation gradient across all features is created in the LH that is strictly decreasing by left-to-right location …"

Although inhibition has been introduced before as a mechanism of interhemispheric communication (see Chiarello & Maxfield, 1996, for a review), there is very little empirical evidence for the specific process suggested by Whitney (2001). The only evidence we could find were two studies by Nazir, Ben-Boutayab, Decoppet, Deutsch, and Frost (2004; Experiments 3 and 4, Roman script). In the first of these studies, the authors briefly presented 5-character strings left or right of the fixation location (i.e., stimuli were presented in such a way that participants either fixated on the first or the last character of the string). Four of the characters were the letter x; the other character was a random letter. Participants had to identify the random letter. In this experiment, Nazir et al. observed the expected RVF advantage (i.e., participants were more likely to identify the letter when they were fixating on the first letter than when they were fixating on the last letter). In the second study, Nazir et al. replaced the 5-character strings by a 9-character string fixated centrally. Again, all but one of the characters were the letter x; participants had to identify the random letter. Under these viewing conditions, Nazir et al. observed that participants were better at identifying the letter in the first part of the character string (i.e., in LVF) than in the last part (RVF), in

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[2] Over 95% of right-handers and 75% of left-handers are LH dominant. Unless otherwise stated, in this text we assume the LH to be language dominant.

line with the idea that verbal information in LVF inhibits information in RVF if both are connected to each other.

In the experiments below we further investigated whether we could find evidence for the temporary inhibition of RVF word information by letters presented in LVF. In particular, we pitted predictions of BPF and SERIOL against each other in a word naming task. According to the BPF model, words presented in LVF are named as fast as words presented in RVF as long as they remain in foveal vision. The reason for this prediction is that words presented in the left part of foveal vision are simultaneously transmitted to LH and RH and thus can easily be named by the language dominant LH (which is required for speech production; Hunter, Brysbaert, & Knecht, 2007; Knecht et al., 2000). However, as soon as the first letter of a word presented in LVF crosses the foveal border, interhemispheric transfer from RH to LH is required and there will be an interhemispheric transfer time cost. Different predictions are made by SERIOL. According to this model a word attached to uninformative letters should be named faster when it is situated to the left of the letters (as in *film*trep) than when it is to the right (trep*film*). The reason for this is that letters before a word will inhibit the processing of the word, even though these letters are irrelevant. Only when there is enough space between the word and the uninformative letters, so that both stimulus parts are perceived as separate entities, will a word to the right of a letter string be named faster than a word to the left of a letter string, because it enjoys the RVF advantage associated with direct access to the language dominant LH. In other words, for the BPF account the distance between the first letter of the word in LVF and the fixation location is the critical variable, whereas for the SERIOL account it is the distance between the last letter of the letter string in LVF and the first letter of the word in RVF that matters.

To test the predictions, we set up two naming experiments, in which words were presented together with meaningless nonwords. The words were presented either to the left or to the right of the fixation position, and the nonwords were presented on the opposite side. In addition, we manipulated the distance between the word and the nonword: The stimuli were either attached to each other (but clearly distinct on the basis of their color) or there were blank spaces between them. According to the SERIOL

model we should find a LVF advantage for words attached to nonwords and an increasing RVF advantage when the distance between the word and the nonword grows. In contrast, according to the BPF model we should find no difference between words in LVF and RVF as long as the words are in foveal vision, and we should observe a RVF advantage as soon as the first letter of the word in LVF is pushed into parafoveal vision. To disentangle the effects of "distance between the word and the nonword" and "distance of the leftmost letter in LVF from the fixation location", we presented words of four letters (Experiment 1) and words of five letters (Experiment 2). Both could be presented within the foveal region, but the former allowed the distance between the stimuli to be larger even though the distance from the leftmost letter to the fixation point was the same. We first present the data of the four-letter words.

Experiment 1

In this naming experiment, 4-letter words were presented together with 4-letter nonwords. For example, the Dutch word *berg* [mountain] was combined with the nonword *nust*. In a first condition both stimuli were attached to each other (i.e., *berg*nust[3] or nust*berg*). In a second condition there were two blank spaces between the word and the nonword (i.e., *berg* nust or nust *berg*). Finally, in the third condition there were four blank spaces between the stimuli. All stimuli were presented within the fovea (i.e., 3° of central vision) and appropriate fixation was ensured with the use of an eye-tracking device.

Method

Participants

The analyses are based on 15 right-handed students (3 male, 12 female; mean age: 21.8) from Ghent University. They all had normal or corrected-to-normal vision, were native Dutch speakers, were free from any known reading impairments, had no color

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[3] In this paper, target stimuli will be italicized. However, all stimuli were presented in standard font during the experiment. Only their color differed.

deficiency, and were paid for their participation. As reported in the Results section, the data from 4 other participants were discarded because of deficient fixation quality.

Participants started by completing a questionnaire about their preferences for handedness (Oldfield, 1971), eyedness, earedness and footedness (Porac & Coren, 1981). They were asked to choose a number between -3 and -1 to indicate their degree of left side preference, and a number between +1 and +3 to indicate their degree of right side preference (Brysbaert, 1994). They also performed the Miles (1930) eye-dominance test, in order to have an indication of eye dominance that is not contaminated by handedness. In the Miles test, participants are asked to put their hands together and to form a small opening between them. Then, they have to look through the opening to a distant object and thereby alternate between binocular and monocular viewing. The eye that sees the target at the same place when viewing with one and two eyes is defined as the dominant eye. Only students that were right-handed and showed right eye dominance based on the Miles test were accepted for participation (the same was true for Experiment 2). Table 1 shows the mean ratings reported in the questionnaire.

TABLE 1

Means and SDs as reported by the fifteen participants in Experiment 1 in the questionnaire about handedness, eyedness, earedness and footedness.

Measure	Mean	SD
Hand	2,55	0,99
Eye	1,13	2,09
Ear	1,22	1,78
Foot	1,97	0,99

Note. N = 15. Scale: -3 = strong left preference; 3 = strong right preference

Stimuli

The stimuli consisted of 240 monosyllabic words and 240 monosyllabic nonwords. Words and nonwords were four letters long. Half of the words had a structure of consonant-vowel-consonant-consonant (e.g., *berg*, meaning mountain), the other half

had a structure of consonant-consonant-vowel-consonant (e.g., *vlag*, meaning flag). They were matched pairwise with the nonwords according to consonant-vowel structure (word-nonword pairs had the same structure), bigram frequency and neighborhood size (ps > .22). The words and their estimates were generated from the CELEX database (Baayen, Piepenbrock, & Van Rijn, 1993) by using the Wordgen software (Duyck, Desmet, Verbeke, & Brysbaert, 2004).

As each word was presented together with a nonword throughout the experiment, four restrictions were made to ensure the comparability of the 8-letter stimuli formed by the combination word-nonword (e.g., *berg*nust) and the combination nonword-word (e.g., nust*berg*): (a) the letters at the first five, six and seven positions and at the last five, six or seven positions of the 8-letter words did not form a Dutch, French, or English word[4] (e.g., *berg*n, *berg*nu, *berg*nus, *g*nust, *rg*nust and *erg*nust are all non-existing words; the same is true for nust*b*, nust*be*, nust*ber*, t*berg*, st*berg* and ust*berg*), (b) the nonword started with a different letter than the word to avoid effects due to the nonword onset (e.g., *berg***n**ust instead of *berg***b**ust), (c) the summated type bigram frequency of the two combinations (e.g., *berg*nust and nust*berg*) were matched (p = .21; mean summed bigram frequency of the word-nonword pairs = 43,256, mean summed bigram frequency of the nonword-word pairs = 43,415), (d) the orthographic neighbourhoodsize of the 8-letter stimuli (e.g., *berg*nust and nust*berg*) were matched (p = .25; mean N of the word-nonword pairs = 0.03, mean N of the nonword-word pairs = 0.05). To make the distinction between words and nonwords clear, words were presented in yellow (RGB 255, 255, 0) against a dark blue background (RGB 0, 0, 100), whereas nonwords were presented in white (RGB 255, 255, 255). In addition, we made sure that the transition between the word and the nonword was very clear (whenever possible, we used illegal sequences of letters in the transition from the word to the nonword). All stimuli were presented in lowercase.

Each word-nonword pair was presented in all 6 conditions to make sure that none of our effects was a confound of the stimuli used in a particular condition. Figure 2

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[4] Most Belgian students are proficient in French and English. Hence, influence of existing words in these languages was avoided.

shows an example of a stimulus in each of the six conditions. The full list of stimuli can be found in the Appendix.
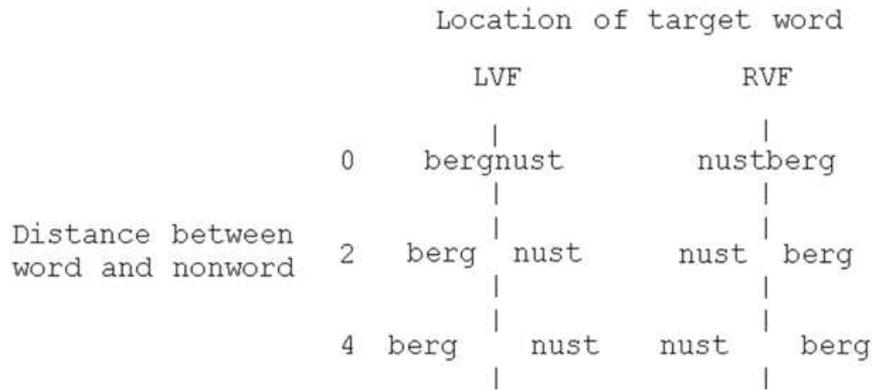
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                                Location of target word

                            LVF                     RVF
                             |                       |
                     0    bergnust             nustberg
                             |                       |
   Distance between          |                       |
   word and nonword    2  berg | nust          nust | berg
                             |                       |
                             |                       |
                     4  berg    nust          nust    berg
                             |                       |
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FIGURE 2. Example of a stimulus in Experiment 1, for the word *berg* (presented in yellow in the experiment) and nonword nust (in white).

Design

There were three factors in this experiment: The location of the target word (2 levels: LVF or RVF), the distance between the target word and the nonword (3 levels: no space, two blank spaces, or four blank spaces), and list version (6 levels). All factors were treated as within-factors. The factor list version referred to the six Latin-square lists made to have each word-nonword pair appear once in each of the 6 location*distance conditions.

Apparatus

A SR Research Eyelink 1000 eye tracking device (Ontario, Canada) was used to record eye movements. Calibration and validation were carried out with a 9-point grid at the beginning of the experiment and after each break. Participants' fixation location was measured every millisecond. Eye movements were recorded from the moment the fixation lines appeared on the screen, but were analyzed only for the time window in which the stimulus was presented. Viewing was binocular, but eye movements were recorded from the dominant right eye only. Head movements were restricted by a chin

rest and a brace at forehead height, without discomforting the participants too much when giving vocal responses. A drift correction was carried out before each trial to control for inappropriate calibration.

Procedure

At the beginning of the session, instructions told the participants to name the yellow words on the screen. The importance of fixating between the two vertically aligned lines in the centre of the screen from the moment they appeared was emphasized. A drift correction was administered at the beginning of the trial, followed by a blank screen during 1000 ms. The stimulus appeared 400 ms after the presentation of the central fixation lines. The position of the word and nonword stimuli changed from trial to trial and depended on the condition. After a presentation duration of 200 ms, the stimulus between the vertical lines disappeared, but the fixation lines remained on the screen until a response was registered by the voice key or until 5000 ms elapsed.

Stimuli were presented in Courier New font, size 15. The CRT display was placed at a reading distance of 110 cm, so that each letter subtended .23°. As such, the maximum region of stimulus presentation on either side of the fixation gap was 1.5 degrees of visual angle (i.e. when there were four blank spaces between the word and the nonword).

Filling in the informed consent and questionnaire, giving instructions, setting up the eyetracking device and presenting all practice and experimental trials took three sessions of approximately 45 minutes. Two lists were presented in each session. There was a time delay of at least half an hour between two sessions in order to avoid fatigue effects. The practice phase was administered at the beginning of each list and contained twelve trials (two of each of the six conditions) which did not return in the experimental phase.

Results

Prior to the analyses of the behavioral data, the stability of eye fixations during the 200 ms stimulus presentation time was checked. Four participants were dropped on the basis of these data, as they made a second fixation on more than 60% of the trials[5].

For the remaining fifteen participants, the analyses were restricted to the trials in which only one fixation was registered during the stimulus presentation and participants were fixating within an area of at most 1 letter position (i.e. 0.23°) on either side of the fixation lines. We further excluded trials with incorrect responses (2.1%), RTs less than 200 ms or greater than 1500 ms, reaction times above or below 2.5 SDs a participant's mean RT (2.6%), and voice key failures (1.9%). Finally, data from 0.2 % of the trials were lost due to interruption of the experimental trials for recalibration. All in all, analyses were based on 43.3% of the trials.

There were not enough naming errors (2.1%) to run reliable error analyses. Therefore the analyses are limited to the reaction times. Naming times were around 600 ms, which is in line with the naming times found in other studies, so that we can safely conclude that the color and the way in which the words and the nonwords had been constructed, made it easy to isolate the word from the nonword.

Naming times were analysed with a repeated measures analysis of variance (ANOVA) with VHF (2 levels: LVF or RVF) and distance (3 levels: 0, 2 or 4 spaces between the word and the nonword) as independent variables. Whenever the assumption of sphericity was violated, Greenhouse-Geisser corrections are reported. The factor VHF did not reach significance [$F(1,14) < 1$]. We did observe a main effect of distance [$F(1.30,18.26) = 4.21$, $MSE = 570.25$, $p < .05$], with mean reaction times of 592 ms, 580 ms and 593 ms for distances of 0, 2 and 4 respectively. In addition, the VHF by distance interaction was significant [$F(1.68,23.49) = 31.24$, $MSE = 207.94$, $p < .001$]. Figure 3 shows the mean RTs for each condition. As can be seen, there was a LVF advantage when the word and the nonword were not separated [$t(14) = -3.03$, $p < .01$]. The VHF-

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[5] The remaining participants made one stable fixation during stimulus presentation on at least 80% of the trials. Mean fixation deviation of the group was 0.05 letters to the right of the fixation lines, with individual data ranging from 1.20 letters to the left to 1.14 letters to the right.

factor did not reach significance with a distance of 2 spaces [$t(14) = 1.24$, $p = .24$], but there was a significant RVF advantage when the stimuli were separated by 4 spaces [$t(14) = 3.33$, $p < .01$][6].

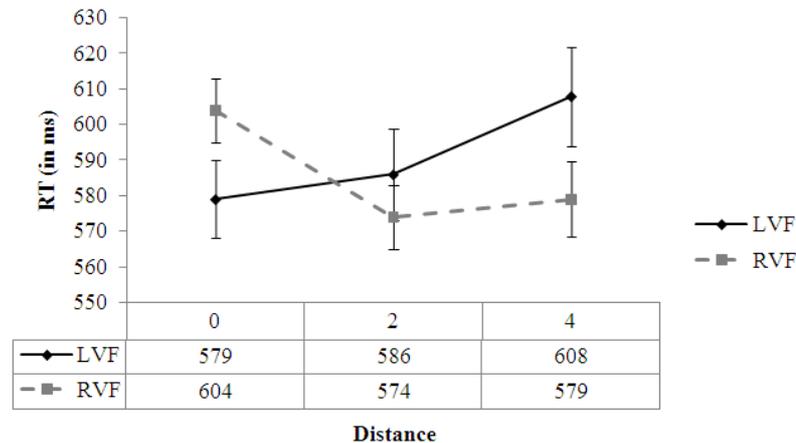|	0	2	4
LVF	579	586	608
RVF	604	574	579

Distance

FIGURE 3. Mean response times for the word targets in Experiment 1 in the LVF and RVF at the three possible distances.

Discussion

The data of Experiment 1 are in line with the predictions of the SERIOL model: When there is letter information to the left of the target word, the processing of the word is inhibited, even when this letter information is irrelevant for the task. This gives rise to a LVF advantage. As soon as there is enough distance between the letters and the target word, so that both are perceived as separate entities, words in RVF can fully profit from the direct connections to the dominant LH and show the RVF advantage typically observed in visual halffield (VHF) experiments with parafoveal vision.

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[6] When the analyses were run without restrictions to the fixation behavior, the LVF-RVF mean RTs were 582 ms – 607 ms [$t(14) = -3.57$, $p < .01$], 585 ms – 568 ms [$t(14) = 2.21$, $p < .05$], and 603 ms – 572 ms [$t(14) = 4.50$, $p < .001$] for space distances 0, 2 and 4 respectively. Although the VHF-factor did not reach significance in the 2 spaces condition in the restricted analyses with only 43.3% of the data, the reaction time pattern remained the same. The percentage of correct fixations and the finding that analyses without fixation restrictions only add noise to the data, are comparable to what was found by Van der Haegen, Drieghe and Brysbaert (2010).

An alternative explanation of the observed LVF advantage with attached words and nonwords may be that it is easier to localize the first letter of a word in the beginning of an orthographic unit than in the middle of a letter string[7]. However, there are three reasons why this explanation is unlikely to apply to our data. For a start, the first letter of the RVF target word in the distance 0 condition was next to the fixation position and was clearly distinct from the competing letters, as the word was presented in bright yellow against a dark background. Second, there was a continuous LVF-RVF difference from 0 letters distance, over 2 letters, to 4 letters distance. It was not the case that the 0-letter distance condition radically differed from the 2-letters and the 4-letters distance conditions, even though the latter two allow the reader to distinguish the letter strings equally easily. Finally, our data replicate those of Nazir et al. (2004), discussed above, which did not involve word segmentation. One reason why our participants may not have had difficulties segmenting the letter strings is that readers of the Dutch language have extensive experience with new words that are compounds of existing words. This is because in the Dutch language, unlike in English, all compound words must be written as single words, even those that are newly formed (e.g. schoolbloem, meaning *school flower*, must be written as a single word).

The data of Experiment 1 are not in line with the BPF model, if it is assumed that the bilateral representation extends 3° (as claimed by Bunt, Minckler, & Johanson, 1977; and also defended by Lindell & Nicholls, 2003, and Bourne, 2006, among others). According to this model, word naming in foveal vision should be equally fast in LVF as in RVF as both have direct access to LH. One way to save the BPF model would be to assume that the region of bilateral projection is smaller (e.g., 2°) and that we obtained a RVF advantage in the 4-space condition, because here the separated stimuli exceeded the 2° foveal region. Indeed, in the literature several estimates of hemifield overlap have been given, going from 0.5° (Wyatt, 1978) to 3° (Bunt et al., 1977), depending on the criteria used.

An easy way to test the "reduced" BPF hypothesis, is to replace the 4-letter words by 5-letter words. As Figure 4 shows, if the pattern of results in Experiment 1

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[7] The authors thank Andy Ellis for this suggestion.

was due to a reduced region of overlap, then we should find the same effect with 5-letter words at distance 0 as with the 4-letter words at distance 2 (i.e., a null-effect). For 5-letter words at distance 2, we should find the same effect as with 4-letter words at distance 4 (i.e. a RVF advantage of 30 ms), because the leftmost letter of a 5-letter word in LVF at distance 2 is equally far from the fixation location as the leftmost letter of a 4-letter word in LVF at distance 4.
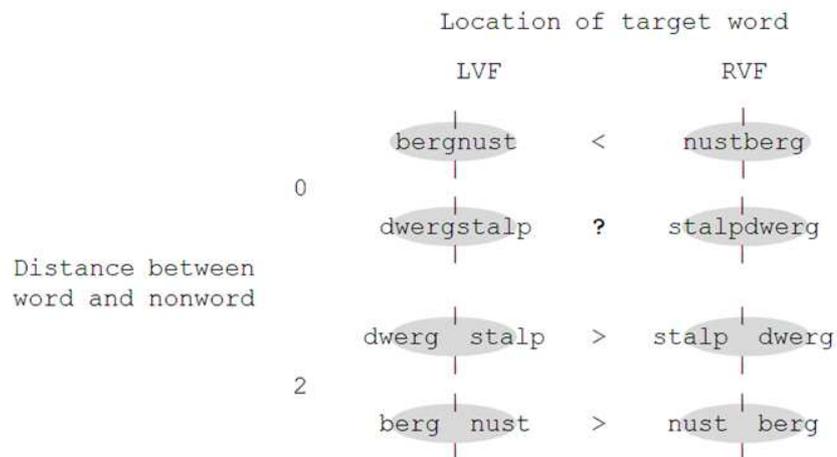
Location of target word

LVF   RVF

bergnust   <   nustberg

0

dwergstalp   ?   stalpdwerg

Distance between
word and nonword

dwerg stalp   >   stalp dwerg

2

berg nust   >   nust berg

FIGURE 4. Illustration of the eccentricity hypothesis tested in Experiment 2, with the target words *berg* [mountain] and *dwerg* [dwarf, gnome] and the nonwords nust and stalp. The grey circle represents a bilateral area of 2° instead of the original 3°.

Different predictions are made by the SERIOL model. Because the pattern of results depends on the *distance* between the stimuli in LVF and RVF, the SERIOL model predicts that the findings with 5-letter words at distance 0 should be the same as the findings with 4-letter words at distance 0 (i.e., a LVF-advantage), and that the findings with 5-letter words at distance 2 should be the same as those with 4-letter words at distance 2 (a null-effect). Experiment 2 tested which predictions were correct.

Experiment 2

Experiment 2 was set up to see whether the findings of Experiment 1 could be explained by assuming a reduced region of bilateral representation. In that case, we should find a different pattern of results if 5-letter words are used as stimuli rather than

4-letter words. In contrast, the SERIOL model predicts exactly the same pattern of results for 5-letter words as for 4-letter words, because not the length of the words is important but their distance from the nonword. Because the critical comparison is between distances 0 and 2, only these conditions were tested.

Method

Participants

Fifteen new right-handed students from Ghent University (3 male, 12 female; mean age: 21.5) received a monetary reward in return for participation in this experiment. They all had normal or corrected-to-normal vision and no color deficiency, were native Dutch speakers, and were free from any known reading or color vision impairments. The data of seven other participants were not analysed, because their fixations were not stable enough.

The same questionnaire as in Experiment 1 was administered in order to test the participants' preferences for handedness (Oldfield, 1971), eyedness, earedness and footedness (Porac & Coren, 1981). The Miles (1930) test of eye dominance was also administered before the participants were selected. Table 2 shows the mean ratings reported in the questionnaire for Experiment 2.

TABLE 2

Means and SDs as reported by the fifteen participants in Experiment 2 in the questionnaire about handedness, eyedness, earedness and footedness.

Measure	Mean	SD
Hand	2,63	0,84
Eye	1,50	1,73
Ear	2,03	1,53
Foot	2,28	0,98

Note. N = 15. Scale: -3 = strong left preference; 3 = strong right preference

Stimuli

160 monosyllabic words and 160 monosyllabic nonwords with a word length of five letters were selected by using the Wordgen software (Duyck et al., 2004) based on the CELEX database (Baayen et al., 1993). Half of the words had a structure of consonant-consonant-vowel-consonant-consonant (e.g., *dwerg*, meaning dwarf), the other half had a structure of consonant-consonant-vowel-vowel-consonant in which the two vowels formed a single phoneme or a diphthong. For half of these stimuli (40) the two vowels were the same (e.g., *draak*, meaning dragon), for the other half they were different (e.g., *groep*, meaning group). The words were matched pairwise with the nonwords according to consonant-vowel structure (word-nonword pairs had the same structure), bigram frequency and neighborhood size ($ts < 1$).

Similar to the stimuli in Experiment 1, four restrictions were made with respect to the combination word-nonword (e.g., *dwerg*stalp) and the combination nonword-word (e.g., stalp*dwerg*): (a) the letters at the first six, seven, eight and nine positions and at the last six, seven, eight and nine positions of the 10-letter word-nonword combination formed no Dutch, French, or English word (e.g., *dwerg*s, *dwerg*st, *dwerg*sta, *dwerg*stal, g*stalp*, rg*stalp*, erg*stalp* and werg*stalp* are all nonwords; the same is true for stalp*d*, stalp*dw*, stalp*dwe* and stalp*dwer*), (b) a word and its paired nonword did not have overlapping letters in order to avoid orthographical and phonological similarity (e.g., *dwerg*st**a**lp instead of *dwerg*st**e**lp), (c) the summated type bigram frequency of the two combinations (e.g., *dwerg*stalp and stalp*dwerg*) were matched ($p = .32$; mean bigram frequency of the word-nonword pairs = 57,403, mean bigram frequency of the nonword-word pairs = 57,378), and (d) the orthographic neighbourhoodsize of the word-nonword combinations (e.g., *dwerg*stalp and stalp*dwerg*) were matched ($t < 1$; mean N of the word-nonword pairs = 0.00, mean N of the nonword-word pairs = 0.01). Target words were again presented in yellow, whereas the nonwords were presented in white on a dark blue background. As in Experiment 1, as much as possible we made sure that the transition between the word and the nonword formed a letter sequence that never occurred within a syllable, so that the distinction between the word and the nonword was very clear. All stimuli were presented in lowercase and can be found in the Appendix.

Design

The same within-factors as in Experiment 1 were manipulated: target word location (2 levels: LVF or RVF), the distance between the target word and the nonword (2 levels: no or two space characters), and list version (4 levels). The four list versions were constructed as in Experiment 1. Again, all participants named all lists.

Apparatus

The eyetracking device and measurement settings were identical to those of Experiment 1.

Procedure

The trial procedure and stimulus presentation settings of Experiment 1 were preserved. Stimuli now subtended 2.3° in the condition without blank spaces between the word-nonword combination, and 2.8° in the condition with 2 blank spaces in-between. The experiment consisted of two sessions of approximately 30 minutes. After two lists, participants were obliged to take a rest of at least 15 minutes in order to avoid fatigue effects.

Results

As in Experiment 1, participants with more than 60% second fixations during stimulus presentation were excluded[8]. This required us to replace seven participants. Based on the data from the participants with adequate fixations, analyses were run on the trials with one stable fixation in the region defined from 1 letter position (i.e. 0.23°) to the left to 1 letter position to the right. RTs less than 200 ms or greater than 1500 ms, RTs above or below 2.5 SDs from the mean (2.2%), and voice key failures (1.3%) were

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[8] As in Experiment 1, the remaining participants made only one fixation on at least 80% of the trials. Mean group fixation deviation now was 0.20 letters to the right of the fixation gap with individual data ranging from from 0.61 letters to the left to 1.25 letters to the right.

discarded as outliers and incorrect responses (1.9%) were deleted. 0.2% of the data were lost due to recalibration. All in all, analyses were based on 38.6% of the data.

Because the percentage of naming errors (1.9%) was very low, no analyses were run on the error data. A repeated measures analysis of variance (ANOVA) was run on the RTs with two independent variables: VHF (2 levels: LVF or RVF) and distance (2 levels: 0 or 2 spaces between the word and the nonword). There was a marginally significant main effect of VHF [$F(1,14) = 4.59$, $MSE = 351.74$, $p = .05$], with faster mean RTs in LVF (549 ms) than in RVF (560 ms). The main effect of distance was also significant [$F(1,14) = 10.14$, $MSE = 122.10$, $p < .01$], with mean RTs of 559 ms and 549 ms for distances 0 and 2 respectively. Finally, VHF and distance interacted significantly with each other [$F(1,14) = 10.97$, $MSE = 197.10$, $p < .01$].

Figure 5 shows the mean RTs in the four conditions. As in Experiment 1, we did planned comparisons between LVF and RVF at distances 0 and 2. These comparisons showed faster RTs in LVF than in RVF when the word and the nonword were concatenated [$t(14) = -4.02$, $p < .01$], but no significant difference with 2 blank spaces between the stimuli [$t(14) = .25$, $p = .81$][9].
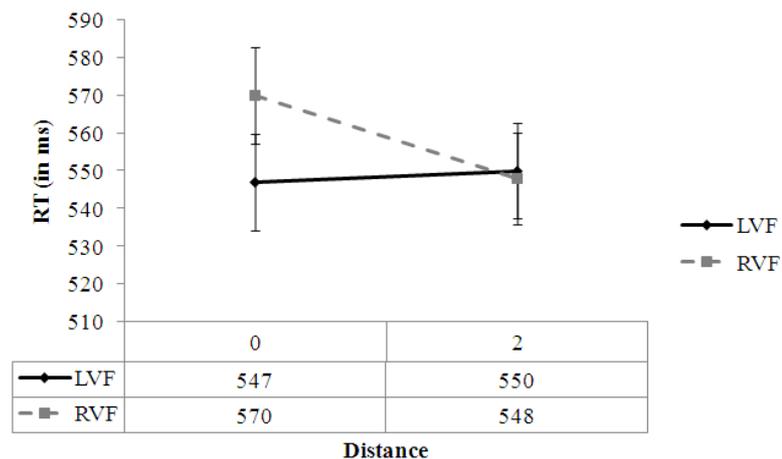

	0	2
LVF	547	550
RVF	570	548

FIGURE 5. Mean response times for the word targets in Experiment 2 in the LVF and RVF at the two possible distances.

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[9] As in Experiment 1, the reaction time pattern did not differ from analyses without fixation restrictions: LVF-RVF differences in these analyses were 550 ms – 568 ms [$t(14) = -4.44$, $p < .01$] and 551 ms – 547 ms [$t(14) = .73$, $p = .48$] in the distance 0 and distance 2 conditions respectively.

A closer look at the condition with two blank spaces between the word and the nonword indicated that this null-effect was not due to the absence of an effect in all participants, but rather to a distinction between participants with a LVF advantage (defined as larger than 5 ms; N = 5, mean LVF advantage = 27 ms) and participants with a RVF advantage (N = 7, mean RVF advantage = 23 ms). A reanalysis of the data of Experiment 1 indicated that something similar happened there, although the mean advantage in LVF (N = 6, mean LVF advantage = 19 ms) was smaller than the mean RVF advantage (N = 8, mean RVF advantage = 36 ms).

Discussion

Experiment 2 was designed to examine whether the data of Experiment 1 could be explained by a BPF model with a reduced (2°) region of bilateral projection. According to this model, 5-letter words at distance 0 should elicit the same VHF difference as 4-letter words at distance 2 (i.e., no significant VHF-difference), and 5-letter words at a distance 2 should induce the same VHF difference as 4-letter words at distance 4 (a significant RVF-advantage of some 30 ms; see Figure 4). Conversely, according to the SERIOL model, 5-letter words at distance 0 should show the same VHF difference as 4-letter words at distance 0 (i.e., a significant LVF-advantage of some 30 ms), and the same should happen for distance 2 (i.e., no significant VHF difference), because what counts is the distance between the word and the nonword: At short distances, the information in RVF is inhibited by the information in LVF; at longer distances this is no longer the case.

A comparison of Figures 3 and 5 clearly shows that the data are much more in line with the SERIOL predictions than with the BPF predictions. Both for 4- and 5-letter stimuli, words in RVF were named more slowly when irrelevant information was attached to them in LVF, leading to a significant LVF-advantage of some 25 ms at distance 0. This effect was reduced by inserting blank spaces between the word and the nonword, leading to a nonsignificant VHF-difference at distance 2.

An intriguing finding was that there was no full conversion from a LVF advantage at distance 0 to a RVF advantage at distance 2. In normal reading, a single blank space suffices to clearly separate the words (although there is evidence that fixation durations are shorter with two or three blank spaces between the words than with one; Drieghe, Brysbaert, & Desmet, 2005; Rayner, Fischer, & Pollatsek, 1998, Experiment 2, wide spacing condition vs. normal spacing condition). In contrast, with 2 blank spaces between the stimuli, we found that 5 out of 15 participants showed a clear LVF advantage (defined as a RT difference larger than 5 ms), as if both words formed one unit, whereas most others showed the expected RVF advantage. A similar pattern was present in Experiment 1: 6 out of 15 participants showed an average LVF advantage of 19 ms, in contrast to 8 participants with a RVF advantage of 36 ms in the 2 spaces condition (i.e. a similar reaction time pattern to that of all the participants in the 4 spaces condition, namely LVF: 608 ms RVF: 573 ms).

In hindsight, the presence of inhibition in the condition with 2 blank spaces may be less unexpected than we thought at the onset of the study. Clearly, the inhibition of LH information by RH information, as postulated by Whitney (2001), must be based on the detection of a contiguity between the information presented in LVF and in RVF. The most likely source for this detection is coarse, low spatial frequency information about the word blobs and their positions relative to each other. Given that our stimuli lighted up against a darker background at the onset of a trial, even at distance 2 they may have looked like a unitary stimulus to many participants (certainly for word length 5) and hence provoked the transcortical inhibition. The strong individual differences in LVF vs. RVF advantage for this particular condition shows that this was more strongly the case for some participants than for others. Although further research is required about this particular aspect of our findings, it does suggest that the transcortical inhibition, hypothesized in the SERIOL model, could very well be an explanation for both the LVF effect at distance 0 and the absence of a clear VHF difference at distance 2. In any case, the reaction time data resemble much more the pattern predicted by the information integration mechanisms of the SERIOL model than the pattern predicted by the bilateral fovea model.

General Discussion

In the introduction we saw that it is tempting to assume that visually presented words, just like auditorily presented words, are immediately available to both cerebral hemispheres. However, we also saw that the organization of the visual system is very different from that of the auditory system, and as far as we can see there have not been strong evolutionary forces (yet) to make the visual cortex adapt to the requirements of fluent reading. A more likely scenario is that the existing organization of the visual system is exploited as best as possible to enable reading. Words differ from most other stimuli, because they require very detailed perception and their interpretation depends critically on the correct alignment of the left and the right part. During reading, they also enter the visual system at a rapid pace (up to 300 words per minute).

To explain how words can be processed by a split fovea, Whitney (2001) proposed an early-integration account, according to which all letter information is brought together in the dominant hemisphere before word processing commences. This required the postulation of an inhibitory process, by which verbal information from RVF is inhibited as soon as it is attached to information in LVF, and delayed until the information from LVF has arrived in LH. This inhibition process was needed to explain why written words, just like spoken words, can be processed in a serial manner from word beginning to word end (see also Whitney, 2008). To our knowledge, the experiments presented here are the first empirical test of the existence of such an inhibition process in word processing (see Chiarello & Maxfield, 1996, for earlier attempts to find evidence for inhibition in interhemispheric collaboration; see Nazir et al., 2004, for evidence based on letter identification).

The hypothesis that all verbal information is combined in LH before word processing starts is in line with fMRI findings, showing a critical role of a region in the left inferior temporal cortex in the early stages of visual word recognition (the so-called "visual word form area"; Cohen et al., 2000), which is active independent of whether words are presented in RVF or LVF. Cai, Lavidor, Brysbaert, Paulignan and Nazir (2008) and Cai, Paulignan, Brysbaert, Ibarrola and Nazir (in press) showed that this

region is lateralized to the LH not because of the left-to-right reading direction in the languages studied (which favors the extraction of information from the RVF), but because this is the dominant hemisphere for speech production in the majority of readers. Participants with RH language dominance (as assessed by measuring which hemisphere controls language production) have their visual word form area lateralized to the RH even though this makes the extraction of information from the RVF more effortful.

The idea of written word information being gathered in the language dominant hemisphere also agrees with recent dynamic causal modeling of fMRI data. By looking at the transitions of brain activations during the execution of a task and fitting them to different types of causal models, it is possible to get a detailed picture of the most likely information flow. Stephan, Marshall, Penny, Friston, and Fink (2007) looked at the most likely flow of information in a letter detection task. Participants had to indicate whether the letter "A" was present in parafoveally presented words. When the word was presented in RVF, very little evidence for interhemispheric transfer was found. However, when the word was presented in LVF there was clear evidence for interhemispheric transfer of information in the inferior temporal cortex. In contrast, when participants had to indicate whether a colored letter was in the first half or the last half of a word, there was enhanced activity in the parietal cortex with symmetrical, bidirectional exchange of information. This clearly shows that the type of interactions between the cerebral hemispheres depends on the task to be performed and that verbal tasks are likely to involve early interhemispheric information transfer from RH to LH.

So, it looks very much like the human brain has solved the problem of how to process written words within the existing human visual system by rapid integration of the information in the language dominant hemisphere (usually the LH) and by temporary inhibition of the information from RVF until the matching information from LVF has arrived. An intriguing question at this point is whether some information is also conveyed to the language non-dominant hemisphere and whether this has any function in reading. Mohr, Endrass, Hauk, and Pulvermüller (2007; see also Mohr, Pulvermüller, & Zaidel, 1994) presented evidence for such a possibility. They showed

that word processing was substantially better when in addition to presentation in RVF, the same word was presented in LVF, so that both hemispheres had direct access to the word. According to Pulvermüller and Mohr (1996), this strongly suggests that visual word representations consist of transcortical cell assemblies, just like spoken word representations. Other evidence for a contribution of the language non-dominant hemisphere was reported by Cai et al. (in press). They reported that vertically presented words activated the non-dominant homologue of the visual word form area, in addition to the visual word form area itself. So, it seems that the resources of the non-dominant hemisphere can be called upon when processing is particularly hard.

Whatever the contribution of the nondominant hemisphere, the present findings strongly suggest that visual word recognition involves temporary inhibition from the RH to the LH in order to assure serial reading. In addition, we observed that this process is activated automatically by verbal information that straddles the visual midline, also in situations where the stimulation in LVF is uninformative and hinders performance in RVF. A further prediction of SERIOL is that the pattern of the currently found results would be different for people with RH language dominance than for LH dominant readers. Because cross-hemispheric inhibition is caused by processing letter strings serially, RH dominant readers would still show a LVF advantage with joined words and nonwords as they also read from the left to the right. However, they would experience less of a RVF advantage in our 4-space condition.[10] This is a hypothesis we intend to test by comparing RH dominant with LH dominant participants.

Finally it is important to stress that our data present solid evidence against the BPF view. This model predicted that we would find the same RVF advantage for 5-letter words presented at a distance 2 as for 4-letter words presented at a distance 4 (Figure 4). There was no evidence at all for this predication, indicating that the RVF-advantage for word recognition in parafoveal vision is not due to the transgression of some magical border between foveal and parafoveal vision, with qualitatively distinct brain circuits involved. Also at a more fundamental level, BPF-protagonists have never explained what the survival benefit of a bilaterally projecting fovea was for our

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[10] The authors thank Carol Whitney for this suggestion.

ancestors. It does not look as if there was a lot of spare tissue in the human brain, given the degree of cortical folding required to make the increase of human intelligence possible. Furthermore, it has been hypothesized that the laterality of higher cognitive functions also emerged to circumvent space limitations (Gazzaniga, 2000; Josse & Tzourio-Mazoyer, 2004). Why then would one argue in favor of a bilaterally projecting fovea, in which information is duplicated and sent to both hemispheres, if the same integration can be achieved by interhemispheric communication? Indeed, one of the first consequences of reading acquisition is an increase of white matter in the splenium of the corpus callosum (Carreiras et al., 2009).

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