Foveal word reading requires interhemispheric communication

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The left cerebral hemisphere is dominant for language processing in most individuals. It has been suggested that this asymmetric language representation can influence behavioral performance in foveal word naming tasks. We carried out two experiments in which we obtained laterality indices by means of functional imaging during a mental word generation task, using fTCD and fMRI respectively. Subsequently, we administered a behavioral word naming task, where participants had to name foveally presented words of different lengths shown in different fixation locations shifted horizontally across the screen. The optimal viewing position (OVP) for left language dominant individuals is located between the beginning and the centre of a word. It is shifted towards the end of a word for right language dominant individuals and, to a lesser extent, for individuals with bilateral language representation. These results demonstrate that interhemispheric communication is required for foveal word recognition. Consequently, asymmetric representations of language and processes of interhemispheric transfer should be taken into account in theoretical models of visual word recognition to ensure neurological plausibility.

Introduction

One of the striking features of the visual system is the crossing of the nasal optic fibers in the optic chiasm. Because of this crossing, stimuli presented in the left visual field (LVF) are initially projected to the right half of the brain and stimuli presented in the right visual field (RVF) are projected to the left hemisphere. This characteristic of the visual field has been used in thousands of experiments to investigate brain asymmetry on the basis of the visual half field (VHF) technique. The split of the visual field in two halves is also the reason why memories of faces are predominantly based on information from the LVF (Brady, Campbell, & Flaherty, 2004).

Surprisingly, limited attention has been paid to the question of what happens at the border where LVF and RVF meet. For a long time the general assumption was that the hemifields overlap in the center of the visual field, so that foveal vision is projected bilaterally and stimuli have to be presented in parafoveal vision in order to ensure unilateral projection (Bradshaw & Nettleton, 1983; Bryden, 1983). This assumption was also shared by psycholinguists whose models of visual word recognition did not include any reference to brain asymmetry or the need of interhemispheric communication.

Several reviews of the literature have shown, however, that the assumption of a bilaterally represented fovea is wrong (e.g., Brysbaert, 1994, 2004; Lavidor & Walsh, 2004). For instance, Corballis and Trudel (1993) examined whether split-brain patients were able to recognize centrally presented four-letter words that could not be guessed on the basis of the first or the last two letters. Two patients were examined (L.B. and D.K.). They were both unable to recognize foveally presented words, even though their performance was good when the stimuli were presented in LVF or RVF. Similar findings were reported by Fendrich and Gazzaniga (1989) and Fendrich, Wessinger, and Gazzaniga (1996) for the patients V.P. and J.W.

A second argument that has been made for the conjecture that cerebral asymmetry and interhemispheric transfer do not constrain visual word recognition in foveal vision, is that in healthy participants interhemispheric communication is so fast and abundant that it does not limit word processing to a greater extent than the equivalent intrahemispheric connections. This view has been phrased most explicitly by Dehaene, Cohen, Sigman, and Vinckier (2005), who wrote (p. 338): “It has been proposed that ‘foveal splitting’, whereby the left and right halves of a centrally fixated word are initially sent to distinct hemispheres, has important functional consequences for reading. However, beyond V1, callosal projections have the precise structure required to guarantee the continuity of receptive fields across the midline and allow convergence to common visual representations. We believe that these connections minimize the functional impact of the initial foveal split.”

Brysbaert (1994) argued that the discussion about whether or not interhemispheric transfer has functional consequences for foveal word recognition can be settled quite easily on the basis of empirical data. All that is needed is to compare a group of participants with right hemisphere language dominance to a group of participants with left hemisphere language dominance. Although language is lateralized to the left in most individuals (Pujol, Deus, Losilla & Capdevila, 1999; Knecht et al., 2000; Szaflarski et al., 2002), there is a small percentage of people with right hemisphere language dominance. Comparing the performance of left and right language dominant individuals in a foveal word recognition task would reveal to what extent higher cognitive processes such as reading rely on interhemispheric transfer and information integration. If foveal vision is bilateral or if interhemispheric connections minimize the functional impact of the initial foveal split, then there should be no difference in the performance of both groups, at least not for short words that subtend a visual angle of less than 2 degrees (under most reading conditions there are 3-4 letters per degree of visual angle).

Brysbaert (1994) made use of the Optimal Viewing Position (OVP) effect (O'Regan & Jacobs, 1992) to investigate the issue. The OVP effect is obtained by asking participants to read words after initial fixation on the first, the second, …, and the last letter. The usual finding is that participants are fastest in recognizing a word when they are allowed to fixate a letter within the first 1/3 of the word (called the OVP) and that there is a considerable time cost for fixations towards the end of the word, in particular for long words (see Figures 3 and 6 below). Brysbaert (1994) recruited a group of 9 participants with atypical brain laterality (i.e. with signs of right hemisphere language dominance or bilateral language representation) and observed that the OVP was shifted more towards the end of the words for these participants compared to a control group of participants with left hemisphere language dominance.

Unfortunately, when Brysbaert (1994) ran his experiments, there were no other noninvasive means of assessing cerebral dominance than VHF tasks. Hence, participants were classified as left or right dominant on the basis of their LVF-RVF asymmetry in a VHF task with parafoveal word presentation. A major weakness of this approach was that variables other than cerebral dominance could account for the correlation between VHF asymmetries and the preferred landing position in the OVP task as observed by Brysbaert (1994). These include, for example, an individual bias in attention allocation across the VHFs (Kim & Levine, 1991), established reading habits and asymmetries in the information distribution within words (Efron, 1990).

In the years since the early 1990s major breakthroughs have been realized to assess cerebral dominance in a noninvasive way. Two techniques stand out. The first involves functional transcranial Doppler sonography (fTCD), through which the differences in blood flow velocity towards the left and right cerebral hemispheres can be measured while participants are performing a language related task, usually word generation. Individuals with left hemisphere language dominance are expected to require a higher blood flow to their left hemisphere than to their right hemisphere while doing the task and this asymmetry can be picked up with fTCD. In a series of studies, Knecht and colleagues showed that the technique makes it possible to reliably assess cerebral dominance in a test session of less than 30 min. Knecht et al. (2001), for instance, applied this technique to a group of 326 healthy participants and obtained evidence for left hemisphere dominance in 264 participants (80%), bilateral representation in 31 participants (10%), and right hemisphere dominance in 31 participants (10%). The technique was further validated by comparing its laterality index to the laterality index based on the well-documented invasive Wada test. Fifteen epilepsy patients underwent both tests as part of a pre-surgery evaluation. The laterality indices of fTCD and WADA agreed in all patients (11 left dominant and 4 right dominant; Knecht et al. 1998).

The second technique that has been used to assess brain dominance in a noninvasive way is functional magnetic resonance imaging (fMRI). Knecht et al. (2003) showed that participants with left and right language dominance (as assessed by fTCD) showed much higher activation levels in the expected hemisphere in the areas related to speech production (Broca's area and the surrounding regions, including BA 44 and BA 45). Similar findings were reported by Pujol, Deus, Losilla, and Capdevila (1999) and Szaflarski et al. (2002).

In the experiments below we will repeat Brysbaert's (1994) OVP study with groups of participants whose brain asymmetry has been assessed either with fTCD or fMRI. If brain laterality has no functional consequences for foveal word recognition, we expect to find similar OVP curves for left dominant and right dominant participants, at least for short words that subtend a visual angle of less than 2 degrees of visual angle. In contrast, if interhemispheric communication constrains foveal word recognition, we expect to find that participants who are left dominant for language will perform better than right dominant participants after fixating the first letters of the words, whereas they will perform worse after fixating the last letters of the words. This is because fixation of the first letters of a word make the word fall mainly in the RVF, whereas if the last letters are fixated the word falls predominantly in the LVF.

Experiment 1

In experiment 1 we tested the OVP effect for German words of 3, 5, and 7 letters in participants whose brain laterality had previously been assessed as typical or atypical by means of fTCD.

Methods

Procedure Participants were chosen from a cohort of people that had previously been assessed for language dominance by fTCD at the Universitätsklinikum Münster (Germany), such that this information was available for pre-selection purpose. All participants gave informed consent and had to complete a questionnaire on handedness based on the Edinburgh Handedness Inventory prior to participation. The experimental paradigm employed in the Doppler-sonography setting is well-documented and has successfully been used in a range of language lateralization studies so far (Knecht et al., 2000, 2001, 2003). All participants were native German speakers.

Because previous laterality assessments had taken place more than a year ago, hemispheric language dominance was reassessed with fTCD during performance of a verbal fluency task. Subsequently, participants performed an OVP task in which they had to name 3-, 5- and 7-letter words presented briefly between two vertically aligned lines at different fixation locations.

Functional transcranial Doppler sonography Twenty participants were selected from the available cohort of people (13 male, 7 female; mean age 28.1; 12 left-handed, 8 right-handed). A 2-MHz transcranial Doppler sonography device (Multidop T; DWL Sipplingen, Germany) was used to measure increases in cerebral blood flow velocity (CBFV) within the left and right middle cerebral arteries (MCAs) during performance of a verbal fluency task. Participants were seated in front of a monitor while a head device, supporting the 2-MHz ultrasound probes, was fitted and the MCAs were located (Ringelstein, Otis, Niggemeyer & Kahlscheuer, 1990). The verbal fluency experiment started out with a 15 s *rest period* followed by an auditory signal that indicated the *cue* phase, during which a random letter of the alphabet was displayed on screen for 5 s. A second auditory signal marked the beginning of the *wordgen* phase, lasting 6 s, which required the participant to silently generate as many words as possible starting with the displayed letter. A third auditory cue signaled the onset of the *speak* phase, during which the words that had been found had to be repeated out loud (12.5 s). The end of the first cycle was indicated by a fourth auditory cue (Figure 1). Twenty of these experimental cycles were recorded, lasting an entirety of approximately 20 min. The Doppler signal resulted in spectral envelope curves which were stored for off-line analysis.

Figure 1 about here.

Data analysis and LI calculations fTCD data were analyzed with the software package AVERAGE (Deppe, Knecht, Henningsen & Ringelstein, 1997). After pre-processing and automatic artifact rejection, the data were integrated over the corresponding cardiac cycles, segmented into epochs which related to the different experimental phases (*rest period, cue, wordgen, speak*) and averaged. Mean CBFV values from the 15 s *rest period* were taken as baseline value. The relative cerebral blood flow velocity (rCBFV) changes in relation to the baseline value were calculated and compared for each experimental phase with the formula:

$$rCBFV = \frac{V_{(t)} - V_{(rest\_mean)}}{V_{(rest\_mean)}} \tag{1}$$

where $V_{(t)}$ is the CBFV over time and $V_{(rest\_mean)}$ refers to the mean velocity in the *rest period*.

The Wilcoxon test was employed to statistically analyze the differences in blood flow velocity between the left and right MCAs at each sample point, resulting in a laterality index (LI) for each participant for the experimentally crucial *wordgen* phase. We found 8 participants to be right-dominant for language with fTCD_LI values ranging from *-1.17* to *-4.93*, while 12 participants showed typical language dominance with values ranging from *1.39* to *7.79* (Table 1). For the current data set and the previously recorded fTCD laterality indices a test-retest correlation was calculated for purpose of comparison ($r = 0.78$, $p < 0.01$, $t(18) = 5.286$), revealing a strong consistency across time for this measurement technique.

Table 1 about here.

Behavioral OVP The behavioral word naming task was performed by the same group of people who were assessed with fTCD.

Stimuli: 70 three-, 70 five- and 70 seven-letter words served as stimuli. The stimulus sample contained German nouns only, which were selected through WinWordGen (downloadable online http://users.ugent.be/ ~wduyck/wwgdown.htm) and were controlled for frequency and neighborhood size. Words were displayed in their common format, with the initial letter capitalized.

Design Each word, independent of its length, could be seen at seven possible fixation locations shifted horizontally across the screen. We chose this design (seven fixation locations even for the shorter words) to be able to present the same number of 3- and 5-letter words as 7-letter words, in equal fixation locations. This design also allowed us to examine whether there was a continuity between foveal and parafoveal word recognition (Brysbaert, Vitu & Schroyens, 1996). A 3-letter word was presented such that participants were fixating the blank space two letter positions before the word (-2; i.e. the complete word was in RVF), the blank space before the word (-1), the first letter of the word (L1), the second letter of the word (L2), the third letter of the word (L3), the blank space after the word (1) or two letter positions after the word (2; see Figure 2). A 5-letter word could be fixated on each letter of the word (L1, L2, L3, L4, L5) or on the space before (-1) or after the word (1). A 7-letter word could be fixated on each possible letter position (L1, L2, L3, L4, L5, L6, L7). Since it would have taken too many repetitions of the stimuli, each participant did not see each individual word at every possible fixation location, but at 3 different positions only (i.e. the set of 210 stimuli were repeated in three lists). Therefore each participant was eventually exposed to 630 trials. The fixation locations for the different words were counterbalanced across the left- and the right-lateralized groups, so that the results could not be due to the words that were seen at the different fixation locations. This was done as follows. First, 7 lists were made according to a latin-square design, so that each list contained all possible words and all possible fixation locations and over the lists all words were presented at all fixation locations. Next *List 1, 2, 3* were seen by the first individual, *List 4, 5, 6* by the second individual, *List 7, 1, 2* by the third, and so forth, such that the OVP-patterns for the left and right dominant groups were independent of the words selected for the experiment.

Procedure Participants viewed a monitor at a distance of ~60 cm and were asked to fixate a gap (fixation-space) between two vertically aligned lines (visible throughout the experiment) in the centre of the screen. The whole set of stimuli was shuffled and presented in pseudo-randomized order, such that there was no blocking of word length. Words stayed on screen for 180 ms each. The participants responded by naming the words as fast as possible. Responses were collected by means of a voice trigger, where the onset of speech was registered as the reaction time for a specific stimulus. To control for eye-movements, digits in the range from 0-9 were presented in the fixation-space at a word/digit ratio of 5.3/1 at randomized time intervals. The digits were on screen for 80 ms only and had to be reported correctly. This was a strong incentive for the participants to constantly fixate the space between the two vertical lines (Brysbaert, 1994). Words and digits were masked with a sequence of ASCII codes 35 (#) that had the same length as the preceding stimulus, in order to prevent any afterimage.

Figure 2 about here.

Results

Preceding the OVP data analysis, timing (>1500 ms) and naming errors were eliminated from the data set (mean mixed error rate 1.77%). Subsequently, mean response times (RT) for each fixation position were calculated, resulting in an OVP curve for each individual and each word length.

The mean RT data were entered in a three-way analysis of variance (ANOVA) including *laterality group* (2 levels, between-subjects), *word length* (3 levels, within-subjects) and *viewing position* (7 levels, within-subjects). We found a main effect of *viewing position* (F (6,108) = 44.184, $p < 0.01$) and an interaction between *laterality group* and *viewing position* (F (6,108) = 5.744, $p < 0.01$), as well as an interaction between *word length* and *viewing position* (F (12,216) = 10.599, $p < 0.01$).

Subsequently, RTs were standardized for every participant per word length by subtracting the overall mean from the observed response times (e.g., a participant who had an average response time of 500 ms for three-letter words and whose response time after fixating the first letter was 490 ms, would get a standardized value of -10 ms for that fixation location). In this way, the curves of the two laterality groups could be compared in a straightforward way by getting rid of the non-significant group differences in reading times. The raw data (before standardization) are given in Table 2.

Table 2 about here.

Figure 3 shows the standardized OVP curves for the group of right-dominant individuals and the group of left-dominant individuals for each of the three word lengths. This figure clearly illustrates the differences between both laterality groups. Participants with left hemisphere dominance named the short words faster when they fixated the space in front of the words or the initial letters, whereas faster reaction times were seen in the right hemisphere dominant participants when they fixated the end letters of the words or the space after the words. Within the group of atypical language dominant participants we found no significant differences in performance between left-handed (4) and right-handed (4) individuals (95% CI = 9 ms for 3-letter words, 95% CI = 10 ms for 5-letter words, 95% CI = 12 ms for 7-letter words; based on the MS_e of the interaction between viewing position and laterality group; Masson & Loftus, 2003).

To measure the correlation of the fTCD laterality indices with the left-right asymmetries of the OVP curves over all participants, we rewrote each OVP curve as a second order polynomial and looked at the regression weight of the linear component[1]. Hence, the OVP curve of each participant was rewritten as:

$$RL_i = a + b(l_i - m) + c(l_i - m)^2 \qquad (2)$$

where RL_i = reaction latency for fixation location i, l_i = rank number of the letter fixated, *m* = middle of the word, *a* = constant, *b* = linear component, *c* = quadratic component.

The linear OVP components ranged from *-12.2* to *+7.1* for the 3-letter words, from *-7.7* to *+18.1* for the 5-letter words and from *-1.0* to *+21.1* for the 7-letter words (Table 1). There were high positive correlations between the slopes of the different word lengths over all participants: r = 0.71, p < 0.01 between 3-letter and 5-letter words, r = 0.61, p < 0.01 between 3-letter and 7-letter words and r = 0.72, p < 0.01 between 5-letter and 7-letter words.

A comparison between the slopes for the atypical and the typical language dominant individuals revealed that the average slopes for the atypical group were *-3.7* for the 3-letter words, *+0.4* for the 5-letter words, and *+4.1* for the 7-letter words. The average slopes for the typical language dominant group were *+1.4*, *+6.2* and *+11.0* respectively (Figure 3). A 2x3 ANOVA including laterality group and word length revealed significant main effects of laterality group (F(1,18) = 12.89, MSe = 39.65, p

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[1] The same results were obtained when the analyses were done on the difference scores between fixations on the last and on the first letter. We prefer the polynomial, because this takes into account all the data that have been gathered and, therefore, is less vulnerable to measurement error.

< 0.01) and word length ($F(2,36) = 39.13$, MSe = 9.18, $p < 0.01$) and no interaction ($F < 1$).

Figure 3 about here.

If we look at the slopes based on the word positions only (L1, L2, L3 for 3-letter words; L1, L2, L3, L4, L5 for 5-letter words; L1, L2, L3, L4, L5, L6, L7 for 7-letter words), we find a difference between the slopes of the laterality groups as well. Average slopes based on word position only were *-1.7* for the 3-letter words, +*0.6* for the 5-letter words, and +*4.1* for the 7-letter words in the atypical group and +*1.6*, +*4.9* and +*11.0* in the typical language dominant group.

Figure 4 shows the correlation between the fTCD Laterality index we obtained for each participant and their average OVP-slope based on the three word lengths. The correlation is significant ($r = 0.55$, $n = 20$, $p < 0.02$), as could be expected from the previous ANOVA. However, a closer look at Figure 4 shows that the effect is mainly due to the difference between the two laterality groups and not to the differences within the laterality groups. As a matter of fact, when we recode the fTCD Laterality index as -1 for the atypical group and +1 for the typical group, the correlation with the OVP-slopes increases ($r = 0.65$, $n = 20$, $p < 0.01$).

Figure 4 about here.

Discussion

Figure 3 clearly shows that the OVP curves of the left dominant participants differ from those of the right dominant participants. Left hemisphere dominant participants have an overall stronger word beginning superiority effect than right dominant participants. This replicates the findings of Brysbaert (1994) in a design that is not subject to the criticism that the relationship between the laterality indices and the left-right asymmetry in the OVP curve could be due to an asymmetrical attention allocation over the visual field.

A second notable finding is that the word beginning superiority is stronger for long words than for short words, both in participants with typical dominance and in participants with atypical dominance. This too is in line with Brysbaert (1994) and indicates that cerebral dominance is not the only factor influencing the left-right asymmetry in the OVP-curve. Other factors that are known to have an impact are the reading direction (left-to-right in the present experiment) and the fact that in general the word beginning is more informative than the word end (Brysbaert & Nazir, 2005; Farid & Grainger, 1996; O'Regan & Jacobs, 1992; Rayner, 1998). The impact of the reading direction and the information asymmetry in words is stronger for long words than for short words. Interestingly, a similar finding has been reported in the VHF literature. It is well documented that the RVF advantage is larger for long words than for short words (Ellis, Young, & Anderson, 1988). Whereas it is possible to find a LVF advantage for 3-letter words (as shown in the upper panel of Figure 3 for the atypical group), one never observes such an advantage for 7-letter words in a language that is read from left to right (see the lower panel of Figure 3).

Finally, we noticed a few limitations of the study. For a start, Figure 4 suggests that the fTCD data were sufficient to determine whether an individual was left or right dominant, but they did not allow us to draw any conclusions about the degree of laterality. This might be a limitation of the fTCD technique or it might indicate that there is no continuous relationship between the OVP slope and the laterality index. Second, our decision to present 3- and 5-letter words at 7 possible viewing positions limited the certainty with which we can conclude that interhemispheric transfer is required for short words (Figure 3). Although there is good evidence for a continuity between foveal and parafoveal word recognition (see also Brysbaert et al., 1996), the evidence for a difference in OVP curve between left and right dominant participants is less strong for the foveal part of the 3- and the 5-letter words. To address these limitations, we ran Experiment 2.

Experiment 2

Given the positive findings of Experiment 1, which reveal a direct relationship between hemispheric dominance for language and OVP task performance on a group level, we decided that it was worthwhile to see whether we could repeat those findings on a single subject level. Regarding the fact that fTCD is a rather crude measure of hemispheric dominance, we wanted to employ a technique that would be able to give us more detailed information on activation patterns in the brain during language tasks. An fMRI set-up, in which the extent of brain activation during a language task can be compared between predefined regions of interest (ROI), allows for a much more detailed investigation of dominance patterns. In addition, we wanted to obtain more reliable estimates of the OVP curves at an individual level. In Experiment 1 we ensured that the OVP-patterns were comparable at the group level; in the present experiment we made sure that the OVP pattern could be interpreted at the individual level and, therefore, could be used to look at the correlation between degree of laterality and degree of word beginning superiority.

A second reason why we examined whether this type of research is possible at an individual level is that we wanted to see whether it can be done without the backup of a large-scale fTCD study involving more than 300 participants. The nice aspect of Experiment 1 was that we already knew on beforehand whether a person was left or right dominant. Do we really need this type of large-scale screening or can we use a more focused (and less expensive) approach? To investigate this, we started from Knecht et al.'s (2000) observation that up to a quarter of the participants who scored high on a questionnaire for left-handedness turned out to have atypical brain dominance (either right dominant or bilateral). We invited left-handed students to take part in a study, which encompassed two VHF tasks for screening purpose, a word production task in an fMRI setting to determine language dominance and, finally, an OVP task to investigate performance in foveal word naming. The VHF tasks involved the naming of short words and the repeated naming of five pictures presented in the LVF and RVF (Brysbaert, 1994). They were administered because we wanted to limit the brain scans to those participants who were interesting, either showing a clear lateralization or evidence for bilaterality. The VHF screening procedure allowed us to strategically search for and select promising candidates.[2]

Methods

Participants All ten participants (4 male, 6 female; mean age 19.8) were English native speakers. Only left-handed participants were tested (based on the Edinburgh Handedness Inventory). They were selected from an original sample of 26 lefthanders, who had taken part in two VHF experiments in which either words or a small set of pictures had to be named (Brysbaert, 1994; Hunter & Brysbaert, in preparation). Six of the participants were chosen because they showed a strong RVF advantage in the VHF tasks (out of 15 showing this advantage), two because they showed no clear VHF difference (out of 7), and two because they showed a clear LVF advantage (out of 4 [3]).

Procedure All participants gave informed consent and subsequently took part in two lines of research which were approved by the departmental ethics committee. All paradigms employed in this study have been well-documented and validated elsewhere (Brysbaert, 1994; Knecht et al. 2003). The task to be performed in the scanner was practiced off-line prior to onset of the experimental trials.

First, we assessed the cerebral dominance of the participants. We used fMRI to scan our participants during performance of a mental word generation task, which was

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[2] Given that the study involved the screening of participants on the basis of VHF tasks, it could be objected that the same validity threat as in Brysbaert (1994) applies. However, because of the clear data of Experiment 1 and since we did not obtain a contradiction between the laterality index obtained on the basis of the VHF experiments and the laterality index obtained on the basis of the fMRI study for any of the participants we examined (Hunter & Brysbaert, in preparation), we feel confident that the results reported below are not a confound of differences in attention allocation across the visual field.

[3] The third and fourth participants with strong LVF advantage could unfortunately not be scanned for the fMRI part of the study.

very similar to the fTCD task used in Experiment 1 and is known to produce marked lateralization (Knecht et al., 2000, 2001, 2003). Subsequently, participants performed an OVP task (Brysbaert, 1994), which required them to name 4- and 7-letter words that were presented briefly between two vertically aligned lines at different fixation locations.

Functional Magnetic Resonance Imaging We employed a mental word generation task to assess hemispheric dominance in a Siemens 3T Magnetom Trio scanner fitted with an eight-channel head array RF coil. Ten single letters with the highest beginning-of-word frequency were presented in randomized order in the activation blocks. Participants had to silently generate as many words as possible starting with the displayed letter. In a control phase the meaningless letter string “dada” was presented and had to be repeated continuously. Each activation and control block lasted 18 s, followed by an 18 s rest interval. The stimulus onset was synchronized with the scanner pulse for each activation block. Blood oxygen-level dependent changes were measured using gradient-echo echo planar T2*-weighted imaging sequences. Whole brain volumes comprising 36 axial slices each were acquired every 3 s (TE 32, flip angle 90º, resolution 3x3x3, matrix 64x64, slice thickness 3 mm, bandwidth 1346). In all, 243 scanning volumes were obtained for each participant. In addition, high resolution anatomical images were acquired (TR 1830, TE 5.56, flip angle 11º, resolution 1x1x1, 256x256 image matrix, 160 sagittal slices).

Data analysis The data were analyzed with the SPM2 software package (available online http://www.fil.ion.ucl.ac.uk/spm/). Images were realigned to the first functional volume to correct for motion artifacts and normalized into standard Talairach-type space using an EPI template. To reduce effects of random noise normalized data were spatially smoothed using a Gaussian kernel (FWHM 6mm). In addition, a high-pass filter was applied to the time series with a cut-off period of 100 s. For statistical analysis the general linear model was employed to map the hemodynamic response curve onto each experimental condition using boxcar regressors. The boxcar function was then fitted to the time series at each voxel resulting in a weighted β-image. The fitted model was converted to a *t*-statistic image which constitutes the statistical parametric map. Images for each individual were corrected for family wise error (FWE) at p = 0.05. The minimum cluster size was set to 20 activated voxels.

LI calculations After pre-processing and statistical analysis of the scanning data, the degree of cerebral dominance was calculated for each participant regarding those voxels that were significantly more active in the activation than in the control phase. Levels of activation were compared between the left and right hemispheres in predefined anatomical regions of interest (ROI), which encompassed regions in the inferior frontal cortex in both hemispheres, including BA 44 and BA 45 (Table 3). Each laterality index (fMRI_LI) was derived by the formula

$$LI = \frac{A_L - A_R}{A_L + A_R} \tag{3}$$

where A_L refers to the number of activated voxels in the left ROI and A_R to the number of activated voxels in the right ROI. Seven participants showed a positive LI, three participants had a negative LI. Those individuals with LI > +0.4 were classed as left-dominant (6), those with indices -0.4 > LI < +0.4 as bilateral (2), and individuals with LI < -0.4 as right-dominant (2).

Table 3 about here.

Behavioral OVP The behavioral word naming task was performed by the same individuals who took part in the scan. Participants viewed a monitor at a distance of ~60 cm and were asked to fixate a gap (fixation-space) between two vertically aligned lines (visible throughout the experiment) in the centre of the screen. 88 four- and 88 seven-letter words were presented in randomized order and stayed on screen for 180 ms each. The stimulus sample contained a mixture of English nouns, verbs, adjectives and function words. These were selected from the Bristol Norms database (accessible online http://language.psy.bris.ac.uk/bristol_norms.html) and were controlled for frequency, age of acquisition, familiarity and imageability. Each word was shown four times, such that for the 4-letter words each letter of each word was presented in the fixation-space once (L1, L2, L3, L4). The 7-letter words were shown four times each, at four different fixation locations (L1, L3, L5, L7), each of which was presented in the fixation-space once. In this way, each participant formed a self-contained N=1 experiment, since their OVP-pattern was independent of the words used. This was done to decrease the noise in the individual data points (which reduces the correlation that can be obtained between the OVP slopes and the laterality indices). The 4-letter words were fixated in each possible letter position to have a more detailed picture of the OVP pattern for short words. In all, participants named a total of 704 words. In addition, digits in the range from 0-9 were presented in the fixation-space at a word/digit ratio of 5.9/1 at randomized time intervals. The digits were on screen for 80 ms only and had to be named correctly. Responses were collected by means of a voice trigger, where the onset of speech was registered as reaction time for a specific stimulus. Words and digits were masked with a sequence of ASCII codes 35 (#) that had the same length as the preceding stimulus.

Results

As before, timing (>1500 ms) and naming errors were eliminated from the OVP data set (mean error rate 1.5%) preceding the analysis. To analyze the OVP data, mean response times for each letter position were calculated, resulting in an OVP curve for each individual. RTs were standardized and mean OVP curves were calculated for the four strongest left-dominant individuals and the two strongest right-dominant individuals, to get an idea of the difference between left and right lateralized individuals, which is shown in Figures 5 and 6 (95% CI = 4.49 for 4-letter words, 95% CI = 16.71 for 7-letter words; based on the MS_e of the interaction effect; Masson & Loftus, 2003). It is clear that these data match those of Experiment 1. There was a stronger word beginning superiority effect in left dominant participants than in right dominant participants, and there was a bigger time cost for fixating the end of a 7-letter word than for fixating the end of a 4-letter word. The raw data are given in Table 4.

A three-way analysis of variance (ANOVA) in a 2*2*4 mixed design including *laterality group* (2 levels, between-subjects), *word length* (2 levels, within-subjects) and *viewing position* (4 levels, within-subjects) demonstrated a main effect of *viewing position* (F (3,12) = 9.153, p < 0.01) and an interaction between *laterality group* and *viewing position* (F (3,12) = 6.306, p < 0.01), as well as an interaction between *word length* and *viewing position* (F (3,12) = 5.268, p = 0.015).

Figures 5 and 6 about here.

To assess the statistical significance of the findings, the linear components of the OVP curves were calculated from the data set in accordance with formula (2). Slopes of the linear component were in the range from *-2.7* to *+10.3* for the 4-letter words and from *+0.9* to *+33.8* for the 7-letter words (Table 3). The slopes of the 4- and the 7-letter words showed a significant positive correlation ($r = 0.67$, $p < 0.05$).

Next, a Pearson correlation was calculated between the OVP slopes and the laterality indices from the fMRI study. This revealed a highly significant positive correlation for the 4-letter words ($r = 0.85$, $p < 0.01$, $t(8) = 4.562$) and a significant positive correlation for the 7-letter words ($r = 0.70$, $p < 0.025$, $t(8) = 2.773$) (Figure 7). The lower correlation for the 7-letter words than for the 4-letter words was due to the results of one left dominant participant, who had a lower slope for the 7-letter words than expected on the basis of the 4-letter words and on the basis of the fMRI laterality index (participant Sub_10 in Table 3).

Table 4 about here.

Figure 7 about here.

Discussion

The data of Experiment 2 show that for words as short as 4 letters, there is a strong relationship between the OVP curve and the participant's cerebral dominance on an individual level. Left dominant participants were 20 ms faster to name a 4-letter word when the word was presented in such a way that they were fixating the first letter, as opposed to when the word was presented in such a way that they were fixating the last letter. In contrast, the two participants with right hemisphere dominance were some 10 ms faster to name the same words after fixation of the last letter than after fixation of the first letter. As in Experiment 1, the word beginning superiority effect could not be reversed for the 7-letter words, but it was substantially smaller for the participants with right hemisphere dominance than for the participants with left hemisphere dominance. The participants with bilateral representation were in-between these two groups, so that across all participants there was a very high correlation between the left-right asymmetry of the OVP pattern and the laterality index calculated upon the fMRI data. In particular for the 4-letter words the correlation reached ceiling level ($r = 0.85$). This means that the issue of interhemispheric transfer in reading can be examined with a psychophysical approach, in which a limited number of participants are tested thoroughly.

General discussion

On the whole, researchers in the last decades have assumed that the distinction between LVF and RVF does not have any implications for the processing of foveally presented stimuli (Brysbaert, 2004). They first pointed to the evidence that the fovea might project bilaterally and, when this evidence could no longer be upheld, to the possibility that interhemispheric communication might be too fast and extensive to put any functional limitation on foveal processing. Given recent advances in noninvasive techniques to assess brain laterality, we can now move beyond the stage of assumption making and empirically test whether cerebral laterality has an impact on the way visually presented stimuli are processed.

Our data are exceptionally clear: As far as the naming of printed words is concerned, there is a significant time cost when part of the word is initially sent to the subdominant hemisphere. This means that for the majority of people (with left hemisphere language dominance) there is an advantage for fixating the left half of the words (i.e., the beginning of the words in a language read from left to right). These individuals show a clear word beginning superiority effect in word naming. For a minority of the people (i.e., those with right hemisphere language dominance), fixating the left half of the word initially sends the word to the subdominant cerebral hemisphere and they show either an advantage for fixating the right half of the word (for short words) or no advantage at all (longer words). The processing costs of interhemispheric communication are in the order of 20 ms for 4 letter words (Figure 6), which is not small when compared to the other effects that have been reported in visual word recognition. In addition, a delay in the magnitude of 15-30 ms accords well with electrophysiological transcallosal conduction plus synaptic transmission delays reported in the literature (Cracco, Amassian, Maccabee & Cracco, 1989).

Our data are particularly strong because we are able to predict the OVP slope for the processing of visually presented 4-letter words on the basis of brain activation patterns in a mental word generation task. Only a few theories would have predicted this (see below). On the other hand, we deliberately have been very selective about the task we used for the OVP experiment. Participants had to name the words aloud, because we saw this as the type of task that comes closest to what happens in the mental word generation task during brain imaging, although we hasten to say that not all processes involved in word naming take place in the region of interest used (e.g., Dronkers, 1996).

Further research will have to elucidate to what extent lateralisation of speech is accompanied by the lateralisation of the earlier stages of word processing (e.g., the visual word form area). There are some indications that the lateralisation of processes that are involved in lexical decision (deciding whether a string of letters is a word or not) may not be completely congruent with the lateralisation of the speech output processes. For instance, Krach, Chen, and Hartje (2006) determined language lateralization using fTCD during a word generation task and correlated the laterality index with the VHF asymmetry in a lexical decision task. They did not find a particularly strong correlation, although in our view this also had to do with the small number of trials in their tasks. Another study was run by Lehericy et al. (2000). They compared the laterality index based on the Wada test with fMRI data in a semantic fluency task (involving the frontal lobes) and story listening (mainly involving temporal regions). The correlation was much stronger in the former task than in the latter. On the other hand, a study by Vigneau, Jobard, Mazoyer and Tzourio-Mazoyer (2005) suggested a leftward lateralization for the processing of visually presented words (but not for non-words) as early as the visual word form area in the occipital-temporal region. Further comparisons of individuals with left and right language dominance will be needed to shed light on this issue. In the mean time, we do not think that it can be assumed that all language processes are lateralized to the same extent within the same hemisphere. Researchers are advised to bare this in mind when designing tasks for language dominance studies.

So far, two computational models have been presented about how the processing costs related to interhemispheric communication can be integrated within theories of visual word recognition. In the first model, SERIOL (Whitney, 2001), interhemispheric transfer is part of the processes that translate the visual input into letter representations. Whitney argues that visual word processing depends on a serial activation of the letter representations from the word beginning to the word end. To achieve this serial firing, two limitations regarding the original input must be overcome: interhemispheric transfer and the fact that information at the centre of fixation has a higher visual acuity than information further away from the fixation location. In languages read from left-to-right, these two constraints have particular relevance for the part of the word that falls into the LVF (i.e., the first few letters of the word). Not only does the visual acuity gradient stand in opposition to the serial processing requirement, but this information is also sent to the right half of the brain, which for the majority of people is the subdominant hemisphere. Whitney (2001) showed that her model could account for the differences in the OVP curves reported by Brysbaert (1994) by assuming a higher inversion cost of the acuity gradient in the subdominant hemisphere, combined with an interhemispheric transfer cost of 9 ms (see also Whitney, 2004; Whitney & Lavidor, 2004, 2005).

Another approach was taken by Shillcock, Ellison, and Monaghan (2000). These authors started out from the problem of how the brain keeps track of the letter positions in a word (e.g. to distinguish SALT from SLAT). Their solution was that the fixation location provides the brain with an extra anchor regarding the letter positions (in addition to the word beginning and the word end). They also ventured that each hemisphere rather independently activates word candidates that agree with the input it receives and integrates this information with that of the other hemisphere only at a relatively late stage. Finally, they assumed that the encoding is coarser in the subdominant hemisphere than in the dominant hemisphere. On the basis of these assumptions, Shillcock et al. were able to simulate the OVP curves. Importantly, in this model, interhemispheric communication does not take place before the word processing ‘as such’ starts (as in the SERIOL model) but is part of the processing itself. Further research (e.g., on the basis of an item analysis of the stimuli presented here) will have to decide which of the two models best captures the data of the participants with right hemisphere dominance and bilateral language representation.

Conclusion

The high positive correlation between laterality indices based on blood flow measures and the left-right asymmetry in visual word recognition points to a direct relationship between hemispheric dominance and word processing in foveal vision, such that it is now firmly established that interhemispheric communication is needed for normal word reading. Our results therefore stand in opposition to Dehaene et al.’s (2005) assumption that the functional consequences of interhemispheric transfer are minimal, and demonstrate that hemispheric dominance does have a strong functional impact and consequently affects word reading.

Our findings have far reaching implications for models of visual word processing. Theoretical modeling approaches, which attempt to integrate interhemispheric transfer into models of visual word recognition (Shillcock et al., 2000; Whitney, 2001; McDonald, Carpenter, & Shillcock, 2005), are now backed up with clear experimental data which proves them to be the most neurologically plausible models.

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Table 1: Gender, handedness, fTCD Laterality indices and OVP slopes for 3-, 5- and 7-letter words are given for each participant (Experiment 1).

	Gender	Handedness	**fTCD_LI**	Dominance	**Slope 3-letter words**	**Slope 5-letter words**	**Slope 7-letter words**
Par_17	m	left	**7.79**	1	**4**	**5.8**	**14.3**
Par_02	m	left	**6.8**	1	**-0.1**	**2.6**	**9.2**
Par_22	m	right	**5.84**	1	**-1.9**	**6.7**	**11**
Par_12	f	right	**3.86**	1	**0.2**	**8.2**	**13.4**
Par_04	m	left	**3.63**	1	**-0.1**	**5.2**	**6.9**
Par_20	m	right	**2.52**	1	**6.2**	**11.2**	**13.2**
Par_10	m	left	**2.34**	1	**2.6**	**1.2**	**3.4**
Par_11	m	right	**2.31**	1	**-2.7**	**3.1**	**7.5**
Par_08	f	left	**2.27**	1	**-2.3**	**3.4**	**8.8**
Par_16	m	left	**2.04**	1	**0.04**	**4.6**	**7.3**
Par_19	m	left	**1.95**	1	**4.1**	**4.5**	**15.8**
Par_07	f	left	**1.39**	1	**7.1**	**18.1**	**21.1**
Par_03	m	right	**-1.17**	-1	**3.2**	**3.2**	**1.2**
Par_21	f	left	**-1.46**	-1	**-5.4**	**-3.3**	**9.1**
Par_18	f	right	**-1.91**	-1	**-3.9**	**-0.6**	**3.6**
Par_14	m	left	**-2.07**	-1	**-4.6**	**5.2**	**-1**
Par_05	m	right	**-2.74**	-1	**-4.3**	**5.5**	**9.5**
Par_15	m	right	**-4.25**	-1	**-12.2**	**-7.7**	**-0.1**
Par_13	f	left	**-4.89**	-1	**-0.6**	**-4**	**2.4**
Par_01	f	left	**-4.93**	-1	**-1.6**	**4.7**	**7.8**

Table 2: Raw average OVP data for the left dominant and right dominant group are given for all seven fixation positions for each word length (Experiment 1).

		pos 1	pos 2	pos 3	pos 4	pos 5	pos 6	pos 7
LD								
	3-letter words	555	542	532	535	535	547	565
	5-letter words	559	551	542	540	546	574	601
	7-letter words	553	539	535	542	557	588	616
RD								
	3-letter words	609	592	569	563	565	578	585
	5-letter words	616	583	574	569	566	589	618
	7-letter words	612	588	575	577	582	598	641

Table 3: Coordinates for the area of strongest activation plus voxel count in the region of interest (ROI), fMRI Laterality indices and linear slopes for 4- and 7-letter words are given for each participant (Experiment 2).

	Active voxels left ROI	MNI coordinates x, y, z	Active voxels right ROI	MNI coordinates x, y, z	**fMRI_LI**	**Slope 4-letter words**	**Slope 7-letter words**
Sub_10	11378	-51 +15 +24	0		**+1.00**	**8.94**	**7.83**
Sub_07	7021	-51 +13 +24	110	+59 +13 +36	**+0.97**	**10.35**	**33.83**
Sub_02	8953	-51 +16 +22	128 100	+49 +17 +29 +43 +5 +31	**+0.95**	**5.37**	**21.81**
Sub_03	5812	-52 +15 +25	169	+49 +16 +5	**+0.945**	**2.43**	**15.27**
Sub_08	9469	-52 +13 +22	2213	+55 +10 +14	**+0.62**	**2.36**	**16.61**
Sub_09	7054	-50 +17 +26	1606 137	+56 +19 +29 +45 +18 +9	**+0.603**	**5.23**	**15.73**
Sub_01	5265	-49 +12 +27	2399	+59 +11 +17	**+0.37**	**4.47**	**6.16**
Sub_04	2940	-50 +10 +22	3029 1214 100	+54 +15 +10 +51 +7 +32 +54 +33 +2	**-0.19**	**1.72**	**7.66**
Sub_06	1076 238 144	-52 +14 +12 -42 +11 +31 -51 +12 +44	7206	+52 +17 +22	**-0.66**	**-2.47**	**5.96**
Sub_05	143	-44 +3 +31	8250	+52 +16 +22	**-0.966**	**-2.73**	**0.86**

Table 4: Raw average OVP data for the strong left dominant and the strong right dominant group are given for all four fixation positions for each word length (Experiment 2).

		pos 1	pos 2	pos 3	pos 4
LD					
	4-letter words	455	444	454	474
	7-letter words	459	453	472	518
RD					
	4-letter words	516	509	507	508
	7-letter words	510	512	510	523

Figure 1 Doppler curves for two representative participants

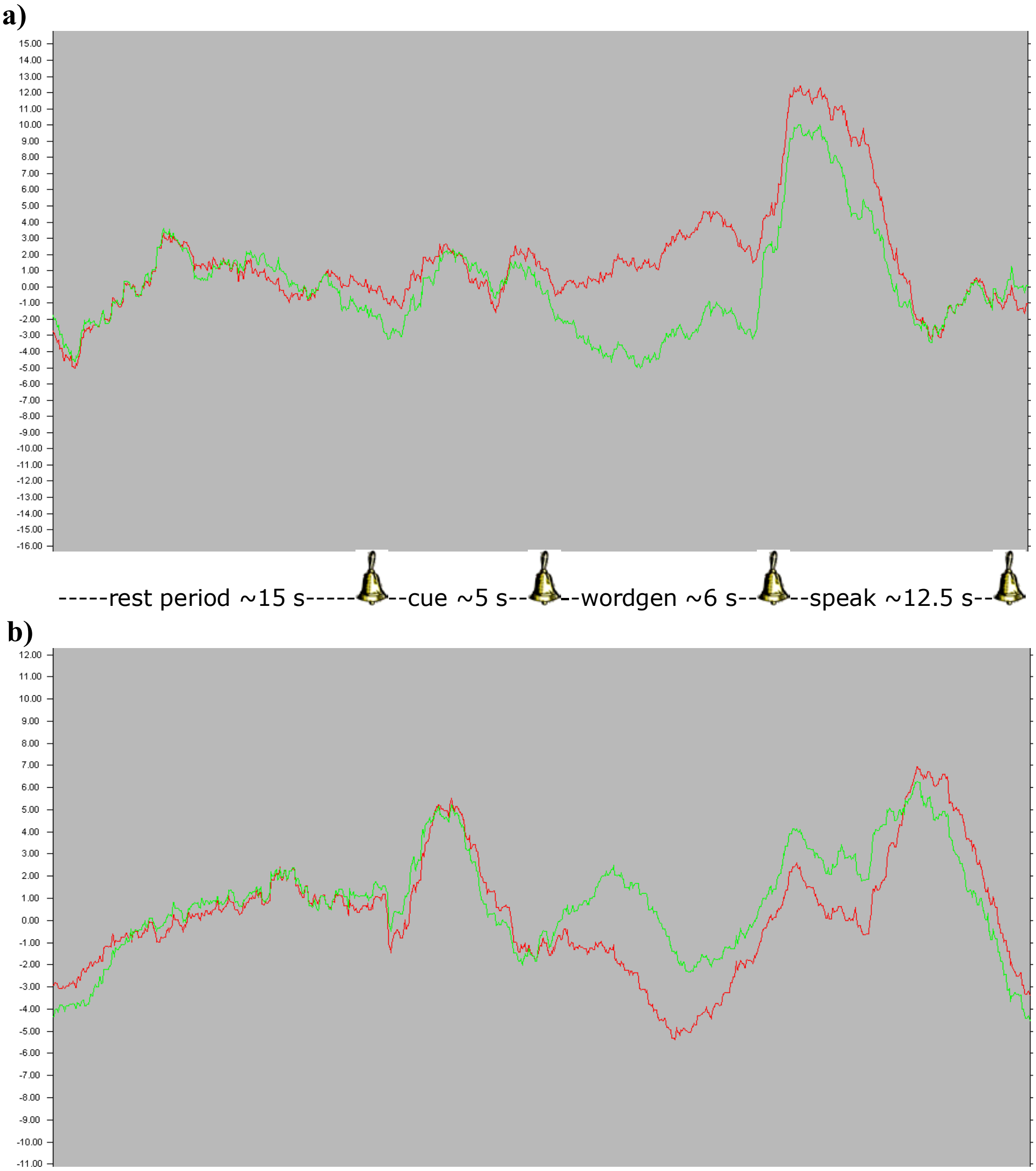


Figure 1 Doppler curves for two representative participants. Average curves for CBFV changes in the left and right MCAs throughout the different experimental phases. Green = *right* MCA; Red = *left* MCA **a)** a clear increase in CBFV in the left MCA during the *wordgen* phase indicates typical left hemisphere language dominance for this individual. fTCD_LI +5.84 **b)** atypical language dominance is illustrated through an increase in CBFV in the right MCA. fTCD_LI -4.25.

Figure 2 OVP design

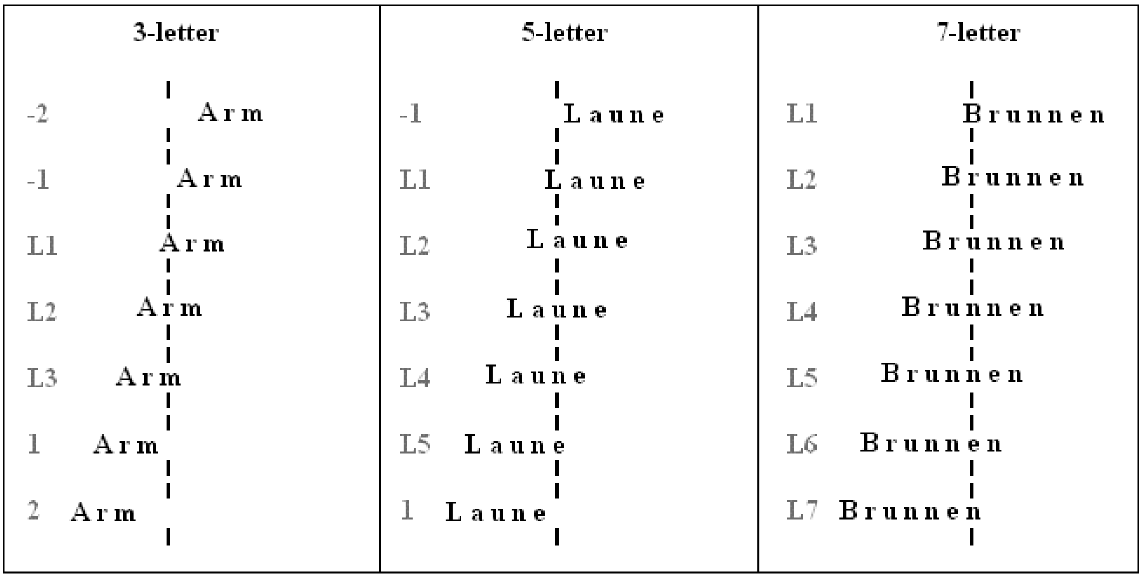


Figure 2 OVP design. Words of all lengths were presented at 7 possible fixation locations (positions 1-7) shifted horizontally across the screen. Participants had to name the word as fast as possible.

Figure 3 OVP curves for 3-, 5- and 7-letter words for the OVP task in Experiment 1

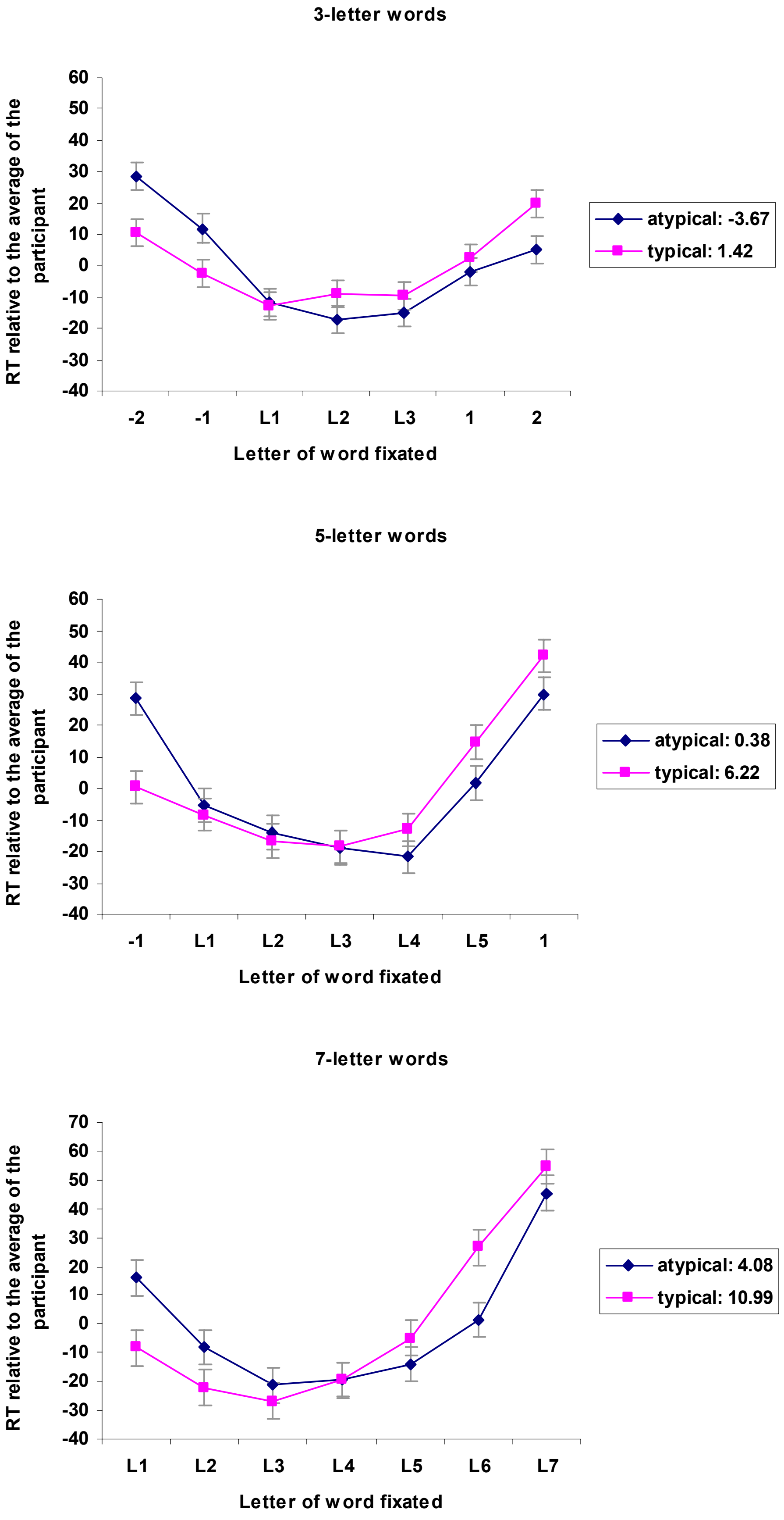


Figure 3 OVP curves for 3-, 5- and 7-letter words for the OVP task in Experiment 1. **typical:** Mean OVP curves for the group of left hemisphere dominant participants, with OVP slopes of *1.42*, *6.22* and *10.99* for 3-, 5- and 7-letter words. **atypical:** Mean OVP curves for the group of right-dominant participants, with OVP slopes of *-3.67*, *0.38* and *4.08* for 3-, 5- and 7-letter words. Intervals indicate the standard errors of the means, based on the MSe of the interaction between laterality group and viewing position.

Figure 4 Scatter plot averaged over all word lengths (Experiment 1)

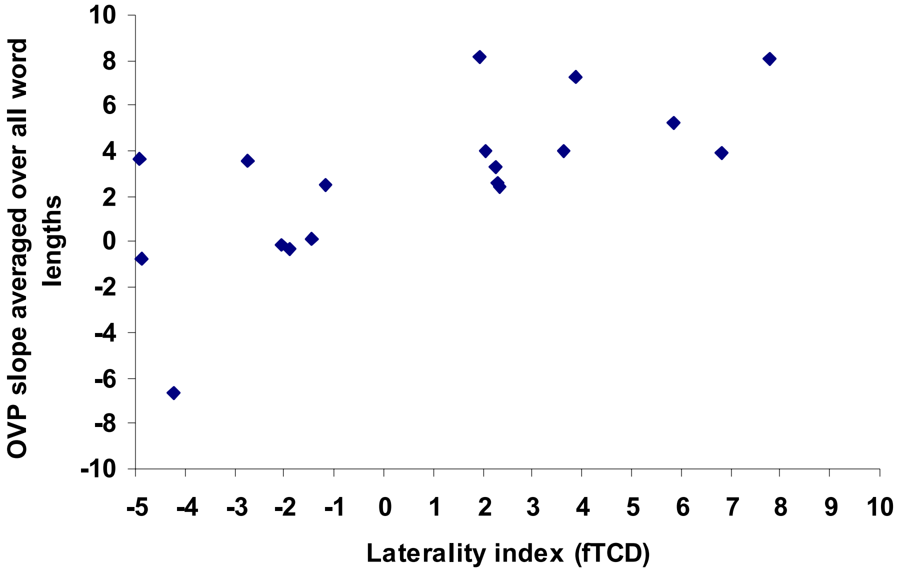
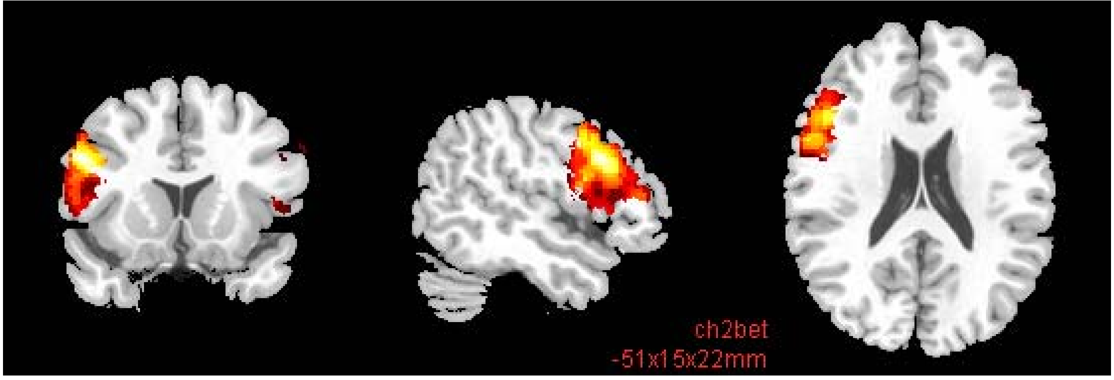


Figure 4 Scatter plot averaged over all word lengths (Experiment 1). fTCD derived laterality indices are compared with the average slopes of the OVP curves .

Figure 5 Language lateralization in two distinct groups

a)



b)

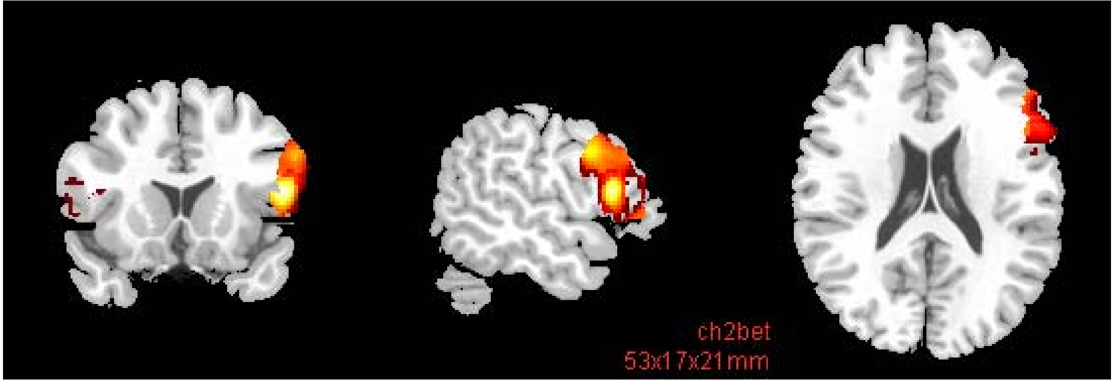


Figure 5 Language lateralization in two distinct groups. **a)** Mean image in ROI for the four individuals with strongest left hemisphere dominance (coronal, sagittal and axial slices at MNI coordinates: x = -51, y = +15, z = +22). **b)** Mean image in ROI for the two individuals with strongest right hemisphere dominance (coronal, sagittal and axial slices at MNI coordinates: x = 53, y = +17, z = +21).

Figure 6 OVP curves for 4- and 7-letter words for the OVP task in Experiment 2

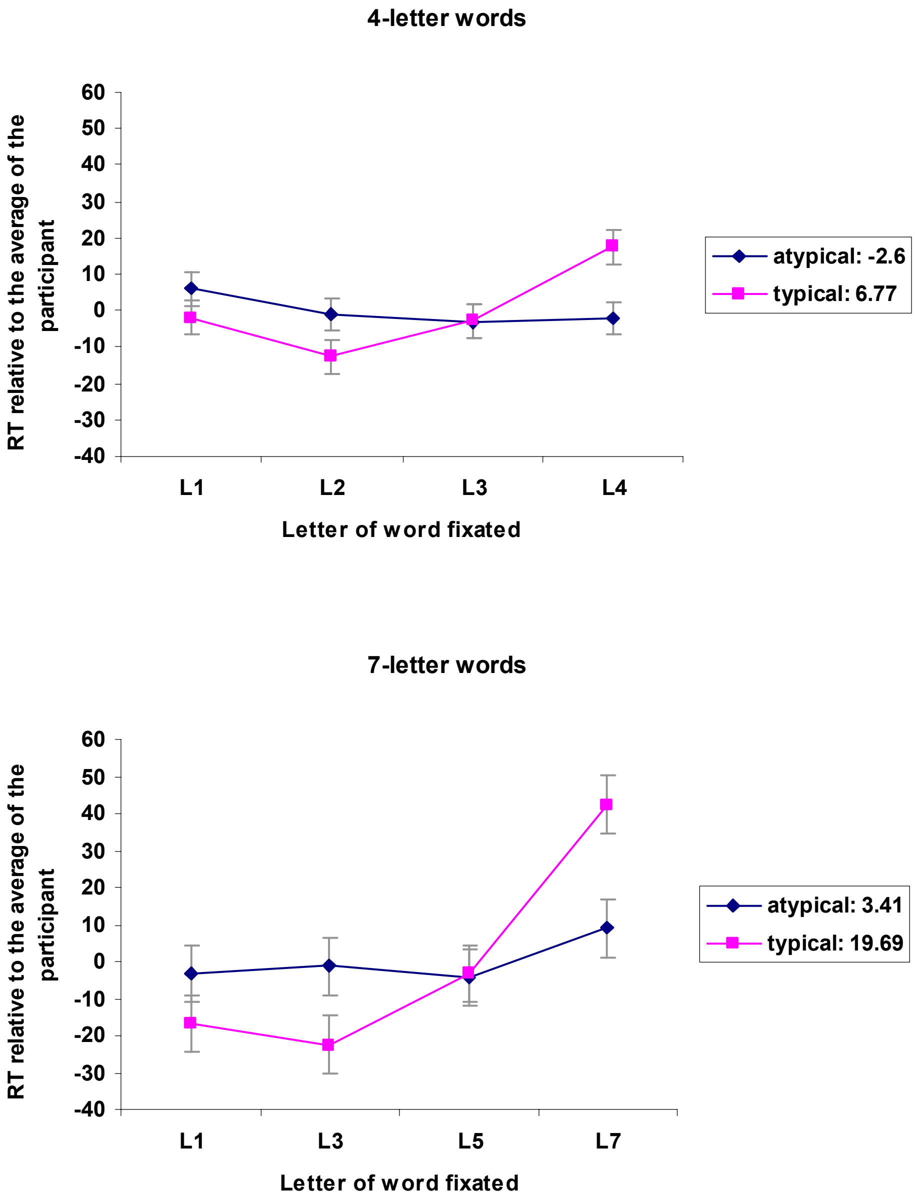
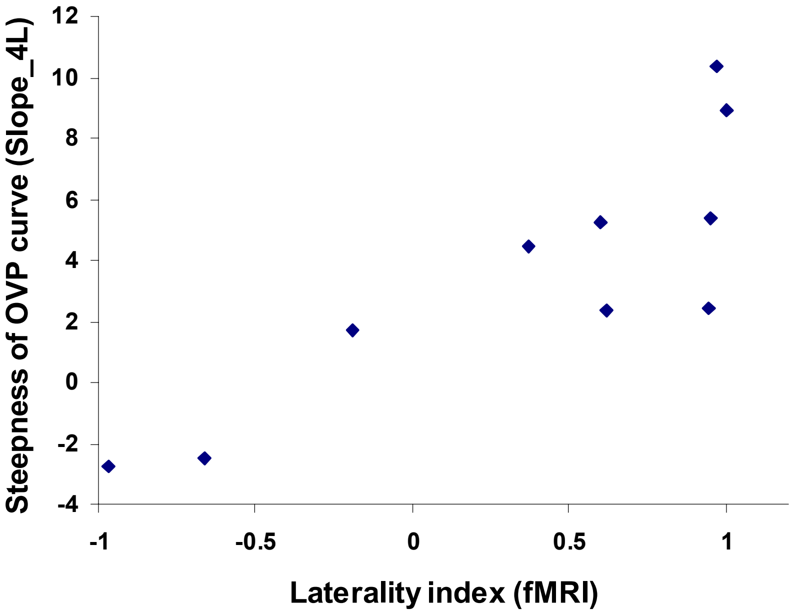


Figure 6 OVP curves for 4- and 7-letter words for the OVP task in Experiment 2. **typical:** Mean OVP curves for the four individuals with strongest left hemisphere dominance, showing a typical OVP effect with the fastest reaction time on fixating the second letter for both 4- and 7-letter words. **atypical:** Mean OVP curves for the two individuals with strongest right hemisphere dominance, depicting an atypical OVP effect with RTs decreasing towards the fourth letter for 4-letter words and towards the third letter for 7-letter words. Intervals

indicate the standard errors of the means, based on the MSe of the interaction between laterality group and viewing position.

Figure 7 Scatter plots (Experiment 2)

a)



b)

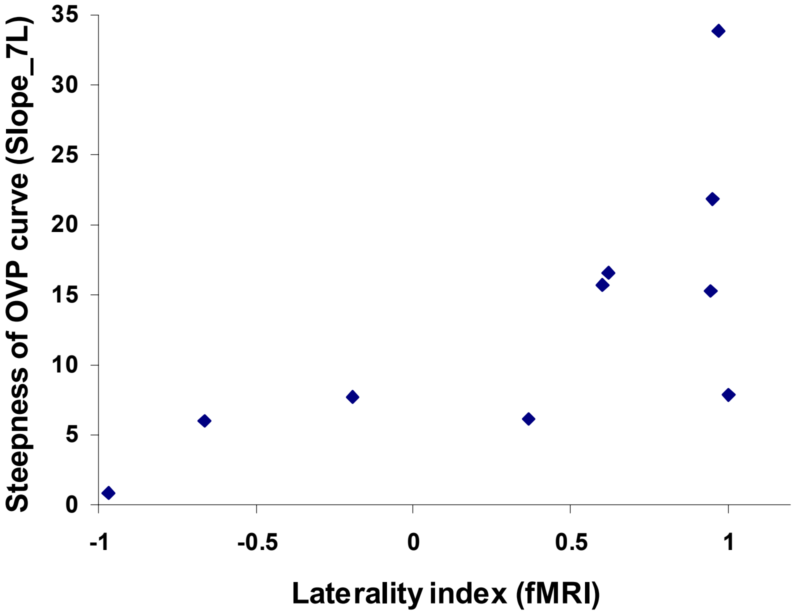


Figure 7 Scatter plots (Experiment 2). Laterality indices calculated upon fMRI data are compared with the slopes of the OVP curves resulting in a significant positive correlations r = 0.85 for 4-letter words **(a)** and r = 0.70 for 7-letter words **(b)**.