Visual Word Recognition in the Fovea

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Our brain is made to work well,
not to be understood well.
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Chapter 1: Introduction
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The complexity of mechanisms underlying reading is easily overlooked. Readers hardly notice that interpreting the black symbols their eyes are currently scanning requires many unconscious and conscious processes that are executed at an amazing speed. Even researchers studying the recognition of visually presented words have to focus on subprocesses because research questions cannot address the whole reading process at once. Studies investigate for example how we encode the letter order of a word, if we need to know how a word sounds before we can access its meaning, etc. Most visual word recognition models start by explaining the reading process from a higher processing level, i.e. from the moment linguistic material has reached the brain. This makes them biologically less than complete. This dissertation examines low-level mechanisms that influence central word recognition from the moment the letters fall on the eye. In particular, the presented studies investigate what happens when letters fall on the fovea, i.e. the central part of the eye where most detailed information is perceived.

This introductory chapter first describes the anatomy of the eye and gives an overview of the brain areas involved and the terms that are necessary for fully understanding the remaining chapters. The second part addresses two visions of interhemispheric communication during foveal word recognition, namely the Bilateral Projecting Theory (BPT) and the Split Fovea Theory (SFT). Two models have explicitly incorporated a split fovea, but have different views on how and when letters are reunited to words: The late integration split fovea model of Shillcock, Ellison and Monaghan (2000) and the early integration account of Whitney (2001). The final part of Chapter 1 will discuss critiques that have been raised against SFT research. From Chapter 2 on, five studies are presented that give an answer to some of the questions raised by the vivid debate between the split fovea and bilateral projecting theory. Chapter 2 refutes the critiques about the methodology of previous split fovea studies. Chapter 3 describes a behavioral and neuroimaging study in which left-handers with typical and atypical language speech dominance were identified. The same sample took part in a neuroimaging reading task reported in Chapter 4. As such, their reading and speech lateralization could be compared. In Chapter 5, right-handers were added to the left-handed sample and evidence was found in favor of the split fovea account under strict methodological settings. Finally, the consequences of a split fovea for
Building blocks of reading: From fovea to cerebrum

Basic pathways: From fovea to v1

When light is projected on the eye, it first reaches the cornea and the pupil (see Figure 1). Visual information is then sent through the lens to the retina at the back of the eye. The outer layer of the retina that is furthest away from the cornea contains about 126 million light-sensitive photoreceptors. About 120 million of them are the so-called rods, responsible for vision in weak light. Cones distinguish blue, green and yellow colours and discriminate fine details. The highest density of cones can be found in the central part of the retina where the thickness of the layers gradually decreases into a pit: The fovea. Hence, sharpest vision can be obtained when visual information falls on the fovea. Parafoveal (up to 5 degrees of visual angle on each side of a central fixation; Yu, Balaratnasingam, Cringle, McAllister, Provis and Yu, 2010) and peripheral vision (beyond the parafovea) is more limited than foveal viewing due to several factors that decline with larger eccentricity, e.g. cone density (Osterberg, 1935; Curcio, Sloan, Kalina & Hendrickson, 1990; cited in Anderson, Mullen & Hess, 1991). At 2° from central fixation, acuity already decreases to 50% (Millodot, 1960, cited in Lindell & Nicholls, 2003).

Figure 1. Anatomical organization of the eye, with indications of the parts relevant for this dissertation.
Eyes are constantly making small and rapid movements (saccades) alternated with rests of about 200-300 ms (fixations) during reading exactly to make letters fall on the central fovea (Rayner, 1998). There is no consensus about how wide the fovea exactly is. Estimates vary from 0.5° (Wyatt, 1978), over 2° (Rayner, 1998; Lavidor & Walsh, 2004) to the most commonly accepted 3° (Bourne, 2006; Bunt, Minckler & Johanson, 1977; Jordan, Paterson & Stachurski, 2008; Lindell & Nicholls, 2003) and 5° (Cohen, 1987), but many studies do not mention any values. In addition, the fovea is often distinguished from the foveola, which is the avascular centre of the fovea with the highest cone density peak of about 150 000 cones/mm² (Cohen, 1987; Hogan, Alvarado, & Esperson Weddell, 1971, cited in Yu et al., 2010). All in all, the boundaries of the eye parts are established by convention rather than by microstructural measurements. Individual differences in the cell structure of the eye (e.g. due to eye length) partly explain this inconsistency (Perry et al., 1990; Li, Tiruveedhula & Roorda, 2010). It is therefore advisable to cautiously make statements about the relative areas of the retina, rather than dividing the eye into subparts on the basis of absolute borders\(^1\). Moreover, it is hard to estimate to what extent tissue in the layers in front of the fovea scatter light (Cohen, 1987).

The photoreceptors in the outer layer of the retina discussed above are nerve cells that send neural electrical signals to the inner layers of the retina (Figure 2). Rods and cones synapse with bipolar, amacrine and horizontal neurons, which in turn are connected to the ganglion cell layer. The axons of the ganglion cells form the optic nerve and from there on, signals are sent to the brain (Cohen, 1987; Leff, 2004; Willoughby, Ponzin, Ferrari, Lobo, Landau & Omidi, 2010).

\(^1\) For simplicity, the term fovea will be used throughout this dissertation to refer to the most central part of vision. An estimate of 3° will be taken to refer to this region, as it is the most widely used estimate in the literature relevant for the presented experiments. However, 3° is not considered as an absolute or precise value.
Figure 2. The three layers of the retina: The outer layer consists of photoreceptors, the two inner layers contain bipolar, amacrine and horizontal cells that synapse with ganglion cells. Source: Dowling and Boycott, 1966

Not only does visual information first have to reach the back of the retina in the eye before processes at the front of the eye can take place, the same remarkable organization holds for visual processing in the brain. Visual information is first sent to the visual cortex, which is situated at the very back of the brain. Before it arrives there, it first undergoes some changes and needs to travel via different pathways.

Figure 3 shows that the nasal optic fibers of each retina (the fibers to the side of the nose) cross at the optic chiasm, whereas the temporal optic fibers go to the ipsilateral hemisphere. The left optic tract (carrying information from the left side of each retina) then goes to the left Lateral Geniculate Nucleus (LGN) in the thalamus and the right optic tract passes the right LGN. There are two important layers that are most apparent in the LGN: (1) The magnocellular (M) layer, originating from 10% of the retinal ganglion cells called parasol cells and responsible for luminance contrast, and (2) The parvocellular (P) layer, which receives input from 80% of the retinal ganglion cells called midget cells and is sensitive to chromatic contrast with high spatial frequency and low temporal frequency (Baseler & Sutter, 1997). Cells projecting to the P-pathway are presumably more present in the fovea relative to M-ganglion cells and the P/M ratio

[^2]: Recent studies assume that the remaining 10% of ganglion cells are bistratified cells, projecting to the so-called koniocellular layers of the LGN. Their precise function remains to be explored, but they have been linked to the blue-on receptive fields in the LGN of macaques (Szmajda, Grünert, & Martin, 2008).
decreases with increasing eccentricity (Baseler & Sutter, 1997; Dacey & Petersen, 1992). After the LGN, the optic tracts change into a range of fibers, the optic radiation, that lead to the primary visual cortex (V1, Brodmann Area [BA] 17, striate cortex). This whole organization makes information from the left visual field (LVF) fall onto the visual cortex of the right hemisphere (RH) and information from the right visual field (RVF) will initially be projected to the left hemisphere (LH). The result is a mirror-reversed projection of the information received by the retinae.

![Diagram](image.png)

Figure 3. Anatomical organization of the visual system, showing that light falling on the retinae is contralaterally sent to the primary visual cortex (V1) via the Lateral Geniculate Nuclei (LGN): Information from the left visual field (LVF) is sent to the right hemisphere (RH), whereas information from the right visual field (RVF) is projected to the left hemisphere (LH). Source: Brysbaert, Cai and Van der Haegen (in press)

Finally, visual information can be further processed by V2 (complex shapes), V3 (orientation and angles), V3A (motion and direction integration), V4 (colour discrimination), V5 (movement) and V6 (depth perception; Carter, 2009). Following V1 processing, information can again be sent over two parallel pathways: The upper dorsal “where” pathway when temporal
frequency is more important than spatial frequency and the lower ventral “what” pathway for object recognition rather than action guiding (Carter, 2009).

**Basic pathways: From v1 to language-related areas**

Once visual information is detected by V1, different brain areas for higher-order processing come into play. There is no strict one-to-one mapping between cognitive functions and anatomical regions (Mesulam, 1990; Price & Friston, 2005). Functions are rather represented in a distributed network of connected areas. It is therefore beyond the scope of the present dissertation to provide an exhaustive overview of language-related brain areas. Only the two most relevant areas for the studies described in the following chapters will be presented: The ventral occipito-temporal area known to be involved in the recognition process of reading and Broca's area, activated during language production. In contrast to lower-level reading processes, it is generally accepted that these areas are lateralized in the human cortex. The third part of this section will discuss cerebral asymmetry and the anatomical structures corpus callosum and anterior commissure that regulate interhemispheric transfer between the two hemispheres (Figure 4).

![Figure 4](image)

*Figure 4.* Panel A shows the most relevant language-related brain areas for the current dissertation. Broca’s area in the frontal lobe is generally assumed to contain the pars opercularis (Brodmann Area [BA] 44) and pars triangularis (BA 45). Studies have claimed that it may also include part of BA 6 (the premotor cortex and Supplementary Motor Area [SMA]), the pars orbitalis (BA 47) and the insula, that lies deeper in the brain than the pars triangularis. On Panel B, the C-shaped corpus callosum can be seen.
Reading and the ventral occipito-temporal area

Cohen et al. (2000) were the first to name one specific region that is indispensable for reading letter strings. They situated the crucial area in the left ventral occipito-temporal sulcus and named it Visual Word Form Area (VWFA). By means of functional Magnetic Resonance Imaging (fMRI), event-related potentials (ERPs) and a behavioural task, they identified the spatial and temporal organization of word and nonword reading. As expected on the basis of the above described visual organization, activation contralateral to the stimulated visual field was activated in the first stages. Up to 160 ms post-stimulus in the ERP-study, contralateral activation was observed. It was related to the extrastriate occipital areas (assumed to correspond to V4) by the high spatial resolution in fMRI. From 180 ms on, activation patterns were similar for LVF and RVF stimuli: The VWFA was then activated in the left hemisphere only. The lexical difference between words and nonwords began to emerge from 220 ms. Cohen et al. concluded that the occipito-temporal VWFA is an exclusive region that is activated more by letter strings than by any other form of visual information. Other studies added to this that the VWFA is active regardless of case, font, script (letters vs. characters such as in the Chinese script), reading direction, word length, etc. (Cai, Paulignan, Brysbaert, Ibarrola & Nazir, 2010; Dehaene, 2009; Dehaene et al., 2004; McCandliss, Cohen & Dehaene, 2003). Laurent Cohen, Stanislas Dehaene and colleagues admit that also other regions are activated during reading, but claim that there is no other area that is exclusively active when recognizing letter strings.

Braet, Wagemans and Op de Beeck (2012) recently further explored the nature of the VWFA. They ran an fMRI study in which subjects were asked to judge the fonts or line drawings of letter strings and pictures in a one-back task (i.e. pressing a button when two consecutive trials contain the same stimulus). Activation patterns could distinguish between individual words but also between objects, showing that the VWFA is not only dedicated to word recognition. On the other hand, orthography turned out to be the driving factor of response patterns when correlating subsets of scans from the different conditions: The correlation of a word with orthographically similar words (defined as number of overlapping letters) was as high as the correlation of a word with itself and significantly higher than correlations with orthographic dissimilar words. Semantic similarity (defined as being synonyms or not) did not have an impact on the correlations, nor did lexical status as the results were confirmed for pseudowords. Objects could
also be distinguished in the nearby lateral occipital control region, but only the VWFA was influenced by orthography, leading Braet et al. to conclude that this could be evidence in favor of the neuronal recycling theory (Dehaene, 2009; Dehaene & Cohen, 2007). According to this view, the VWFA developed as a region specialized for reading as a specific form of object recognition, in which the recognized units grow larger from a letter level over bigrams to short words when moving from the posterior to the anterior part of the VWFA (Dehaene et al., 2004).

Cathy Price, Joseph Devlin and colleagues have questioned the claim that the VWFA is specialized for reading, because the activation depends on the task used, and the area can also reflect other cognitive processes (Devlin, Jamison, Gonnerman & Matthews, 2006; Duncan, Pattamadilok & Devlin, 2010; Price & Devlin, 2003, 2011; Twomey, Kawabata Duncan, Price & Devlin, 2011). For example, damage to the left ventral occipito-temporal cortex mainly impairs object naming and not reading. As stated before, functions that are located in a certain area are also interacting with a network the area belongs to (Kherif, Josse & Price, 2011; Price & Friston, 2005), calling into question the plausibility of a region that is uniquely dedicated to a function.

Twomey et al. (2011) illustrated the flexibility of the VWFA in two fMRI lexical decision tasks: (1) In an orthographic task, participants had to decide whether letter strings that formed words (e.g., brain) or pseudohomophones (e.g. brane) were existing English words or not; (2) In a phonological task, they had to judge whether pseudohomophones (e.g., beest) and pseudowords (e.g., beal) sounded like existing words or not. Pseudohomophones always elicited the most activation in the VWFA, regardless of whether participants were focusing on visual or nonvisual, phonological features. More activity was observed in the phonological task compared to the orthographic task. If the VWFA was independent of other language-related regions related to meaning and phonology such as Broca’s area, activity should have increased with increasing importance of orthographic features.

**Production and Broca’s area**

(C)overtly pronouncing a word is a second important language-related process. Only Broca’s area will be described in more detail as a region involved in speech production, because it is one of the most relevant areas for the present dissertation.
The surgeon Paul Broca became known as the first to localize human speech production in the third convolution of the left frontal lobe, even though Marc Dax already presented similar results in 1836 at a conference (Broca, 1865; M. Dax, 1836; G. Dax, 1865; see Buckingham, 2006 for a detailed historic description of Broca’s area). From 1861 to 1863, Broca noticed that twenty-five patients that could maximally utter one monosyllabic word all had a lesion in the left frontal lobe. The first patient Leborgne, known as Tan because that was the only word he could pronounce, became the most famous case with Broca’s aphasia.

Today, the network subserving language production is much more complicated than Broca described it, although the term Broca’s area is still used to refer to the core region in the inferior frontal lobe. First, the boundaries of Broca’s area cannot be well-defined. BA44 (approximately corresponding to pars opercularis) and BA45 (approximately pars triangularis) are classically seen as Broca’s area. They are known to be involved in semantic, phonological and syntactic processes (Amunts et al., 2004; Heim, Eickhoff & Amunts, 2008). Several authors have claimed that other parts should also be included in Broca’s area (e.g., Hagoort, 2006, 2009). For example, BA47 (approximately pars orbitalis) has also been found to be involved in semantic processing (De Carli et al., 2007) and the processing of fine-grained temporal sequences (Vuust, Roepstorff, Wallentin, Mouridsen, & Østergaard, 2006). The insula should be included because it is involved in speech motor control (Ackermann & Riecker, 2010). Finally, BA6 (the supplementary motor area and premotor area) is responsible for the programming of overt speech (Shuster & Lemieux, 2005).

The second remarkable difference with Broca’s initial theory is that we now know that language production is not always localized in the left hemisphere. The localization of language processes is important to minimize the loss of linguistic abilities when brain tissue has to be removed, for example to limit cortical spreading of epileptic seizures. The most widely used language lateralization test is the Wada-test. In this invasive test, one hemisphere is anaesthetized by injecting one of the internal carotid arteries with sodium amobarbital. The hemisphere that is active while the subject can still speak aloud is indicated as the dominant one (Wada & Rasmussen, 1960). Due to its invasiveness, alternative behavioural and/or neuroimaging paradigms have been developed. Their validity was often tested by comparing the lateralization patterns with the results from the Wada-test (e.g., Binder et al., 1996; Hirata et al.,
Knecht et al. (2000) tested 188 right-handed and 138 left-handed healthy volunteers in a word generation task while measuring their blood flow velocity in the middle cerebral arteries by means of functional transcranial Doppler sonography. Subjects saw a letter presented on a computer screen for 15 s and were asked to silently generate as many words as possible starting with the target letter. This verbal fluency test is nowadays used in many lateralization studies and leads to activity in Broca’s area (e.g., Abbott et al., 2010; Badzakova-Trajkov, Häberling, Roberts & Corballis, 2010; Cuenod et al., 1995; Friedman et al., 1998). Knecht et al. calculated lateralization indices based on the maximum difference of blood velocity in the left and right hemisphere. They found a left hemispheric dominance for most participants, with a clear interaction between speech dominance and handedness: The left hemisphere was dominant in more than 95% of right-handers, while the percentage decreased to about 75% in left-handers. The exact prevalence of typical left speech lateralization and atypical right or bilateral dominance differs across studies, but most studies reported results that were in line with those of Knecht et al. (e.g., Pujol, Deus, Losilla & Cadevila, 1999; Szaflarski et al., 2002). More details about the methodology of determining language lateralization indices will be described in the large-group study of Chapter 3, comparing laterality indices from an fMRI silent word generation task with a behavioural picture and word naming task.

Finally, it should be noticed that most researchers use the concept language lateralization to refer to lateralization of speech production and thus mainly allude to the functional asymmetry in Broca’s area. However, even if production and in particular phonological and articulatory processes are seen as the most lateralized human function (Kosslyn, 1987; Hughdal & Westerhausen, 2010), various linguistic subprocesses such as speech perception, reading, prosody etc. can all have deviating regional lateralization indices. These variations cannot be captured by one global index used as an indication of the language dominance of an individual (Seghier, Kherif, Josse & Price, 2011). We therefore calculated lateralization indices from an fMRI lexical decision task in Chapter 4, in addition to the silent word generation indices presented in Chapter 3.
Cerebral asymmetry and the corpus callosum

Cerebral asymmetries always represent a relatively higher contribution of one of the hemispheres over the other in a particular cognitive function. Even though the brain halves have been depicted as a complementary dichotomy (e.g., the verbal LH vs. the non-verbal RH, the spatial RH vs. the non-spatial LH), there is no function that is fully lateralized. Lindell (2006) reviews the involvement of the RH in language acquisition, visual word recognition, lexical processes such as phonology, orthography and imageability, and also syntax and semantics. In other words, the RH is partly involved in linguistic subprocesses that are typically ascribed to the LH. How much cooperation between the hemispheres is demanded, depends on the function and task being executed (Boles, Barth, & Merrill, 2008). If it is so important for the two brain halves to work together, how can they communicate fast enough to ensure a sufficient fluency of cognitive functions?

By far the most important anatomical structure for interhemispheric communication is the corpus callosum. Other commissures, including the anterior commissure and dorsal and ventral hippocampal commissures among others, can also transfer information, but will not be discussed further as they are not involved in the interhemispheric transfer of visual information. The corpus callosum is the largest white matter fiber tract connecting many homologue areas of the cortex. It is ten times larger than the anterior commissure and contains 200 to 800 million axons (Banich, 1995). The corpus callosum forms the C-shaped structure seen on a mid-sagittal brain slice (Figure 4). It is divided in different parts that form independent pathways. There are many homotopic fibers, connecting homologue cortical areas, and heterotopic fibers, that have a lower density because they connect an area to a non-homologue set of cortical areas in the contralateral hemisphere (Kennedy, 1991 cited in Hoptman & Davidson, 1994). The dorso-ventral dimension of the corpus callosum mainly connects cortical areas on the medio-lateral axis (Innocenti, 1994). The antero-posterior dimension connects areas in a topographic way: The anterior part, called the genu, connects prefrontal regions, the middle part (truncus) interconnects motor and somatosensory brain areas, more posterior lays the isthmus that connects auditory cortices and the most posterior splenium connects dorsal parietal and occipital regions.

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3 The anterior commissure does transfer visual information in primate nonhumans, but not in humans (Foxman, Oppenheim, Petito & Gazzaniga, 1986).
splenium is most important for this dissertation as it connects the visual areas. Dougherty, Ben-Shachar, Bammer, Brewer and Wandell (2005) showed that the inferior-anterior part of the splenium receives projections from the ventral V1 (upper visual field) and that the more superior-posterior splenium is connected with the dorsal V1 (lower visual field). Saenz and Fine (2010) reported a similar organization by following the track of water molecules in the white matter corpus callosum with the diffusion-weighted imaging technique. They additionally showed that fibers from central V1 (< 4° across the vertical meridian) project to the superior-anterior part of the splenium, whereas fibers from the more peripheral visual field (up to 18°) project to the inferior-posterior splenium. Several studies reported differences in the size of the corpus callosum according to handedness and gender, although there is a remarkable inconsistency in the literature. For example, Luders et al. (2010) argued that larger callosal fibers in the anterior and posterior midbody were related to more weakly pronounced handedness preferences, independent of the direction of handedness. Josse, Seghier, Kherif and Price (2008) however reported larger corpus callosum sizes for subjects with stronger left frontal language dominance, even when controlling for handedness, gender and age. The associations are generally estimated to be rather small, as confirmed by Cherbuin, Luders, Chou, Thompson, Toga and Anstey (2012).

There is also disagreement in the literature on how the corpus callosum functionally establishes interhemispheric communication. Studies not only tested healthy subjects, but also split-brain subjects in which the corpus callosum and/or the anterior commissure were removed to prevent the spread of seizures in epileptic patients (Gazzaniga, 2000; Sperry, 1974). Two visions came forward. First, the corpus callosum can be seen as an excitatory body that integrates information from the two complementary brain halves. The excitatory view was supported by studies testing split-brain patients because they experience difficulties when information that is projected to different hemispheres has to be integrated. For example, they cannot name objects (with the speech dominant LH) when they are in their left hand (projecting to the RH). Thus, hemispheres have to share and not suppress information, in line with an excitatory function of the corpus callosum. A similar view was proposed in the callosal relay model by Moscovitch (1970). He stated that only one hemisphere can perform a function and that information has to be transferred if the stimulus first arrived in the non-dominant brain half. Another view considered the corpus callosum to execute inhibition to the other hemisphere in order to leave the dominant
hemisphere undisturbed. Evidence was found in favor of three possible inhibition mechanisms (Chiarello & Maxfield, 1996): (1) Interhemispheric suppression in which one hemisphere prevents parallel processing in the other hemisphere; (2) Isolation when processes in the other hemisphere are not suppressed but the transfer of the information is prevented; or (3) Interference when irrelevant or conflicting information is sent to the other side to decrease the efficiency. Evidence suggesting that the corpus callosum rather functions according to one of these three inhibitory mechanisms than according to excitatory processes comes from the dichotic listening task, in which subjects hear two simultaneously presented sounds (one in each ear) and have to report which sound they heard best. Most LH dominant subjects show a right ear advantage for processing speech while their performance is not decremented by the information in the left ear (with stronger contralateral pathways to the RH than ipsilateral projections to the LH). This suggests that the corpus callosum can block information coming from the other side (Bloom & Hynd, 2005; Milner, Taylor & Sperry, 1968 cited in Hugdahl, 2005).

The fact that the debate about the exact functioning of the corpus callosum is still going on can be ascribed to at least four impeding factors. First, the need for interhemispheric transfer varies across tasks. The corpus callosum cannot be labeled as an excitatory or inhibitory structure without considering the amount of conflicting information in the task being executed. For example, Barca et al. (2011) presented words that had to be named either in LVF or in RVF. Their magnetoencephalography results showed a RVF/LH advantage for word naming for both RVF and LVF presentations: The LH received the RVF words directly, but also showed strongest activation for LVF words after they were transferred from the RH. This is in line with an excitatory view of the corpus callosum, as both hemispheres need to work together to process one word. If Barca et al. would have presented a distractor word in the other visual half field of the target word, they would most likely have observed more inhibition, as the corpus callosum then had to transfer conflicting information. Second, interhemispheric communication also varies across cognitive functions so that different parts of the corpus callosum can act according to different excitatory or inhibitory mechanisms. Even closely related functions can already induce differences. Hemond, Kanwisher and Op de Beeck (2007) for example found stronger contralateral activation for objects than for faces, implying that the spatial location of the stimulus had most influence on the callosal transfer time when objects had to be recognized. In addition, connections can be excitatory at a neurochemical level, but inhibitory when performing
in a network of inhibitory neurotransmitters and neurons (Bloom & Hynd, 2005). Finally, studies with split-brain patients or patients with epilepsy make it hard to generalize callosal mechanisms to the total population because the brain can compensate for lesions by developing an alternative functional organization (Thivard et al., 2005). The following chapters will focus on a specific part of interhemispheric transfer of information, namely whether transfer is needed for foveal word processing.

**Information from the fovea: Split or duplicated?**

The description of basic pathways from the fovea to V1 made clear that the visual system is contralaterally organized: Information on the left side of a fixation point will initially be projected to the right V1 and information from RVF will be sent to the left visual cortex. The question whether the same organization holds for centrally presented stimuli was raised decades ago. It was assumed that information falling on a small strip along the vertical meridian is available in both hemispheres. This duplication implies a discontinuity at about 1.5° along fixation. Nasotemporal fibers within that area do not cross but overlap, or ipsilaterally and contralaterally projecting cells intermingle in the small strip. This view is called the Bilateral Projecting Theory (BPT). However, the BPT is not fully accepted, as later studies pointed to flaws in the original evidence. As an alternative, the Split Fovea Theory (SFT) states that the same mechanism holds within the central 3° and beyond that border, namely that visual information projected onto the fovea is (precisely) split and sent to the contralateral V1. The main aim of this dissertation is to pit the two visions against each other. Remember though that the borders of the fovea cannot be defined with an accuracy of one minute of arc (i.e. 1/60\textdegree{} of a degree of visual angle) and that there is not even consensus of the exact boundaries at the level of visual degrees. We will consider the most accepted 3° as definition of the fovea as this is the standard width taken in the relevant literature. The following introductory part reviews previous studies that provided direct or indirect evidence for the BPT and SFT. The overview does not aim to be exhaustive, but is restricted to the most important findings that outlined the debate.
Macular sparing in hemianopia patients

The earliest evidence favoring the BPT comes from the ophthalmologist Tatsuji Inouye who examined wounded soldiers in the beginning of the 20th century. He observed many soldiers with hemianopia (i.e. visual loss of either the LVF or RVF, often after a stroke or brain injury in a unilateral striate cortex) that preserved normal vision in the central fovea, a phenomenon called macular sparing. Inouye (1909, cited by Leff, 2004) attributed this preservation to a duplication of foveal information in LH and RH. So, normal foveal vision was maintained in these patients because the undamaged hemisphere receives all necessary information. Other researchers followed Inouye's reasoning, enforcing the belief in a BPT (e.g., Huber, 1962).

Years later, alternative explanations for macular sparing in hemianopia were put forward, weakening the BPT evidence. Previous experiments often let patients indicate whether they could observe a light spot presented in LVF or RVF. Studies that controlled fixation positions better discovered that their hemianopia subjects regularly made saccades towards the light spots presented in the undamaged field (Bischoff, Lang & Huber, 1995). Related to this, Reinhard and Trauzettel-Klosinski (2003) argued that the foveal sparing observation in Huber (1962) could have been due to light scattering. Patients may have been able to confirm the presence of stimuli not on the basis of recognition, but because scattering of the light flashes fell on preserved retinal areas.

A second alternative explanation for macular sparing is that many hemianopia patients show incomplete damage of the striate cortex and connections to it. The undamaged parts could lead to macular sparing in central vision. Unilateral visual loss is often caused by a stroke after arteries supplying blood to the occipital lobe are blocked by a blood clot. In many patients, branches of the crucial arteries for central vision are preserved. It is rarely the case that all arteries leading to the central part of V1 (four main branches of the posterior cerebral artery and the superior temporo-occipital sylvian artery coming from the middle cerebral artery; Leff, 2004) are blocked.
Finally, if central vision is preserved because of a bilateral representation in the visual cortex, then all hemianopia patients with unilateral damage should show macular sparing. This is not at all the case (Celesia, Meredith & Pluff, 1983, cited in Brysbaert, 2004; Trauzettel-Klosinski and Reinhard, 1998). Even patients with bilateral damage can preserve normal central vision (Symonds & MacKenzie, 1957).

**Anatomical evidence for the BPT**

A second line of evidence that made researchers believe in the BPT came from anatomical monkey studies that injected the retrograde transneuronal tracer horseradish peroxidase in different areas of V1. The tracer marks the pathway going to the LGN and goes retrogradely to the ganglion cells in the retina. Stone, Leicester and Sherman (1973) additionally sectioned part of the optic tracts of macaque monkeys to simulate hemianopia. They observed spared ganglion cells in a vertical strip of about 1° around the vertical midline. Similarly, Bunt, Minckler and Johanson (1977) saw traces of the marker in the ganglion cells on both sides around the fovea although horseradish peroxidase was unilaterally injected.

The main problem with this line of evidence is that it draws conclusions about the fovea based on ganglion cells. As can be seen on Figure 2, the foveal photoreceptors are only indirectly connected to ganglion cells via bipolar, amacrine and horizontal cells. The fovea itself does not contain ganglion cells. Synapses can be formed between a cone at the nasal side of the fovea and a ganglion cell at the temporal side (Leff, 2004).

Second, although the striate cortex of macaques have been shown to be similar to those of humans, research also pointed to differences between them so that these anatomical findings form no convincing data to prove the BPT in humans (Matsuno & Fujita, 2009; Sereno & Tootell, 2005). It definitely does not provide any evidence that functional processes such as reading are influenced by a bilateral representation of foveal information. More convincing anatomical evidence would be to show that not all nasal fibers cross at the optic chiasm, but that some of them continue on the ipsilateral pathway. Until now, no study has ever shown this. Nor was it ever proven that foveally presented visual stimuli have an extra representation in the occipital cortex (one on the contralateral side and one on the ipsilateral side) compared to
extrafoveally stimuli (one in the contralateral hemisphere). Tootell, Switkes, Silverman and Hamilton (1988) also failed to find evidence for bilateral representations in monkeys: They injected C2-deoxy-D-Glucose to see which part of V1 was visually stimulated. The eyes of the monkey were stabilized in this experiment and a measurement accuracy of 0.15° was reached. Tootell and colleagues did not observe a bilateral representation of their stimuli in the occipital cortex. Of course, human data would provide more convincing evidence than generalized conclusions from monkey studies.

**Split Fovea Theory: Information split along the vertical meridian**

**SFT research in split-brain patients**

The SFT claims that the vertical meridian is precisely split in the middle, so that extrafoveal and foveal stimuli in LVF are sent to RH and vice versa. One line of evidence favoring the SFT comes from split-brain patients (Corballis & Trudel, 1993; Fendrich & Gazzaniga, 1989; Fendrich, Wessinger & Gazzaniga, 1996). If foveally presented stimuli are split and contralaterally sent to the visual cortex they require interhemispheric communication. It is hypothesized that split brain patients are unable to recognize words in central vision, because their brain halves can no longer communicate with each other. The words in this experiment should of course be unpredictable on the basis of the letters on one side of fixation. The prediction was confirmed in two patients of Corballis and Trudel (1993): Performance was at chance level in a lexical decision task when the fixation point of a four-letter word was presented between the second and third letter, but parafoveal words and nonwords were correctly judged on at least 73% of the trials (Brysbaert, 1994a). BPT supporters have criticized this study (Jordan & Paterson, 2009), because fixation was not strictly controlled and because stimuli subtended 4° in total, exceeding a foveal area of 3°.

Fendrich and Gazzaniga (1989) did control eye fixation behavior and let their split-brain patient V.P. compare target line figures within the central 1° with parafoveal reference figures in the same or opposite visual half field (VHF). The reference line figure was presented 2.5° from the midline and before the target appeared. It remained on the screen during the 200 ms target presentation. V.P. was asked to judge whether the target and reference figures were the same or
not. Targets in the same field as the reference outperformed those in the opposite field. Fendrich and Gazzaniga concluded that these results were clearly in line with the SFT and against BPT. Although their accuracy scores on figures such as a square or asterisk tell nothing about the time course in reading, it is a clear and well-controlled indication for the SFT.

Fendrich et al. (1996) let split-brain patient J.W. judge whether the orientation of two bilaterally presented square wave gratings were the same or not, while eye fixations were again controlled. When the medial edges of the gratings were horizontally presented at 2° from central fixation, J.W. performed at chance level. A presentation duration of 2 s or 200 ms did not make a difference. Performance neither improved when the stimuli were 200 ms on the screen with their medial edges 1° from the vertical meridian. Only when stimuli were 1° close to the centre and presented for 2 s did performance raise above chance. In other words, only when the split-brain patient had 2 s time to transfer information about the orientation of the gratings could he extract sufficient information to make a similarity judgement. As reading requires much faster communication, it can be assumed that J.W. would not have duplicated representations of close stimuli that are fast and qualitative enough to be used in reading (Ellis & Brysbaert, 2010).

**SFT research in healthy subjects**

Many studies investigating visual lateralization make use of so-called visual half field tasks, in which reaction times to stimuli can be compared for different eccentricities away from the fixation point. One of the oldest tasks used is the Poffenberger paradigm (Poffenberger, 1912). In this paradigm, the participant is asked to press a button with his left or right hand as soon as a stimulus appears in the LVF or RVF (in the original Poffenberger task, light flashes were used as stimuli). An interhemispheric transfer time (IHTT) can then be calculated because hand motor responses are also contralaterally connected with motor areas. The IHTT in the Poffenberger task is the difference in reaction time between uncrossed and crossed conditions. Reactions to LVF stimuli with the left hand and to RVF stimuli with the right hand belong to the uncrossed condition because they do not require interhemispheric transfer of low-level processes. Crossed reactions are obtained when one has to respond with the right/left hand to respectively LVF/RVF information. In this case, transfer time is needed. Harvey (1978) applied the Poffenberger paradigm to the recognition of the stimulus O. His participants unimanually
responded to the location of the target by pressing a left or right button with their left or right hand (response mapping was counterbalanced throughout the experiment). He found an IHTT of 25 ms. This is remarkably higher than IHTTs observed with light flashes (about 2-3 ms, Brysbaert, 1994b), which is probably due to the somewhat more complex stimulus O compared to light flashes. Harvey observed the same results for stimuli presented 0.25° and 4° from fixation, which is in line with the SFT. Lavidor and Ellis (2003) also found the same reaction time patterns when comparing physical matching of letters (A-A) to abstract matching (A-a) for letters presented extrafoveally (2° from fixation) and foveally (0.4° from fixation). At both eccentricities, the physical task yielded faster times than the abstract task and was performed fastest when the stimuli were presented in the same visual half field, whereas the abstract task was carried out fastest when letters were presented across visual fields. Both Harvey (1978) and Lavidor and Ellis (2003) concluded that comparable transfer times within and outside the fovea indicate that there are similar processes going on at both eccentricities.

VHF tasks using more complex stimuli such as letters and words were promising as a paradigm for laterality research, but also as a cheap and fast noninvasive screening tool for language dominance determination when vocal responses are collected. A VHF task can give a first indication of language dominance before more clinical tests such as the Wada test are used. They were however criticized because VHF results can be modulated by attentional and perceptual effects (Bryden & Mondor, 1992). Bourne (2006) and Hunter and Brysbaert (2008) therefore formulated methodological recommendations to improve the reliability and validity of VHF tasks. An overview will be presented here; More details can be found in Chapter 3.

First of all, previous studies may not have found reliable IHTTs or LVF-RVF differences due to unilateral stimulus presentation. Bilateral stimuli combined with a central fixation point avoid an unequal difficulty and attention level in the two visual half fields. Second, the number of trials included in past studies did not suffice so that high variability in RTs and practice effects could have lead to unstable lateralization indices. Third, complex stimuli such as pictures and words in LVF and RVF should be matched instead of counterbalanced in order to maintain reliability at an individual level. The fourth recommendation was to use a stimulus presentation duration of 150 ms in order to avoid saccades towards the target and at the same time preserve a reasonable stimulus visibility. Further, a word task should only contain short words to restrict the
more natural RVF-advantage. A reading direction from left to right, the fact that the left hemisphere is the most common language dominant hemisphere and the word beginning superiority effect that increases with longer words all favor the RVF. Finally, Hunter and Brysbaert (2008) recommended naming latencies over reaction times of button presses when using the VHF task as language dominance indicator, because speech production is the most lateralized human function and the Wada test and most other tasks determining language laterality correlate best with this function.

Apart from the Poffenberger paradigm and VHF tasks, a third line of experiments supporting the SFT in healthy subjects made use of the different cognitive characteristics of the RH and LH. For example, word length has a larger influence on recognition in LVF compared to RVF (Bub & Lewine, 1988; Young & Ellis, 1985). Lavidor, Ellis, Shillcock and Bland (2001) therefore hypothesized that if the SFT is correct, varying the number of letters left to fixation should influence lexical decision latencies, whereas the number of letters at the right side of fixation should have no effect. Lavidor et al. used five- and eight-letter words with the same two initial or final letters. Participants were asked to fixate between the second and third initial or final letters. Word length indeed interacted significantly with the position of the shared letters: Latencies were only longer for eight-letter words than five-letter words when the fixation was between the second and third last letter. The eight-letter words then had six letters in LVF, compared to only three letters for the five-letter words. In a second control experiment, they replicated the word length effect in LVF and not in RVF for lateralized stimuli. This time, the position of shared letters did not affect RTs. Similar experiments were run testing the LVF effect of case alternation (Ellis, Brooks & Lavidor, 2005) and neighbourhood size (defined as the number of existing words when replacing one letter in the target word; Lavidor, Hayes, Shillcock & Ellis, 2004).
Finally, Brysbaert (1994a) argued that the dispute between BPT and SFT can easily be settled by using yet another paradigm: the Optimal Viewing Position task (OVP; O'Regan & Jacobs, 1992). In this task, words are presented between two vertically aligned fixation lines. The lines remain at the centre of the screen, while the position of the word is horizontally shifted so that the first, second, third etc. letter of the word is fixated on different trials (Figure 5). The OVP effect implies that there is an optimal fixation position whereby readers are fastest to name a word or to decide whether the presented stimulus is a word or nonword. O’Regan and Jacobs (1992) showed that this position is situated near the middle or slightly to the left of the middle of the fixated word. In a review article, Brysbaert and Nazir (2005) attributed the OVP to four factors: (1) Visual acuity decreases when the distance between fixation location and a letter increases; (2) The first letters of a word contain most information about the word identity; (3) Words are typically identified from the first part of the word so readers are more experienced at this location; and (4) Letters in the RVF are initially projected to the LH, which is the dominant language hemisphere for most readers. The last factor is what Brysbaert (1994a) discovered by comparing left and right speech dominant participants (identified on the basis of a VHF word naming, object naming and clockfase reading test). Participants named three-, four-, five-, seven-, and nine-letter words that were presented between two vertically aligned lines. Only the odd letter positions were included for the seven- and nine-letter words. Participants were told to fixate the gap between the lines that always stayed on the screen. To ensure central fixation, briefly presented digits between zero and nine followed by a mask had to be identified at random.
trials (Mean accuracy: 98%). Reading distance was approximately 57 cm (without head movement control), so that 1 cm equalled about 1°. Each letter had a width of 0.33°. Stimuli were presented for 160 ms followed by a mask of the same length as the target word. Every subject completed 15 sessions of 482 trials. Figure 6 shows the results: Subjects with typical left hemispheric dominance showed a larger word beginning effect than right dominants. When fixating at the beginning of a word, most letters fall in RVF and are sent to the LH. The time cost for transferring letters to the dominant hemisphere is thus limited for most readers if they are fixating at the first letters. In contrast, right dominants limit the transfer time when fixating more towards the end of a word. The OVP-curves are not reversed for the two groups, because the first three factors involved in the OVP effect mentioned above are the same for subjects with atypical dominance. In sum, Brysbaert (1994a) demonstrated that interhemispheric transfer is needed for foveally presented words, which provides support for the SFT.

![Figure 6](image.png)

*Figure 6. Results of the optimal viewing position paradigm in Brysbaert (1994a). The curves show the naming latencies for three-, four-, five-, seven- and nine-letter words. Source: Brysbaert (1994a)*

Visual Word Recognition in the Fovea
Hunter, Brysbaert and Knecht (2007) replicated Brysbaert's results for German three-, five- and seven-letter words. The main difference was that they estimated the language dominance of their participants in a more reliable way than the VHF tasks used in Brysbaert (1994a). Blood flow velocity was measured in a word generation task by using the functional Transcranial Doppler Sonography technique. Eight participants with a higher velocity in the right middle cerebral artery were classified as being right dominant, twelve others were left dominant. Again, the letter position with the fastest RTs was more towards the word end for the right dominants than for the left dominants, with a clearer difference in OVP curves for longer words.

**Recombining letters in a split fovea: Early versus late integration views**

Based on the evidence favoring the SFT, two models incorporating a split fovea in visual word recognition were presented in the literature. They both propose detailed mechanisms in order to explain how letters are recombined after an initial split. The Split fovea model of Shillcock, Ellison and Monaghan (2000) hypothesizes that the integration of visual information in the LVF/RVF is part of the word recognition process. This is called a late integration view. On the other hand, the *Sequential Encoding Regulated by Inputs to Oscillations within Letter units* or SERIOL model introduced by Whitney (2001) assumes that visual information is first integrated in the language dominant hemisphere, before word recognition starts. It is therefore called a model that supports the early integration view.

**Late integration view**

Shillcock et al. (2000) were the first to explicitly incorporate a split fovea and its consequences for visual word recognition in a model. They explicitly state that the fovea is initially precisely split at the anatomical level and that visual information is contralaterally sent to the visual cortex. The main assumptions of Shillcock et al.’s split fovea model are summarized below.
The most important claim is that part of the visual word recognition process takes place intrahemispherically. This claim is supported by different characteristics that have been assigned to the two hemispheres. For example, the LH is specialized in recognizing functions words (Mohr, Pülfmüller & Zaidel, 1994). In addition, the LH is the dominant hemisphere for most language-related functions, but the RH is also capable of recognizing words. These are two examples of arguments Shillcock et al. refer to as an indication that word recognition is partly performed by both hemispheres and that it is rather unlikely that the recognition process can only start when all information is gathered in the dominant LH. In order to facilitate word recognition, the labor should be divided over the hemispheres. After all, interhemispheric transfer has been estimated to cost about 20 ms per letter. In other words, the two hemispheres have to interact in order to achieve word recognition, and this interaction can involve orthographic, semantic and phonological information, but the integration of information is part of the recognition process. The model therefore belongs to a late integration view.

In addition, Shillcock et al. simulated how much information is needed to determine the position of a letter. They argue that readers only have to know the identity of the letter being fixated, the visual field the letter belongs to, and the identity of the left and right outmost letter. Overall, 98.6% of 1- to 21-letter words included in the CELEX database (Baayen, Pipenbrock & Gulikers, 1995) could be recognized based on information about the two letters around central fixation or one letter left from fixation in the case of word lengths with an odd number of letters. When adding the identity of the outmost letters, the recognition rate even raised until 99.8%. Shillcock et al.’s model hence suggests that the optimal viewing position is situated at or near the centre of a word and is influenced by the position of the letters that are most informative for the word.

**Early integration view**

Shortly after Shillcock et al. (2000) published their late integration view, Whitney (2001, see also Whitney, 2008; Whitney & Berndt, 1999; Whitney & Cornelissen, 2008) presented the
SERIOL model as an alternative view on how letters are recombined after an initial split.\textsuperscript{4} The model consists of five layers that will be described in more detail.

At the edge or retinal level, an acuity gradient represents the activation from the primary visual cortex. Activation is highest at the fixation point and decreases symmetrically with increasing eccentricity. The SERIOL model assumes that this layer is retinotopically organized (i.e. central fixation positions correspond to central locations in V1) and that it is split at the vertical meridian.

The second layer is called the feature layer. It consists of nodes or groups of neurons that fire when they recognize their feature (e.g. an oblique line / as part of the letter W) on a preferred location with less activation when the input deviates from the optimal feature location. The SERIOL model assumes that there is no overlap around the vertical meridian and that feature nodes in LH and RH have different characteristics. The translation of the acuity gradient into a locational gradient at the feature level hence occurs differently for features in LVF and RVF. In RVF/LH, the acuity gradient already has the correct decreasing slope for the locational gradient (i.e. for languages read from left to right). In LVF/RH, the acuity gradient must be inverted in order to obtain the highest activation for the leftmost features (see Figure 7, Panel A). This inversion is achieved by stronger bottom-up, excitatory edge-to-feature connections in LVF compared to RVF. In addition, lateral inhibitory connections inhibit features from left to right. The first letter thus fires first, because it does not receive any inhibition. As the locational gradient now corresponds to the ordinal position of letters in a word, it creates the positional gradient.

At the interhemispheric level, RH features inhibit LH features until information from LVF is transferred from RH to the dominant LH (i.e. for most readers processing language dominantly in the LH; see Figure 7, Panel B). Features are then reunited in the dominant hemisphere with features firing from left to right.

\textsuperscript{4} Recently, a revised SERIOL model has been developed (Whitney & Marton, submitted). Whitney (2011) summarizes the SERIOL2 model. However, because the main mechanisms supporting an early integration view are comparable to those in the SERIOL(1) model and have no influence on the experiments presented in this dissertation, only the original model will be described.
Figure 7. Two assumptions made at the feature level in the SERIOL model. Panel A shows the locational gradient: The acuity gradient of the letters left from fixation is inverted so that the first letter receives the highest activation, followed by the second, etc. Panel B illustrates the interhemispheric inhibition assumption: LVF/RH features temporarily inhibit RVF/LH features. As a result, the LVF letters receive the highest activation and are recognized first. LVF/RVF = left/right visual field respectively; LH/RH = left/right hemisphere respectively.

Letter nodes are firing in the third layer of the SERIOL model. Previous layers caused a decrease of input activation from left to right. At the letter layer, excitability increases over time, so that the first letter can fire based on its high input level and the following letters can fire subsequently because of increasing excitability. Lateral inhibition between letters ensures high activation for the processed letter, but decreases in time so that the next letter can fire from the moment that its received inhibition can be overruled. Letters only fire once, because they receive inhibition after being activated. Studies often observed a final-letter advantage, implying faster/better recognition of the final letter than what would be expected based on a monotonically decreasing activation gradient. The SERIOL model explains this by the fact that the final letter does not receive any lateral inhibition from letters to the right.

The bigram layer is the fourth layer in SERIOL. It consists of open bigram-nodes, i.e. bigrams contain two letters in the same order as in the target word but the letters are not necessarily next to each other. Bigrams of contiguous letters do receive more activation than bigrams of letters further away from each other, e.g. WO will be highly activated in the target WORD, compared to WD that receives much weaker activation. Edge bigrams introduced in Whitney (2008) are bigrams that uniquely code the outmost letters, e.g. *W will fire for the first letter of WORD.
The bigram nodes activate word nodes, taking into account the relative weights of the bigrams as described in the previous paragraph. Lateral inhibition is also present at the word level, so that words compete to be activated and recognized.

**The BPT returns: Criticisms on SFT research**

The studies and models discussed above suggest that both foveal and extrafoveal word recognition need interhemispheric transfer. However, previous SFT research was recently criticized, mainly by researchers of Leicester University. Their main concern is the accuracy of measurements. The critiques can be summarized in four points and were published in eight articles (Jordan & Paterson, 2010; Jordan, Paterson & Kurtev, 2009; Jordan, Paterson & Stachurski, 2008, 2009; Jordan, Paterson, Kurtev & Xu, 2009, 2010a, 2010b; Paterson, Jordan & Kurtev, 2009) and one review (Jordan & Paterson, 2009). The four critiques will be briefly described; they are discussed in more detail in Chapter 2.

First, fixation location was not always strictly controlled. If the SFT claims that the fovea is precisely split, one should be able to prove that subjects are fixating exactly at the intended location (either between two letters or at a letter). High accuracies on a secondary fixation task such as briefly presenting a digit (used in Brysbaert, 1994a and Hunter et al., 2007) do not suffice according to Jordan and colleagues, because it does not ensure adequate fixation on every trial and does not guarantee that the subjects’ fixation was stable throughout a trial.

Second, stimuli often exceeded the foveal borders of 1.5° on each side of fixation. Therefore, reported SFT results can mimic the contralateral projection of parafoveal stimuli because they fall at least partly in the parafovea. In Brysbaert (1994a) only the three- and four-letter words fell within the area of 1.5° away from fixation.

The third main critique on previous SFT research concerns the fixation disparity between the two eyes. The left and right eye can differ temporally (e.g., the peak velocity of saccades; Williams & Fender, 1977) and spatially (different landing positions; Heller & Radach, 1999). Heller and Radach (1999) asked their participants to read passages with six lines per screen. They found that binocular disparity could lead to fixation differences up to two characters. This can contaminate the results of SFT research according to Jordan et al. Paterson, Jordan and
Kurtev (2009) demonstrated that in a lexical decision of five-letter words and nonwords about 50% of the fixation did not fall on the same letter that subtended 0.25°, hence concluding that not only in reading but also in single word processing disparities regularly occur. They however note that this had no influence on the results: Mean RTs for word decisions were 532 ms when fixations were aligned, 529 ms for crossed fixations, and 532 ms for uncrossed fixations.

Finally, naming overstates SFT results according to Jordan and colleagues because recognition of visual words can be done bilaterally, while pronouncing them evokes unilateral activation of the language production dominant hemisphere. Jordan et al. (2008) recommend the Reicher-Wheeler task as an alternative. After flashing a word for a few milliseconds, subjects are asked to make a forced choice between two letters that could have been present at a given position. For example, if snow was the stimulus, the alternatives can be an n or h at the second position because both form an existing word (snow and show). An accuracy rate of 66% is pursued.

Jordan et al. strengthen their critiques by their failure to replicate the word length effect found in the fovea and parafovea (Lavidor et al., 2001; see the section above). Jordan, Paterson and Stachurski (2009) found no interaction between the fixation position and the position of shared letters in the same five- and eight-letter words used by Lavidor et al. They point to the extremely small size of the stimuli used in that study: Letters only occupied 0.10°, which makes it highly unlikely that participants were fixating properly. In a second experiment, Jordan et al. (2009) adjusted the letter size to explore the word length effect with improved stimulus perceptibility. Letters now subtended 0.14°. Note that this is still only half the width Rayner and Pollatsek (1989) recommend for normal reading (i.e. 0.25° per letter). An eye-tracker revealed that eye fixations were on the intended letter in only 52% of trials. Despite this fixation control, the word length effect was still not found for the foveal lexical decisions. In the third experiment, an eye contingent technique ensured that stimuli only appeared when participants made a stable fixation for 400 ms. Stimulus duration was limited to 50 ms in order to avoid saccades. Again, no word length effect was found. Jordan and colleagues concluded that SFT research cannot be replicated when the methodology is strictly controlled and that previous evidence in favor of the SFT is hence invalid.
In sum, the debate between the BPT and SFT is still going on, leaving the question whether interhemispheric communication is needed in foveal word recognition unanswered. Many experiments favoring the BPT could be refuted or clarified by alternative explanations, whereas experiments favoring SFT were criticized because of methodological shortcomings. The following chapters will present a series of experiments that were set up to decide between the BPT and SFT.

Outline of this dissertation

The main aim of this dissertation was to investigate how visually presented words are recognized in the fovea. If the SFT is correct, information is initially split and contralaterally sent to the cortex. This can have major implications on our understanding of reading, as it implies that the two hemispheres have to communicate in order to recognize words.

Chapter 2 presents three experiments that evaluated the methodological critiques raised by Jordan and colleagues. The OVP paradigm was tested by letting right-handers (assumed to be LH dominant for speech) name six-letter words under varying methodological settings. A baseline OVP curve was obtained, using the same settings as previous studies did (e.g., Brysbaert, 1994a). This curve was compared to naming latencies when (1) The right eye of the participant was monitored or controlled by means of an eye-tracking device, (2) Stimuli were carefully controlled so that they did not exceed the foveal boundaries defined as 1.5° on either side of fixation, and (3) Viewing was monocular instead of binocular. Only main effects were observed, indicating that stricter methodological settings increased the overall reaction times. Fixation position latencies did not interact with the modifications introduced in the experiments. We therefore concluded that the critiques raised by Jordan et al. point to origins of noise in previous SFT studies.

In Chapter 3, left-handers with typical left and atypical right speech dominance were recruited. Two behavioral VHF tasks were used as a first screening method in 250 students. Naming latencies for pictures and words presented in the LVF/RH and RVF/LH were compared, taking into account methodological recommendations mentioned in Bourne (2006) and Hunter et al. (2008). Fifty participants were then scanned during an fMRI silent word generation task and a...
lateralization index was calculated for Broca’s area. The behavioral results could not perfectly predict the language lateralization measured in fMRI, but the two indices did correlate considerably. Depending on the index threshold taken, we showed that the visual half field technique can be a useful language lateralization indicator.

Chapter 4 extended the results of Chapter 3, by scanning participants of the same sample during a lexical decision task. This time, the lateralization index was calculated based on the activity in the ventral occipito-temporal region, known as the visual word form area. Word generation and lexical decision indices correlated significantly, indicating that the hemisphere dominant for speech is also dominant for reading for the majority of participants. However, reading turned out to be less lateralized, as more than half (31/57) of the left-handers did not show a clear lateralization pattern in favor of one or the other brain half.

The main hypothesis of this dissertation was tested in Chapter 5. Naming latencies of left and right speech dominant participants were compared in an optimal viewing position paradigm. Three-, four-, and six-letter words were presented between two vertically aligned fixation lines. On different trials, their position was shifted horizontally across the screen so that participants named all words while fixating at all possible letter positions. Eyes were binocularly monitored to fulfill the methodological requirements raised in the literature about SFT research, and trials on which participants did not fixate properly were excluded from the analyses. Speech lateralization had a clear influence on the naming latencies: Left speech dominants named the words fastest when fixating at the word beginning, whereas the optimal viewing position of right speech dominants was situated more towards the word end. The effect was found for all word lengths. Only the split fovea theory and not the bilateral projecting theory predicts faster naming times when most letters directly fall onto the dominant hemisphere.

Finally, Chapter 6 investigated whether the need for interhemispheric transfer can also be observed in more natural text reading. The left and right speech dominant participants now read word series containing ten words of six- or eight-letters long and three texts involving newspaper articles, short stories and country descriptions. Speech lateralization indeed had an influence on the initial landing positions: Right speech dominants landed on average further in a word than left speech dominants (on average 0.41 letters in the word series task, 0.23 letters during text reading). The effect was caused by the difference in speech lateralization;
Handedness was not driving the effect as the reading behavior of both left dominant right- and left-handers differed from the fixations of the right speech dominants, but no differences were observed within the left dominant group. The lexical decision lateralization indices obtained in Chapter 4 could not explain any variability, presumably because reading was more bilaterally distributed than speech in the current sample and was thus unable to differentiate two clearly separated groups. The influence of speech lateralization on fixation durations was negligible, in line with the hypothesis that when eyes move during reading is determined by high-level linguistic characteristics such as word frequency and context predictability, whereas the position of the eyes is modified by low-level factors such as saccade length, word length and, as we can now add, speech lateralization.


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Visual Word Recognition in the Fovea


Chapter 2: The Split Fovea and the Leicester critique: What do the data say?
According to the Split Fovea Theory (SFT) recognition of foveally presented words involves interhemispheric transfer. This is because letters to the left of the fixation location are initially sent to the right hemisphere, whereas letters to the right of the fixation position are projected to the left hemisphere. Both sources of information must be integrated for words to be recognized. Evidence for the SFT comes from the Optimal Viewing Position (OVP) paradigm, in which foveal word recognition is examined as a function of the letter fixated. OVP curves are different for left and right language dominant participants, indicating a time cost when information is presented in the halffield ipsilateral to the dominant hemisphere (Hunter, Brysbaert, & Knecht, 2007). The methodology of the SFT research has recently been questioned, because not enough efforts were made to ensure adequate fixation. The aim of the present study is to test the validity of this argument. Experiment 1 replicated the OVP effect in a naming task by presenting words at different fixation positions, with the experimental settings applied in previous OVP research. Experiment 2 monitored and controlled eye fixations of the participants and presented the stimuli within the boundaries of the fovea. Exactly the same OVP curve was obtained. In Experiment 3, the eyes were also tracked and monocular viewing was used. Results again revealed the same OVP effect, although latencies were remarkably higher than in the previous experiments. From these results we can conclude that although noise is present in classical SFT studies without eye-tracking, this does not change the OVP effect observed with left dominant individuals.
**Introduction**

When we perceive visual stimuli, input from the left visual field (LVF) is initially projected to the right hemisphere (RH), whereas input from the right visual field (RVF) is sent to the left hemisphere (LH). This well-known organization of the visual system is a consequence of the fact that the fibers from the nasal hemiretina cross at the optic chiasm whereas those from the temporal hemiretina do not (see Gazzaniga, 2000, for a review).

There has been a lot of debate, however, about what happens in central vision, and what consequences this has for visual word recognition. The issue is whether visual information in the fovea, the center of the visual field that subtends about 3 degrees of visual angle, is split or not. For many years, projection of foveally presented stimuli was thought to be bilateral. According to this vision, the same information is sent to both hemispheres when words are fixated centrally (e.g., Bunt, Minckler, & Johanson, 1977). However, an increasing number of researchers have reported evidence in favor of the Split Fovea Theory (SFT) (e.g., Brysbaert, 1994a; Brysbaert, 2004; Brysbaert, Vitu, & Schroyens, 1996; Ellis, Brooks, & Lavidor, 2005; Harvey, 1978; Haun, 1978; Hunter, Brysbaert, & Knecht, 2007; Lavidor, Ellis, Shillcock, & Bland, 2001; Lavidor & Walsh, 2004; Martin, Thierry, Démonet, Roberts, & Nazir, 2007). According to this theory, letters presented to each side of the fixation position are projected to the contralateral hemisphere and interhemispheric communication is needed for the recognition of centrally fixated words.

One line of evidence for the SFT came from research on the Optimal Viewing Position (OVP) effect (Brysbaert, 1994a). The OVP effect is obtained when participants are asked to read words at different fixation positions (O’Regan & Jacobs, 1992). For example, a six-letter word is presented such that the first, the second, the third, the fourth, the fifth, or the sixth letter falls between two vertically aligned fixation lines (Figure 1). Participants are asked to name the word or to perform a lexical decision on the letter string. Generally, processing times are fastest when words are fixated in the first half of the word compared to fixations in the second half. More specifically, the fastest reaction times are observed when fixations fall slightly to the left of the word center, whereas words fixated at the last letter position take the longest time to be recognized.
Figure 1. Example of the OVP-paradigm with the Dutch six-letter word ballon (meaning balloon). On different trials (according to a Latin-square design) the word is presented in such a way that each letter position is fixated. Participants have to name the word as fast as possible.

The OVP effect is the outcome of four factors (Brysbaert & Nazir, 2005): (1) the first letters contain the most information about the identity of the word; (2) visual acuity decreases when the distance between the fixation location and the letter increases; (3) the eyes tend to land on the first half of the word, so that readers have more practice processing words from this location; and (4) fixating the left side of a word makes most letters fall in RVF and hence most information is sent directly to the LH, the language dominant hemisphere for the majority of readers.  

Evidence for the hypothesis that brain laterality is involved in the OVP-effect was obtained by comparing the OVP effect for participants with left and right hemisphere dominance (Brysbaert, 1994a; Hunter et al., 2007). For left dominant participants, factors 1, 3 and 4 result in a word beginning advantage and, hence, we can expect to find a hefty processing cost when

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5 About 75% of left-handed and 95% of right-handed university students have left hemisphere language dominance; the others have bilateral or right hemisphere dominance for language processing (Hunter & Brysbaert, 2008b; Knecht et al., 2000).
participants are forced to fixate on the last letters. In contrast, for right dominant participants factor 4 results in a word end advantage, so that the OVP curve is expected to be flatter for these individuals. The OVP curve of right dominant participants is not the mirror image of that of the left dominant participants, because laterality is only one of the four factors affecting the curve; the higher informativeness of the word beginning is the same for left and right dominant readers.

To test this prediction, Hunter et al. (2007, Experiment 2) assessed the laterality of speech production in left-handed individuals by means of fMRI. On the basis of this measure, groups of left and right dominant students were identified. These participants were subsequently asked to name four- and seven-letter English words. Stimuli were presented following the OVP paradigm (Figure 1). As predicted by SFT, participants with left hemisphere dominance were faster at naming words fixated at the beginning; in contrast, participants with right hemisphere dominance showed a flat OVP curve (Figure 2).

![Figure 2. OVP curves for naming seven-letter English words in participants with left language dominance (light gray line) and right language dominance participants (dark gray line). The left dominant participants show a strong word beginning superiority effect, whereas the right dominant participants show a flat curve. The difference between both groups is in line with SFT. Given that left dominant participants are better at extracting verbal information from RVF, they have an advantage when fixating on the first letters. In contrast, right dominant participants have an advantage for fixation at the end of a word, because they are better at extracting verbal information from LVF. Source: Hunter et al. (2007, Figure 6)
The finding of Figure 2 indicates that interhemispheric transfer is needed for foveal word recognition: There is a time cost when letters of a word are initially sent to the non-dominant hemisphere. If the letters of the foveally presented words had been sent simultaneously to both hemispheres, the OVP would have been the same for left and right language dominant participants.

However, the OVP-evidence for SFT has recently been criticized by a group of researchers working at the University of Leicester (e.g., Jordan & Paterson, 2009; Jordan, Paterson, & Stachurski, 2008, 2009). Their objections concern the methodology used in previous SFT research. Four shortcomings have been singled out: (1) the fixation location was not adequately controlled; (2) the size of the foveally presented stimuli was not appropriate; (3) binocular viewing may have contaminated the results; and (4) the naming task may have exaggerated the need for interhemispheric transfer.

The first shortcoming mentioned by the Leicester group concerns the lack of fixation control. Given that SFT sees a sharp divide between LVF and RVF it is critical to know where exactly participants are looking at the moment the word is presented. According to Jordan et al., merely instructing participants to fixate the designated location is insufficient to guarantee proper fixation. Even adding a fixation control task, such as asking participants to name briefly presented digits that appear on some of the trials (e.g., Brysbaert, 1994a; Hunter et al., 2007), does not fulfill the requirement. The only way to properly control fixation positions is by using an eye-tracking device.

The second Leicester criticism involves the fact that the stimuli used in OVP research often exceed the area of foveal vision. In order to increase the precision of the measurements, letters in OVP research typically cover an angle between one third and one half of a degree (in most OVP experiments participants are free to choose their position in front of the computer screen, so that there is some variation in the distances between the eyes and the screen). Specifically, with respect to the data reported in Figure 2 it can be objected that the 7-letter words extended an area of more than 1.5°, so that fixations on the first and the last letter made some letters fall outside the bilaterally projecting fovea. As a result, findings such as those of Figure 2 cannot differentiate between interhemispheric transfer in foveal and parafoveal vision. At the same time, Jordan et al. question other research for making their stimuli too small, which
in their view magnifies the issue of good fixation control. For instance, they criticized the five-letter word stimuli used by Lavidor et al. (2001) because these only subtended 0.5°, whereas five letters usually occupy 1.25° in reading (Rayner & Pollatsek, 1989). According to Jordan et al., it is unlikely that such small stimuli can be fixated adequately.

A third point of criticism made by the Leicester group concerns the fact that binocular viewing was used during testing. Given that the two eyes may not look at exactly the same location, binocular viewing may provide the cerebral hemispheres with different information from around the fixation location. Such disparities could undermine the conclusions of SFT research.

Finally, Jordan et al. criticized the use of the naming task to investigate SFT. Given that word production is the most lateralized brain function, data with the naming task are likely to result in exaggerated differences between left and the right dominant participants. In their own words (Jordan et al., 2008, p.741): “because speech production in right-handed individuals is lateralized to the LH, using naming as a measure of perceptual performance is likely to produce a spurious advantage for stimuli projected to the LH that does not reflect hemispheric asymmetries in perception.”

Although it is tempting to comment on each of the criticisms now, we will refrain from doing so until the General Discussion, as it seems critical first to empirically evaluate the impact of the objections. In particular, although the Leicester group has repeatedly shown that fixations are less than adequately controlled by simple instructions, they have never tested the effects of this confound on the OVP curve. Similarly, although they have repeatedly criticized the stimuli for being either too large or too small, they have never examined the consequences of differences in letter size on the OVP effect. So, the first thing to do is to evaluate the Leicester critique properly. Is it the case that the OVP effect for left dominant participants will become flatter when eye fixations are controlled tightly, when the size of the words is made smaller, and/or when participants are forced to look monocularly?

A yes-answer to any of the above questions would force the SFT-proponents to reconsider their position. No-answers to all the above questions would seriously undermine the Leicester critique and would mirror what happened with Jordan’s previous critique about
inadequate fixation control in studies with parafoveal word presentation in the visual half-field (VHF) paradigm. After having published several papers showing that eye fixation is not well controlled by simply instructing the participants to look at the fixation stimulus in the center of the visual field (e.g., Jordan, Patching, & Milner, 1998) Jordan and Patching (2005) decided to directly compare free vision and proper fixation control with an eye-tracker. Contrary to their previous claims about the possible dire consequences of sloppy fixation control in the VHF-paradigm, they observed that fixation control had no effect at all on the RVF advantage in the word recognition task they used, forcing them to conclude that (p. 686): “both techniques produced the same pattern of visual field effects, indicating that the demands of fixating a fixed central point do not confound performance with lateralized words.” Of course, the main difference between parafoveal and foveal word presentation is that faulty fixations potentially have a much higher impact in the latter condition than in the former. Therefore, it is necessary to test the Leicester critique anew for the OVP curve.

In the experiments reported below we repeated the OVP studies reported by Brysbaert (1994a) and Hunter et al. (2007) and introduced various degrees of fixation control. In addition, we made the stimuli small enough to fit within the foveal area and used monocular viewing. According to the Leicester critique these changes should result in a reduction of the asymmetry in the OVP curve. Because precise assessment of language dominance requires fMRI testing of left-handed participants (Hunter & Brysbaert, 2008b), we limited our studies to right-handed individuals who in addition were right eye dominant (needed because we tracked the right eye). The default expectation for these participants is that they will be left hemisphere dominant and, indeed, none of our participants showed the flat curve typically observed in right dominant participants (Brysbaert, 1994a; Hunter et al., 2007; Hunter & Brysbaert, 2008a).

**Experiment 1**

In the first experiment, we ran a naming task with six-letter words using the experimental settings previously applied. Stimulus size was not adjusted to the boundaries of the foveal visual area, participants were asked to sit at a reading distance of approximately 60 cm, and they were allowed to watch binocularly. As in Brysbaert (1994a) and Hunter et al. (2007), on a limited
number of trials a briefly presented digit had to be named to ensure that the participants were fixating properly. As such, we aimed to obtain an OVP curve for left-hemisphere dominant participants similar to the one shown in Figure 2 (light gray line), which could serve as the baseline for Experiments 2 and 3.

Method

Participants

Participants were twelve students from Ghent University (9 female, 3 male; mean age: 21.1). All were native Dutch speakers, had normal or corrected-to-normal vision, and were naive with respect to the purpose of the experiment.

Prior to participation, the students were asked to fill in a questionnaire about their preferences for handedness (Oldfield, 1971), eyedness, earedness and footedness (Porac & Coren, 1981). They were asked to use 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, 1994b). Additionally, participants were asked to perform the Miles (1930) test of eye dominance. In this test participants are asked to look at a distant target through a small opening formed by putting together the thumbs and index fingers of both hands. Then, binocular viewing through the opening is alternated with monocular viewing by each eye. The eye that sees the target when it is opened is selected as the dominant eye. The Miles test was administered to determine the participant’s eyedness by means of an unconscious sighting task, which controls for contamination of handedness. Only students that were right-handed and showed right eye dominance based on the Miles test were accepted for participation. Table 1 shows the mean ratings reported in the questionnaire.

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6 For example, participants may indicate a right eye preference for sighting down a rifle, simply because they prefer to have their right hand on the trigger (Porac & Coren, 1976).

7 Two students reported to be left eye dominant in the questionnaire. We did not exclude these participants as they showed right eye dominance when performing the more objective Miles test. Moreover, the OVP effect in the repeated measures ANOVA’s across participants (F1) and across items (F2) for the six fixation positions remained the same without these participants [F1(1.88,16.91) = 15.64, MSE = .00048, p < .001; F2(4.62,1062.39) = 7.20, MSE = .0057, p < .001]
TABLE 1.
Mean self-ratings (and SDs) of handedness, eyedness, earedness and footedness as reported by the twelve participants included in each of the Experiments of this study

<table>
<thead>
<tr>
<th>Measure</th>
<th>Experiment 1</th>
<th>Experiment 2</th>
<th>Experiment 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hand</td>
<td>2.69 (0.63)</td>
<td>2.70 (0.76)</td>
<td>2.67 (0.88)</td>
</tr>
<tr>
<td>Eye</td>
<td>1.88 (1.84)</td>
<td>2.04 (1.57)</td>
<td>2.02 (1.79)</td>
</tr>
<tr>
<td>Ear</td>
<td>2.21 (0.99)</td>
<td>2.35 (0.96)</td>
<td>2.40 (1.09)</td>
</tr>
<tr>
<td>Foot</td>
<td>2.25 (0.86)</td>
<td>2.50 (0.88)</td>
<td>2.15 (1.70)</td>
</tr>
</tbody>
</table>

*Note. N = 12 in each Experiment. Scale: -3 = strong left preference; 3 = strong right preference.

Materials

The total stimulus set used in the experiments consisted of 600 words (all were nouns and six letters long) and 60 digits between 1 and 9. The word stimuli were extracted from the CELEX database (Baayen, Piepenbrock, & Van Rijn, 1993) by using the Wordgen software (Duyck, Desmet, Verbeke, & Brysbaert, 2004). The digits were added to ensure that the participants fixated between the two vertically aligned fixation lines.

To mimic the statistical power obtained in Experiments 2 and 3, the stimulus list was divided in two halves. Half of the participants received the first 300 stimuli, the other half received the last 300 stimuli. Thirty digits were included in each list, which is ten percent of the word trials. The words could be presented at six different locations (i.e. with the first, the second, the third, the fourth, the fifth, or the sixth letter between the fixation lines; see Figure 1). To eliminate stimulus confounds, each set of 300 stimuli was divided into six matched groups of 50 words. These groups were matched with respect to word class (all words were nouns), number of syllables, log frequency per million, summed type bigram frequency, and neighborhood size (all *ps* > .34). Estimates for the matching process were retrieved from the Wordgen software (Duyck et al., 2004).

A Latin square design was used to ensure that across participants each stimulus was seen in all possible conditions. The full set of stimuli can be found in the Appendix.
**Procedure**

All participants were tested individually. Each session lasted approximately 25 minutes. The experiment started with a practice phase, containing 24 six-letter words (four at each of the six possible fixation positions), which did not return in the experimental phase, and 6 digits between 1 and 9.

The experimenter gave the following instructions (in Dutch) to the participants: "*In this experiment, Dutch words will be presented. Name these words as fast and as accurately as possible. The presentation of each word will be preceded by two vertically aligned lines in the middle of the screen. It is of high importance to always fixate between these vertical lines from the moment they appear on the screen until the presentation of the word. From time to time, you will have to name a digit instead of a word. These digits will appear briefly. So, it is important to fixate properly in order to be able to name these digits.*" Participants were also told that they would be paid extra if they named 24 out of the 30 digits correctly. This incentive was added because in a previous experiment without the incentive 8 of the first 15 participants had to be excluded because they made more than 20% errors on the digit trials; once the incentive was introduced, no participants had to be excluded any more (Van der Haegen, Brysbaert, & Davis, 2009, Experiment 1).

Stimuli were presented in Courier New font, size 15, on a CRT display. Participants were sitting at a viewing distance of approximately 60 cm, such that the visual area of the words subtended 2.5 degrees.

Each trial started with the presentation of two vertical fixation lines in the middle of the screen. After 400 ms the word stimulus was presented for 150 ms between the two lines and participants had to name the word. The fixation lines remained on the screen until the voice key was triggered or until 5000 ms elapsed. In the digit trials, a digit was presented between the two fixation lines for 80 ms, followed by a mask (#) also presented for 80 ms. Participants had to name the digit, which was registered by the experimenter. The intertrial interval was 1500 ms.
Results

Incorrect responses (1.2%), trials with voice key failures and responses shorter than 200 ms or longer than 1500 ms (1.2%) were excluded from the analyses. Also, RTs more than 2.5 SDs above or below participant’s mean RT in a condition were discarded as outliers (2.5%). The mean percentage of errors for the digits was 0.6%; the maximum number of errors made was one digit, so that none of the participants had to be excluded based on the 80% correct criterion. No participants or items had to be excluded on the basis of the errors or latencies of the word naming task.

Analyses of variance (ANOVA) were run across participants (F1) and across items (F2) for the remaining latencies with fixation position (at letter 1, 2, 3, 4, 5 or 6) as a repeated factor. Due to the positive skewness of the data distribution the ANOVA’s were run on the logarithms of the RTs. Greenhouse-Geisser corrections are reported where the assumption of sphericity was violated.

Reaction time analysis. Figure 3 shows the mean response times for the word naming task. The ANOVA of the mean RTs revealed a main effect of fixation position \( F(1.93,21.26) = 16.59, \ MSE = .00044, p < .001; F(4.62,2089.88) = 18.07, \ MSE = .0061, p < .001 \), with the fastest response times when participants fixated at the third letter position (500 ms) and the slowest response times when they fixated at the sixth letter position (553 ms).

\[ n^\text{8} \] In psycholinguistic research, effects are usually analyzed both across participants and across items to make sure that any effect observed is not only generalizable to other participants, but also to other items (i.e., is not due to a few deviating items).
Error analysis. Mean percentages of errors were 0.5% (position 1), 1.2% (position 2), 0.3% (position 3), 0.3% (position 4), 1.2% (position 5) and 3.7% (position 6), so lowest at positions 3 and 4 and highest at position 6, as indicated by the significant main effect of fixation position \( F(1,2.37,26.01) = 7.49, \ MSE = .00057, p < .01; F(2,2.86,1714.35) = 8.37, \ MSE = .020, p < .001 \).

Discussion

Experiment 1 was run to provide a baseline OVP curve for six-letter words, which can be used to compare the data from the further experiments. In this experiment, none of the Leicester critiques was taken into account. We simply copied the parameters of the previous OVP experiments. As expected, the naming data yielded the familiar OVP curve for LH dominant readers, with the shortest latency (500 ms) when the stimuli were fixated at the third letter (the position slightly to the left of the word center) and the longest latency (553 ms) when the fixation fell on the sixth letter (the last letter of the word).

The difference in naming latency between fixation on the last letter and fixation on the first letter was 43 ms. This compares well with the 23 ms for 5-letter words and the 55-63 ms for
7-letter words reported by Hunter et al. (2007, Table 2; the OVP is known to become more asymmetric as the words are longer). It also compares well with the estimate of 31 ms predicted by the SERIOL model of word recognition (Whitney, 2001). This model has been developed on the basis of the data reported in Brysbaert (1994a) and assumes a split fovea with a time cost for interhemispheric communication (see Hunter & Brysbaert, 2008a for a detailed calculation of the expected values and the application of the model to the Hunter et al., 2007, data).

Now that we have the “traditional” OVP curve, we can assess the impact of the Leicester critiques. Following the SERIOL model, we can even be more specific and predict that the difference between fixation on the first and the last letter will shrink to 13 ms if there is no need for interhemispheric transfer any more.

**Experiment 2**

In Experiment 2, the same task and stimulus set as in Experiment 1 were used. This time, two of the aforementioned shortcomings raised by Jordan et al. (2008, 2009) were taken into account. First, stimuli were presented in such a way that they did not exceed the three degrees of visual angle of the fovea. The stimulus size of Experiment 1 was kept the same, but the reading distance was adjusted. In this way, the stimulus quality was not degraded because the letters consisted of less pixels. Second, an eye-tracking device was used to provide detailed information about the fixation positions of the participants. In the first part of the experiment, participants’ dominant right eye was monitored and the stimuli were presented without restrictions. This will be referred to as the EM condition (eye-monitoring condition). In the second part, an eye position contingent stimulus display technique was used. This means that the stimulus was not presented until the participant properly fixated the designated location between the two vertically aligned lines. In the remainder of the text, this condition will be called the EPC condition (eye position contingent). No digits had to be named, and viewing was binocular. If the OVP curve differs from the one observed in Experiment 1, then controlling fixation by means of an eye-tracker is indeed necessary in SFT research.
Method

Participants

Sixteen students from Ghent University (13 female, 3 male; mean age: 20.9) were paid for their participation in this experiment. All were native Dutch speakers, had normal or corrected-to-normal vision, and were naive with respect to the purpose of the experiment. None of the participants had taken part in Experiment 1.

As in the previous study, the students were asked to fill out the questionnaire about their preferences for handedness (Oldfield, 1971), eyedness, earedness, footedness (Porac & Coren, 1981), and they performed the Miles (1930) test. One participant had to be excluded because the Miles test revealed a left eye dominance. Two other participants were removed from the analyses because of unreliable eye movement data due to a large amount of blinking. Finally, a fourth subject was excluded because of poor performance in the naming task relative to the twelve remaining participants (mean percentage of errors: 7.8%; mean reaction time: 910 ms). Excluded participants were replaced by participants who received the same distribution of stimuli over conditions, to make sure that we ended with a complete Latin square design. The mean ratings reported in the questionnaire are shown in Table 1.

Materials

The stimulus set was the same as in Experiment 1. There were no digits included. Again, the stimulus list was divided in two halves. In this experiment, each participant had to name all 600 stimulus words. Half of the participants received the first 300 stimuli in the first part of the experiment (with eye-monitoring) and the last 300 stimuli in the second part (with eye position contingent stimulus presentation). The order of blocks of stimuli was reversed for the other half of the participants. Words were again presented at six different fixation positions (Figure 1). Hence, two factors were manipulated as repeated measures: display type (2 levels: EM vs. EPC) and fixation position (6 levels: at letter position 1, 2, 3, 4, 5 or 6). A Latin square design was used to make sure that each word was presented in each display type condition and at each letter position. Lists were created in the same way as in Experiment 1.
Apparatus

Eye movements were recorded with a SR Research Eyelink 1000 eye tracking device (Ontario, Canada), which monitored participants’ fixation location every millisecond. In the EPC condition stimuli were presented only when the eye-tracker detected 20 consecutive millisecond samples in the area within 0.5 character spaces on each side of the vertical midline. Calibration and validation were carried out with a 9-point grid. Eye movements were recorded from the moment the stimulus appeared on the screen. Viewing was binocular throughout the experiment, but eye movements were recorded for the dominant right eye only. A chin rest and a brace at forehead height were used to restrict head movements.

Procedure

Participants were tested individually. The experiment consisted of two sessions of approximately 45 minutes with a minimum of one week in-between. In the first session, participants were asked to complete the questionnaire described above, followed by the EM condition; the second session consisted of the EPC displays. All participants started with the EM condition, to make this condition as similar as possible to a “traditional” OVP experiment. We did not want participants to start with the EPC condition, because this might have beneficial effects on their performance in the EM condition.

The same instructions (in Dutch) as in Experiment 1 were given to the participants before the beginning of the EM condition. The information that eye movements would be registered and stimuli would appear only if the participants fixated between the two vertical lines was added to the instructions of the EPC phase. Completing the questionnaire, giving the instructions and setting up the eyetracking system took approximately 10 minutes.

Before the experimental trials started, a practice phase was administered, containing twenty-four stimuli (four at each of the six possible fixation positions), which did not return in the experimental phase.

Stimuli were presented in Courier New font, size 15. Participants were sitting at a viewing distance of 101 cm, such that the maximum region of stimulus presentation on either
side of the fixation gap was 1.5 degrees of visual angle (i.e. the width of the fovea as suggested by Jordan et al., 2008).

Trials began with a drift correction, followed by a blank screen. After 1000 ms, two vertically aligned lines were presented in the middle of the screen for 400 ms. Thereafter, the stimulus was displayed for 150 ms. In the first experimental session, the stimulus was presented immediately between the two lines; in the EPC session, 20 consecutive millisecond samples from the eye-tracker in the crucial fixation region were required for stimulus presentation. The fixation lines remained on the screen until the voice key was triggered or until 5000 ms elapsed.

**Results**

Incorrect responses (1.5%) were removed from the reaction time analyses. RTs shorter than 200 ms or longer than 1500 ms, inadequate voice key registrations (0.4%), and RTs above or below 2.5 SDs from the mean RT of a participant’s condition (2.2%) were deleted. Trials on which the first fixation was shorter than 150 ms (i.e. the duration of stimulus presentation) were removed from the EPC data-analysis (0.7%). Finally, 0.9% of the data were lost due to inadequate calibration settings. Eye fixation analyses, latency analyses and error analyses were run on the remaining data.

Eye fixation analysis. Analyses included eye fixation locations during the 150 ms when the stimulus was presented on the screen. Figure 4 shows the distribution and percentages of fixations at the different letter positions for both the EM phase and the EPC phase. The boundaries per letter position were calculated based on the number of pixels covered by the letters.

As can be seen in Figure 4, participants fixated on the letter between the vertical lines on 34.4% of the trials in the EM condition and on 71.9% of the trials in the EPC condition. In both conditions, there was a fixation bias towards the left (31.4% fixations on letter -1 in the EM condition and 16.4% in the EPC condition). The average deviation from letter position 0 was -0.57 letter positions or -0.16 degrees of visual angle in the EM condition and -0.13 letters or -0.04 degrees of visual angle in the EPC condition.
Notice that 71.9% of fixations at position 0 in the EPC condition is lower than what could be expected if the stimuli were presented only when participants fixated properly. This is because eye fixations either slightly to the left or to the right of the critical fixation area occasionally included the required 20 millisecond samples in the critical region, hence triggering the stimulus presentation. Indeed, if we made the boundaries of the critical fixation position less strict (up to 0.5 letter positions extra on either side of position 0), fixation accuracy reached 97.9% in the EPC phase and 61.9% in the EM condition. Although there still is a leftward deviation when corrected, the degree of misfixations is much smaller in the EPC condition.

Figure 4. Percentages fixation positions at the different letter positions for the two conditions in Experiment 2. Note: Letter position −5 = the leftmost possible fixation position, 0 = the fixation position between the vertical fixation lines, 5 = the rightmost possible fixation position; EM= eye-monitoring condition; EPC = eye position contingent condition; one letter position subtends 0.27°.

Reaction time analysis. Repeated measures analyses of variance (ANOVA) were run across participants (F1) and across items (F2) with fixation position (6 levels: at letter 1, 2, 3, 4,
5 or 6) and display condition (2 levels: EM vs EPC) as repeated measures. RTs were log-transformed as the distribution of the data was positively skewed. If necessary, Greenhouse-Geisser corrections were applied to correct for sphericity violation.

The ANOVA revealed a main effect of display type \(F_1(1,11) = 14.07, \ MSE = .0038, p < .01; \ F_2(1,319) = 311.04, \ MSE = .0049, p < .001\], with longer mean latencies in the EPC condition (524 ms) compared to the EM condition (476 ms). The main effect of fixation position was also significant \(F_1(2.77,30.48) = 21.07, \ MSE = .00050, p < .001; \ F_2(4.15,1324.98) = 15.15, \ MSE = .012, p < .001\], with the fastest latencies when fixating at position 3 (485 ms) and the slowest latencies for position 6 (533 ms). There was no significant interaction between fixation position and display condition \(Fs < 1\).

As can be seen in Figure 5, the shape of the OVP curves is very similar in the two experimental conditions, as indicated by the non-significant interaction between fixation position and display type. For comparison purposes, the OVP curve of Experiment 1 is also displayed in Figure 5. ANOVA’s with fixation position (6 levels: positions 1, 2, 3, 4, 5 or 6) as within-subjects factor and Experiment (2 levels: Experiment 1 vs. Experiment 2 EM condition; or 2 levels: Experiment 1 vs. Experiment 2 EPC condition) as between-subjects factor indicated that there was no significant interaction between experiment and fixation position \(Fs < 1\).
Figure 5. Mean response times for the word naming task at the six possible fixation positions in the two display conditions of Experiment 2 and in Experiment 1. EM = eye-monitoring condition; EPC = eye position contingent condition.

**Error analysis.** Mean percentages of error rates were 1.0%, 0.2%, 0.0%, 0.2%, 1.0% and 2.4% in the EM condition, and 1.7%, 0.8%, 1.3%, 1.7%, 1.7% and 5.7% in the EPC condition for fixation positions 1, 2, 3, 4, 5 and 6 respectively. The ANOVAs on error rates yielded a main effect of display type $[F1(1,11) = 6.49, \ MSE = .0011, p < .05; F2(1,539) = 17.87, \ MSE = .015, p < .001]$, with higher error rates in the eye position contingent condition (2.2%) than in the eye-monitoring condition (0.8%). The main effect of fixation position was also significant $[F1(1.98,21.79) = 8.80, \ MSE = .0011, p < .001; F2(3.48,1877.76) = 10.36, \ MSE = .020, p < .001]$, with the lowest error rate at position 2 (0.5%) and the highest error rate at position 6 (4.0%). Finally, there was no significant interaction between fixation position and display type $[F1(2.69,29.56) = 1.31, \ MSE = .00085, p = .29; F2(3.62,1951.55) = 1.86, \ MSE = .019, p = .12]$. 
Discussion

In Experiment 2 we replicated Experiment 1 with two major changes. First, the word size was decreased from about 2.5° to 1.5°, so that the stimulus remained in foveal vision even when fixated on the first or the last letter. Second, participants’ eye movements were monitored to examine the alleged confound between fixation position and OVP curve. In the first part of the experiment, the eye movements were simply monitored (EM condition); in the second part, the stimuli were not displayed until the participants fixated appropriately (EPC condition).

As can be seen in Figure 5, none of the changes had any effect on the OVP-curve. In all conditions, naming latencies were the fastest when stimuli were fixated slightly to the left of the word center and slowest at the rightmost fixation position. The difference in naming latency between fixation on the first and the last letter was 35 ms in the EM condition and 37 ms in the EPC condition (remember that a difference of 31 ms was expected on the basis of the SERIOL model of word recognition; see the discussion of Experiment 1). Error rates were in line with the latency analysis: most errors were made at position 6 (4.0%) and least errors were made at position 3 (0.5%).

We also replicated Jordan et al.’s (2009) finding that participants are not always fixating exactly where they have been instructed to if no eye position contingent stimulus presentation is used. On two thirds of the trials they were looking at a different letter position than they were supposed to. Most of these deviations were to the letter position left of the instructed location. Interestingly, the distribution of eye fixations in degrees of visual angle was very similar in our experiment as in Jordan et al. (2009, Figure 3): The vast majority of fixations in both experiments were in the region between -0.25° and +0.25°. A difference between our data and those of Jordan et al. (2009) is that in their experiment the distribution was symmetric whereas in our study there is a bias to the left. This bias remains to some extent in the EPC condition.

When participants look one position to the left of the required location in the OVP paradigm, they look at the blank space before the word when it is presented at position 1 and they look at the second last letter of the word when it is presented at position 6 (Figure 1). The most likely interpretation of this bias is that participants try to optimize their performance. Given that performance deteriorates rapidly for fixations towards the end of the word and changes little
for fixations towards the beginning, it is more efficient to look slightly to the left of the fixation location. Forcing participants to look at the required fixation location slightly deteriorates their performance and somewhat increases the left-right asymmetry, as can be seen in Figure 5. As no performance asymmetry was present in Jordan et al.’s (2009) task, participants had no incentive to bias to one or the other side.

As a whole, the eye position contingent stimulus display session was experienced as much more fatiguing by the participants, despite the fact that there was more than a week between the first and the second experimental session. The error rate and the response latencies were significantly higher and we had to exclude 2/16 participants for reasons related to the eye-tracking. The main effect of display type with longer latencies and higher error rates in the EPC condition compared to the EM condition was partially due to the fixation behavior of the participants. On several trials in the EPC condition they had to search for the exact fixation location that would trigger the stimulus display. As such, participants were more insecure about the exact moment the stimulus would appear on the screen and were less prepared to respond than in the EM condition.

Most importantly, however, was the observation that despite the eye fixation noise in the EM condition there was no difference in the OVP curves of the two conditions. If anything, the OVP-curve was slightly “clearer” (i.e., a stronger left-right asymmetry and a higher impact of the distance between the extreme letters and the fixation location) in the EPC condition than in the EM condition. This agrees with the claim that the deviations from the intended fixation location induce noise rather than a systematic bias. As mentioned in the Introduction, this was also the conclusion Jordan and Patching (2005) reached on the basis of their VHF-study.

A remaining possibility is that the OVP-effect might be affected by fixation disparities between the two eyes. Eye-movement research in reading has indicated that the eyes are not always moving in a fully yoked way, so that disparities of up to two letter positions are not uncommon (Kirkby, Webster, Blythe, & Liversedge, 2008). Although these deviations are obtained with moving eyes, Jordan et al. (2008; 2009) conjectured that similar disparities might be present in OVP experiments and might invalidate the conclusions. Therefore, in Experiment 3, we tested the effect of monocular viewing. We also tested whether the fixation control task used in Experiment 1 could reduce the leftward bias observed in the EM condition.
**Experiment 3**

Given the results of Experiments 1 and 2, a final experiment was run to test the validity of the Leicester objection that binocular viewing contaminates the results of SFT research. The same displays as in Experiment 2 were used, but viewing in the EPC was monocular (with the dominant eye) instead of binocular. In addition, we added the eye fixation control task of Experiment 1 to the EM condition to see whether this would improve the fixation accuracy. To maximize the comparability of this condition with Experiment 2, we used binocular vision. As in Experiment 2, the EM condition was run before the EPC condition and the sessions were run on different days to avoid fatigue effects.

**Method**

**Participants**

Sixteen students from Ghent University (11 female, 5 male; mean age: 20.6) were paid to participate in the experiment. All students were native Dutch speakers, had normal or corrected-to-normal vision, and were naive with respect to the purpose of the experiment. None of them had participated in Experiments 1 or 2.

The data from the questionnaire about preferences for handedness (Oldfield, 1971), eyedness, earedness, and footedness (Porac & Coren, 1981) can be seen in Table 1. All participants also performed the Miles (1930) test and were confirmed as right eye dominant. Two participants were excluded in the second session because they reported that the task was too difficult and hence the session had to be cancelled. One participant had to be excluded because of an insufficiently corrected vision. The data of one more participant were lost due to technical problems with the eye-tracking device. All these participants were replaced to complete the Latin square design of the experiment. None of the twelve remaining participants had to be excluded on the basis of the digit naming results (mean error rate: 4.2%).
Materials

The same stimulus materials as in Experiment 2 were used. Additionally, 30 digits (10% of the word trials) between 1 and 9 were randomly intermixed in the EM condition. The 2 (display type: EM vs. EPC) x 6 (fixation position 1, 2, 3, 4, 5 or 6) design was also identical to that of Experiment 2.

Apparatus

The same eye-tracking device and settings as in Experiment 2 were used. One adjustment was made with respect to the task in the EPC condition: By covering the left eye with an eye patch, we forced the participants to view with their dominant right eye only, which was being tracked.

Procedure

Experimental procedure, stimulus presentation, and trial outline were identical to the settings of Experiment 2. Instructions in the EM condition were adjusted with the additional information that there would also appear a digit from time to time that had to be named. Participants were informed that they could earn extra money by naming 24 out of the 30 digits correctly.

Results

Prior to the analyses, data from five categories of inaccuracies were removed: (1) incorrect responses (1.5%); (2) RTs shorter than 200 ms or longer than 1500 ms and inadequate voice key registrations (1.5%); (3) RTs above or below 2.5 SDs from the mean RT of a participant’s condition (2.7%); (4) trials on which the first fixation was shorter than 150 ms (i.e. the duration of stimulus presentation) in the EPC condition (1.3%); and (5) trials on which inadequate calibration settings had to be corrected (0.4%).

Eye fixation analysis. The data of the eye fixation analysis were calculated in the same way as in Experiment 2. Figure 6 shows the results. In the EM condition, participants fixated on
36.4% of the trials between the boundaries of the letter presented in the gap between the fixation lines. In the EPC condition, this increased to 71.7%. Again, a leftward bias was observed, particularly in the EM condition: 36.9% of the fixations in this condition fell on letter position -1, in contrast to 12.4% fixations on letter position +1. Mean misfixation distance from letter position 0 was -0.68 letters or -0.19° in the EM condition and +0.05 letters or +0.01° in the EPC condition.

As in Experiment 2, many deviations straddled the border between letter positions -1 or +1 and 0. If we enlarged the boundaries of the critical fixation area by 0.5 letters, fixation accuracy increased to 96.8% in the EPC condition and to 66.2% in the EM condition.

![Figure 6. Percentages fixation positions at the different letter positions for the two conditions in Experiment 3. Note: Letter position -5 = the leftmost possible fixation position, 0 = the fixation position between the vertical fixation lines, 5 = the rightmost possible fixation position; EM= eye-monitoring condition; EPC = eye position contingent condition; one letter subtends 0.27°.](image)

Visual Word Recognition in the Fovea
Reaction time analysis. Repeated measures analyses of variance (ANOVA) were run by participants (F1) and by items (F2). Within variables were fixation position (6 levels: at letter 1, 2, 3, 4, 5 or 6) and display type (2 levels: EM vs. EPC). ANOVAs were conducted with log-transformed RTs to reduce the positive skew in the distribution. Wherever the assumption of sphericity was violated, Greenhouse-Geisser corrections are reported.

The latencies ANOVA indicated a main effect of display type \( [F1(1,11) = 21.04, \ MSE = .0060, \ p < .01; \ F2(1,274) = 613.49, \ MSE = .0049, \ p < .001] \): mean latencies in the EPC condition (629 ms) were higher than in the EM condition (544 ms). The data also showed a significant main effect of fixation position \( [F1(3.01,33.13) = 17.83, \ MSE = .0037, \ p < .001; \ F2(4.72,1293.09) = 13.15, \ MSE = .0079, \ p < .001] \): latencies at position 3 (571 ms) were the fastest, whereas latencies at position 6 (618 ms) were the slowest. The interaction between fixation position and display type was not significant (Fs < 1).

Figure 7 shows the OVP curves of the EM and EPC condition in Experiment 3, together with the OVP curve from Experiment 1. Again, the shape of the OVP curves were very similar, as indicated by the non-significant interactions between fixation position and Experiment. A repeated measures ANOVA with fixation position (6 levels: position 1, 2, 3, 4, 5 or 6) and experiment (3 levels: Experiment 1, Experiment 2 EPC and Experiment 3 EPC) as between variable confirmed this similarity. The interaction between fixation position and experiment was not significant (Fs < 1).
Mean response times for the word naming task at the six possible fixation positions in Experiment 1 and in the two conditions of Experiment 3 (EM = eye monitoring with binocular vision; EPC = eye position contingent stimulus presentation with monocular vision).

Figure 7. Error analysis. Mean percentages of error rates were 0.5%, 0.8%, 0.7%, 0.3%, 0.5% and 1.3% in the EM condition, and 1.7%, 1.2%, 1.0%, 1.0%, 2.2% and 6.4% in the EPC condition for fixation positions 1, 2, 3, 4, 5 and 6 respectively. ANOVAs on the error rates revealed a main effect of display type \([F(1,11) = 10.73, \text{MSE} = .00084, p < .01; F(1,572) = 30.04, \text{MSE} = .014, p < .001]\). Error rates were higher in the EPC condition (2.2%) than in the EM condition (0.8%). The main effect of fixation position was also significant \([F(1,572) = 11.63, \text{MSE} = .020, p < .001]\), with the lowest error rate at fixation position 4 (0.7%) and the highest error rate at fixation position 6 (3.9%). However, there was also a significant interaction between fixation position and display type \([F(2,11,23.24) = 6.30, \text{MSE} = .00075, p < .01; F(3.56,2037.49) = 6.27, \text{MSE} = .021, p < .001]\). In the EM condition, error rates ranged from 0.3% (position 4) to 1.3% (position 6); in the EPC condition, error rates ranged from 1.0% (positions 3 and 4) to 6.4% (position 6).
Discussion

In Experiment 3, three changes to the usual OVP design were made to meet the objections raised by Jordan et al. (2008; 2009). First, the stimuli were presented within the foveal area. Second, eye-tracking was used to control the fixation accuracy. Third, monocular vision was used to exclude the possibility of fixation disparities between the eyes affecting the data.

As in Experiment 2, the effect on the OVP curve was minimal and non-significant. The difference in response latency between fixation on the first letter and fixation on the last letter was 30 ms in the EM condition and 40 ms in the monocular EPC condition (compared to a difference of 43 ms in Experiment 1). Again the OVP-curve tended to be flatter in the EM condition than in the EPC condition, in line with the idea that variation in the fixation positions adds noise to the curve.

Although the OVP curves in the different conditions were very similar, there were consistent variations in the overall RTs. In general, adding a digit fixation control to the OVP paradigm seems to involve a time and error cost (compare the EM condition of Experiment 2 - without digit fixation control - with Experiment 1 and the EM condition of Experiment 3 - with fixation control). The same is true for the registration of eye movements (compare the EM condition of Experiment 3 with Experiment 1), the use of eye position contingent stimulus presentation (compare the EM and EPC conditions of Experiments 2 and 3), and the use of monocular viewing (compare the EPC condition of Experiment 3 with the EPC condition of Experiment 2). So, whereas the Leicester objections do not change the OVP curve, they do make the task considerably harder for the participants. Even more than in Experiment 2, the participants did not like the EPC condition of Experiment 3 with monocular viewing. We lost 3/16 participants due to performance problems.

In the EM condition, we additionally examined the effect of the secondary digit fixation control task, used in Experiment 1 and in the previous OVP studies. Overall, the influence of this task in the current experiment was minimal: with strict boundaries only 36.4% of the trials in Experiment 3 were correctly fixated, compared to 34.4% in Experiment 2. The outcome was slightly better when boundaries of plus or minus 1.5 letter positions were used: Then, accuracy increased to 66.2% in Experiment 3, compared to 61.9% in Experiment 2. Nevertheless, we still
observed a leftward fixation bias in both experiments and the scatter in the fixation data was comparable. In this regard, it must be taken into account, though, that performance was quite good in Experiment 2. As mentioned in the Method section of Experiment 1, Van der Haegen et al. (2009) had to exclude nearly half of their participants because they failed to identify enough digits. Only when they were paid for good performance, did they perform properly. So, although the digit fixation control task does not guarantee that the participants will look at the exact fixation location, it arguably does help to detect participants with deviations of more than one letter position. A way to further improve the utility of the digit fixation control task may be to decrease the presentation time of the digits. The current digit naming task was not experienced as difficult by the participants; indeed they performed at ceiling level. It can be expected that the harder the digit task, the more carefully participants will have to look between the fixation lines. At the same time, it will make the task harder, without much effect on the shape of the OVP curve.

**General discussion**

In recent years, a group of researchers at the University of Leicester (Jordan & Paterson, 2009; Jordan et al., 2008, 2009) have strongly criticized research on the Split Fovea Theory (SFT), including the findings of Brysbaert and colleagues with the Optimal Viewing Position (OVP) paradigm. The core of the criticism is that all findings interpreted as evidence for a split fovea could be confounds of inadequate fixation control. This critique continues an objection Jordan and colleagues previously raised against VHF experiments (e.g., Jordan et al., 1998), but which they were unable to substantiate in a study directly comparing free vision with tight fixation control on the basis of an eye-tracker (Jordan & Patching, 2005).

The present study is an attempt to assess the impact of inadequate fixation control on the OVP effect, in particular on the left-right asymmetry between fixations on the word beginning and the word end, which has been interpreted as evidence for interhemispheric transfer in foveal word recognition (Brysbaert, 1994a; Hunter et al., 2007).
According to Jordan and colleagues, the existing evidence for a split fovea is flawed for four reasons: (1) participants’ eye fixations have not been controlled adequately; (2) stimulus sizes exceeded the foveal area or were too small to ensure adequate fixation control; (3) binocular viewing may have contaminated the measurement of precise fixation position; and (4) tasks such as naming are inappropriate. Three experiments were run to evaluate the first three objections (see below for our response to the last objection).

In our experiments, using free vision, monitored vision, and eye position controlled stimulus presentation with binocular and monocular vision, we found that (1) there is indeed some scatter in the fixation positions of the participants from trial to trial (Figures 4 and 6); (2) in the OVP paradigm with word naming there is a bias towards fixations slightly to the left of the required position (Figures 4 and 6); (3) these deviations are not much improved by requiring participants to do a secondary digit identification task on a limited number of trials; and (4) the deviations add noise to the OVP curve, but do not change the curve in such a way that the SFT is called into question. If anything, the OVP-effect becomes stronger when accurate fixation is ensured (Figures 5 and 7), but this has a nonnegligible cost on the participants’ performance and their comfort.  

Now that we know the empirical data, we are in a better position to theoretically evaluate the specific objections made. As indicated, the core issue identified by Jordan and colleagues is that inadequate fixation control calls into question all existing evidence in favor of the SFT, including the research based on the OVP effect. Importantly, Jordan et al. have never put forward a mechanism to explain how inadequate fixation control could give rise to the difference in OVP curve observed between left dominant and right dominant participants (Figure 2); all they argued was that the data were suspect. It is not easy to find a mechanism that on the basis of inadequate fixations could lead to a strong left-right asymmetry in participants with left hemisphere dominance and to a flat curve in participants with right hemisphere dominance. The only one we were able to find was Kinsbourne’s (1970) theory of lateral asymmetries in attention allocation. According to this theory, when one hemisphere is active attention is shifted to the contralateral

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9 The cost can also be illustrated with the results of Jordan et al. (2009). In their third experiment, lexical decision times for words were on average 807 ms for five-letter stimuli and 888 ms for eight-letter stimuli. Mean error rates were between 18% (five-letter words) and 23% (eight-letter words), much worse than what is usually reported in psycholinguistic studies.
VHF. Assuming that there is a fixation bias towards the attended VHF, this theory could predict that left dominant participants show a systematic fixation bias towards RVF while naming words, whereas right dominant participants show a systematic shift towards LVF. As a result, the left-right asymmetry in word processing would be enhanced in left dominant participants and attenuated in right dominant participants. Needless to say, this interpretation is completely at odds with our empirical data. Not only does the OVP curve stay the same under tight fixation control, we also observe a fixation bias in the opposite direction to the one predicted by Kinsbourne’s theory: left hemisphere dominant participants have a bias towards LVF not towards RVF, presumably because fixations slightly to the left of the required location improve the overall performance (see the discussion of Experiment 2).

A much simpler hypothesis is that the lack of fixation control in OVP experiments introduces trial-to-trial noise, making the OVP curve slightly flatter than it could be under optimal circumstances (because participants sometimes fixate at position -1 or +1, while the experimenters assume them to be on position 0). This hypothesis is fully in line with our findings and, as it happens, with some of Jordan’s own previous work (Jordan & Patching, 2005).

A second objection, related to the first, is that fixation disparities between the left and the right eye might somehow confound the OVP curve. Again, no mentioning has been made of possible mechanisms. Only suspicion was raised on the basis of findings in text reading. As before, we failed to find any corroborating evidence: The OVP effect was in all relevant aspects the same under monocular viewing conditions as under binocular viewing conditions.

This leaves us with two remaining criticisms that have been raised against the interpretation of the OVP effect as influenced by interhemispheric transfer. The first is that the stimuli in most experiments were too wide, exceeding the region of ‘bilateral projection’. We have addressed this concern in Experiments 2 and 3 by limiting the size of the words to 1.5°. Given that we did not observe any difference with the data of Experiment 1 or with previous experiments, we can safely conclude that the alleged bilateral projection does not include the 3° often claimed. A more tricky question is whether it could be smaller, say only 1°. We admit that the present studies cannot convincingly refute this possibility. This can only be done by comparing the OVP effect of left and right hemisphere dominant participants for very short words (of 3 and 4 letters). Such studies have been reported by Brysbaert (1994a) and Hunter et
al. (2007) with the expected difference between the left and the right dominant participants, but these studies did not involve fixation control and they were based on binocular vision. All we can say at the moment is that an overlap of 0.5° to either side of the fixation location does not really change the underlying issue, as it implies that centrally fixated words longer than 5 letters require interhemispheric communication to be processed. The most appealing aspect of a bilaterally projecting fovea indeed was that it discharged researchers of visual word recognition from having to consider the anatomical divide between the brain halves in their theories at all.

Finally, there is the criticism that the naming task might be an inappropriate task because it is too lateralized. The reasoning here is that visually presented words can be processed bilaterally but require the dominant hemisphere to be pronounced. This is exactly the reason why we have been using the naming task, because the laterality of Broca’s area is easy to establish with the current brain imaging techniques. Knecht, Deppe, Ebner, Henningsen, Huber, Jokeit, and Ringelstein (1998) showed that laterality measures based on differences in blood flow to the left and the right frontal cortex during a word generation task are perfectly correlated with the best available clinical tool to determine language dominance, the WADA test. Jordan and colleagues object against the word naming task, because the differences between left and right dominant participants on this task seem to imply that visual word recognition entirely depends on the dominant hemisphere, whereas in reality the lateralization may be limited to the word production part (Broca’s area).

We agree that the OVP naming task only tells us something about the need for interhemispheric transfer in speech production. However, we fail to see how this could be an argument against the split-fovea theory. SFT does not claim that all word processing is limited to the dominant hemisphere. It only says that interhemispheric communication is needed for the processing of centrally fixated words. It also argues that this communication in healthy participants has a time cost long enough to be measurable (typically in the order of 10-20 ms depending on the length of the word) and that the requirement of interhemispheric transfer predicts problems for people with a severed corpus callosum, such as split-brain patients and individuals with callosal agenesis. A bilateral account of foveal processing would predict no differences in the naming pattern of right and left dominant participants, as no transfer is needed. However, studies as Brysbaert (1994a) and Hunter et al. (2007) did observe a time cost when
comparing the OVP curves of both groups. The naming task is perfectly suited to measure the need for interhemispheric communication. Other techniques (fMRI, MEG) are much more appropriate to study the laterality of the word processes in the temporal cortex (see, e.g., Cai, Lavidor, Brysbaert, Paulignan, & Nazir, 2008; Cohen, Dehaene, Naccache, Lehericy, Dehaene-Lambertz, Henaff, & Michel, 2000; Gold & Rastle, 2007).

The limits of the objection against the naming task can be compared with the problems related to the task favored by the Leicester group. Their task of choice is the Reicher-Wheeler task (e.g., Jordan et al., 2008b). In this task participants see tachistoscopically presented words and have to indicate which letter was presented at a given position. For instance, the stimulus “snow” is flashed for a few milliseconds and participants have to indicate whether the letter “n” or “h” was presented at the second position. Typically, stimulus presentation time is limited to ensure some 66% correct identification. Using this task, Jordan et al. (2008) showed that participants performed better with presentation in RVF than in LVF when parafoveal presentation was used (more than 2° away from the fixation location), but not when foveal vision was used (less than .5° from the fixation location). On the basis of this finding, Jordan et al. claimed to have evidence for a bilateral representation of the central 1° of the visual field. They additionally claimed that their result questioned all existing evidence for SFT (because it had failed to take into account proper fixation control, etc.).

We do not question Jordan et al.’s (2008) finding. We simply notice that the Reicher-Wheeler task is an offline task, in which conclusions are drawn on the basis of accuracy data. There is big difference between saying that interhemispheric transfer requires some 10–20 ms extra in healthy participants (which can be measured in carefully designed studies) and claiming that the extra time cost must result in a drop of performance accuracy. Offline tasks based on accuracy data are most interesting when there is evidence for suboptimal processing, for instance in the case of split-brain patients. They are a crude measure when it comes to study the fine-grained, online processes involved in normal word recognition. High accuracy in the Reicher-Wheeler task can be reached on the basis of correct perceptual identification instead of recognition at word level (Grainger & Jacobs, 1994) and can thus reflect other processes than we intend to measure. Jordan et al. (2008) counter this criticism by pointing to the clear difference between the parafoveal LVF and RVF conditions, showing that the technique is capable of
picking up this effect. Unfortunately, the most likely interpretation of the difference between parafoveal LVF presentation on the one hand and foveal presentation or parafoveal RVF presentation on the other hand is that English reading participants have virtually no practice recognizing words in parafoveal LVF vision. One of the consequences of this difference in practice is that words in LVF parafoveal vision are processed much less in parallel than words presented in foveal or RVF parafoveal vision (Nazir, Ben-Boutayab, Decoppet, Deutsch, & Frost, 2004).

All in all, we agree that reasonable confounds must be checked. This is why we invested heavily in the current series of experiments. At the same time, it cannot be denied that the benefits of experimental control follow an inverted U shaped curve with an optimal value somewhere in the middle: not enough control is bad, but too much control is counterproductive as well. Given the present findings, we hope the Leicester group will agree with us that for a valid OVP study it is not required to fully immobilize participants by means of a bite bar and a headrest, to continuously monitor their eyes with two dual-Purkinje eye-trackers, and to present the stimuli only when both eyes are exactly on the indicated spot of the computer screen. Indeed, Jordan and Patching’s (2005) findings remind us that initially justified concerns about confounds need not imply that all previous research was invalid, just that the validity of the findings must be assessed properly.
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Chapter 3: Further fMRI validation of the visual half field technique as an indicator of language laterality: A large-group analysis
The best established lateralized cerebral function is speech production, with the majority of the population having left hemisphere dominance. An important question is how to best assess the laterality of this function. Neuroimaging techniques such as functional Magnetic Resonance Imaging (fMRI) are increasingly used in clinical settings to replace the invasive Wada-test. We evaluated the usefulness of behavioral visual half field (VHF) tasks for screening a large sample of healthy left-handers. Laterality Indices (LIs) calculated on the basis of the latencies in a word and picture naming VHF task were compared to the brain activity measured in a silent word generation task in fMRI (pars opercularis/BA44 and pars triangularis/BA45). Results confirmed the usefulness of the VHF-tasks as a screening device. None of the left-handed participants with clear right visual field (RVF) advantages in the picture and word naming task showed right hemisphere dominance in the scanner. In contrast, 16/20 participants with a left visual field (LVF) advantage in both word and picture naming turned out to have atypical right brain dominance. Results were less clear for participants who failed to show clear VHF asymmetries (below 20 ms RVF advantage and below 60 ms LVF advantage) or who had inconsistent asymmetries in picture and word naming. These results indicate that the behavioral tasks can mainly provide useful information about the direction of speech dominance when both VHF differences clearly point in the same direction.
Introduction

Since Dax (1865) and Broca (1865) localized speech production in the left cerebral hemisphere, a large number of researchers have investigated the functional asymmetry of the two brain halves, which look so similar at the anatomical level. Today, language processing is still one of the most frequently investigated lateralized functions (Hugdahl & Westerhausen, 2010). It is now well-established that speech production is not always controlled by the left hemisphere, not even in healthy right-handers. Some 1-5% of the right-handers are right language dominant or have bilateral language control (Knecht et al., 2000; Pujol, Deus, Losilla & Cadevila, 1999). Surprisingly, the majority of left-handers are left dominant as well (against Broca’s initial assumption). Only 20-25% of the left-handers are thought to be right language dominant or to have bilateral control. Because of the limited covariation between handedness and cerebral dominance, it is important for researchers to have a reliable measure of language lateralization. Simply comparing a group of left-handers with a group of right-handers is unlikely to provide clear findings.

Localization of language functions has been studied most intensively in patients undergoing brain surgery (e.g., to remove the seizure-causing tissue in epilepsy). For these patients, it is important to know where the language areas are, so that they can be spared (Möddel, Lineweaver, Schuele, Reinholz, & Loddenkemper, 2009). Traditionally, the Wada test was used (Wada & Rasmussen, 1960). This test consists of the injection of sodium amobarbital in the left or right internal carotid artery while the subject performs a language task such as counting aloud. The Lateralization Index (LI) is then calculated by comparing the performance after left and right injection (Binder et al., 1996). The Wada test is clearly invasive and does not provide intrahemispheric information. In recent years, a range of neuroimaging paradigms have been used as an alternative. These are non-invasive techniques such as functional Magnetic Resonance Imaging (fMRI) and magnetoencephalography (MEG). The validity of LIs based on these techniques was established by comparing them with results from the Wada test both in healthy and epileptic populations (e.g., Binder et al., 1996; Hirata et al., 2010; Jansen et al., 2006; Pirmoradi, Béland, Nguyen, Bacon & Lassonde, 2010).
Although fMRI and MEG are much less invasive than the Wada-test, they have some drawbacks for every-day laterality research. First, they are expensive and time-consuming. Second, a considerable percentage of participants do not qualify for this type of research, because they suffer from claustrophobia or because their body contains irremovable ferromagnetic matter. Finally, there may be concerns about repeated, intensive testing (e.g., to try out various manipulations or to establish psychophysical functions). Although some of the disadvantages can be overcome, behavioral LI measures would be an interesting alternative for fast, less expensive language lateralization of large groups and for repeated, intensive testing.

Surprisingly, despite decades of research only a few studies have looked directly at the validity of behavioral laterality measures by comparing them with brain imaging data (e.g., Bethmann, Templemann, De Bleser, Scheich & Brechmann, 2006; Gonzalez & Goodale, 2009; Hunter & Brysbaert, 2008a; Krach, Chen & Hartje, 2006). In addition, Hunter and Brysbaert (2008a) criticized most of these studies, because they were not well designed.

Hunter and Brysbaert (2008a) examined the visual half field (VHF) task with bilateral stimulus presentation. In this task participants fixate the middle of a screen where a fixation cross appears and after 500 ms is replaced by tachistoscopically presented parafoveal stimuli in the left visual field (LVF) and the right visual field (RVF), together with a central arrow pointing to one of them. Participants are asked to name the stimulus to which the arrow points. LIs are calculated by subtracting the mean reaction time (RT) to stimuli in RVF from the mean RT to stimuli in LVF. This method is based on the contralateral projection of visual information in humans (e.g., Bradshaw & Nettleton, 1983; Bryden, 1982). Due to the partial crossing of the human visual pathways, stimuli from LVF/RVF are sent to the right hemisphere (RH)/left hemisphere (LH) respectively. As a result, participants with left brain dominance are expected to name stimuli faster in RVF, whereas participants with right dominance are expected to name stimuli faster in LVF.\(^\text{10}\)

Hunter and Brysbaert (2008a) used two different types of stimuli: words and pictures. They obtained high correlations between the LIs of these tasks and fMRI brain activity measured

\(^{10}\) The VHF technique is usually not criticized when the stimuli are presented outside central vision (i.e., parafoveally, about 1.5° of visual angle away from the centre), although evidence motivated by the split fovea theory indicates that laterality effects can also be found in central vision (see Ellis & Brysbaert, 2010 for a review).
in a silent word generation task (for more details about the tasks, see below). The correlation was $r = 0.63$ for word naming and $r = 0.77$ for picture naming. Furthermore, Hunter and Brysbaert (2008b) claimed that the combined results of word and picture naming allowed them to predict brain dominance as measured with fMRI with 100% accuracy.

A main problem with the Hunter and Brysbaert (2008a) study, however, is that it was based on a very small sample. Only 26 left-handers took part in the behavioral VHF-tasks, and only 10 of them were selected for the fMRI task. Six of these showed clear RVF advantages in both VHF tasks and, as expected, turned out to be left dominant in the scanner. Two participants had clear LVF advantages and were confirmed as right dominant. Two final participants showed an LVF advantage in the word task, but no clear advantage in the picture naming task, and they were classified as bilateral in the fMRI task.

All in all, although Hunter and Brysbaert’s results look promising, for two reasons it would be good to have a retest on a larger group. First, it would be good to see a confirmation of the RH dominance in participants with clear LVF advantages, given that this group is rare and that there were only two hits in Hunter and Brysbaert. Second, it would be interesting to know what can be concluded of the many participants who do not show a clear VHF advantage. Do these participants have a reduced LI, or is their VHF measure simply less informative?

In the current study, we present data of 250 left-handed students who participated in the behavioral tasks (word and picture naming) and of whom 50 were scanned. We were particularly interested in those participants that deviated from the mainstream pattern (i.e., those that did not show a RVF advantage indicative of LH dominance). As a result, the majority of our findings involve participants either showing a clear LVF-advantage or a reduced VHF-asymmetry.

We adopted the method of Hunter and Brysbaert (although we had to use Dutch stimuli). We used the naming VHF task, because this task comes closest to the brain activation measured by the silent word generation task and because naming is the most lateralized function (see Ellis & Brysbaert, 2010 vs. Jordan & Paterson, 2009, for a discussion of this).

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11 The relationship between the laterality of the frontal language regions and the occipito-temporal language regions is an interesting topic as well (see Cai, Lavidor, Brysbaert, Paulignan & Nazir, 2008; Cai, Paulignan, Brysbaert, Ibarrola & Nazir, 2010 vs. Pinel & Dehaene, 2010), but one that is orthogonal to the subject of the present paper. If language comprehension or the relationship between production and comprehension is the focus of research, other
We also introduced some improvements. A first change was that we monitored eye-position with an eye-tracker, to directly test the extent to which VHF data may be invalidated by imperfect adherence to the central fixation instruction (Bourne, 2006). It has been claimed that participants in VHF tasks do not always fixate at the instructed location and that this may invalidate the findings (Jordan, Patching & Milner, 1998), although in a previous study we failed to find evidence for this possibility, at least when the stimuli were presented in such a way that one letter always fell on the fixation position (i.e., the so-called optimal viewing position paradigm; Van der Haegen, Drieghe & Brysbaert, 2010). Eye movement monitoring also allowed us to check to what extent participants make eye movements in a VHF-task. Although stimulus presentation time was tachistoscopic in Hunter and Brysbaert (2008a), the authors did not explicitly test the presence of fast eye movements, for which they have been criticized (Jordan & Paterson, 2009).

The second improvement of our study was that we calculated the fMRI LIs in a different way. Recent studies have pointed out that different definitions of region of interest (ROIs), statistical thresholds of brain activity, boundaries of LIs to classify dominance, and baseline conditions may result in different LIs (Abbott, Waites, Lillywhite and Jackson, 2010; Chlebus, Mikl, Brazdil, Pazourkova, Krupa & Rektor, 2007; Jansen et al., 2006; see Seghier, 2008 for a review). Wilke and Schmithorst (2006) proposed a combination of a bootstrapping procedure and histogram analysis to calculate robust LIs in neuroimaging data (see the Method section for a more detailed description of this technique). Hunter and Brysbaert used a normalized subtraction of the number of activated voxels in each hemisphere as LI, which may not always have resulted in the best estimate for each participant. In order to have more robust LIs, we used the approach of Wilke and Schmithorst to calculate a global mean LI for activation in the pars opercularis (approximately BA 44) and the pars triangularis (approximately BA 45). These two regions are the most active areas in the silent word generation task we adopted. They are known to be involved in many linguistic functions, including semantic, phonological and syntactic processes (Amunts et al., 2004; Heim, Eickhoff & Amunts, 2008), with semantic processing located more anterior than syntax and phonology. In addition, we looked at the LIs in the pars orbitalis (approximately BA 47), the insula, and the ventral premotor cortex (BA6), as these regions are tasks are more appropriate (see for example van Ettinger-Veenstra et al., 2010 and Pirmoradi et al., 2010 for a discussion of appropriate tasks to assess LIs in posterior brain areas such as Wernicke).
more and more considered as part of the language production network as well. BA 47 is cytoarchitectonically more similar to BA 45 than BA 44, because it is part of the same granular layer of the cortex (Hagoort, 2006, 2009). BA 47 has also been found to be involved in semantic processing (De Carli et al., 2007) and the processing of fine-grained temporal sequences (Vuust, Roepstorff, Wallentin, Mouridsen, & Østergaard, 2006). The insula is involved in speech motor control (Ackermann & Riecker, 2010). Finally, BA 6 has been found active when overt speech is programmed (Shuster & Lemieux, 2005).

Method

Behavioral VHF tasks

Participants

A total of 250 students from Belgian universities and higher education schools participated in this experiment (68 males, 182 females; age ranging from 17 to 30 with mean age = 19.9 years). They were recruited via advertisements on a research website, e-mail, or word of mouth. All participants were left-handed native Dutch speakers and had normal or corrected-to-normal vision. Sixty-four students earned credit points for a psychology course by participating, the others were paid. We recruited more widely than the traditional undergraduate psychology students because we needed a large number of left-handers. This group shows a higher incidence of atypical brain laterality (Knecht et al., 2000; McKeever, Seitz, Krutsch & Van Eys, 1995; Pujol et al., 1999). By not including right-handers we excluded confounds related to handedness. We also wanted to have extra variability in our sample.

Handedness was assessed with a Dutch version of the Edinburgh Handedness Inventory (Oldfield, 1971). This was combined with a questionnaire about eyedness, earedness and footedness (Porac & Coren, 1981). Participants 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). Additionally, they performed the Miles (1930) test of eye dominance. In this test participants are asked to look at a distant target through a small opening formed by putting together the thumbs and index fingers of both hands.
Binocular viewing through the opening is alternated with monocular viewing with each eye. The eye that sees the target when it is open is selected as the dominant eye. The Miles test was administered to determine the participant’s eyedness by means of an unconscious sighting task, which controls for contamination of handedness. For example, participants may indicate a right eye preference for sighting down a rifle, simply because they prefer to have their right hand on the trigger (Porac & Coren, 1976). The questionnaire and the Miles test were administered prior to participation. Only students that reported to write and draw with their left hand were accepted. We did not include participants based on a cut-off value for left-handedness in order to obtain large variability. The Appendix shows the mean ratings reported in the questionnaires for the 50 students who also participated in the fMRI study. The data of all 250 participants are available as electronic supplementary materials.

**Stimuli**

*Picture naming.* The line drawings used in the VHF picture naming task were adopted from Hunter and Brysbaert (2008a). Five pictures were randomly presented: a boat ([boot] in Dutch), a book [boek], a house [huis], a lamp [lamp] and a star [ster]. The figure of a tree in Hunter and Brysbaert (2008a) was replaced by a symmetrical figure of a star, because of the large phonological overlap between the Dutch words *boom* (tree) and *boot* (boat). All names were monosyllabic and all stimuli were symmetrical not to favor a VHF. The five pictures are displayed in Figure 1.
**Word naming.** A list of 96 Dutch three-letter words and a list of 96 four-letter words were selected for the VHF word naming task. Half of them served as targets, half as filler words to create matched word pairs. Targets and fillers of each pair had an equal number of letters, belonged to the same word class (substantive or adjective), and were pairwise controlled for summated type bigram frequency, log frequency per million and number of neighbors in the CELEX database ($ps > .40$; Baayen, Piepenbrock, & Van Rijn, 1993). Words were selected with the Wordgen software (Duyck, Desmet, Verbeke, & Brysbaert, 2004). Similar to Hunter and Brysbaert (2008a) the three-letter and the four-letter words were matched on initial phoneme as this is the best predictor of naming latencies (Balota, Cortese, Sergent-Marshall, Spieler & Yap, 2004). Finally, targets and fillers that formed a bilateral pair never started with the same letter, so that errors could easily be detected and participants would not be able to start their response on the basis of the wrong stimulus. The full list of word pairs can be found in the electronic supplementary materials.
Design

There was only one repeated-measure variable in the naming tasks, namely VHF. In the picture naming task, each of the five line drawings was presented four times in combination with each of the other four pictures: once as a target in the LVF, once as a target in the RVF, once as a filler in the LVF and once as a filler in the RVF. As a result, each picture was presented 16 times in the 40 possible stimulus pairs (5*4*2). A randomized sequence of these 40 trials was repeated four times during the experiment.

In the word naming task, each of the 96 target words was presented twice with its matched filler word: once in LVF and once in RVF. Hence, the participants named 192 trials in total. The trials were divided in two blocks, in such a way that all targets were named once before the second presentation block began. Two lists were created and distributed over the participants, with a counterbalanced order of the VHF in which the trials were presented.

The VHF task has been criticized because possible confounding variables have not always been controlled for. Therefore, we paid attention to the variables that have been mentioned. First, bilateral presentation was used, so that participants were not subject to attentional biases due to the sudden appearance of a stimulus in LVF or RVF. Second, participants only had to name the stimulus the arrow pointed to. When participants have to process two stimuli and are free to choose which half field is processed first, the VHF differences are confounded by individual attention strategies (Voyer & Boles, 2007). The central arrow pointing to the target stimulus further ensured that participants were motivated to pay attention to the fixation location rather than look around (Schmuller & Goodman, 1980). Stimulus duration was limited to 200 ms, which was short enough to prevent eye movements in a paradigm with bilaterally presented stimuli (Hulme, 1979; Walker & McSorley, 2006) but long enough to make the stimulus perceptible. The stimuli in the parafovea were also large enough to make sure that participants could see them reasonably well. Each participant responded to all stimuli both in LVF and RVF, so that the individual LIs were not influenced by the stimuli presented in RVF and LVF. Finally, we presented enough stimuli to make sure that the VHF estimates had reasonably small confidence intervals (Brysbaert & d’Ydewalle, 1990).
Apparatus

Fixation locations were monitored with an Eyelink 1000 eye tracking device (SR Research, Ontario, Canada) and naming response latencies were registered with a voice key. Head movements were restricted with a chin rest and a brace at forehead height, without discomforting the participants too much when giving vocal responses. Appropriate calibration and validation were carried out with a 9-point grid. The drift between the computed fixation location based on the calibration and the current fixation was checked after each trial by displaying a single fixation target. If the drift was too large, calibration was rerun. Participants’ fixation location was measured every millisecond (sampling rate of 1000 Hz). Eye movements were recorded from the moment the trial started. For the fixation analyses only fixation locations during stimulus presentation were taken into account. Viewing was binocular throughout the experiment, but the eye-tracker only recorded the dominant eye (as assessed by the above described Miles test).

Procedure

Figure 2 illustrates the procedure of the VHF tasks. Participants were instructed to fixate the center of the screen placed at a reading distance of 60 cm from the moment the fixation cross appeared. At a viewing distance of 57 cm, an image size of 1 cm corresponds to 1 degree of visual angle. Participants were told that the fixation cross after 500 ms would be replaced by a tachistoscopically presented arrow and two stimuli (one in LVF and one in RVF). The arrow pointed in the direction of the target stimulus, which had to be named as fast and accurately as possible. The target and filler stimulus were presented for 200 ms and followed by a mask. The mask consisted of randomly oriented lines in the picture naming task, and four ASCII codes 35 (#) in the word naming task. At the onset of the mask, the arrow was replaced by the fixation cross, which remained visible until the voice key registered a response, or until 5000 ms elapsed.
The two stimuli were presented at an equal distance from the screen center. Pictures subtended a visual angle between 1.91° and 10.98°. Words were presented in Courier New font, size 15, between 1.6° (four letter words) or 2.07° (three letter words) and a fixed outer edge of 3.39°.

Each participant received the same practice trials before the beginning of the experimental blocks. These consisted of 8 randomly chosen picture pairs or 16 word pairs that did not return in the experimental phase. All participants first performed the picture naming task, as the word task was experienced as more difficult. Because we wanted the procedure to be standardized for all participants, we did not counterbalance the order of the VHF tasks but presented them in increasing order of difficulty. A limitation of this decision is that we cannot generalize the results across presentation order of the VHF tasks.

Completing the questionnaire and the informed consent form, giving instructions, setting up the eye-tracking device and presenting all practice and experimental trials took about 60 minutes.
Participants

We selected a subgroup of 50 participants from the behavioral VHF tasks. All selected participants who were willing to undergo the fMRI test fulfilled all conditions to be scanned. They signed an informed consent form according to the guidelines of the Ethics Committee of the Ghent University Hospital. Because we especially wanted to find participants with atypical language dominance, all participants with a LVF advantage of at least 10 ms on both the picture and word naming task were asked to take part in the fMRI study. Twenty participants did so; participants 58, 61, 65 and 66 were also invited but refused to take part. We further included the following comparison patterns: no clear advantage on either task (N = 1), a clear RVF advantage on both tasks (N = 14), a clear RVF advantage for picture naming, but no clear advantage for word naming (N = 1), a clear LVF/RVF advantage for word naming, but not for picture naming (N = 7 and 4 respectively), and a LVF/RVF advantage for picture naming, but a RVF/LVF advantage for word naming (N = 2 and 1 respectively). Figure 3 shows the distribution of the 250 VHF differences. The height of the black bars reflects the number of participants that were selected to take part in the fMRI study.
Figure 3. Distribution of VHF differences in the picture (upper histogram) and word (lower part) tasks. Grey bars represent the number of subjects in the behavioral tasks (N = 200), black bars reflect the number of subjects in addition participated in the fMRI study (N = 50). Digits indicate the proportion of fMRI participants per category of 25 ms VHF difference.
**Task design**

A silent word generation task was used to determine language dominance. It is the task used by Hunter and Brysbaert (2008a) and others interested in hemispheric dominance (e.g., Abbott et al., 2010; Badzakova-Trajkov, Häberling, Roberts & Corballis, 2010; Knecht, Henningsen, Deppe, Huber, Ebner & Ringelstein, 1996). Participants were asked to mentally think of as many words as possible beginning with a letter presented in the middle of the screen for 15s. Ten different letters were presented in randomized order. The baseline condition consisted of ten 15s blocks with silent repetition of the non-word *baba*. Experimental and baseline blocks were alternated with 20 rest periods of again 15s, during which a horizontal line was displayed at the screen centre. Subjects were familiarized with the method prior to scanning.

**Image acquisition**

Images were acquired on a 3-Tesla Siemens Trio MRI scanner (Siemens Medical Systems, Erlangen, Germany) with an 8-channel radiofrequency head coil. First, a high-resolution anatomical image was collected using a T1-weighted 3D MPRAGE sequence (TR = 1550 ms, TE = 2.39 ms, image matrix = 256 × 256, FOV = 220 mm, flip angle = 9°, voxel size = 0.9 × 0.9 × 0.9 mm³). Functional images were then obtained using a T2*-weighted gradient-echo EPI sequence. Forty axial slices covering the whole brain were acquired (TR = 2630 ms, TE = 35 ms, image matrix = 64 * 64, FOV = 224 mm, flip angle = 80°, slice thickness = 3.0 cm, distance factor = 17%, voxel size = 3.5 * 3.5 * 3 mm³).

**Data analysis**

Data analysis was performed using SPM5 software (Wellcome Trust Centre for Neuroimaging, London, UK). The first four acquired images were eliminated for each participant, due to the stabilizing of the magnetic field. Data preprocessing consisted of (1) slice time correction because slices were acquired in an interleaved way; (2) realignment using rigid body transformations to correct for movement artifacts; (3) coregistration of the anatomical image to mean functional image; (4) normalization to the Montreal Neurological Institute (MNI) T1 template; and finally (5) spatial smoothing with an isotropic Gaussian Kernel (8 mm full width at half-maximum). Data-analysis was done by using the general linear model (GLM) for
modeling the experimental (target letter) and control (non-word baba) condition with a boxcar function, convolved with a canonical haemodynamic (BOLD) response function.

**Results**

**LI calculations**

Prior to LI calculation for the VHF studies, some elementary data cleaning was done. The following trials were excluded: naming corrections or errors (Picture: 3.5%, Word: 10.0%), voice key failures (Picture: 0.7%, Word: 1.2%), data loss due to eye-tracker recalibration (0.2% in each task), RTs less than 200 ms or greater than 1500 ms (Picture: 1.4%, Word: 1.6%), and for the remaining trials latencies above/below 2.5 SDs from the participant's mean RT (Picture: 2.5%, Word: 2.6%).

LIs were calculated in two different ways. Analysis1 included all trials, whereas Analysis2 took into account the quality of central fixation. This analysis excluded all trials on which the subject initiated a saccade in the 200 ms stimulus presentation period (Picture: 1.8%, Word: 17.2%) or fixated more than .5° to the left or the right of the screen center (Picture: 16.4%, Word: 14.0%). Eye movements of 11/250 participants could not be registered because their pupil was not clearly visible (indicated by * in the Appendix and in the supplementary materials). The data of these participants were all treated as unreliable fixations outside the critical region of 1° in the above described data trimming.

All in all, the behavioral LIs in Analysis 1 were based on 91.9% of the trials for picture naming and on 84.4% of the trials for word naming. In Analysis 2, they were based on 73.5% (Picture) and 55.0% (Word) of the data. LIs of less than -10 ms were considered as evidence for a LVF/RH advantage, LIs of more than 10 ms were considered as evidence for a RVF/LH advantage. Values in between were classified as unclear. On the basis of these criteria, 24 participants showed a clear LVF advantage on both tasks, 143 showed two clear RVF advantages, and the remaining showed either a mixed pattern (N = 81) or no clear VHF advantage (N = 2). Overall, the picture and word VHFs correlated significantly, but not very highly with each other (r = .45, p < .001, both in Analysis1 and Analysis2).
Because the intercorrelation of measures depends on the reliability of the individual measures, we calculated the split-half reliability by correlating the first and second half of each test and attenuating the correlation for length with the Spearman-Brown formula \[ r_{\text{attenuated}} = \frac{2 \cdot r}{1 + r} \]. Reliability of LI index in the picture naming VHF task was .79 in Analysis1 and .73 in Analysis2; for the word VHF tasks the values were .91 and .85 respectively.

Finally, we compared the LIs of Analysis1 and Analysis2 in the 239 participants whose eye movements could be measured, to investigate to what extent the findings in a VHF-task were invalidated by inadequate fixation control. A first informative finding was the very high correlation between the LIs of both analyses: \( r = .98, p < .001 \) for picture naming and \( r = .94, p < .001 \) for word naming. When we looked at our initial classification of the participants (clear LVF or RVF advantage, no clear advantage), we saw that 16 participants or 6.7% got a different classification in the picture naming task and 23 or 9.6% in the word naming task if we used the data of Analysis2 rather than those of Analysis1. Note that Analysis2 was based on very strict selection criteria: A trial was invalid from the moment the eye-tracking device registered an eye movement, regardless of the position or duration of the resulting fixation. When we made the criterion of an eye movement less strict and defined it as no eye movement on the parafoveal stimulus instead of no eye movement at all, the VHF classification changed for only 2.6% of the participants in the picture naming task and 5.7% in the word naming task. In other words, for 95% of the participants eye movement control did not have added value. The small extra value of fixation control was confirmed when we looked at the correlations between the VHF differences and the fMRI LIs \( [r = .66, p < .001 \) and \( r = .67, p < .001 \) in Analysis1 (N=50) vs. \( r = .65, p < .001 \) and \( r = .64, p < .001 \) in Analysis2 (N=49) for the picture and word VHF respectively].

As indicated above we used a different approach than Hunter and Brysbaert (2008a) for the fMRI LIs. Instead of taking a certain statistical threshold to calculate the normalized difference of number of activated voxels in each hemisphere, we used the LI Toolbox 1.02 provided by Wilke and Lidzba (2007). For each region on which the LI scores were based, 20 equally sized steps from 0 to the maximum \( t \)-value were taken as thresholds. At each level, 100 bootstrap resamples with a resample ratio of \( k = 0.25 \) were taken in the left and right investigated area. Then, all 10 000 possible LI combinations were calculated but only the central 50% of data were kept in order to exclude statistical outliers. In the last step, a weighted mean LI for each
individual was calculated with higher thresholds receiving a higher weight. A more detailed description of this procedure can be found in Wilke and Schmithorst (2006).

Individual fMRI LIs were calculated from the activation in the areas formed by the pars opercularis (approximately BA44) and the pars triangularis (approximately BA45) together, in the pars opercularis and pars triangularis separately, in the pars orbitalis (approximately BA 47), in the insula, and in the precentral cortex (according to the AAL template; Tzourio-Mazoyer et al., 2002). All six resulting LIs per participant can be found in the supplementary materials. The analyses below are based on the areas classically seen as Broca's area, namely the combination of BA 44 and 45, because these showed the highest correlations with the VHF data. This measure is included in the Appendix as well. FMRI LI values range from -1 (when there are only voxels active in the right hemisphere) to +1 (when there is only signal in the left hemisphere) as they reflect the normalized difference of activated voxels in the left and the right hemispheres. When running the study we used the following criteria to classify participants: Participants with LI < - .60 were classified as RH dominant (N = 20), those with LI >+ .60 as LH dominant (N = 25), and those with LI between –.60 and +.60 as bilateral (N = 5).

**Comparison of LIs based on VHF and fMRI**

Figure 4 shows the correlation between LIs based on the VHF tasks (Analysis 2; see description in 3.1) and LIs based on the fMRI task (BA44+45). The VHF data vary along the y-axis (two data points per participant), the fMRI data along the x-axis. The data of Participant8 are not included, as there were no eye-monitoring data for this right dominant participant. Panel A shows the data for all 49 participants; Panel B shows the results for the participants with consistent VHF asymmetries in word and picture naming (N = 34). The upper right and lower left quadrant include data indicative of respectively LH/RH dominance both in VHF and fMRI.
Figure 4. Individual scores based on the activation in BA44 + 45 in the absent word generation task (x-axis) and RT differences in the picture and word VHF task (y-axis). Panel A shows the data for all participants (N = 49). Panel B only contains those participants that had the same VHF advantage in the picture and word task (N = 34).
It is clear from Figure 4 that fMRI makes a much sharper distinction between LH and RH dominance than the VHF task. There is a distinct gap between both groups, with only two or three participants falling in-between. In contrast, the transitions from LVF advantage to RVF advantage in the VHF tasks are much more continuous, with an unpredictable relationship to the fMRI outcome in the region from -60 ms to +25 ms. All participants with a RVF advantage of more than 25 ms were classified as LH dominant in the scanner, and all but one participant with a LVF advantage of more than 60 ms were classified as RH dominant. Participants with VHF asymmetries between -60 and +25, however, could go either way in the scanner. A comparison between Panel A and Panel B shows that this was particularly true for participants who showed opposite VHF advantages for word and picture naming.

Overall, the fMRI LIs correlated positively with both the picture ($r = .65, p < .001$) and word ($r = .64, p < .001$) naming LIs. As expected on the basis of Figure 4, the correlations were even higher when only the consistent participants were taken into account (Panel B; picture: $r = .76, p < .001$; word: $r = .74, p < .001$). It is clear that a stricter threshold than +/- 10 ms should be taken for clear-cut classifications, but the current data show that the VHF tasks are a useful screening tool for laterality research.

A stepwise multiple regression analysis with four predictor variables (word VHF and picture VHF according to Analysis1 and Analysis2) returned significant effects for word VHF ($t(46) = 3.14, p < .01$) and picture VHF ($t(46) = 2.75, p < .01$) according to Analysis1, and no further contribution of word VHF and picture VHF according to Analysis 2. Apparently, the addition of eye fixation control was not an asset for better prediction of brain dominance as determined with fMRI (see the Appendix for the raw data).

**Correlations with the questionnaire data of lateral preferences**

We also correlated the VHF and fMRI LIs with the laterality indices based on the questionnaire data. None of the questionnaire preferences correlated significantly with the behavioral data or with the LI from BA44 and 45 ($p$s > .11), although footedness seemed stronger for the right dominant group as assessed with fMRI (mean = -1.8) compared to the left.
dominant group (mean = -0.8). Other authors also reported higher correlations with footedness than with other variables (Day & Macneilage, 1996; Searleman, 1980), although Brysbaert (1994) reported a higher correlation between language laterality and earedness. When interpreting the present null-effects it is important to keep in mind that only left-handers were tested, which seriously reduced the range of laterality indices in the questionnaire data.

**Discussion**

We examined the usefulness of VHF tasks to assess language laterality in a large sample of left-handed, healthy participants (N = 250). All participants took part in two VHF tasks (word naming and picture naming) and the participants we thought most likely to have atypical language dominance were invited to take part in an fMRI validation study, together with a control group of 14 participants with a consistent RVF advantage on both tasks. We additionally examined the influence of saccades and imprecise eye fixation positions in VHF tasks. The following were the main findings.

First, it is clear that both VHF tasks can be used to screen participants for atypical language laterality. Chances of finding such a laterality pattern are much higher for participants with LVF advantages than for participants with RVF advantages. Although it is possible that we would have found a participant with clear RVF advantage in the VHF tasks and RH dominance in the scanner if we had scanned all 250 participants, our data strongly suggest that such occurrences would be very rare (Figure 4; see also Hunter & Brysbaert, 2008a). In contrast, of the 20 participants with consistent LVF advantages we scanned, 16 turned out to have atypical dominance (i.e., a hit rate of 80%). The fact that the classification was better for participants with consistent VHF advantages than for participants with inconsistent advantages indicates that the combination of the word and picture naming VHF task was worthwhile. We thus recommend using the picture and word VHF as a combined laterality indicator.

The main limitation of the VHF tasks is what to do with participants not showing a clear VHF asymmetry and participants with inconsistent VHF asymmetries. As for the participants with reduced VHF asymmetries, it is not the case that they also have reduced laterality in the
scanner (based on the LIs of BA 44 and 45, which had the highest correlations with the VHF tasks). Rather they seem to divide into a group with LH dominance and a group with RH dominance. Further testing is also needed to have more information about participants with opposite VHF asymmetries in the word and picture naming task, because financial constraints prevented us from fully testing them. We were able to test only two participants with a LVF advantage in word naming and a RVF advantage in picture naming (P22, P43), one of whom turned out to be bilateral in the scanner (P22: word -49 ms, picture +37 ms, fMRI -0.23), and one LH dominant (P43: word -16 ms, picture +88 ms, fMRI +0.89). Of the two participants with a LVF advantage in picture naming and a RVF advantage in word naming, one turned out to be RH dominant (P19: word +10 ms, picture -38 ms, fMRI -0.65) and one LH dominant (P46: word +38 ms, picture -42 ms, fMRI +0.93).

On the one hand, these deviating patterns may point to differences in laterality patterns between brain regions responsible for word reading and speech production in a subset of participants (as argued by Pinel & Dehaene, 2010). On the other hand, they could also be due to the fact that VHF tasks and fMRI tasks use different dependent variables (RTs vs. BOLD signal) or to the fact that although the tasks are similar they are nevertheless different paradigms (stimulus naming vs. silent word generation).

The fuzzy boundary between LH and RH dominant participants in VHF measures means that researchers can use various criteria to select their participants, depending on the constraints under which they are working. If they have easy access to a large pool of left-handers, but difficult access to an fMRI scanner, they are advised to include only those participants who show an LVF advantage both in word and picture naming. Alternatively, if access to large groups of participants is a problem whereas scanning costs are not prohibitive, all LIs smaller than +20 ms become interesting, because this is where we found our RH dominant participants (Figure 4).

The addition of eye movement control to the VHF tasks did not have additional value in the present study. The corrected VHF asymmetries did not differ much from the uncorrected ones and, more importantly, did not correlate more with the fMRI validation data. This agrees with Van der Haegen et al.’s (2010) conclusion that deviations in the fixation position are noise, rather than systematic biases that invalidate the conclusions, as argued by Jordan and colleagues.
(Jordan et al., 1998; Jordan & Paterson, 2009). In this respect, it is important to keep in mind that our study already contained a fixation incentive in the form of the central arrow pointing to the target stimulus to be named. Results may be different if participants have no incentive at all to properly look at the fixation position when the trial starts. Another way to put control on the participants’ fixation behavior is to add a secondary task, such as naming briefly presented digits at random intervals (Van der Haegen, Brysbaert & Davis, 2009). The fact that strict eye movement control is not needed for valid laterality research, is interesting because it takes away much of the burden for the participants and also makes the testing more mobile. Without the need for an eye-tracking device, larger (left-handed) samples can be tested for screening under more comfortable circumstances. In addition, it must not be forgotten that eye-tracking results in the exclusion of potentially interesting participants. For instance, we had to decline participants with strong glasses and even then we had problems to monitor the eyes of 11 out of 250 participants (including one who turned out to be RH dominant; P8).

Finally, for the interpretation of our findings it is important to keep in mind that only left-handers were tested. It will be interesting to see how a similar group of right-handers perform on our battery of tasks and measures. Given that less than 5% of them are expected to be right language dominant, we would expect very few participants to show a clear LVF advantage both in word and picture naming. However, of these we would expect an equally high percentage (80%) to be right dominant in the word generation task. The most interesting subgroups arguably would be those with reduced VHF asymmetries and inconsistent VHF asymmetries: Would they all be left-dominant given the prevalence of this type within the right-handers or would they divide in two subgroups like the lefthanders?
References


Brysbaert, M. (1994). Lateral preferences and visual field asymmetries: Appearances may have been overstated. *Cortex, 30*, 413-429.


Appendix

Data from the 50 participants who participated in both the behavioral VHF tasks and the fMRI silent word generation task. The various columns include respectively: mean scores for handedness, earedness, eyedness, footedness, and an overall sidedness score (as reported in the questionnaires); the mean RT difference between LVF and RVF on the picture and the word naming task (both when uncorrected and corrected for imperfect fixation positions); and the fMRI Laterality Index for BA44+45. We also include the initial assessments we gave to the participants on the basis of the data. A VHF advantage of at least 10 ms was considered as evidence for a reliable VHF difference; advantages below this criterion were classified as “unclear”. fMRI LIs between -.60 and +.60 were considered as evidence for bilaterality. Participants are ordered and numbered according to fMRI LI for the first 50 participants, and according to the picture VHF difference for the remaining 200 participants (who did not take part in the fMRI task). Participants of whom no eye-tracking could be collected (e.g. when the eyelid or eyelashes are too close to the pupil, the eye-tracker receives insufficient contrast to localize the pupil position) are indicated by an asterisk.
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Chapter 3 | fMRI validation of the VHF technique as language laterality indicator
Chapter 4: Colateralization of Broca's area and the visual word form area in left-handers: fMRI evidence
Chapter 4: Colateralization of Broca's area and the visual word form area in left-handers: fMRI evidence


Language production has been found to be lateralized in the left hemisphere (LH) for 95% of right-handed people and about 75% of left-handers. The prevalence of atypical right hemispheric (RH) or bilateral lateralization for reading and colateralization of production with word reading laterality has never been tested in a large sample. In this study, we scanned fifty-seven left-handers who had previously been identified as being clearly left (N = 30), bilateral (N = 7) or clearly right (N = 20) dominant for speech on the basis of fMRI activity in the inferior frontal gyrus (pars opercularis/pars triangularis) during a silent word generation task. They were asked to perform a lexical decision task, in which words were contrasted against checkerboards, to test the lateralization of reading in the ventral occipitotemporal region. Lateralization indices for both tasks correlated significantly (r = 0.59). The majority of subjects showed most activity during lexical decision in the hemisphere that was identified as their word production dominant hemisphere. However, more than half of the sample (N = 31) had bilateral activity for the lexical decision task without a clear dominant role for either the LH or RH, and three showed a crossed frontotemporal lateralization pattern. These findings have consequences for neurobiological models relating phonological and orthographic processes, and for lateralization measurements for clinical purposes.
Introduction

Language processing is considered as one of the most lateralized cerebral functions in humans. At the anatomical level, the hemispheric asymmetry has been attributed to a larger size of the left planum temporale (a posterior region of the Sylvian fissure), and to different slopes of the Sylvian fissures in the two hemispheres (Geschwind & Levitsky, 1968; Josse, Mazoyer, Crivello & Tzourio-Mazoyer, 2003). At a functional level, a left hemispheric specialization was reported for a variety of language-related regions, among which the inferior frontal gyrus (IFG) crucial for speech production and more posterior brain regions such as the ventral occipitotemporal (vOT) region involved in reading.

Despite the well-established role of IFG for speech production and the vOT for reading, it is still not clear how these frontal and occipitotemporal regions interact with each other. If they are closely interrelated, one would expect the anterior and posterior regions to lateralize to the same hemisphere in order to decrease the time costs of information exchange.\(^{12}\) Psychological models of visual word recognition nearly all incorporate a contribution of phonological information to visual word recognition based on a large variety of behavioral evidence (e.g., Dimitropoulou, Duñabeitia & Carreiras, 2011; Ferrand & Grainger, 1992; Rastle & Brysbaert, 2006), but fast interactions between IFG and vOT are not yet widely integrated in neurological models of reading (e.g., Cohen et al., 2000; Dehaene et al., 2004; Dehaene, Cohen, Sigman & Vinckier, 2005). Dehaene and colleagues believe that the vOT is specifically specialized for the binding of letters into words. They called it the visual word form area (VWFA; Cohen et al., 2000) as it responded to orthographic letter strings, invariantly of retinal location, case, font or horizontal/vertical format (see also Cai, Paulignan, Brysbaert, Ibarrola & Nazir, 2010; Dehaene et al., 2004; McCandliss, Cohen & Dehaene, 2003). Others believe that the vOT is not dedicated to visual word form processing because it also responds to picture naming, repeating auditory words etc. (e.g., Devlin, Jamison, Gonnerman & Matthews, 2006; Duncan, Pattamadilok & Devlin, 2010; Price & Devlin, 2003, 2011; Twomey, Duncan, Price & Devlin, 2011). The latter view considers the vOT as an interface in the reading process: The neurons in vOT that are

\(^{12}\) Note that the direction of laterality within an activated region can be influenced by both excitatory and inhibitory connections from the LH/RH homologue areas. For example, Seghier, Josse, Leff and Price (2011) and Seghier, Kherif, Josse and Price (2011) found lateralities to vary according to the amount of right hemispheric activity in a word matching task. This could also indirectly influence the colateralization patterns between two or more regions.
sensitive to visual bigrams (and to whole words more anteriorally) are in constant interaction with neurons coding for the nonvisual characteristics of the stimuli such as their phonology or meaning. Such fast interactions would predict that the vOT is lateralized to the same side as the IFG, assuming that the cross-talk between these areas would be slowed down if their activity were dominantly situated in different hemispheres.

Indeed, studies reported left hemispheric lateralizations in language-related tasks for both IFG and vOT (e.g., Xue et al., 2005; Seghier, Kherif, et al., 2011). Seghier, Kherif, et al. (2011) for example, compared the degree of lateralization during a semantic vs. perceptual word matching task in 50 brain regions. Their voxel-based laterality maps showed consistent LH lateralization in frontal regions and the vOT at group level.

However, a number of studies have reported individual cases of crossed frontal and temporal language dominance (e.g., Baciu et al., 2003; Jansen et al., 2006; Kamada et al., 2006; Lee et al., 2008), with for example speech being controlled by the left hemisphere (LH) and reading by the right hemisphere (RH). Similarly, in a large-scale fMRI study Pinel and Dehaene (2010) argued against an overall dominance view of brain regions because very few regions related to sentence processing (situated in the posterior superior temporal sulcus and the middle frontal gyrus) colateralized with brain areas involved in mental arithmetic (in particular a horizontal segment of the intraparietal sulcus and the superior parietal lobule). Even the correlations between the laterality indices (LIs) in vOT and frontal areas (inferior, pre-central, mid-frontal) in sentence processing often were not significant (Pinel & Dehaene: Table 1), making the authors conclude that “… although all of these regions are highly asymmetrically activated, always in favor of the left hemisphere, correlations between the LI of the fusiform gyrus and of frontal areas are weak.” (Pinel & Dehaene, 2010, p.53). Pinel and Dehaene claimed that the brain should be seen as a mosaic of independently lateralized regions, although one has to keep in mind that their findings point to an absence of a correlation in the degree of lateralization in right-handed LH-dominant participants rather than colateralization across hemispheres itself.

So far, only two small-scale studies directly investigated the colateralization of the IFG during speech (measured as activity in the so-called Broca’s area, i.e. pars opercularis (Brodmann Area [BA] 44) and the pars triangularis (BA 45)) and vOT during reading at an individual level.
Cai, Lavidor, Brysbaert, Paulignan and Nazir (2008) assessed the lateralization of speech by comparing event-related potentials (ERPs) in the left and right IFG during a verb generation task. The lateralization of word reading was tested in a lexical decision task (LDT). Eight right-handed subjects showing a typical frontal lateralization for speech in the left hemisphere (LH) also showed the strongest negative mean ERP in the LH for the visual word form area during word reading in the LDT. Four RH speech dominant participants consistently showed stronger reading ERPs in the RH compared to the LH. Cai et al. (2008) attributed the perfect collateralization of the frontal and occipito-temporal language areas to the need for fast interactions between these regions during word reading. In a second study run by Cai et al. (2010), 11 participants were identified as LH lateralized in the word generation task and five participants were atypically RH lateralized. The LIs of the vOT during reading in a LDT again correlated significantly with the LIs calculated from the IFG ($r = 0.59$), but one right-handed person with LH dominance in IFG and one left-handed participant with RH dominance in IFG showed crossed laterality. Cai et al. (2010) pointed to the possibility that weak activity during the word reading task could have caused the exceptions. In particular, the pattern of the right-handed participant was not clear, as she showed the expected LH dominance of vOT when the words were presented vertically (when there was more activity in vOT).

All in all, the evidence about the collateralization of frontal and occipito-temporal language processing brain areas is far from clear. As we have argued a number of times (Ellis & Brysbaert, 2010a, 2010b; Hunter & Brysbaert, 2008; Van der Haegen, Cai, Seurinck & Brysbaert, 2011), the best way to examine laterality patterns is to compare a group of participants with typical LH language dominance (found in about 95% of right-handers and 75% of left-handers; Knecht et al., 2000) with a group of participants with atypical RH or bilateral language dominance. Cai et al. (2008, 2010) followed this approach, but only tested small samples of four and five participants with atypical dominance so that only coarse conclusions about the variability of frontotemporal laterality patterns could be drawn. Other studies did report large-scale results, but their correlations between LIs were based on a homogeneous sample of participants with typical language dominance, mostly right-handers (e.g., Pinel & Dehaene, 2010). Still other studies did not analyze lateralization data at the individual level, but only reported collateralizations at group level (e.g., Seghier, Kherif, et al., 2011). It is important however to investigate the degree of inter-subject variability in language lateralization across
different functions both for theoretical and clinical purposes. As for the latter, large variability would indicate that an overall lateralization index of language is misleading for preoperative assessments when surgeons want to minimize the damage in the dominant hemisphere (Seghier, Kherif et al., 2011). Rather, separate LIs for different language functions should be obtained.

In the present study, we explored the relationship between the occipitotemporal word reading region vOT and the frontal phonology-related speech region IFG in a sample of 57 participants who reported to write and draw with their left hand. If these regions are lateralized independently for most of the participants, we should see many cases of crossed laterality. On the other hand, if the lateralization of vOT is influenced by the laterality of the speech areas, we would expect that if the asymmetry of IFG changes, the lateralization of vOT will shift as well for the majority of participants.

We could test a large number of participants with atypical brain dominance in IFG because we first screened 265 left-handed participants with a behavioral picture and word visual half field task (see Method section). Participants showing an indication of atypical speech laterality in these tasks were invited for a fMRI study that contained a silent word generation task and the currently discussed LDT. In addition, participants that presumably had LH speech dominance were selected as control participants.

**Method**

**Participants**

In a previous study (Van der Haegen et al., 2011), 50 participants were selected from a large group of 250 left-handers to take part in a fMRI silent word generation task. The selection was based on their performance in a behavioral picture and word visual half field task. Pictures or words were shown in the parafovea. Stimuli were presented in bilateral pairs to avoid attentional biases. The target that had to be named was indicated by an arrow in the middle of the screen. Hunter and Brysbaert (2008) demonstrated that these tasks can serve as a screening method to find people with atypical speech dominance. The partial crossing of optic fibers makes
stimuli presented in LVF/RVF initially fall into the RH/LH respectively, so that shorter naming latencies for stimuli in LVF can point to a RH dominance for speech (see also Barca et al., 2011). In Van der Haegen et al. (2011), we invited participants who were faster in naming pictures and/or words in LVF than in RVF to the fMRI study with a silent word generation task as they were potential atypical subjects. A control group of left-handed participants with RVF advantages were also scanned to compare the data of the atypical participants with those who had typical LH dominance.

For the present study, 7 extra participants were scanned bringing the total sample to 57 left-handers (41 females, 16 males; age ranging between 18 and 29 years with mean age = 20.8 years). All were students of Belgian universities or higher education schools with Dutch as their native language and with normal or corrected-to-normal vision. Table 1 shows their mean handedness scores obtained via a Dutch translation of the Edinburgh Inventory Questionnaire (Oldfield, 1971). The scale ranged from –3 (extreme left preference) to +3 (extreme right preference). All participants reported to write and draw with their left hand. Three out of 57 participants had a positive handedness value, because they did not use their left hand for the eight actions other than writing and drawing in the handedness questionnaire (e.g. using scissors). We did not consider them as an exclusion criterium to increase variability of the sample and thus increase the chances of finding a broad range of LI scores. Participants fulfilled the conditions to be scanned and signed an informed consent form according to the guidelines of the Ethics Committee of the Ghent University Hospital.
TABLE 1.
Individual handedness scores (mean preference score between -3 and +3), LIs in inferior frontal gyrus during silent word generation (target letter vs. *baba* repetition) and LIs, left and right hemispheric peak coordinates and Z-scores in vOT during LDT (horizontal words vs. checkerboards).

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<th>Z-score</th>
<th>RH vOT peak (x, y, z)</th>
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Note that subjects are sorted with ascending LI values in inferior frontal gyrus in the interest of readability of the table (i.e., from most RH dominant to most LH dominant). vOT peaks of subjects showing strong activity in vOT (Z > 3.7) after small volume correction are highlighted in bold, those with Z scores between 3.0 and 3.7 are written in normal font. Subjects without reported vOT peaks had Z-scores below 3.0.
Tasks and Stimuli

Word generation task

The lateralization of speech was measured by activity in the inferior frontal region (Broca’s area: pars opercularis + pars triangularis) during a silent word generation task. The same task was previously used by Cai et al. (2010) among others (Abbott, Waites, Lillywhite & Jackson, 2010; Badzakova-Trajkov, Häberling, Roberts & Corballis, 2010; Hunter & Brysbaert, 2008; Knecht et al., 1996). Participants were asked to silently generate as many words as possible starting with a letter presented in the middle of the screen (b, d, k, l, m, n, p, r, s or t) during ten blocks of 15s. Ten other blocks of 15s contained the control task: The letter string baba appeared on the screen and participants were asked to silently repeat this nonword as long as it was presented. Finally, activation and control blocks were alternated with rest blocks of 15s indicated by a horizontal line on the screen, in which participants were asked to relax. A practice phase outside the scanner ensured that everyone understood the task correctly.

Lexical decision Task

The LDT task aimed to assess the lateralization of word reading by looking at activity in the vOT. Stimuli consisted of 24 high frequent words (mean log10 Frequency/million = 2.16, range 1.89-2.44), 24 low frequent words (mean log10 Frequency/million = 0.61, range 0-1), 24 consonant strings and 24 scrambled words. Words were 4-7 letters long, with six words of each word length. The length of the consonant strings was equal to the word lengths. Scrambled words were created by scrambling images of word stimuli at the pixel level; they matched the words in length/size. Stimuli were displayed in Courier New, in black on a white background.

An event-related design was used for this task. Each trial began with a centrally presented fixation cross. After a variable duration of 500-2000 ms, a stimulus was displayed for 800 ms followed by a short horizontal line for 2s until the end of the trial. Participants were required to press the yes button with the left index finger if the stimulus was a word and to press the no button with the right index finger if the stimulus was no existing word. They were told to perform the task as fast as possible from the moment the stimulus appeared. All stimuli were displayed once in random order.
Stimulus presentation and fMRI Data Acquisition

Stimuli were presented using Presentation software (NeuroBehavioral Systems, CA, United States) and projected onto a translucent screen. Participants watched the screen via a mirror installed in front of their eyes in the scanner.

Whole-brain images were acquired using a 3-Tesla Siemens Trio MRI scanner (Siemens Medical Systems, Erlangen, Germany) at the Ghent University Hospital with an 8-channel radiofrequency head coil.

Functional images were obtained using a T2*-weighted gradient-echo EPI sequence [TR = 2630 ms, TE = 35 ms, image matrix = 64 * 64, FOV = 224 mm, flip angle = 80°, slice thickness = 3.0 cm, distance factor = 17%, voxel size = 3.5 * 3.5 * 3 mm³]. These settings gave 40 axial slices parallel to the anterior-posterior commissure. A high-resolution anatomical image was obtained using a T1-weighted 3D MPRAGE sequence [TR = 1550 ms, TE = 2.39 ms, image matrix = 256 * 256, FOV = 220 mm, flip angle = 9°, voxel size = 0.9 × 0.9 × 0.9 mm³].

fMRI Data Analysis

FMRI data analysis was performed with SPM5 (Wellcome Trust Centre for Neuroimaging, London, UK). The first four images were discarded in each session in order to obtain a magnetization equilibrium. Functional images were preprocessed by (1) a correction for slice time delays caused by the interleaved acquisition of images; (2) spatial realignment using rigid body transformation to correct for head movements; (3) coregistration of individual anatomical images to a mean functional image; (4) normalization to the Montreal Neurological Institute (MNI) T1 template; and (5) spatial smoothing with a 3 mm full width at half maximum (FWHM) Gaussian Kernel to optimize the images for individual analyses. The pre-processed data from each participant were then entered into first-level statistical analysis. For the word generation task, experimental conditions were modeled using a canonical hemodynamic response function (HRF; Friston, Jezzard & Turner, 1994) convolved with a boxcar function in a General Linear Model (GLM). Error trials and six estimated head movement parameters were added into the models as regressors-of-no-interests.
Individual contrast images in the word generation task were obtained by contrasting the word generation condition (target letter display) with the control condition (babab repetition). For the LDT task, modeling consisted of convolving the onset time series of the different stimulus types with canonical HRF with time derivatives. The contrast of interest was the horizontal word condition against the scrambled word condition.

Individual LIs for production in the word generation task were calculated for the region formed by the pars opercularis (approximately BA44) and pars triangularis (approximately BA45) in the AAL template (Tzourio-Mazoyer et al., 2002). For the LDT, we adopted the predefined vOT mask used in Twomey et al. (2011). This box ranged from X = -30 to -54, Y = -45 to -70 and Z = -30 to -4 and a mirror-reversed box in RH, excluding cerebellar regions. We further restricted this mask to the fusiform and inferior temporal gyri. Participants showing no activation at an uncorrected $p < 0.01$ level in this mask were excluded because their vOT activity would be too weak to calculate reliable LIs.

LI values were computed with the LI Toolbox 1.02 of Wilke and Lidzba (2007). We decided to use this toolbox as it has been shown that traditional LI calculations based on a normalized difference of number of activated voxels in LH and RH surviving an arbitrarily chosen threshold produce fluctuating estimations (e.g., Abbott et al., 2010; see Seghier, 2008 for a review). In contrast, the LI toolbox produces a weighted mean LI. For each ROI, 20 thresholds levels were defined by equal steps from 0 to the maximum t-value. Hundred bootstrap resamples (sample ratio $k = .25$) were taken in all ROIs in LH and RH. Only the central 50% of those 10 000 possible were preserved to avoid statistical outliers. A weighted overall mean LI was calculated on the basis of the remaining data by assigning a higher weight to the higher thresholds. More details can be found in Wilke and Schmithorst (2006). Final LI values ranged from -1 (only active voxels in RH) to +1 (only active voxels in LH). Participants with LI > 0.5 were considered as left dominant, those with LI < -0.5 were defined as right dominant.
Results

Behavioral results

No participant reported any difficulty in completing the word generation task. In the LDT, participants made on average 2.9% errors, proving that everyone found the task easy to perform. Overall mean RT was 601 ms, with no significant difference in latencies between the word and nonword stimuli \( F < 1 \). The fMRI analysis was based on all correct trials. Behavioral LDT data of five LH speech dominants (participants 32, 33, 35, 40 and 50 in Table 1) failed to be recorded. We decided to leave these participants in the sample, given the high overall performance.

fMRI results

Figure 1 shows the lateralization patterns of all subjects for IFG activity (Broca's area: pars opercularis + pars triangularis) during silent word generation and vOT activity during LDT. Individual LI values, calculated by the LI toolbox of Wilke and Lidzba (2007), can be seen in Table 1. Finally, Table 2 gives an overview of percentages of LH/RH or bilateral dominance based on the LIs for IFG/word generation and vOT/LDT word reading.

| TABLE 2. |
|---|---|---|---|
| **Percentages of participants showing right hemispheric (RH), left hemispheric (LH) or bilateral dominance for the word generation task (i.e., activation in the inferior frontal gyrus, IFG) and lexical decision task (LDT; i.e. activation in the ventral occipito-temporal region, vOT). Percentages of IFG are based on all 57 participants; percentages of vOT are based on 55 participants, because 2 participants showed unreliably low activity in this task.** |
| **IFG (word generation)** | **vOT (LDT)** |
| RH dominant | 35,1 | 10,9 |
| LH dominant | 52,6 | 32,7 |
| Bilateral | 12,3 | 56,4 |
Figure 1. Lateralization patterns for 55 participants. Two participants without significant vOT activation at an uncorrected $p < .01$ level are not shown. The x-axis displays the LIs based on activity in the IFG during silent word generation; The y-axis shows the LIs in vOT during lexical decision making.

For the word generation task, group analyses for the participants with LH dominance showed strong activity in the left inferior/middle frontal gyrus (with a peak in the pars opercularis) extending to the cingulate gyrus, the precentral gyrus and the SMA, the left angular gyrus, bilateral putamen and thalamus, bilateral precuneus, and the right cerebellum. A reversed pattern was observed for the RH dominant participants. No regions other than the IFG ROI showed robust activity for all individuals (at $p < .05$, FWE corrected). At the individual analysis level, 30 participants showed a clear left lateralized activation pattern in IFG (i.e. with LIs score above + 0.50 in the combined activity of pars opercularis and triangularis; 21 females and 9 males) with values ranging from 0.51 to 0.94, 20 participants showed a clear right lateralized pattern (LI < -0.50; 16 females and 4 males) with values ranging from -0.62 to -0.94, and 7
participants can be considered as more or less bilateral for speech (LIs between -0.50 and +0.50; 4 females and 3 males) with LIs between -0.50 and 0.29.

For the LDT, both RH and LH speech dominant groups showed right lateralized activity in the postcentral and precentral gyri, and in the left cerebellum, which corresponds to the left finger tapping for words. The activation further extended to the right thalamus and the putamen. For the group of participants with typical LH speech dominance, we also observed left-lateralized vOT activity at the same threshold ($p < 0.001$ uncorrected, k=10). No vOT activity was observed for the group of atypical RH participants at the same threshold ($p < 0.001$) but a right vOT activity was observed at a slightly lower threshold ($p < 0.005$; peak at 46, -60, -21, t=3.81). At an individual level, two participants (one RH and one LH dominant) were excluded from further analyses because they showed no significant activation at an uncorrected $p < .01$ level in the predefined vOT box. Among the remaining participants, 18 showed clear LH reading laterality with vOT LI values higher than +0.50, ranging from 0.52 to 0.89. Sixteen of them were also clearly left lateralized for speech. Subject 18 had a clear crossed lateralization pattern as her IFG LI was -0.69 and her vOT LI +0.60. Subject 21 had an IFG LI of -0.50 combined with a vOT LI of +0.60. Only six participants were clearly RH lateralized in vOT with LIs ranging from -0.78 to -0.51. Among them, five were also clearly RH lateralized in IFG and one showed bilateral speech activity with an IFG LI of -0.43.

Next, a correlational analysis based on the individually calculated LIs was performed. The overall correlation between IFG LIs in word generation and vOT LIs in LDT (N = 55) was strongly significant in the positive direction ($r = .59; p < .001$), indicating that both regions collateralized.

At the same time, Figure 1 illustrates that the laterality pattern was much less clear for vOT than for IFG. The majority of the participants (N = 31) had bilateral vOT activity with LIs between -0.49 and +0.44. For the participants with a positive LI values for both tasks, the mean IFG LI was 0.73 (N = 31) and mean vOT LI was +0.48 (N = 34). For participants with negative values, the means were -0.75 for IFG (N = 24) and -0.41 for vOT (N = 21). About half of these participants were LH dominant for speech, the other half was RH dominant. In particular the participants with RH dominant IFG seemed to be less lateralized in vOT. Here we also saw the two clearest cases of crossed lateralization (the abovementioned Subjects 18 and 21). Subject 39
can be considered as a third participant with crossed laterality, with an IFG LI of +0.76 and a vOT LI of −0.49. This means that 3/55 or only 6% of all participants showed a clearly crossed lateralization pattern.

To further investigate the individual vOT activity pattern, we checked the strength of the vOT activity during the LDT for each participant within the pre-defined bilateral region of interest. A small volume correction was applied (Worsley et al., 1996). The threshold \( p < 0.05 \) after correction for number of independent comparisons within the pre-defined region corresponded to a voxel threshold of \( Z > 3.7 \). All peaks of vOT activation surviving this threshold are reported in Table 1. We also report peaks of \( Z > 3.0 \) as trends. It can be noticed that for 17/55 or 29.8% of the participants, no significant vOT activity could be reported.

**Discussion**

In this study, we further explored the collateralization between 1) speech production as assessed by the activity in IFG (Broca's area: pars opercularis and pars triangularis) measured in a silent word generation task and 2) word reading as defined by the activity in the vOT region during a LDT with horizontally presented words. Previous small-scale studies such as Cai et al. (2008, 2010) located both functions in the same hemisphere for 26 out of 28 participants in total. This seems to be in line with the scarcity of single case studies reporting crossed lateralities in both healthy participants and patients (Baciu et al., 2003; Jansen et al., 2006; Kamada et al., 2006; Lee et al., 2008). The use of a global language LI was also criticized by Seghier, Kherif et al. (2011), because they found large inter-subject variabilities of lateralization across language-related brain regions.

By testing a large sample of left-handers we explored the degree of frontal-temporal lateralization variability in healthy participants. Similar to Cai et al. (2008, 2010), the vast majority of participants showed most vOT activation in the same hemisphere as the one with the most activity in IFG, leading to a positive correlation of 0.59 between both LIs. As a matter of fact, only 3/55 participants (6%) showed clear evidence for a cross-lateralization if laterality was defined as a LI index of +0.50 or −0.50. With a slightly lower criterion, two more participants would qualify.
We can assume that the number of crossed lateralizations would be even smaller among right-handers. Genetic models of left-handedness attribute hand preference in these individuals to a chance factor. For instance, the model of McManus (1985) focuses on the relationship between handedness and cerebral dominance. In particular, it tries to explain why the correlation between hand preference and language dominance is much higher among right-handers (less than 5% crossed laterality: right-hand preference and RH language dominance) than among left-handers (more than 70% crossed laterality: left-hand preference and LH language dominance). McManus's (1985) theory claims that handedness is determined by a gene with two alleles. A homozygous gene with two D (Dextral) alleles always leads to right-handedness and left hemisphere dominance, a homozygous gene with two C (Chance) alleles produces random preferences (both for handedness and language laterality), and a heterozygous DC type leads to a pattern in-between. Because left-handers always possess at least one C-allele, they are expected to show much more variability in language dominance and, arguably, in the lateralization of other brain areas as well. Only the right-handers with one or two C-alleles are expected to show crossed lateralities. The frequency of the C-allele is estimated to be around .15, so that only a small percentage of right-handers is expected to have crossed laterality. As a result, left-handers may be more prone to crossed laterality of speech production and visual word recognition, although this explanation is still speculative at present and only one of several potentially genetic influences. In line with these predictions, Cai et al. (2010) reported more variability in their atypical (left-handed) participants than in their typical (predominantly right-handed) participants.

The high correlation between IFG and vOT lateralizations in our study was accompanied by a higher percentage of bilateral language representation in vOT than in IFG. The evidence for stronger asymmetry in IFG than vOT agrees with the hypothesis that speech production is the most lateralized function (Kosslyn, 1987), because the rapid coordination of movements involved in speech require a single control center. There may be more scope for bilateral representation in the word reading system. This by itself could be the reason for the low incidence of crossed laterality, as persons with inverse lateralities of vOT and IFG might be more liable to involve the contralateral vOT tissue in order to optimize the interactions with IFG.

Another interesting finding of the current study is that there was a tendency towards more LH vOT involvement in participants with RH dominant IFG than there was RH vOT activation.
in participants with a LH-asymmetry for IFG. The higher incidence of finding opposite LI values for vOT and IFG in RH speech dominants was also observed by Cai et al. (2010), who mentioned a possible explanation for this. Reversed functional asymmetries are not always associated with deviations at the anatomical level (Sun & Walsh, 2006). In addition, given that the anatomic frontotemporal connections seem to be stronger in LH than in RH (Glasser & Rilling, 2008; Powell et al., 2006), this could imply that some right IFG dominant participants have less developed connections between their RH IFG and RH vOT cortex, even though their speech production is atypical at the functional level. This suggestion of course is a general observation and needs future research by for example Diffusion Tensor Imaging techniques in the same group of participants.

Reading direction could be a second factor in the shift towards a stronger LH vOT involvement in RH dominant participants. As all participants were native Dutch speakers, they all read from left to right. It is well known that readers have an asymmetric perceptual span in line with their reading direction. For left to right readers the span is estimated to go from about three to four letters at the left side to about 14-15 letters at the right side (Rayner, 1998). This means that more information is extracted from the right visual field than the left visual field, putting the left vOT in the lead. Interestingly, the reading direction did not result in a massive shift of vOT asymmetry to LH dominance, suggesting that the impact of the reading direction on vOT asymmetry is rather limited.

The observed data agree with Pinel and Dehaene (2010) in showing that the interhemispheric interactions do not seem to preclude a rather large variety of LI indices in different brain regions. It is not the case that strong laterality in one region is indicative of similar strong laterality in another region, even not when both regions are assumed to interact intensely. In other words, the degree of lateralization of two language functions is not as consistent as the direction of these lateralities. This has implications for preoperative examinations in patients. Seghier, Kherif et al. (2011) already argued for measuring regional instead of global LIs when they found a combination of strongly left lateralized activity in angular gyrus with relatively low lateralized activity in the ventral precentral gyrus in their 82 subjects (44 right-handers, 38 left-handers) performing a semantic word matching task. Similarly, Tzourio-Mazoyer, Josse, Crivello and Mazoyer (2004) found LH/LH, LH/RH and RH/RH patterns during a PET study of a word
generation (IFG) and story listening (middle and inferior temporal regions) task. The independence of LIs in various regions is likely to be clearer the more different the functions are.

At present, our conclusions are limited to the collateralization of speech production in IFG with LDT word reading in vOT. The language network obviously goes far beyond these two regions and the many-to-many mapping of brain structures and functions makes the collateralization analysis incomplete. For example, the superior temporal sulcus (STS) is another important node in the lateralized language network. Richardson, Seghier, Leff, Thomas and Price (2011) investigated different possible pathways including the posterior inferior occipital region, vOT and anterior/posterior STS by means of dynamic causal modeling. They concluded that different routes can be followed between these regions to link orthographic, phonological and semantic processing, which illustrates that linking two language areas is only part of the complex language network. Similarly, Pinel and Dehaene found weak correlations between the LIs of the fusiform gyrus and frontal regions, but observed strong collateralizations between the posterior STS and fusiform/frontal areas. They discussed that the STS may be a keystone in the language network, because previous studies demonstrated an early leftward temporal lateralization for speech listening that can already develop after two or three months (Dehaene-Lambertz, Dehaene & Hertz-Pannier, 2002). Only nine participants showed superior temporal activity in our sample (at an uncorrected $p < 0.01$ level with $Z > 3$, defined as a sphere ROI of 15 voxels around $x = -53, y = -13, z = 0$; see Jobard, Crivello & Tzourio-Mazoyer, 2003), but this could be attributed to an overall high activity level around the STS, so that no conclusions about STS can be made in our sample with this LDT. Jobard et al. (2003) argued that superior temporal activity is part of a network converting graphemes into phonemes when reading words or pseudowords. The decision between words and nonwords in our LDT presumably did not require phonological computations.

Future research is needed to complete the currently presented collateralization results between vOT and IFG with LIs of for example the STS. It would then be possible to see how different subareas of the language network are linked to each other in terms of lateralization. Moreover, additional LI values of other regions are needed because the vOT is not purely dedicated to LDT word reading (Dehaene et al., 2004; Price & Devlin, 2003, 2011), and the IFG is activated in more tasks than word generation as well (Hagoort, 2009; Lindenberg, Fangerau &
Seitz, 2007). Other tasks will also create the possibility to perform other analyses than correlational analyses. For example, a dynamic causal modeling analysis allows to test which connections between different regions fit best with the acquired activation maps (Friston, Harrison & Penny, 2003). This could not be applied to the current data, because the IFG and vOT ROIs were defined in two different tasks (word generation vs. LDT respectively) and because there was too much variability in ROI activation at the individual level. In addition, functional and anatomical connectivity analyses could explore whether the different patterns of asymmetry can be associated with differences in connection strength.

Finally, future research can investigate whether opposite asymmetries have processing consequences. Would participants with deviating LI s in IFG and vOT rely less on phonology in visual word processing than participants with similar LIs? There is a large range of tasks that can be used to address these questions (e.g., Rastle & Brysbaert, 2006).
References


Chapter 5: Speech lateralization influences word reading: Evidence from the optimal viewing position paradigm
Chapter 5: Speech lateralization influences word reading: Evidence from the optimal viewing position paradigm


The question whether foveal processing requires interhemispheric communication forms a long-standing and lively debate. Visual information in patients with hemianopia or callosal deficits seems to be split in the fovea, with stimuli presented in the left visual field sent to the right hemisphere and right visual field information projected to the left hemisphere. The present study tested the consequences of a foveal split for word reading in healthy subjects. We compared naming latencies to three-, four-, and six-letter words while subjects with typical left and atypical right hemispheric speech dominance fixated at all possible letter positions. An eye-tracking device monitored the fixation position of both eyes. Results showed that speech lateralization has a major influence on word reading. The beginning of a word was the optimal viewing position for readers with typical left hemispheric language dominance, i.e. when most letters fall to the right of fixation and are thus directly projected to the left dominant hemisphere. Atypical right speech dominants were faster when they fixated towards the end of the word. These results can only be obtained when letters of foveally presented words are split and sent to the contralateral cortex, and invalidate the existence of bilateral cortical representations. Consequently, visual word recognition models should take into account that interhemispheric transfer is needed for both parafoveal and foveal word recognition.
**Introduction**

Optic fibers coming from the nasal hemiretinae cross at the optic chiasm, whereas the temporal optic fibers lead to the ipsilateral hemisphere. There is a general consensus that information is then carried via the thalamic lateral geniculate nuclei and optic radiation to the contralateral primary visual cortex. As a consequence, visual stimuli presented in the left visual field (LVF) are projected to the right hemisphere (RH), and information from the right visual field (RVF) is sent to the left hemisphere (LH). It is anatomically and functionally unclear whether a similar contralateral projection applies to visual information presented in the fovea (i.e., the center of vision generally estimated to subtend 3 degrees of visual angle). Three lines of evidence have investigated whether the fovea is split or not.

First, ophthalmologists and psychologists long believed that macular and foveal sparing in hemianopia patients (i.e. preservation of vision despite unilateral damage to the occipital cortex) was caused by a bilateral cortical representation of central visual information (e.g., Huber, 1962). Trauzettel-Klosinsky and Reinhard (1998) were the first to test macular sparing under strict methodological conditions. They asked hemianopic patients to report the number of dots presented on a screen. The dots were vertically aligned triplets shown at different eccentricities up to 10° in peripheral vision. Trauzettel-Klosinsky and Reinhard used black dots against a red background to avoid a halo of light scattering in the seeing field. Presentation duration was limited to 120 ms to avoid saccades. A laser ophtalmoscope scanned the fixation position and blood vessels of 13 human eyes. Results of previous studies that did not control eye fixations or used conventional perimetry were probably contaminated by saccades towards the hemianopic side. Hence, patients could report visually presented stimuli because they moved the visual half field borders or because they saw light from the stimulus scattering into the seeing field (Bischoff, Lang & Huber, 1995; Schuett, Kentridge, Zihl & Heywood, 2009). Hemianopic patients indeed develop adaptive oculomotor strategies to complete their visual image (Leigh & Kennard, 2004). Trauzettel-Klosinsky and Reinhard observed macular sparing ranging from 2° to 5° in four patients. They all had an occipital vascular lesion, making the authors conclude that macular sparing is not caused by a bilateral projection of visual stimuli, but can be attributed to a dual blood supply in the occipital cortex (McFadzean, Brosnahan, Hadley & Mutlukan, 1994). Four other patients showed no macular sparing at all. This could point to a foveal split at 0°, but
a nasotemporal overlap of 0.5° is still possible given that spatial accuracy was limited to 0.5° horizontally.

Reinhard and Trauzettel-Klosinsky (2003) investigated foveal sparing around the vertical midline in a larger sample of hemianopic patients. They measured 36 eyes from 20 patients using the above described method. Stimuli were presented from 1° in the seeing hemifield to 10° in the blind hemifield. Reinhard and Trauzettel-Klosinsky found no cases at all with a spared strip around the vertical midline that had a convex shape in the fovea. They did find a straight foveal strip of 0.5° with preserved vision in 12 eyes, a preserved strip with concavity in the central 1.5° in 22 eyes and a straight (13 eyes) or widening (18 eyes) strip of preserved perception in the periphery. In sum, macular sparing has been observed but alternative explanations exclude a bilateral presentation of visual information; foveal sparing has not been detected under strict methodological conditions, even though a very small area of 0.5° (i.e. the diameter of the dot) could still exist.

![Figure 1. Results from Reinhard and Trauzettel-Klosinsky (2003). Importantly, they found no eyes with convex foveal sparing in hemianopia patients (B). They did observe preserved foveal vision, but only in a continuous strip (A), or with concavity (C). In the periphery, foveal sparing could be straight (D) or widening (E). Source: Reinhard and Trauzettel-Klosinsky (2003)］
A second line of research investigating the existence of a foveal split tests patients with callosal transfer deficits such as split-brain patients whose corpus callosum was sectioned to limit spreading of epileptic seizures (e.g., Corballis & Trudel, 1993; Fendrich & Gazzaniga, 1989; Fendrich, Wessinger & Gazzaniga, 1996). Luo, Shan, Zhu, Weng and He (2011) tested a patient with a lesion in the splenium (i.e. the most posterior part) of the corpus callosum, impairing interhemispheric transfer, and a lesion in the left medial occipitotemporal region. Stimuli were only presented within the central 3°, because the patient suffered from right homonymous hemianopia beyond 1.5°. Luo et al.’s patient misread significantly more unilaterally presented Chinese one- and two-character words in LVF than RVF, and failed to identify the left components of centrally presented Chinese words. This was confirmed in a functional Magnetic Resonance Imaging (fMRI) study: The so-called visual word form area (Cohen et al., 2000) in the occipito-temporal sulcus was only activated in the LH when stimuli were presented in RVF. LVF words were not correctly read because they could not be transferred from the RH to the LH via the damaged corpus callosum. If the bilaterally projecting theory had been correct, RVF/LVF words should also have activated the RH/LH respectively. Luo et al. reported similar findings for chimeric face processing, when the patient could only make gender judgments on the basis of the face presented in LVF (projecting to the right fusiform face area). Remarkably, LVF (but not RVF) words activated the primary visual areas bilaterally. The authors concluded that the fovea might be functionally split for both word and face processing, but that there may still be some evidence in favor of bilateral representations at a lower level (see Discussion).

However, the most generalizable consequences of a split fovea for word reading and other high cognitive functions can only be revealed by testing healthy subjects. If central information is indeed split in the same way as extrafoveal stimuli, this should lead to substantial differences between readers with typical left and atypical right or bilateral speech lateralization. Brysbaert (1994) and Hunter, Brysbaert and Knecht (2007) used the Optimal Viewing Position (OVP) paradigm (O'Regan & Jacobs, 1992) to differentiate between a bilateral account and a split fovea. The OVP for reading is assessed by shifting words horizontally across the screen between two vertically aligned fixation lines, so that naming latencies are registered at all possible letter fixation positions of a word (see Figure 2). As predicted by a split fovea, the OVP varied according to the speech dominance of the subjects: Typical left hemispheric dominant
readers (more than 95% of right-handers and about 75% of left-handers; Knecht et al., 2000) showed a J-shaped OVP curve with fastest naming times when they fixated at the word beginning because then most letters fall in the RVF and are sent to the dominant LH. The OVP of atypical speech dominants was located at the word end, when most letters fall in LVF/RH. The OVP curves of LH and RH dominant subjects are not mirror-reversed, because three other factors that are similar for both groups play a role in word naming: (1) The first letters contain most information about the word identity; (2) Visual acuity of letters decreases with an increasing distance from fixation; and (3) Fixating at the word beginning makes word recognition easier because eyes tend to land more often at the word beginning and frequently fixated locations improve reading performance (Nazir, Ben-Boutayab, Decoppet, Deutsch & Frost, 2004).

Figure 2. Example stimulus in the OVP paradigm with a four-letter word. On different trials, the word is presented in such a way that participants fixate the first, second, third or last letter.

The studies of Brysbaert (1994) and Hunter et al. (2007) showed that the fovea is functionally split, but were criticized because of several factors. First, the speech dominance of subjects in Brysbaert (1994) was only measured by behavioral visual half field tasks, in which participants were asked to name parafoveally presented words or objects. Hunter et al. (2007) used more reliable laterality indicators, by running a silent word generation task in fMRI and functional Transcranial Doppler Sonography, but only tested a small sample of 8 RH and 12 LH dominant subjects. Moreover, both studies did not present all of their three- to nine-letter words within the foveal boundaries of 3° and did not use an eye-tracking device to control fixation.
positions (Jordan & Paterson, 2009, but see Ellis & Brysbaert, 2010; Van der Haegen, Drieghe & Brysbaert, 2010).

In the current study, we tested the OVP naming task in a large sample of atypical RH dominant left-handers, and typical LH dominant left- and right-handers. Their lateralization was defined by the activity in LH Broca’s area (Pars triangularis/BA44 and pars opercularis/BA45) or the RH homologue area during a silent word generation task in fMRI. Stimuli were three-, four-, and six-letter words that fell within the central 3°. An eye-tracking device measured fixation positions binocularly. This is the first well-controlled study that can decide to what extent the human fovea is split and which consequences this has for the high cognitive function of reading.

Method

Participants

Forty-nine Belgian students (11 males, 38 females; mean age: 20.6 years, SD: 2.9) with normal or corrected-to-normal vision were included in the analyses reported below. Their handedness, footedness, eyedness and earedness was tested on a scale ranging from -3 (extreme left preference) to +3 (extreme right preference) in a Dutch version of the Edinburgh Handedness Inventory (Oldfield, 1971) and Porac and Coren (1981) questionnaire. All left-handers reported to at least write and draw with their left hand. There were no restrictions applied to the remaining items (e.g. using scissors). Table 1 shows the mean scores for the RH and LH dominant group. Individual preferences can be found in the Appendix. Participants all signed an informed consent form approved by the ethics committee of Ghent University.
TABLE 1.
Mean scores on the questionnaire asking participants to indicate their preference for handedness, earedness, eyedness and footedness. The rightmost columns show the mean lateralization indices (LIs) for speech and lexical decision reading for each group.

<table>
<thead>
<tr>
<th>RH speech dominant</th>
<th>Left-handers (N = 17)</th>
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<td>Footedness</td>
<td>Speech LI</td>
<td>Reading LI</td>
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<td>Reading LI</td>
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Language dominance assessment

Typical and atypical speech dominant left-handers were screened by a word and picture visual half field naming task in order to increase the chance of finding RH dominant readers. An fMRI silent word generation task confirmed the lateralization of all participants. Lateralization indices were calculated by Toolbox 1.02 of Wilke and Lidzba (2007), that estimates a bootstrapped weighted mean of active LH and RH voxels in the left and right pars opercularis (approximately BA44) and pars triangularis (approximately BA45), classically seen as Broca's area (Figure 3). More information about the lateralization assessments of these subjects can be found in Van der Haegen, Cai, Seurinck and Brysbaert (2011). Table 1 shows the mean lateralization indices for the LH and RH dominant group. Individual values can be found in the Appendix. A score of -1 represents a complete right lateralization; +1 would mean that language production is fully left lateralized. Participants were classified as being LH/RH dominant if their indices were above +0.60/below -0.60 respectively.
Materials

Stimuli consisted of 75 three-letter words, 100 four-letter words, and 300 six-letter words. All stimuli were selected by using the Wordgen software (Duyck, Desmet, Verbeke, & Brysbaert, 2004) that is based on the CELEX database (Baayen, Piepenbrock, & Van Rijn, 1993).

The three-letter words were divided into three groups of 25 stimuli, matched independently on log frequency per million, summed type bigram frequency, and neighborhood size ($F_s < 1$). They were all nouns. Similarly, the four-letter nouns were distributed over four groups of 25 stimuli and matched on the same variables as the three-letter words ($F_s < 1$). The 300 six-letter nouns were split up in six matched groups of 50 words ($p_s > .23$).

Design

All words were presented with one letter between two vertically aligned fixation lines. The position of the fixated letter was manipulated by horizontally shifting the word. We treated every subject as a single case study because it is very effortful to find participants with atypical speech dominance and because we knew the strict fixation control was going to force us to exclude a substantial number of trials. All participants named all words at all possible fixation positions (i.e., three times 25 words per position for the three-letter words, four times 25 words per position for the four-letter words, two times 25 words per position for the six-letter words because in the latter condition six times 25 words per position would have been too fatiguing).
The data of Brysbaert (1994) and Hunter et al. (2007) already showed that the OVP curves can be obtained in a psychophysical way by treating every subject as an experiment on their own.

Lists were created for the 3- and 4-letter words according to a Latin square design such that each word only appeared once in each list but at a different fixation position. The order in which the lists were administered was counterbalanced over participants.

**Apparatus**

Fixation positions of both eyes were monitored with a SR Research Eyelink 1000 eye tracking device (Ontario, Canada). Coordinates were recorded every millisecond. At the beginning of the experiment and after each break, calibration and validation were carried out with a 9-point grid. The experimenter could also perform a recalibration during the experimental blocks if necessary. Only eye fixation positions during stimulus presentation were used for data-analysis. A chin rest and a brace at forehead height were used to restrict head movements.

**Procedure**

Stimuli were presented in Courier New font, size 15. A CRT display was placed at a viewing distance of 101 cm. One letter subtended .27° such that the maximum distance from the central fixation position (i.e. when fixating at the middle of an outer letter) was .68° for 3-letter words, .95° for 4-letter words and 1.50° for 6-letter words.

Each trial contained the following steps: 1) Two vertical fixation lines were presented in the middle of the screen for 400 ms; 2) The word stimulus was presented for 150 ms between the lines with the to be fixated letter position exactly in the center; 3) The fixation lines remained on the screen until the voice key registered a response or until a time-out of 5000 ms was reached; and 4) An intertrial interval of 1500 ms was followed by a central dot on the screen to check the calibration accuracy (see Figure 4). A break was provided after 38 (three-letter words) or after each 50 (four- and six-letter words) trials, or whenever the participant indicated that (s)he needed a break.
Instructions were given that there would appear a Dutch word between two vertical lines in the middle of the screen. It was stressed explicitly and repeatedly that it was important to fixate between the two lines when these lines were presented on the screen. Participants were asked to name the words as fast and as accurately as possible. They were informed that they could ask for a break whenever they wanted.

**Results**

The following trials were excluded from the naming latencies analyses: (1) pronunciation errors (0.3%); (2) voice key trigger errors (1.8%); (3) RTs smaller than 200 ms or greater than 1250 ms (1.2%); (4) RTs deviating more than 2.5 standard deviations from a participant's mean (1.9%); (5) 1.5% of the data were lost due to recalibration and incomplete trial transfer from the host pc to the display pc. Finally, two left-handed participants did not name all word lengths because of a randomization error in the program and six (two left-handers, four right-handers) did not finish the experiment because it was too hard to calibrate at least one of their eyes to continue the program. As left-handed participants were selected from the fMRI word generation task, they could not be replaced. Seventeen left-handed students formed the left dominant group with LIs above +.60, 17 participants were classified as being right dominant,
with LIs below -.60. In addition, 20 right-handers were tested. Left speech dominance (found in more than 95% of right-handers, Knecht et al., 2000) was confirmed for 15 students, 5 others refused to be scanned or did not fulfill scanning conditions as their body contained irremovable ferromagnetic matter and they were excluded from the analyses.

The analysis reported below included only trials on which participants (1) made only one stable fixation throughout the 150 ms stimulus presentation, (2) fixated within the boundaries of the letter presented between the two vertical fixation lines (i.e. .25°), and (3) showed binocular disparity of less than 1 letter. In order to reject unreliable OVP curves, we decided to exclude participants that had less than ten trials left per fixation position after these strict fixation control criteria, i.e. 30 for three-letter words (hereafter OVP3), 40 for four-letter words (hereafter OVP4) and 60 for six-letter words (hereafter OVP6). This included data of 28/32 LH (15 left-handers: Mean LI = +.79, SD = .10; 13 right-handers: Mean LI = +.80, SD = .11) and 14/17 RH (mean LI = -.83, SD = .12) dominant students for OVP3, 26/32 LH (13 left-handers: Mean LI = +.79, SD = .10; 13 right-handers: Mean LI = +.80, SD = .10) dominants for OVP4, and 27/32 LH (14 left-handers: Mean LI = +.78, SD = .10; 13 right-handers: Mean LI = +.80, SD = .11) and 12/18 RH (mean LI = -.82, SD = .12) dominants for OVP6. The remaining data contained 47.4%, 66.5% and 35.5% of the original data for OVP3, OVP4 and OVP6 respectively.

The OVP data were analyzed using linear mixed effects (LME) modelling with naming reaction times (RTs) as dependent variable. Fixed factors of the LME analysis included fixation position (relative to the word centre), speech dominance (2 levels: LH and RH dominant) and word length (3 levels: 3-, 4-, and 6-letter words). Within-subject variables were also entered as random factors. For participants, random factors were word length and fixation position as these factors were repeated within participants. For items, speech dominance and fixation position were specified as random factors. The LME analysis additionally tested whether significant interactions between fixation position and laterality group were due to a linear (i.e. OVP3: -1, 0, +1; OVP4: -1.50, -.50, +.50, +1.50; OVP6: -2.50, -1.50, -.50, +.50, +1.50, +2.50) or quadratic trend (i.e. OVP3: +1, 0, +1; OVP4: +2.25, +.25, +.25, +2.25; OVP6: +6.25, +2.25, +.25, +.25, +2.25, +6.25). If LH/RH dominants are indeed faster when fixating at the word beginning/end respectively, this should be captured by the linear component of the interaction. A difference in
the quadratic trend would mean that the two groups differ in terms of visual acuity (Brysbaert and d'Ydewalle, 1991).

Figure 5 shows the 3, 4-, and 6-letter OVP curves for LH and RH speech dominants. Most importantly for the current issue, the linear component of fixation position interacted significantly with speech dominance \([\chi^2(1) = 11.45, p < .001]\), whereas the quadratic term did not \([\chi^2(1) = 1.56, p = .21]\). The slope of the OVP curve from the LH speech dominants increased 3.64 ms per letter fixated more towards the word end \([\beta = 3.64, z = 4.49, p < .001]\) whereas the slope of the RH dominants’ OVP curve did not differ significantly from zero \([\beta = -1.10, z = -0.93, p = .35]\). All other interactions did not reach significance \((ps > .41)\), including the linearly defined fixation position by word length interaction \((\chi^2 < 1)\). Differences in naming RTs while fixating at the word beginning versus the word end when comparing LH and RH dominants were thus found for 3-, 4-, and 6-letter words.

Main effects were found for (1) The intercept \([\chi^2(1) = 5544.00, p < .001]\), simply indicating that the mean naming RT was different from zero; (2) Speech dominance \([\beta = 29.2, z = 2.41, p = .02]\), with RH dominants being on average 29.2 ms faster at word naming than LH dominants; (3) Word length \([\chi^2(2) = 12.37, p < .01]\) with 3.94 ms slower naming RTs for OVP4 compared to OVP3 \([\beta = 3.94, z = 1.09, p = .27]\) and OVP6 being on average 22.26 ms slower than OVP3 and OVP4 \([\beta = 22.26, z = 4.88, p < .001]\); and (4) The main effect of fixation position was marginally significant \([\beta = 1.27, z = 1.76, p = .08]\) but as described above, the fixation position factor significantly interacted with speech dominance.
Figure 5. Optimal viewing position curves for left hemisphere speech dominants (L, left panel) and right hemisphere dominants (R, right panel) for 3- (lower panel), 4- (middle panel), and 6- (upper panel) letter words. The x-axis shows all possible fixation positions relative to the word centre (0); the y-axis displays the mean naming reaction times (RTs) with 95% confidence intervals (CIs) based on the regression weights (i.e. the value of the CIs) and variance-covariance matrices (i.e. length of the CIs) of the fixed effects. The black circles represent the fitted data, the red lines show the observed mean RTs.

Handedness was collapsed across the LH speech dominants in the above described results. As a control, we reran the LME analysis with 3 levels for the factor speech dominance: LH dominant left-handers, LH dominant right-handers and RH dominant left-handers. Again, the linear fixation position factor interacted with speech dominance \( [\chi^2(2) = 12.01, p < .01] \), whereas the quadratic component did not \( [\chi^2(2) = 1.79, p = .41] \). The word beginning and word end naming times interacted with the speech dominance of LH dominant left-handers versus RH dominant left-handers \( [\beta = 5.16, z = 3.24, p < .01] \), with the speech dominance of LH dominant
right-handers versus RH dominant left-handers [$\beta = 4.35$, $z = 2.68$, $p < .01$], but not with the speech dominance of LH dominant left-handers versus LH dominant right-handers [$\beta = .81$, $z = .51$, $p = .61$]. Similar to the above described analysis with two groups for speech dominance, the slope of the OVP-curves from LH dominants increased towards the word end [$\beta = 4.04$, $z = 3.64$, $p < .001$ for left-handers; $\beta = 3.23$, $z = 2.78$, $p < .01$ for right-handers], but the slope of the OVP curve from RH dominants did not reach significance [$\beta = -1.12$, $z = -.96$, $p = .34$].

**Discussion**

The present experiment investigated whether foveally presented visual information is split and which consequences this has for readers with typical or atypical speech lateralization. Previous studies reported that no bilateral representations were found in patients with hemianopia or callosal deficits. We found clear differences in the linear component of the optimal viewing curves for healthy participants with either left or right hemispheric speech dominance. LH dominant subjects were faster to name a central word when they fixated at the beginning (when most letters fall into RVF) than at the end, whereas RH dominant subjects showed flatter curves or were even faster when fixating at the word end (when most letters fall into LVF). The difference was found for 3-, 4- and 6-letter words, comprising .27° per letter and thus falling within the foveal area of 3°. It was clear that the differences were caused by the linearity of the curves, and not by the quadratic components. Only speech dominance influenced the slope of the curves, no effect of handedness was found. The RH dominant group was faster compared to the LH dominants, but there is no reason at present to assume that this would alter the conclusion that the fovea is split. Brysbaert (1994) and Hunter et al. (2007) also found an interaction between laterality group and fixation position, but in their OVP studies the RH dominants named the words more slowly relative to the LH dominants.

The present results are in line with a split fovea theory and demonstrate that foveally presented letters are not duplicated in both hemispheres during naming. If there were bilateral representations, we should not have found a difference between the laterality groups. It is thus more likely that foveally presented words follow the contralateral projection of parafoveally words than that there is a discontinuity between the central 3° and parafoveal vision. It can still
be discussed to what extent the fovea is exactly split. There remains a possibility that two-letter words are projected bilaterally as these were not tested in our sample. However, the impact of such a duplication on daily reading would be negligible, because two-letter words only account for 0.5% of the Dutch language (Keuleers, Brysbaert & New, 2010).

A closer look at Figure 5 suggests that fixating at a non-optimal position in a word is more detrimental for LH dominants than for RH dominants. For the six-letter words for example, the RT difference between the fifth and sixth letter is 15 ms for the LH dominants, compared to a difference of 10 ms between the first and second letter for RH dominants. The difference even becomes more clearly for four-letter words: It is then predicted that LH dominants show a 8 ms differences between letters 3 and 4, whereas RH dominants only have a predicted difference of 2 ms between letters 1 and 2. This could be due to two other factors apart from speech dominance that account for the OVP effect, namely that the first letters of a word are most informative for the word identity and that eyes most frequently land at the word beginning (Brysbaert & Nazir, 2005). Both factors favor fixations at the word beginning and could partially compensate for the letter transfer time cost RH dominants experience when fixating at the first letters. LH dominants on the other hand, cannot benefit from factors that facilitate naming while fixating at the last letters, so that the time cost caused by the transfer of letters from LVF/RH to LH cannot be reduced.

The question remains whether bilateral representations do exist in low-level visual information. As Corballis (1995) pointed out, some split brain patients who have undergone forebrain commissurotomy or corpus callosum sectioning can still perceive visual information in the hemisphere ipsilateral to the visual field in which a foveal stimulus was presented (e.g., Fendrich et al., 1996). This information is generally limited in spatial and temporal resolution, which made Corballis suggest the existence of two visual systems: One that processes low-level information such as location and movement, and a higher visual system used for fine-grained processing that is needed in for example object or word recognition. The detection of low-level information in both hemispheres can point to bilateral representations, although interhemispheric transfer from the retina to the primary visual areas via the superior colliculi instead of the geniculostriate route might be an alternative explanation. Similarly, Luo et al. (2011) observed bilateral activity in the striate cortex when presenting LVF words (not when presenting RVF
words), but only unilateral LH activity in the higher processing visual word form area. The present study indicates that in healthy subjects, at least high-processing word naming cannot make use of bilateral representations. Future research might investigate whether the same conclusion holds for object processing, although word recognition provides a stricter test as words are almost all asymmetrical so that their identity cannot be guessed on the basis of visual information from one visual half field.

Now that we know that the fovea is split in word naming, the precise mechanisms of foveal word processing remain to be explored. Brysbaert (2004) already stated that the importance of interhemispheric transfer for foveal vision is a factor that has often been overlooked in theories of visual word recognition. It is now time to investigate how foveal information is integrated after an initial split. Thus far, only two models explicitly described how letters can be integrated after an initial split. The split fovea model of Shillcock, Ellison, and Monaghan (2000) states that each hemisphere starts recognizing the letters it receives and generates word candidates that could fit the input. In a later stage information from both sides is integrated as part of the word recognition process. However, Van der Haegen, Brysbaert and Davis (2009) failed to find evidence for this hypothesis. They did not find any influence of high-frequent hemifield competitors when participants fixated for example between the second and third letter of in-come (then indeed and become should slow down recognition) compared to fixation between the fourth and fifth letter of inco-me (then there are no longer LVF competitors as inco- is a unique beginning of English 6-letter words). The SERIOL model of Whitney (2001) provides an alternative mechanism, in which foveal letters are reassembled in the dominant hemisphere before recognition starts. For LH dominant participants, this means that letters at the word end (in RVF) are directly sent to the dominant LH, but have to be temporarily inhibited until letters at the word beginning (in LVF) are transferred from the non-dominant RH to LH. Van der Haegen and Brysbaert (2011) found evidence in line with this inhibition mechanism: A RVF naming advantage was found when words were presented at a reasonable distance from a nonword in LVF compared to presentation of the target word in LVF and nonword in RVF. When the target words were concatenated to the nonwords, participants named them faster in LVF than RVF, indicating that RVF information is indeed temporarily inhibited until LVF information is being transferred from the non-dominant RH to the dominant LH and can be recognized first. These first studies on how foveally presented letters are integrated after an
initial split thus found evidence that interhemispheric transfer takes place before word recognition starts, rather than being part of the recognition process.
References


Appendix

The appendix shows individual scores of all subjects on handedness, earedness, eyedness and footedness (ranging from $-3 = $ strong left preference to $+3 = $ strong right preference). In addition, the table lists the speech lateralization indices (LIs) calculated on the basis of activity in Broca’s area during a silent word generation. Subjects are ordered and numbered according to ascending speech LIs and according to handedness: Subjects 1-17 are the left-handed right hemisphere speech dominants, subjects 18-34 formed the left-handed left hemisphere speech dominant group, and subjects 35-49 are the right-handed left speech dominants.
## Mean Scores Questionnaire

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Chapter 6: The consequences of a split fovea on reading
Chapter 6: The consequences of a split fovea on reading


The results of Chapter 5 revealed that typical left hemisphere (LH) speech dominant subjects are fastest to name a word when they fixate at the word beginning, whereas atypical right hemisphere (RH) dominants show the shortest naming latencies when fixating more rightwards. The interaction between speech lateralization and the optimal viewing position indicates that foveally presented words are initially split when they are sent to the cortex, and that interhemispheric communication is needed during word identification. In the current chapter, we examined the consequences of a split fovea on eye movements during word reading in a context. Our sample of LH and RH speech dominants read texts and word series in silence. They were asked to summarize the texts in the first task and to press a button from the moment they identified a word belonging to a pre-specified semantic category (e.g. vegetables) in the word series task. Linear mixed effects analyses showed that speech lateralization interacts with reading behavior: The eyes of the RH dominant group landed more towards the right relative to the initial fixation positions of the LH dominants. Handedness did not influence the results as both LH dominant left- and right-handers significantly differed from the RH dominant participants. The shift of the preferred landing position was predicted by the lateralization indices obtained during a silent word generation task (Chapter 3), but not by the more bilaterally distributed lexical decision reading indices (Chapter 4). We found a minimal influence of speech lateralization on fixation durations, in line with previous studies stating that non-linguistic variables, such as speech lateralization, modify where eyes tend to land but not when eyes move during reading. We conclude that interhemispheric communication is not only needed in central visual word recognition, but that reading behavior is also optimized in function of speech lateralization.
**Introduction**

Our eyes continuously make saccades so that detailed visual information such as letters falls on the foveal part of the retina where vision is sharpest. Outside the fovea (i.e. the parafovea up to 10° from the center of vision, and the periphery beyond the parafovea), acuity severely drops because of a decreased density of cone photoreceptor cells (see Chapter 1). Besides acuity limitations, oculomotor processes seem to be influenced by two types of variables: Low-level or non-linguistic variables such as word length and saccade length modify where the eyes tend to land (McConkie, Kerr, Reddix, & Zola, 1988), whereas higher-level or linguistic variables such as word frequency and predictability of the context influence when the eyes move while reading (Rayner & Duffy, 1986).

Within the fovea, the amount of information that can be extracted from a fixation is asymmetrically distributed: The perceptual span of alphabetic orthographies read from left to right (e.g., English) is estimated to be 3-4 letters to the left of fixation and 14-15 letters to the right of fixation (Rayner, 1998). Letter identification is further restricted to 8 letters to the right of fixation (Underwood & McConkie, 1985). The asymmetrical perceptual span has been attributed to a covert attention mechanism that makes most information being extracted from the direction in which the eyes are about to move next. For example, the perceptual span of English-Hebrew bilinguals was asymmetric to the right when reading English sentences, but asymmetric to the left when reading in Hebrew (Pollatsek, Bolozky, Well & Rayner, 1981).

The previous chapters of this dissertation pointed out that one factor which may affect the perceptual span and fixation positions and their duration has been overlooked in the past decades of reading research: Language lateralization. Chapter 5 made clear that the partial crossing of optic fibers at the optic chiasm not only makes parafoveal information being projected to the primary visual cortex contralateral to the visual field in which the stimuli were presented, but that also foveally presented words are initially split. Left hemisphere (LH) speech dominant left- and right-handers and right hemisphere (RH) speech dominant left-handers showed different Optimal Viewing Position curves (OVP, O’Regan & Jacobs, 1992): The OVP curves of the LH speech dominants had an increasing slope, whereas the RH dominants had a flat OVP curve. In other words, LH dominants were fastest when fixating at the word beginning, when most letters fall in the right visual field (RVF) and are directly sent to the dominant LH. The left-handed RH
dominants did not have a word beginning advantage. The observation that the OVP curves were
influenced by speech lateralization can only be explained by assuming that visual stimuli need
interhemispheric transfer when they are presented in the foveal area.

The question remains whether a split fovea not only affects naming latencies of words
presented in isolation, but also influences where the eyes tend to land in a more natural text
reading context. In the current study, we compared the reading behavior of the same typical LH
and atypical RH speech dominant subjects that took part in Van der Haegen, Stevens and
Brysbaert (in preparation, Chapter 5). We expected LH dominant readers to fixate more towards
the left in a word compared to RH dominants. Participants read two short stories, four newspaper
articles and two country descriptions. In addition, they were asked to read series of ten words
with a fixed word length of six or eight letters and to press a button if the series contained a word
belonging to a pre-specified semantic category (e.g. vegetables). As these tasks do not involve
naming but silent reading, we used both speech and reading lateralization indices as predictors of
fixation landing positions. The speech indices were taken from Van der Haegen et al. (2011,
Chapter 3); The reading indices were calculated based on the activity in the ventral occipito-
temporal region during a lexical decision task (see Van der Haegen, Cai, & Brysbaert, 2012;
Chapter 4).

Method

Participants

Participants were recruited from Van der Haegen et al. (in preparation, see Chapter 5). They
were all willing to take part in the current reading study, but data from five participants were not
collected for all subtests as their eyes could not be calibrated accurately enough (in the OVP task
trials were excluded when the eyes did not fixate the intended fixation location). The remaining
44 Belgian students (10 males, 34 females; Mean age: 20.7 years old, SD: 3.0 years) from
universities and higher education schools filled in a questionnaire in which their handedness,
eyedness, earedness and footedness was tested on a scale ranging from -3 (extreme left
preference) to +3 (extreme right preference) in a Dutch version of the Edinburgh Handedness
Inventory (Oldfield, 1971) and Porac and Coren (1981) questionnaire. Participants reporting to at
least write and draw with their left hand were classified as being left-handed. Table 1 shows the mean scores on the questionnaires for the right-handers (N = 15), left-handers with LH language dominance (N = 13) and left-handers with RH language dominance (N = 16). Individual scores can be found in the Appendix. All participants signed an informed consent form approved by the ethics committee of Ghent University.

TABLE 1.
Mean scores of handedness, earedness, eyedness and footedness on a scale ranging from -3 (strong left preference) to +3 (strong right preference) for the right hemisphere (RH) dominant left-handers and left hemisphere (LH) left- and right-handers. The rightmost columns show the mean lateralization indices (LIs) for speech and lexical decision reading for each group.

<table>
<thead>
<tr>
<th>Identification of language lateralization</th>
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<td>Speech lateralization</td>
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Van der Haegen et al. (2011, Chapter 3) describe in detail how speech lateralization patterns were measured. In short, typical and atypical speech dominant left-handers were screened by a word and picture visual half field naming task in order to increase chances of finding RH dominant readers. Twenty right-handers were added to the current study to control for handedness effects. An fMRI silent word generation task confirmed the lateralization of all participants. In this widely used paradigm (e.g., Abbott et al., 2010; Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Hunter & Brysbaert, 2008, Knecht et al., 1996), an experimental condition in which the subject is asked to generate as many words as possible starting with a target letter is contrasted against a condition in which the subject has to silently repeat a non-word (see Figure 1A). Lateralization indices were calculated by using the Toolbox
1.02 of Wilke and Lidzba (2007). A weighted mean of the activity in LH and RH so-called Broca’s area (pars opercularis/Brodmann Area [BA] 44 and pars triangularis/BA45) resulted in a speech LI for each individual, ranging from -0.94 (i.e. most extremely lateralized RH dominant) to +0.94 (i.e. most extremely lateralized LH dominant, see Appendix for individual scores). Table 1 shows the mean lateralization indices for the RH speech dominant left-handers (LIs below -0.60; A value of -1 would mean complete RH lateralization), and the LH speech dominant left-handed and right-handed group (LIs above +0.60; A value of +1 would mean complete LH lateralization).

**Reading lateralization**

In a similar vein, reading LIs were calculated for each individual. The fMRI paradigm consisted of a lexical decision task in which words of four to seven letters were contrasted against images of words that were scrambled at pixel level (see Figure 1B). Weighted mean LIs were now calculated based on the activity in the LH and RH ventral occipito-temporal region (i.e. the so-called visual word form area, Cohen et al., 2000). Indices ranged from -0.78 to +0.89. Mean values for the LH and RH speech dominant left- and right-handers can be found in Table 1; Individual scores are included in the Appendix. Speech and reading LIs correlated significantly: Most brain activity during lexical decision reading was localized in the same hemisphere as the participants’ speech dominant hemisphere (Van der Haegen et al., 2012, Chapter 4). It is however clear from Table 1 and the Appendix that lexical decision reading is more bilaterally distributed than word generation representing naming. We therefore classified our participants as LH or RH language dominant based on the naming task, and additionally ran analyses using the continuous speech and reading LIs.
Figure 1. Procedures of the silent word generation task (Panel A) and lexical decision task (Panel B; targets could be either scrambled words that had to judged as a non-word or words presented in normal font) in fMRI, used as indicators for naming and reading lateralization respectively.

Tasks and Procedures

Word series reading task

In the first task, initial fixation landing positions were examined in a reading context of words with a fixed word length. On each trial, ten six-letter words or ten eight-letter words with one space in between were presented in a series in the middle of the screen. The two word lengths were presented in two separate blocks. Participants were asked to read the series in silence. They were told to do so in a natural way, as if they were reading a newspaper or a book. They had to press a button with their left index finger if the series contained a word belonging to a pre-specified semantic category (i.e. animals in the first half of the experiment, vegetables/fruit in the second half), and a button with their right index finger if the series did not contain a target word in order to move on to the next trial. Stimuli consisted of 1250 words, divided into groups of ten words that were presented in a randomized order. Target words were included in 1/5 word
series. Trials containing a target were excluded from further analyses to avoid deviating eye movement patterns due to identifying a target word. Analyses reported below are thus based on 80% of the data or 200 trials of 10 words in total. Words belonged to various grammatical classes (verbs, nouns, adjectives, prepositions) with a log frequency per million ranging from 0 to 3.88 (Mean: 1.19, SD = 0.69), summed type bigram frequency ranging from 5515 to 122569 (Mean: 49909, SD = 20901), and neighborhood size ranging from 0 to 19 (Mean: 2.78, SD = 3.33) based on the CELEX database (Baayen, Piepenbrock & Van Rijn, 1993). The words were presented in Courier New font, size 14. A CRT display was placed at a viewing distance of approximately 75 cm. One letter subtended .30°.

Figure 2A displays the procedure of the word series reading task: 1) A fixation dot was presented one line above and one letter to the left of the location of the first stimulus to ensure that eye fixations started from the same position in each trial; 2) After calibration checking based on the fixation dot, the experimenter started the presentation of a series of ten words; The words were presented until either the left or right button was pressed; 3) An inter-trial interval of 1500 ms was inserted prior to the next fixation dot. A break was provided after 63 word series, or whenever the participant indicated that (s)he needed a break. The practice phase consisted of five times ten words that did not reappear in the experimental phase.

Text reading task

The second behavioral task consisted of reading two short stories, four newspaper articles and two descriptions of countries (containing information about their history, geography and population) in order to obtain reading data in a setting reflecting natural reading. Each screen contained five lines of text with maximum 80 characters on each line. Participants were asked to read the texts as naturally as possible and to press a button with their dominant hand at the end of each screen to move on to the next trial. The procedure is illustrated in Figure 2B. Prior to the start of the experiment, participants wrote down what they knew about the topics of the texts to ensure that all participants had an equal amount of knowledge of the content. They were also asked to shortly summarize each text at the end of the experiment. Texts included 6117 words in total. Analyses only included data of four- (N = 840, mean log frequency: 2.55, SD: 1.54), five- (N = 489, mean log frequency: 1.42, SD: 1.28), six- (N = 641, mean log frequency: 1.17, SD: 1.36), seven- (N = 405, mean log frequency: 0.82, SD: 1.00), and eight-letter words (N = 407,
mean log frequency: 0.62, SD: 0.92). Proper names were not excluded as they were the same for LH and RH dominants. Stimulus presentation was similar to the word series reading task. A break was provided after every seven screens, or upon request.

Figure 2. Procedures of the word series reading task (Panel A) and text reading task (Panel B).

**Apparatus**

Fixation positions of both eyes were monitored with a SR Research Eyelink 1000 eye tracking device (Ontario, Canada). Coordinates were recorded every millisecond. At the beginning of the experiment and after each break, calibration and validation were carried out.
with a 9-point grid. The experimenter could also perform a recalibration during the experimental blocks if necessary. Calibration accuracy was checked after each trial by letting the participant fixate a dot presented one line above and one letter left from the first stimulus. A chin rest and a brace at forehead height were used to restrict head movements.

**Results**

The fixation position analyses reported below only included fixations that were longer than 80 ms and shorter than 800 ms. Analyses were further limited to fixations that did not fall on the first word of a line, fixations that were the initial landing fixations on a word, and resulted from a forward saccade. For the initial fixation position analyses, words that were fixated more than once were excluded. This also eliminated those words that were fixated twice or more within the same fixation run, i.e. when the word was fixated more than once before moving to the next word (22.5 % of the word series data, 20.2 % of the text reading data). These data inclusion criteria were also used for the fixation duration analyses so that both analyses were based on the same dataset. In the text reading task, only four- to eight-letter words were examined. In the word series task, trials that included a target word were excluded, i.e. 20% of the total number of trials. Mean accuracy rates in the word series reading task were very high: A word belonging to the pre-specified semantic category was on average detected in 90.0% (word length 6; SD = .07) and 88.4% (word length 8; SD = .09) of the trials. Word series that did not contain a target word were on average correctly judged in 99.1% (word length 6; SD = .01) and 97.2% (word length 8; SD = .15) of the trials.

The fixation behavior of LH and RH language dominant participants was compared by running a linear mixed effects (LME) model. The dependent variable was the initial landing position of a word. For both the text and word series reading task, three fixed effects variables were examined: Speech dominance (2 levels: LH and RH dominant), Eye (2 levels: left eye and right eye) and Word length (2 levels for the word series: 6- and 8-letter words; A centered continuous variable for the text reading data with a length varying from 4 to 8 letters). A random intercept and a random slope for word length were entered as random effects for eyes and participants; For items, a random intercept and random slopes for speech dominance and eye
were used. P-values reported below are based on a Type III ANOVA using a $\chi^2$- distribution. Statistically significant main effects and interactions were further explored using generalized Wald tests on the variance/covariance matrices of the fixed effects.

**Initial fixation position analyses**

**Text reading**

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

We further observed the following significant main effects and interactions, which are mentioned for completeness: (1) A main effect of Eye, with the right eye fixating on average 0.15 letters more to the left than the left eye [$\chi^2(1) = 14.91, p < .001$]; (2) A main effect of Word length, with fixations landing on average 0.13 letters more to the left per additional letter [$\chi^2(1) = 39.79, p < .001$]; (3) An interaction between Eye and Word length, with an increasing binocular disparity for longer words [$\chi^2(1) = 13.29, p < .001$].
Chapter 6 | The consequences of a split fovea on reading
Figure 3. The initial fixation position curves for the left hemisphere (L, black lines) and right hemisphere (R, red lines) speech dominant participants in the text (upper panel, page 183) and word series (lower panel, current page) reading task. The curves are based on the mean and standard deviation of a normal distribution obtained from a non-linear mixed effects model with the following specifications: The dependent variable was the frequency of landing positions (around the word centre 0) for each participant, eye and word length collapsed over items (i.e. the densities on the y-axis); Speech dominance, eye and word length were modeled as fixed factors with a random intercept and a random effect of word length for each participant and each eye. The solid lines on each panel show the fitted results, the dotted lines display the observed values.
Word series reading

Very similar results were found for the 6- and 8-letter words in the word series task (see Figure 3B). The intercept again was significant, with fixations now falling on average 0.44 letters to the right of the word centre \( \chi^2(1) = 38.93, p < .001 \). Most interestingly, mean initial landing positions again differed between the LH and RH speech dominants \( \chi^2(1) = 8.65, p < .01 \), with RH dominants fixating 0.41 letters more towards the right than LH dominants [LH dominants: \( \beta = 0.24, z = 2.75, p < .01 \); RH dominants: \( \beta = 0.65, z = 5.76, p < .001 \)]. As in the text reading results, Speech dominance interacted with Word length \( \chi^2(1) = 4.42, p < .001 \): The word length effect did not reach significance for the LH dominants \( \chi^2(1) = 3.17, p = .07 \), but RH dominants did fixate more towards the right for 8- compared to 6- letter words \( \chi^2(1) = 15.80, p < .001 \); with \( \beta = 0.91, z = 6.10, p < .001 \) and \( \beta = 0.39, z = 3.58, p < .001 \) for 8- en 6-letter words respectively].

The same remaining main effects and interactions as for the text reading data were observed: (1) A marginally significant main effect of Eye, with the two eyes fixating on average 0.11 letters from each other \( \chi^2(1) = 3.78, p = .05 \); (2) A main effect of Word length, with fixations landing on average 0.18 letters more towards the right per additional letter \( \chi^2(1) = 17.74, p < .001 \); (3) An interaction between Eye and Word length, with more binocular disparity for 8- than for 6- letter words \( \chi^2(1) = 5.18, p = .02 \).

Effect of handedness on initial fixation positions

In the previous analyses, we did not make a distinction between right-handers and left-handers in the LH dominant group. The RH dominant group only contained left-handers. To control whether Speech dominance and not handedness influenced the initial landing positions, the analysis was rerun with a three-level Speech dominance factor, i.e. LH dominant left-handers, LH dominant right-handers and RH dominant left-handers.

Text reading

Exactly the same effects were found compared to the analysis with two levels for Speech dominance. The initial fixation positions differed between the three groups \( \chi^2(2) = 13.95, p < \)
When contrasting the groups, the mean fixation positions of the LH dominant left-handers did not differ from those of the right-handers \( [\beta = -0.02, z = -0.23, p = .82] \), but both the left-handers and the right-handers landed more towards the word beginning than the RH dominant left-handers \( [\beta = -0.24, z = -3.35, p < .001 \text{ and } \beta = -0.22, z = -3.10, p < .01 \text{ respectively}] \).

**Word series reading**

Similar results can be reported for the word series task. The main effect of Speech dominance with three group levels was again significant \( [\chi^2(2) = 8.45, p < .05] \), and with no differences within the LH dominant group \( [\beta = 0.02, z = .10, p = .92] \), but fixations further in the word for RH dominants when compared to both LH dominant left-handers and right-handers \( [\beta = 0.42, z = 2.49, p < .05 \text{ and } \beta = 0.41, z = 2.48, p < .05 \text{ respectively}] \).

**Initial fixation positions predicted by continuous speech and reading LIs**

Instead of dividing the participants into two discrete groups (LH versus RH speech dominants), we entered the Speech dominance factor as a continuous measurement in this analysis. In addition, the LIs calculated on the basis of an fMRI lexical decision task were included as reading LIs because the currently investigated tasks involved silent reading (see Table 1 and the Appendix for individual reading LI values).

**Text reading**

Main effects and interactions did not change compared to the pattern found when Speech dominance was included as a discrete factor. Most importantly, Speech dominance still had an influence on the initial fixation position \( [\chi^2(1) = 13.83, p < .001] \), but Reading dominance could not predict the fixation pattern \( [\chi^2(1) = 2.18, p = .14] \). In other words, the lexical decision LIs did not contribute to the variance of fixation positions when combined with a continuous measure of Speech dominance.

**Word series reading**

The word series data analysis lead to similar conclusions: The effect of Speech dominance remained significant \( [\chi^2(1) = 5.34, p < .05] \), but the Reading LIs did not explain
anything in addition \( \chi^2(1) = 0.17, p = .68 \). Two interactions changed compared to the two-level Speech dominance analysis: The interaction between Eye and Word length disappeared \( \chi^2(1) = 0.90, p = .34 \), and we observed a three-way interaction between Speech dominance, Reading dominance and Eye \( \chi^2(1) = 4.50, p < .05 \).

**Fixation duration analyses**

In the final analyses, we investigated the influence of the initial fixation positions of LH and RH dominants on fixation duration. The same data inclusion criteria as above were used so that duration analyses were based on exactly the same data as in the fixation position analyses. The dependent variable of the LME analysis now was the duration of fixations when words were fixated once. The fixed factors were Speech dominance (2 levels: LH vs. RH), Fixation position (centered around the middle of the word and modeled as a linear or a quadratic term to test whether the results were respectively due to a difference in laterality, resulting in differences at the word beginning/end or due to a difference in visual acuity, Brysbaert & d’Ydewalle, 1991), Word length (2 levels: 6- or 8-letter words for the word series task; A centered continuous variable containing 5 word lengths from 4- to 8-letter words for the text reading task). As for the random effects, we modeled a random intercept and slope for Speech dominance, Eye and Fixation position at the item level, and a random intercept and slope for Word length and Fixation position at the level of participants and eye.

**Text reading**

Of most interest for the current study, we found a three-way interaction between the linear component of Fixation position, Speech dominance and Word length \( \chi^2(1) = 14.38, p < .001 \). Figure 4B shows that LH dominant subjects fixated words more shortly at the word beginning than at the word end, whereas the optimal viewing position of the RH dominant subjects was situated more towards the word end, in line with the OVP data from Chapter 5. The interaction was however only present for the shortest word lengths, from 6-letter words on it no longer reached significance [4-letter words: \( \chi^2(1) = 10.92, p < .001 \), 5-letter words: \( \chi^2(1) = 6.77, p < .01 \), 6- to 8-letter words: \( ps > .14 \)].
In addition, the following main effects and interaction were significant and are mentioned for completeness: (1) A significant intercept \( \chi^2(1) = 2246.47, p < .001 \) with a mean fixation duration of 223 ms; (2) Fixation position modeled as a quadratic term was significant \( \chi^2(1) = 30.81, p < .001 \) with longer fixation durations around the word centre than at the extremes; (3) Fixations lasted on average 3.18 ms longer when the word length increased with one letter \( \chi^2(1) = 9.37, p < .01 \); (4) A significant interaction between the linearly modeled fixation position variable and eye \( \chi^2(1) = 4.10, p < .05 \), but neither slope was significantly different from zero when tested separately for each eye \( ps > .29 \); (5) The inverted U-shape of the fixation positions was more pronounced for shorter than for longer words, but reached significance for all word lengths \( \chi^2(1) = 7.54, p < .01 \); (6) LH dominants did not show a word length effect \( \beta = 1.64, z = 1.45, p = .15 \), in contrast to the RH dominants \( \beta = 4.71, z = 2.17, p < .001 \), resulting in a speech dominance by word length interaction \( \chi^2(1) = 4.05, p < .05 \).

**Word series reading**

As in the text reading task, we observed a three-way interaction between the linearly modeled Fixation position variable, Speech dominance and Word length \( \chi^2(1) = 30.88, p < .001 \), illustrated by Figure 4A. The Fixation position by Speech dominance interaction was however not significant for neither the 6-letter words \( \chi^2(1) = 1.16, p = .28 \), nor the 8-letter words \( \chi^2(1) = 2.81, p = .09 \), indicating that LH vs. RH speech dominance differences in fixation durations based on the initial fixation positions were negligible.

We again mention the remaining significant main effects and interactions: (1) The intercept reached significance with fixation durations lasting on average 258 ms \( \chi^2(1) = 1471.79, p < .001 \); (2) Both the linear \( \chi^2(1) = 20.50, p < .001 \) and quadratic \( \chi^2(1) = 47.80, p < .001 \) term of the Fixation position variable were significant, with on average shorter fixations towards the word beginning and an inverted U-shaped curve respectively; (3) There was a small but significant duration difference between the left and right eye \( \chi^2(1) = 16.28, p < .001 \), with the left eye leaving the word on average 1.69 ms earlier than the right eye; (4) The quadratic term of Fixation position interacted with Eye \( \chi^2(1) = 23.34, p < .001 \), but was also present in the three-way interactions with Speech dominance \( \chi^2(1) = 18.38, p < .001 \) and Word length \( \chi^2(1) = 7.44, p < .001 \). Only the interaction mentioned in the previous paragraph is shown in Figure 4 given the relevance for the research question of the current study; (5) The linear
component of Fixation position interacted with Word length [$\chi^2(1) = 21.01, p < .001$], but the interaction was also involved in the three-way interaction with Eye [$\chi^2(1) = 6.92, p < .01$]; (6) Finally, Speech dominance interacted with Eye [$\chi^2(1) = 7.33, p < .01$] and with Word length [$\chi^2(1) = 6.04, p < .05$], with in addition a significant three-way interaction between all three variables [$\chi^2(1) = 5.60, p < .05$].
Figure 4. The three-way interaction between Initial fixation position (on the x-axis, displayed around the word centre 0; The linear and quadratic term are combined in these curves), Speech dominance (Left (L, in black) and Right (R, in red) hemisphere dominants) and Word length (6- and 8- letter words in the upper panel on page 189; 4- to 8- letter words from left to right in the lower panel) in the word series reading task (upper panel) and text reading task (lower panel). The y-axis shows the mean fixation duration in milliseconds. The solid lines represent the fitted curves, whereas the dotted curves display the observed values.
Discussion

In Chapter 5, we found that speech lateralization modified the optimal viewing position during an isolated word naming task. In the current study, we investigated whether language lateralization also interacts with fixation position in more natural, everyday reading circumstances. It has been argued that the OVP effect can change in a linguistic context (Vitu, O’Regan, & Mittau, 1990). When reading texts or word series, words can be skipped, the identity of upcoming words can be predicted from the context, attention is constantly shifted, parafoveal words can be previewed, words can be refixated, etc. It thus involves a much more dynamic context with saccades and fixations, whereas fixations were forced to be stable at a predefined position in the isolated OVP word naming experiment.

Our main research question was to examine whether the preferred initial landing position is shifted more towards the word end for RH language dominant subjects compared to LH dominants. If visual information in the fovea is split, it would be less detrimental for RH dominants to fixate towards the right because more letters fall in the left visual field and are directly sent to the dominant RH. The time cost caused by the transfer of letters from the non-dominant to the dominant hemisphere is then limited. Shillcock and McDonald (2005) attributed the OVP effect to an attempt to equally divide the labor during orthographic, phonological and semantic processing across the two hemispheres. They showed that the OVP resembles the position at which information uncertainty is optimized, i.e. at the word centre or slightly to the left in order to favor the LH which is the most important hemisphere for most readers. Our results indeed showed an influence of speech lateralization on initial fixation positions: In both the text and word series reading task, RH dominants fixated more rightward than LH dominants did (i.e. 0.11 vs. 0.34 letters to the left of the word centre in the texts, 0.65 vs. 0.24 letters to the right of the word centre in the word series for RH and LH dominants respectively). The difference was rather limited, but it was a stable observation that was highly significant. It can be assumed that the RH dominants did not fixate even further into the word because of three other factors that contribute to the OVP-effect (Brysbaert & Nazir, 2005): (1) The word beginning is most informative; (2) Reading is easier when looking at the word beginning because the first letters are most frequently fixated in languages read from left to right; and (3) Visual acuity of
letters decreases with an increasing distance from fixation. The first two factors may limit the rightward OVP shift for RH dominants.

Apart from the main effect of speech lateralization on initial landing position, three other observations were made. First, the OVP in the word series was slightly to the right of the word centre, whereas the OVP is usually situated at the word centre or slightly to the left (Rayner, 1979). The nature of the task probably induced a rightward bias: Participants were asked to press a button from the moment they noticed a word belonging to a pre-specified semantic category or to continue to the next trial when there was no target present in the series. In other words, they had to scan the series until the end before they could make a decision. In the text reading, task performance was not evaluated at the end of each line. Participants were simply asked to summarize the text when they finished reading it. Second, the effect of speech dominance increased for longer words. The differences between LH and RH dominants were .05, .14, .23, .31 and .40 letters for 4- to 8-letter words in the text reading and .24 and .54 letters for 6- and 8-letter words in the word series reading task. This is in line with the split fovea account, stating that the preferred OVP depends on the number of letters that have to transferred to the dominant hemisphere. Third, the left and right eye were not always aligned during reading as observed in many other studies (see Kirkby, Webster, Blythe & Liversedge, 2008 for a review). In both tasks, we observed a crossed fixation disparity with the right eye landing on average 0.15 (reading task) or 0.11 letters (word series task) in front of the left eye. This binocular disparity interacted with word length, but not with speech dominance. Shillcock, Roberts, Kreiner and Obregón (2010) argue that more crossed disparity is observed in reading studies where fusion between the images of the two eyes is not problematic, e.g. when dark letters are presented on a light background as was the case in the current study. Shillcock et al. further varied four parameters in a model simulating when most information can be extracted from visually presented letters and found that crossed fixations facilitate lexical access more than uncrossed fixations regardless of the assumed precision of foveal splitting (no overlap or 1.2° overlap), the amount of contralateral preference (i.e. the human visual system prioritizes contralateral input) or left or right ocular prevalence (i.e. the fact that one eye produces more cortical activation than the other). Producing more crossed than uncrossed fixations thus optimized reading for both LH and RH dominant subjects in the current experiments.
Our second analyses indicated that the shift of the OVP was due to the side of speech lateralization, and not due to handedness. The OVP of both LH dominant right- and left-handers differed from RH dominant left-handers, whereas the preferred fixation position was comparable for the LH dominant groups. This illustrates that consequences of lateralized cognitive functions should be investigated by comparing LH to RH (speech) dominant subjects, and not only by including left-handers as a more atypically lateralized group. This is in line with Vingerhoets et al. (2012, in press), who found only marginal differences between the cortical activation pattern of left- and right-handers during a tool use pantomiming task (i.e. most LH activity in dorsolateral prefrontal, premotor and posterior parietal regions, but reduced LH activity for left-handers in the parietal lobule), but a completely reversed pattern when comparing LH and RH speech dominant left-handers (i.e. the ventral and dorsal premotor cortex, dorsolateral prefrontal cortex, posterior parietal cortex and supplementary motor area were lateralized to the same side in the word generation and tool use task). Similarly to Vingerhoets et al.’s results implying that praxis representations are related to speech dominance and not to handedness, we can conclude from the current results that differences in reading are associated with speech dominance but would not have been observed when only taking handedness into account.

Third, a shift of the OVP could be predicted by a discrete or continuous speech dominance variable, but lateralization indices obtained during the lexical decision task could not explain any additional variance. Theoretically, it seems plausible that silent reading behavior is more related to lexical decision LIs calculated from activity in the ventral occipito-temporal region than word generation LIs based on activity in Broca’s area. It is however important to note that the reading LIs were less lateralized compared to naming. Indeed, naming is generally seen as the most robustly lateralized human function (Kosslyn, 1987). Van der Haegen et al. (2012) showed that reading and naming LIs are significantly correlated. In the current sample, the LIs also correlated \( r = 0.57, p < .001 \), but when taking the same cut-off value +/-0.60 as was used to classify the participants into LH or RH speech dominants, only 3/44 were clearly RH dominant and 8/44 were clearly LH dominant for lexical decision with one participant (S14 in the Appendix) from the latter group showing a crossed frontotemporal lateralization pattern. It can thus be assumed that the lexical decision LIs could not differentiate the reading behavior of our participants because the cortical activation is too bilaterally distributed to have an effect on the initial fixation positions. Also note that our participants were first recruited based on the
speech dominance LIs. We predict that the OVP effects can be explained by the reading LIs in a sample of more extremely lateralized subjects during a lexical decision task, because it can be expected that one hemisphere will also be clearly dominant for speech during a silent word generation task. The cortical differences between the groups would then be distinct enough to capture the shift in preferred fixation position even though our data suggest that a minority of the population will be strongly lateralized for reading.

In the final analyses, we explored whether the preferred fixation positions could be called the optimal viewing positions by looking at the consequences for fixation durations. We decided to only include those fixations that were the single fixations on a word in order to run the analyses on exactly the same dataset as was used for the fixation position analyses. The initial fixation durations were thus equal to the total time spent on the word or gaze duration. For all word lengths and in both tasks, we observed the inverted OVP-effect previously reported in word reading (e.g., Vitu, Lancelin & d’Unienville, 2007) but also in natural reading (e.g., Kuperman & Van Dyke, 2011): Fixation duration were longest near the word centre, with decreasing latencies when moving towards word extremes. More importantly, fixation durations were influenced by fixation position, speech dominance and word length. The fixation position by speech dominance interaction was however limited to the 4- and 5- letter words in the text reading task. RH dominants fixated slightly longer at the word beginning (i.e. when most letters are sent to their non-dominant hemisphere) than at the word end, whereas the reversed pattern was observed for LH dominants. The minimal influence of the OVP’s on the duration of fixations is in line with the distinction that has been made between factors that influence where the eyes tend to land and factors that determine when the eyes move on (Rayner, Binder, Ashby & Pollatsek, 2001). Differences in durations have been attributed to high-level linguistic factors such as word frequency and predictability based on the context. Different landing positions have been ascribed to low-level variables such as word length and the distance from the previous fixation (launch site). We can now add speech dominance as a non-linguistic determinant that significantly influences initial fixation positions along with an increase of the effect for longer words, but that has a smaller effect on the fixation durations.
References


Appendix

In the appendix, the following variables are included from left to right: (1) Subject numbers ordered according to ascending speech LIs and handedness; (2) Individual mean values of handedness, earedness, eyedness and footedness with a general mean score, all ranging from -3 (strong left preference) to +3 (strong right preference); (3) Speech dominance categories divided in a right (lateralization indices [LI] below -0.60) en left (LIs above +0.60) hemisphere dominant group based on the activity in Broca’s area during a silent word generation task; (4) Reading LIs and the appropriate categories based on the activity in the ventral occipito-temporal region during a lexical decision task (LIs between -0.60 and +0.60 are classified as bilateral; three subjects had too weak activity to calculate reliable LIs, two other subjects could not be scanned during the lexical decision task due to technical problems, see Van der Haegen et al. (2012)).
## Mean Scores Questionnaire | Speech | Reading

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Chapter 7: General discussion
Chapter 7: General discussion

This dissertation aimed to investigate whether foveal and parafoveal visual word recognition is organized in the same way. A similar organization would imply that words presented in the central 3 visual degrees are initially split and contralaterally sent to the cortex: Letters on the left side of the fixation point are sent to the right visual cortex, whereas letters from the right visual half field are projected to the visual cortex of the left hemisphere. The two hemispheres consequently have to collaborate in order to recognize a word. This view is supported by the split fovea theory (SFT). In contrast, the bilateral projecting theory (BPT) argues that letters presented in the fovea are duplicated, so that each hemisphere receives all letters and no interhemispheric transfer is needed in order to recognize the word.

Evidence in favor of the BPT comes from hemianopia patients whose vision was spared in the fovea despite unilateral damage to the visual cortex (Huber, 1962), and from anatomical studies that observed traces of a retrograde transneuronal marker on both sides of the central vertical midline although the tracer was unilaterally injected (Stone, Leicester & Sherman, 1973). The results of these studies could be refuted or clarified by alternative explanations. For example, the hemianopia patients made saccades towards the stimuli they had to detect (Bischoff, Lang & Huber, 1995), and the anatomical studies derived their conclusions from ganglion cells that are only indirectly connected to the fovea (Leff, 2004).

The SFT was supported by split-brain patients who could not read centrally fixated words as their sectioning of callosal fibers precluded interhemispheric communication (Corballis & Trudel, 1993), and from behavioral studies with healthy subjects that for example found a different optimal viewing position (OVP) for left hemisphere (LH) and right hemisphere (RH) speech dominants, resulting in an optimized number of letters that had to be transferred to the dominant hemisphere (Brysbaert, 1994; Hunter, Brysbaert & Knecht, 2007). Studies favoring the SFT were criticized because of methodological shortcomings regarding precise fixation control or could not be replicated (Jordan & Paterson, 2009).

In this General discussion, an overview will be given of the studies that put the discussion between the SFT and BPT under scrutiny. Then, recent studies examining whether letters of an
initially split word are reunited in an early or late stage of visual word recognition will be discussed, followed by a description of possible implications for reading when interhemispheric transfer is impaired. Finally, the consequences of a split fovea in other visual processes than reading will be outlined.

**Research overview**

In Chapter 2, the impact of critiques raised against previous SFT studies was evaluated. Jordan and Paterson (2009) reviewed the four main methodological flaws in SFT research: (1) Fixation location control was inappropriate; (2) Words were not always presented within the foveal borders of 1.5° on each side of fixation; (3) Eyes are not always aligned so that a precise split is contaminated by binocular disparity; (4) Naming tasks overestimate the need for interhemispheric transfer because language production is the most lateralized function. Van der Haegen, Drieghe and Brysbaert (2010) showed that these shortcomings indeed induced noise in previous OVP curves, but strictly controlling the methodological settings did not alter the OVP effect in left speech dominants. In Experiment 1, an OVP curve for six-letter words was obtained using the same settings as in previous studies (i.e. no fixation control, binocular viewing, stimuli exceeding the foveal borders etc.). Experiment 2 did monitor the eyes of the participants, or made use of an eye contingent display technique. In addition, the size of the six-letter words was carefully controlled so that the outmost letters were maximally 1.5° away from fixation. The OVP curve was replicated, with the fastest naming latencies observed when participants were fixating at the third letter. The final experiment added a secondary fixation task (i.e. at randomly presented trials participants had to name a briefly presented digit) to the eye monitoring condition, and viewing was monocular instead of binocular in the eye contingent condition. The OVP curve never interacted with methodological adjustments; Reaction times only increased when the conditions were more fatiguing for the participants. The results can be best explained by assuming that previous SFT studies were contaminated by trial-to-trial noise. The overall conclusion remains the same, namely that LH speech dominants are fastest to name a word when most letters are directly projected to their dominant hemisphere.
The fourth critique raised by Jordan and colleagues (i.e. naming would overestimate the split fovea effects) was not taken into account by Van der Haegen et al. (2010). Word recognition is indeed more bilaterally represented in the human brain than word production as was shown in Chapter 4. However, this cannot explain why the OVP curves were so similar in the three experiments. Moreover, not finding the typical J-shaped curve in a strongly lateralized task such as naming would have been even stronger evidence against the SFT than a failure to replicate the OVP effect in a word recognition task such as lexical decision. Production is clearly dominated by one hemisphere. As a result, a need for transferring letters should become clear when comparing word naming latencies from LH or RH dominant subjects. No difference in naming between the two groups would show that words are not split in the fovea, whereas lexical decision latencies can also be influenced by stimulus-response compatibility effects, the non-words that are used in the experiment, different strategies to decide whether the presented letter string is a word or not etc. A third advantage of the naming task is that it can reveal time costs related to rapidly transferred letters, whereas tasks focusing on accuracy such as the Reicher-Wheeler task (e.g. deciding whether the letter n or h was presented at the second letter position after a brief presentation of the word snow) are not sensitive enough to capture the consequences of a split fovea.

The studies of Chapter 2 do not provide direct evidence that words are indeed split when being recognized, but they do indicate that the results from previous SFT studies (e.g. Brysbaert, 1994; Hunter et al., 2007) are not invalid because their data contained noisiness. A more convincing test would be to compare the OVP curves in a large sample of typically left and atypically right language dominant subjects.

Chapter 3 described the method used to recruit these left and right speech lateralized subjects. First, visual half field tasks screened 250 left-handers for a left or right visual field (LVF or RVF respectively) advantage when naming pictures or words. A subgroup of 50 subjects was then scanned in an fMRI silent word generation task, in which they were asked to mentally generate as many words as possible starting with a predefined letter. Weighted mean lateralization indices (LIs) were calculated based on the activity in Broca’s area (i.e. pars opercularis and pars triangularis in the inferior frontal gyrus). Twenty-five participants had an LI
above +0.60, meaning that they could be considered as being left speech dominant, 20 participants had an LI below -0.60, being right speech dominant, and the remaining five participants did not show clear activity differences in the left and right hemisphere. Overall, the behavioral visual half field tasks correlated significantly with the fMRI word generation task, with most correspondence when only subjects whose visual field advantages were the same in the picture and word task were included ($r = 0.76$, $p < 0.001$ and $r = 0.74$, $p < 0.001$ respectively). In line with the results reported in Chapter 2, strict eye fixation control did not alter the results.

The main purposes of Chapter 3 were twofold. First, the left and right speech dominant groups were recruited in order to compare their word naming behavior in Chapter 5. As such, the need for interhemispheric transfer in central word recognition could be evaluated in an OVP paradigm. Second, we evaluated behavioral tasks as a fast and cheap screening tool for (a)typical speech dominance. The VHF tasks can give a first indication before more time-consuming and expensive techniques such as fMRI are used to obtain a more detailed lateralization index. Moreover, clinical tests are generally more invasive such as the Wada-test, in which one of the hemispheres is temporarily anaesthetized and then production performance for each brain half is evaluated. Future laterality research can make use of our data to estimate the lateralization pattern of their participants. The visual half field tasks should be used as a screening method. We do not argue that the results provide equal reliable and detailed information as fMRI results, especially not when the differences between the hemispheres are less pronounced. Correct predictions can be improved when using a more conservative LI threshold, or when combining language tasks such as word generation, naming words based on a description etc. (see for example Niskanen et al., 2012 for an evaluation of combined lateralization tasks).

It has become clear in recent years that the term language lateralization should be used with caution. It is well-known that language processing consists of various subprocesses such as speech production, speech perception, reading, prosody etc. with production being the most lateralized function (Kosslyn, 1987). Different subprocesses can yield different regional LIs, as argued by Seghier, Kherif, Josse and Price (2011). We therefore tested our sample of LH and RH speech dominant subjects in an additional fMRI task, namely a lexical decision task described in
Chapter 4. Responses to horizontally presented words were contrasted against scrambled words of the same length. LIs were calculated with the same LI toolbox used in Chapter 3, but now focused on activity in the ventral occipito-temporal (vOT) region, known as the visual word form area (Cohen et al., 2000). Fifty-seven participants were scanned: 30 of them were clearly left speech dominant, 20 had a clear right speech dominance, and seven participants were considered as having bilateral speech representations, as their LI in the silent word generation task was between -0.60 and +0.60. Speech and reading LIs correlated significantly \((r = 0.76, p < 0.001)\), meaning that the dominant hemisphere for speech was the same hemisphere that was dominant in reading for most participants. It was however remarkable that reading was overall less lateralized, with 18 left reading dominants, six right reading dominants and no less than 31 left-handers without a clear lateralization pattern (two participants had to be excluded due to unreliably weak activation in the region of interest). Three subjects even showed a crossed lateralization pattern, either processing speech dominantly in the LH and reading in the RH or vice versa.

As in Chapter 3, the study of Chapter 4 was set up because of two reasons. First, reading LIs were obtained in order to evaluate the differences in fixation behavior for subjects with typical left or atypical right lateralized reading (Chapter 6). If the SFT is correct, it would be beneficial for right dominants to fixate more towards the word end, so that most letters are directly projected to their dominant vOT in the RH. Only using the speech LIs from Chapter 3 as predictors for a shift in initial landing positions during reading would go against the recent claim that laterality research should calculate regional LIs instead of one global language LI. We would then have only been able to predict reading behavior based on speech LIs. Second, comparing speech and reading LIs in a larger sample than previous studies tested (e.g. Cai, Lavidor, Brysbaert, Paulignan & Nazir, 2008; Cai, Paulignan, Brysbaert, Ibarrola & Nazir, 2010) could shed light on the phonological and orthographical mechanisms active during word recognition. If reading orthographic codes is influenced by the phonology of words, we expected speech and reading to lateralize to the same hemisphere in order to rapidly share information. Top-down influence of the phonological code during visual word recognition has been found in numerous behavioral studies (e.g., Dimitropoulou, Dunabeitia & Carreiras, 2011), but is not yet widely integrated in neurological models of reading (see the discussion between Cohen et al., 2000; Dehaene et al., 2004 who consider the vOT as a region dedicated to reading, and Price &
Devlin, 2003, 2011 who point to the constant interaction between neurons active during phonological, semantic and orthographical processing). The large correspondence between the hemisphere dominant for speech and reading signifies that time costs to share phonological and orthographical information are reduced by a lateralization of both functions to the same side. The high incidence of bilateral activation during the lexical decision task indicated that reading is less extremely lateralized than speech, as already stated by Kosslyn (1987).

**Chapter 5** described a crucial test for deciding between the SFT and BPT. We adopted the same method as Brysbaert (1994) and Hunter, Brysbaert and Knecht (2007) used: If foveally presented words require interhemispheric transfer, then this should be reflected in the OVP curves of LH and RH speech dominants. Under strict methodological settings, we confirmed that RH dominants name words fastest when they are fixating more towards the word end compared to LH dominants. We monitored the eyes of the participants binocularly while they named three-, four-, and six-letter words that fell within the foveal boundaries of 1.5° on either side of the central fixation lines. Trials on which participants did not fixate properly were excluded from the analyses. This was the first study that took into account the critiques raised against previous SFT studies, even though Chapter 2 already provided evidence that OVP curves include noisiness but do not change substantially with less strict stimulus and fixation control. As expected, LH dominants showed a larger word beginning effect than RH dominants did. The difference between the groups was due to the linear component of the naming curves, and not due to differences in visual acuity which would have been captured by the quadratic term of the curves. The shift of the OVP effect was found for all word lengths, and did not depend on handedness as both right- and left-handers from the LH dominant group significantly differed from the RH dominant group.

These results indicate that interhemispheric transfer is needed in central visual word recognition: Letters that are projected to the non-dominant hemisphere have to be transmitted to the dominant hemisphere, resulting in a time cost. Chapter 5 also supports the view that observations of preserved foveal vision in hemianopia patients were caused by experimental artefacts. Trauzettel-Klosinsky and Reinhard (1998) for example argued that saccades towards the seeing field made it possible for hemianopia patients to report the presented stimuli. Our results indeed indicate that there is no hemiretinal overlap along the vertical meridian in the
fovea. It can be questioned to what extent foveal splitting has an influence on word reading. As
the shortest words we included in our experiment were three letters long, it is still possible that
two-letter words or single letters are sent to both the LH and RH primary visual cortices. Two-
letter words however only comprise 0.5% of the Dutch language (Keuleers, Brysbaert & New,
2010), limiting the relevance of a possible different mechanism for the central two letters. Hence,
we did find strong evidence in favor of the SFT, but we should be cautious when claiming that
the fovea is precisely vertically split (e.g., Jordan & Patterson, 2009; Shillcock, Ellison &
Monaghan, 2000).

The final empirical chapter of this dissertation, Chapter 6, investigated whether a split
fovea also influences the way our eyes move during everyday reading. LH and RH speech
dominants read texts involving newspaper articles, short stories and country descriptions, in
addition to 200 word series of ten words with a length of six or eight letters. The linear mixed
effects analyses revealed significantly different initial landing positions for the LH and RH
dominants: In the texts, right speech dominant subjects landed on average 0.23 letters further in
the word than left speech dominants; In the word series task, the difference was 0.41 letters. The
more rightward landing positions were more pronounced for longer words than for short words,
from only 0.05 letters difference between the groups in the case of four-letter words to 0.40
letters for eight-letter words (texts) and differences of 0.24 and 0.59 for six- and eight-letter
words respectively (word series). As in the OVP task of Chapter 5, speech lateralization caused
the effect, not handedness. Remarkably, lexical decision reading LIs could not predict different
landing positions of the LH and RH dominant group. The average degree of the individual LIs
was probably not extreme enough to categorize the landing positions in two groups. The lexical
decision LIs were however correlated to the speech LIs (see Chapter 4). Fixation durations were
not affected by speech lateralization. Both LH and RH dominants showed an inverted U-shape
curve with longest fixations at the center of the words, known as the inverted OVP effect. The
absence of an interaction between lateralization indices and fixation durations is consistent with
the literature: Previous studies only identified high-level linguistic factors (e.g. context
predictability, word frequency) as variables influencing gaze durations. The current results
suggest that speech lateralization should be incorporated in models explaining reading behavior,
even though the impact on initial fixation positions might be more limited than the distance from
the previous fixation and the word length. RH dominants seem to have optimized their reading behavior by slightly fixating more towards the right, but their preferred landing position is not too far away from the first letters of the word that contain most information about the word identity (Brysbaert & Nazir, 2005).

**Early versus late integration of a split word**

Now that we found evidence that interhemispheric transfer during foveal word recognition is needed, it can be questioned how our two brain halves communicate fast enough in order to read fluently. In the introductory Chapter 1, two visions that explain how letters of an initially split word can be reunited were described: The late integration view proposed by Shillcock, Ellison and Monaghan (2000) in their split fovea model and the early integration view incorporated in the SERIOL model of Whitney (2001).

Shillcock et al. (2000) assume that the integration of letters is part of the word recognition process. In the first stages, each brain half starts recognizing the letters it receives from the contralateral visual field. Word candidates are generated intrahemispherically, before the two hemispheres start integrating the letters. Interhemispheric transfer is thus part of the word recognition process. In terms of functional mechanisms of the corpus callosum described in Chapter 1, the late integration can be seen as an example of interhemispheric interference when the target word identity has to be selected based on the word candidates generated independently by the LH and RH (Chiarello & Maxfield, 1996): One hemisphere will provide information that is in conflict with the word information generated by the other hemisphere. The information is only combined in a later stage when the target word is selected and recognized.

The hypothesis of a late integration was tested by Van der Haegen, Brysbaert and Davis (2009) and McCormick, Davis and Brysbaert (2010). Both studies started from the prediction that each fixation position provides unique information to each hemisphere if the late integration account is correct. Varying the fixation position should thus lead to different words generated by the hemispheres and this should be reflected in the reaction times for word recognition. In Experiment 1, Van der Haegen et al. compared lexical decision latencies for target words following a transposed letter prime (e.g. graden – GARDEN) or a replaced letter prime (e.g.
gsuden – GARDEN). Perea and Lupker (2003) showed that transposed letters yield significantly more priming than replaced letters, indicating that letter positions are less strictly encoded than letter identities. The transposed or replaced letters in Van der Haegen et al. could be at positions 2-3 (e.g. graden – GARDEN) or 4-5 (e.g. garedn – GARDEN) of the six-letter words. Fixation lines were placed between letters; Lexical decisions were compared for words fixated between the letters 1-2, 2-3, 3-4, 4-5 and 5-6. If the split fovea model of Shillcock et al. is correct, the difference between transposed and replaced letters should be less pronounced when fixating at positions 2-3 (e.g. gr-aden versus gs-uden) and 4-5 (e.g. gare-dn versus gari-ln), because the hemispheres then receive information that is incompatible with the target word GARDEN. At the remaining positions, incorrect letter positions but correct letter identities are sent to each hemisphere so that the input is more informative for lexical decision. However, priming only increased when the distance between the fixation position and the transposed/replaced letters increased. The left panel of Figure 1 shows the prediction of the data by a model that assumes less priming when the transposed letters are sent to different hemispheres. Model 2 in the right panel predicts more priming when the transposed letters are further away from fixation, because the incorrect letter positions then become less visible. Dixon’s (2003) likelihood ratio λ indicated that the second model explained the data 21.4 times better than the first model.
Figure 1. Two models explaining the priming effects in Van der Haegen et al. (2009) when either letters at positions 2-3 (upper panel) or at positions 4-5 (lower panel) are transposed: Model 1 predicts less priming when the transposed letters are sent to different hemispheres in line with Shillcock et al. (2000), Model 2 predicts that the magnitude of the priming depends on the distance between the fixation position and transposed letters. Source: Van der Haegen, Brysbaert and Davis (2009)

The priming effects cannot be explained by the late integration view. Experiment 2 in Van der Haegen et al. (2009), investigating the influence of hemifield competitors, and McCormick et al. (2010), analyzing semantic categorizations of embedded words, also failed to observe performance differences based on dissimilarities between the two hemispheres.

Another vision that can possibly explain how letters are reunited after an initial split was presented in Whitney’s (2001) Sequential Encoding Regulated by Inputs to Oscillations within Letter units or SERIOL model (see also Whitney, 2008; Whitney & Berndt, 1999; Whitney & Cornelissen, 2008). At the feature level, the model assumes that an acuity gradient is converted into a locational gradient so that the first letter receives most activation and a word is read out serially. Letters in the RVF are directly sent to the LH, but are temporarily inhibited by letters in the LVF, until the latter are transferred from the non-dominant RH to the dominant LH (see
Chapter 1, Figure 6). Once all letters are gathered in the dominant LH, word recognition starts. Letters are thus integrated in an early stage of the visual word recognition process. The early integration view in the SERIOL model can be considered as an example of interhemispheric suppression (Chiarello & Maxfield, 1996): The left hemisphere dominates the cognitive process and RVF letters are inhibited so that letters are recognized in a serial order. The suppression is thus based on the spatial location of the letters (coming from LVF or RVF) and takes place before the letters are identified.

The interhemispheric inhibition assumption of the SERIOL model was tested by Van der Haegen and Brysbaert (2011). They asked right-handed subjects to name four-letter words of a word-nonword pair while fixating between the two stimuli (Figure 2A). Words could be presented in LVF or RVF and were separated by 0, 2 or 4 space characters from the nonword. The target word was printed in yellow; The nonword was white on a dark blue background. According to the SERIOL model, a concatenated stimulus pair should result in a LVF word naming advantage, as the letters of the nonword in RVF are being inhibited until the word is transferred from RH to LH and the leftmost letters are recognized first. When the word and nonword can be seen as separate identities, the fastest naming times should be observed in RVF/LH, in line with the frequently obtained RVF advantage for LH speech dominant right-handed subjects. Figure 2B validates this hypothesis: Naming times were significantly faster in LVF in the 0-space condition, whereas the results turned into a RVF advantage when the distance between the word and nonword increased (albeit a non-significant advantage in the 2 character spaced condition). A second experiment replicated the results with five-letter words, suggesting that the fovea is split in at least the central 2°.
Figure 2. Panel A: Example stimulus from Van der Haegen and Brysbaert (2011): Participants were asked to name the word berg (printed in yellow in the experiment), that was separated from the nonword nust (printed in white) by 0, 2 or 4 space characters. The target word could be presented in the left or right visual field (LVF/RVF). Panel B: naming times were fastest when the word was presented in LVF in the 0-space condition. This turned into a RVF advantage when the word and nonword were separated. Source: Van der Haegen and Brysbaert (2011)

Further evidence in favor of the early integration account comes from Jordan, Fuggetta, Paterson, Kurtev and Xu (2011), who measured event-related potentials during a lexical decision task. Words and pseudowords were unilaterally displayed in the fovea or parafovea. An eye-tracking device ensured that the participants were fixating at the screen centre. Within the early time-windows of 100-150 ms and 150-200 ms after stimulus onset, activation of parieto-occipital electrodes peaked earliest in the hemisphere contralateral to the visual field in which the letter string was presented. Ipsilateral activation peaked later than contralateral activation. Importantly, the early contralateral activation was obtained regardless of presentation position (foveal or extrafoveal) or word type (word or pseudoword). Words were only distinguished from pseudowords after 300-350 ms, indicating that the early asymmetric activation must have been achieved before word recognition started. Activation latencies in the later time window were however only fastest in the hemisphere contralateral to the visual field in which extrafoveal (pseudo)words were presented; When activation for foveally presented stimuli peaked was not influenced by the visual field. This is in line with Cohen et al. (2000) who claimed that word recognition mainly activates the left ventral occipito-temporal region regardless of the presentation position and also agrees with the SERIOL model in that words are reassembled in the dominant hemisphere in a pre-stage of word recognition. Jordan et al. (2011) do not provide
direct evidence in favor of the SERIOL model, as they tested unilaterally presented words and looked at the differences in peak latencies in only one brain region (i.e. the parieto-occipital electrodes P07/08), but their results are in line with an early integration account.

At present, an early integration of letters before word recognition starts seems more plausible than a late integration as part of the recognition process itself. Only few computational models of visual word recognition have taken the need for interhemispheric transfer into account. If the integration of letters is indeed completed before letter identification begins, this may not be problematic for these models as it does not affect the high-level processes they describe. The Self-Organising Lexical Acquisition and Recognition (SOLAR) model of Davis (1999; see also Davis, 2010a for a comparison between the SOLAR and SERIOL model, and Davis, 2010b) for instance does assume that interhemispheric transfer of letters is needed before word recognition. The position-independent letter units of the SOLAR model recognize letters in the dominant LH, so information first has to be collected in one hemisphere. According to Davis (1999), the need for interhemispheric communication in the SOLAR model is further illustrated by the explanations it can provide for letter-by-letter reading in the case of pure alexia. First, letter-by-letter reading is not intrinsically problematic as also control subjects without any brain lesions read in a serial way. The slow reading of alexics could be caused by a more time-consuming transfer of letters from the non-dominant RH to the dominant LH. Binder and Mohr (1992) indeed attributed alexia to lesions in the callosal pathways, for example in the splenium of the corpus callosum. Second, degraded orthographic input in alexia can lead to malfunctioning of the spatial code in the SOLAR model. Apart from context- and position-independent letter units, serial spatial coding is a second important assumption of the model: Input words are compared with representations of words that are already present in the lexicon; Letter positions are determined by a fast left-to-right scan that connects the identity of letters to their position in the word. Reading in patients with alexia can then be explained by a slower spatial coding process because it is hard to match the degraded input to learned representations.
Consequences of impaired interhemispheric transfer

The interhemispheric transfer costs observed in the OVP experiment of Chapter 5 are in line with previous estimates. Whitney (2001) calculated interhemispheric transfer times (IHTTs) based on the OVP data of Brysbaert (1994). She included two factors: (1) The time cost related to the inversion of the acuity gradient and (2) The time it takes to transfer letters from the non-dominant to the dominant hemisphere. The first factor is dependent on the number of letters in the LVF: The slope of the acuity gradient in LVF is increasing whereas the locational gradient needs to be decreasing from the word beginning to the word end. The inversion cost will be higher if letters from the LVF are initially sent to the non-dominant hemisphere (i.e. in the case of LH dominant participants) than to the dominant hemisphere (i.e. in the case of RH dominant participants). Whitney (2001) took 9 ms as an average time cost for the transfer of letters, the second factor determining the total IHTT. For four-letter words, the difference in time when fixating at the first or last letter was estimated to be 4 ms for RH dominants (i.e. 9 ms callosal transfer for first letter fixations, 5 ms inversion time for last letter fixations, see Whitney, 2001 and Hunter & Brysbaert, 2008 for detailed calculations) and -17.5 ms for LH dominants (i.e. no costs for first letter fixations, 9 ms callosal transfer and 8.5 ms inversion time for last letter fixations). Hunter and Brysbaert (2008) report that the transfer costs for the four-letter OVP curves reported in Hunter et al. (2007) were 8 ms for RH dominants and -16 ms for LH dominants. They additionally argued that the inversion cost can theoretically be replaced by a perception cost accounting for the higher informativeness of first letters when identifying words. On the basis of the regression weights of the current Chapter 5, we obtained very similar time costs. LH dominants named the words on average 3.6 ms more slowly per letter that they fixated more towards the right, whereas RH dominants were on average 1.1 ms faster. For four-letter words, the maximum number of letters that have to be transferred was 3.5, i.e. when fixating at the first or final letter. This results in an estimated IHTT of -13 ms for LH dominants and 4 ms for RH dominants. In other words, transfer costs in visual word recognition are relatively consistent across three OVP studies testing four-letter words, despite methodological differences (laterality indications based on less reliable behavioral visual half field tasks in Brysbaert, 1994; small samples of 6 LH dominants and 2 RH dominants and laterality indices based on a normalized difference of number of activated voxels in Hunter et al., 2007; 26 LH dominants and 16 RH dominants based on weighted mean indices in Chapter 5).
The transfer times imply that interhemispheric transfer is needed in visual word recognition. What are the consequences when callosal transfer is impaired? The previous section briefly described how the SOLAR model can account for letter-by-letter reading in alexic subjects whose lesions include callosal pathways (Binder & Mohr, 1992; That alexics have lesions in for example the splenium of the corpus callosum was already reported by Dejerine, 1892, cited in Cohen et al., 2000). Impaired interhemispheric transfer has also been related to developmental dyslexia, a reading disorder that is characterized by a persistent reading difficulty that cannot be expected based on the person’s age, intelligence, sensory acuity or educational opportunities (World Health Organization, 2007). Various neurocognitive causes have been described in the literature. Dyslexia has been attributed to impaired phonological awareness, the ability to divide speech into constituent sounds (Snowling, 2000). The phonological deficit theory has been linked to an inadequate reading network in the LH, including inferior frontal, occipito-temporal and inferior parietal regions (Richlan, 2012). On the other hand, the visual deficit account states that dyslexia originates when rapid integration of visual information is problematic. Magnocellular cells in the dorsal visual pathway, responsible for the localization of visual stimuli such as letters, would be less sensitive compared to control subjects (Livingstone, Rosen, Drislane & Galaburda, 1991).

Impaired interhemispheric transfer is another potential cause that can contribute to the understanding of dyslexia. Studies have found differences in the corpus callosum size of dyslexics compared to control subjects: The callosal midbody seems to be reduced in dyslexics, whereas the splenium has been found to be enlarged, hampering rapid interhemispheric integration (Paul, 2011; Note that results have been inconsistent and that the precise underlying mechanisms remain unclear). Monaghan and Shillcock (2008) successfully simulated developmental surface dyslexia, in which nonwords can be read correctly, but grapheme-to-phoneme conversion rules seem to be over-generalized, resulting in pronunciation errors when reading irregular words (e.g. pint vs. mint). Monaghan and Shillcock’s model assumed a split fovea and manipulated the amount of possible transfer between the hemispheres during mapping of orthography onto phonology. As predicted, performance of reading exception words mostly decreased when the hemispheres were disconnected, whereas nonword reading differed only marginally from a model with interhemispheric connections.
Finally, Henderson, Barca and Ellis (2007) assigned the absence of a bilateral field advantage (BFA) in dyslexics to impaired interhemispheric transfer. When identical words are presented in LVF and RVF, increased temporal activity has been observed in both hemispheres compared to unilateral presentation (Mohr, Endrass, Hauk & Pülvermüller, 2007). Henderson et al. investigated this BFA effect by comparing dyslexic and control subjects on their accuracy of typing stimulus words that appeared for only 60 ms on the screen. Parafoveal stimuli could be presented bilaterally, both in LVF and RVF, or unilaterally. In the unilateral condition, X’s were shown in the opposite visual half field. Dyslexics did not benefit from the bilateral presentations, resulting in a performance equal to the unilaterally presented words. The control subjects did show a BFA. The difference between the groups was particularly clear in LVF, suggesting that impaired callosal connections could not transfer the letters from LVF/RH fast enough to the dominant LH in order to increase accuracy. The results are in line with Martin, Thierry, Démonet, Roberts and Nazir (2007) who compared event-related potentials when subjects were fixating at the first or final letter of a word. The IHTT was slightly shorter for control subjects than for subjects with dyslexia. Remarkably, an asymmetric transfer time with faster transfer from RH to LH than from LH to RH was only found for the control subjects, but not for the dyslexics. The difference in LVF performance reported by Henderson et al. could thus indeed be caused by slower LVF/RH transfer to the dominant LH. It would be interesting to investigate the impaired interhemispheric transfer account of dyslexia in an OVP task. If subjects with dyslexia indeed have problems with the fast transfer of letters to their dominant LH, the difference in the slope of their OVP curves compared to RH dominants’ OVP curves should be even more pronounced than the slope differences of the RH and LH dominants tested in Chapter 5. Dyslexics can benefit even more from the limited number of letters that have to be transferred when fixating more towards the left in a word, whereas fixations at the word end would increase the IHTT to a larger extent. This prediction is supported by Kelly, Jones, McDonald and Shillcock (2004) who found that dyslexics fixated more towards the word beginning than control subjects. In addition, the difference in fixation duration between the two groups was largest at the word end, suggesting that dyslexics need more time to transfer letters when they fixate at the word end.
**Split fovea in non-reading tasks**

If a split fovea influences word naming and reading, does it also affect the processing of other visual stimuli? Letters seem to be reassembled in the dominant speech or reading hemisphere according to an early integration account (Whitney, 2001). The splitting and reuniting of visual information in the fovea is thus a low-level process that may not be inherent to other visual processes such as object or face recognition, but it is not unlikely that all visual information is initially sent to the contralateral hemisphere, regardless of the exact nature of the stimulus. The time needed to reintegrate information may depend on the task being executed.

Luo, Shan, Zhu, Weng and He (2011) found evidence for a split fovea in both word and face recognition. They tested a Chinese patient who had a lesion in the splenium of the corpus callosum and a damaged left medial occipitotemporal region. The patient was asked to read compound words that were centrally presented, with one character to the left of fixation and one character to the right of fixation. His low reading performance was mainly caused by misreading the character presented in LVF, presumably because he was unable to transfer LVF information from the RH to the LH and the LH lacked a representation of the left character. In the face recognition task, the patient was asked to make gender judgments of centrally presented chimeric faces (i.e. half of the face was female, the other half was male). His responses were clearly based on the left half of the faces that were projected to the intact RH face processing area, again in line with a split fovea. Luo et al. thus show that the split fovea for words can be generalized to face recognition, but cannot provide any insights into possible different transfer mechanisms in reading compared to object/face recognition, simply because their patient could not transfer information or process faces in RVF/LH.

An important difference between word recognition and object or face recognition is that words are nearly almost asymmetric, whereas most objects or faces are symmetric or nearly symmetric. This can have major implications for a split fovea in healthy subjects. If the stimulus is asymmetric, information across visual fields has to be integrated before the information can be uniquely identified. If however the information in LVF and RVF is (nearly) identical, one can assume that the hemispheres detect this redundancy of information and transfer is limited. This could still be in line with the SERIOL model (Whitney, 2001) stating that the recognition process only starts after information integration. Treder (2010) concludes in his review that symmetry
detection is quick and automatic, and can occur in a two-stage process: Spatial filters first preprocess the (a)symmetry of the object, whereafter actual symmetry detection takes place and is based on the result of the preprocessor. The preprocessed symmetry judgment could provide an estimation of the amount of transfer needed, even though this account is still speculative.

Conclusion

The studies of this dissertation tested the hypotheses made by the BPT and the SFT. We demonstrated that the critiques raised against previous SFT studies did not invalidate previous findings that central information is split. Under strict methodological controls, we replicated different optimal viewing positions for left and right speech/reading dominants. In line with the SFT, left language dominants were fastest to name words when they fixated at the word beginning, limiting the number of letters that have to be transferred. Right language dominants were fastest at the word end, making most letters directly fall into their dominant right hemisphere. The split fovea even affected reading behavior, although the implications are limited when reading in context. Future research will have to clarify how letters are reunited after an initial split and whether the SFT can be generalized to other processes in the visual domain.
References


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Lezers beseffen nauwelijks hoeveel (on)bewuste processen zich in onze hersenen afspelen om de zwarte tekens die je ogen momenteel bekijken te interpreteren. Tijdens het lezen van een woord activeren we onder andere orthografische, fonologische en semantische codes. Onderzoek focust dan ook op deelaspecten van het leesproces. De studies uit deze doctoraatsverhandeling onderzochten hoe visueel gepresenteerde woorden worden herkend van zodra letters op onze retina’s geprojecteerd worden. Meer bepaald werd nagegaan of de twee hersenhelften met elkaar moeten communiceren wanneer woorden worden aangeboden in de fovea, het centrale gebied van onze ogen waar de meeste visuele details onderscheiden kunnen worden.

**Inleiding**

Licht dat op onze ogen valt, wordt via de cornea, de pupil en de lens naar de retina aan de achterkant van een oog geprojecteerd. De retina bevat 126 miljoen fotoreceptoren, de zogenaamde staafjes die stimuli in zwak licht detecteren en kegeltjes die de kleuren blauw, groen en geel onderscheiden en fijne details opmerken. De meeste kegeltjes bevinden zich centraal in de fovea. Door onze ogen voortdurend te bewegen zorgen we ervoor dat letters in het foveale gebied vallen zodat we de verschillende tekens scherp zien. Algemeen wordt aangenomen dat de fovea de 3 centrale visuele graden omvat (Bourne, 2006; Jordan, Paterson & Stachurski, 2008). Dit is vergelijkbaar met de centrale 12 letters op een normale leesafstand van 60 cm. Het gebied tot ongeveer 5° rond het fixatiepunt wordt het parafoveale gebied genoemd, daarbuiten spreekt men over perifeer zicht (Yu et al., 2010).

De fotoreceptoren zenden neurale signalen uit naar de binnenste lagen van de retina. Staafjes en kegeltjes staan daar in verbinding met bipolare, amacrine en horizontale neuronen, die op hun beurt gelinkt zijn aan ganglioncellen. De axonen van de ganglioncellen vormen de optische zenuw. Figuur 3 uit Hoofdstuk 1 toont dat informatie daarna opgesplitst wordt en naar de gekruiste of contralaterale hersenhelft gezonden wordt (Cohen, 1987). De nasale banen (dichtst bij de neus) kruisen ter hoogte van het optisch chiasme, in tegenstelling tot de temporale banen die niet kruisen en naar de ipsilaterale hersenhelft leiden. Via de laterale geniculate nuclei
in de thalamus loopt tenslotte een linkse en rechthoekige optische vezelbundel naar de primaire visuele cortex (V1) in de occipitale hersenkwaab achteraan in de hersenen, van waaruit informatie naar gespecialiseerde hersengebieden wordt gestuurd voor verdere verwerking (Carter, 2009).

Naast achtergrondinformatie over de weg die visuele informatie aflaat van onze ogen tot onze hersenen, zijn twee taalgerelateerde hersengebieden van belang voor het onderzoek uit deze verhandeling: De Visual Word Form Area (VWFA) die gerelateerd wordt aan lezen, en het gebied van Broca dat sterk geactiveerd wordt tijdens het spreken. Een derde hersenstructuur, het corpus callosum, wordt kort voorgesteld omdat het een belangrijke rol speelt bij de communicatie tussen de twee hersenhelften (zie Hoofdstuk 1, Figuur 4).


Broca’s area ligt in de inferieure frontale gyrus, en wordt gevormd door de pars opercularis (bij benadering Brodmann Area [BA] 44) en de pars triangularis (bij benadering BA 45). Hoewel ook dit gebied betrokken is bij verscheidene functies, wordt het vooral gelinkt aan spraakproductie (Broca, 1865; M. Dax, 1836, G. Dax, 1865). Broca’s area is dominant in de linkerhersenhelft (LH) voor meer dan 95% rechtshandigen en ongeveer 75% linkshandigen; Slechts 5% rechthandigen en 25% linkshandigen verwerken spraakproductie voornamelijk in de rechterhersenhelft (RH; Knecht et al., 2000). Spraak wordt beschouwd als de meest gelateraliseerde cognitieve functie (Kosslyn, 1987).

Het corpus callosum is de C-vormige anatomische structuur die een brug vormt tussen de LH en RH. Verschillende delen van het corpus callosum verbinden andere hersengebieden. Het belangrijkste deel voor de huidige studies ligt meest posterieur, namelijk het splenium dat
occipitale en parietale informatie uitwisselt. De grootte van het corpus callosum werd gelinkt aan de dominantie van spraak, maar recente meta-analyses tonen aan dat deze verschillen gering zijn wanneer gecontroleerd wordt voor handvoorkeur, geslacht en leeftijd (Cherbuin et al., 2012; Josse, Seghier, Kherif & Price, 2008). Het is niet duidelijk hoe informatie functioneel wordt uitgewisseld tussen de LH en RH: Het corpus callosum kan afhankelijk van de taak en de aangeboden stimuli excitatorisch (i.e. informatie vanuit de LH en RH wordt geïntegreerd) of inhibitorisch (e.g. informatie vanuit een hersenhelft wordt onderdrukt zodat de andere hersenhelft optimaal werkt) functioneren.

Het is algemeen aanvaard dat visuele informatie initieel wordt gezonden naar de contralaterale hersenhelft, en van daaruit door een dominante hersenhelft wordt verwerkt. Of hersenhelften moeten samenwerken tijdens centrale visuele woordherkenning wordt echter nog in vraag gesteld. De huidige studies onderzochten of informatie in de fovea ook gesplitst wordt (Split Fovea Theory, SFT), of gedupliceerd wordt zodat zowel de LH en RH representaties ontvangen van de centraal aangeboden letters (Bilateral Projecting Theory, BPT).

De eerste studies hieromtrent wezen in de richting van de BPT: Hemianopia patiënten (i.e. zichtsverlies in het linker- of rechter visueel halfveld [LVV of RVV] na een beroerte of hersenschade unilateraal in V1) bleken een normaal zichtsvermogen te behouden in de fovea (Huber, 1962). De patiënten werden gevraagd om lichtpunten in LVV of RVV te detecteren. Binnen het gebied van de fovea observeerden zij zowel links als rechts van het fixatiepunt licht, wat erop wijst dat hun unilateraal hersenletsel hun prestatie op de test niet hinderde omdat foveale stimuli toch naar beide hersenhelften worden gezonden. Latere studies die een striktere methodologie volgden wezen er echter op dat hemianopia patiënten vaak saccades maakten naar de stimuli (Bischoff, Lang & Huber, 1995), of het licht konden zien doordat het verspreid werd tot gevrijwaarde visuele gebieden (Reinhard & Trauzettel-Klosinski, 2003).

Een tweede reeks studies vond evidentie voor de SFT. Deze studies maakten gebruik van de Optimal Viewing Position (OVP) taak (O’Regan & Jacobs, 1992) om na te gaan of interhemisferische communicatie noodzakelijk is tijdens centrale woordherkenning. In deze taak worden participanten gevraagd om te fixeren tussen twee verticale lijnen. Daarna verschijnt een woord tussen de fixatielijnen dat zo snel mogelijk benoemd moet worden. De positie van de
woorden kan over trials heen horizontaal verschoven worden, zodat men op de eerste, tweede, derde etc. letter van het woord fixeert (zie Hoofdstuk 1, Figuur 5). Brysbaert (1994) en Hunter, Brysbaert en Knecht (2007) vonden dat de benoemingscurves verschillen voor LH en RH spraakdominante personen. De LH dominanten waren snelst wanneer ze links van het midden van het woord fixeerden, terwijl de OVP van RH dominanten meer naar het woordeinde toe lag. Brysbaert en Nazir (2005) verklaarden de J-vormige OVP-curve van de LH dominanten aan de hand van vier factoren: (1) Visuele scherpte neemt af wanneer de afstand tussen een letter en de fixatielocatie toeneemt; (2) De eerste letters van een woord zijn meest informatief voor de identiteit van het woord; (3) Lezers fixeren meestal in de eerste helft van een woord; (4) Letters in RVV worden rechtstreeks gezonden naar de LH, de dominante sprakhemisfeer voor de meerderheid van de populatie. De laatste factor is wat de SFT voorspelt: LH dominanten zullen snelst zijn wanneer ze links in het woord fixeren, aangezien dan de meeste letters in RVV vallen, en dus naar hun dominante LH worden geprojecteerd. RH dominanten zullen een minder sterk stijgende of zelfs dalende curve vertonen, omdat de eerste drie factoren behouden blijven, maar de vierde factor ervoor zorgt dat een fixatie later in het woord voordeliger is aangezien dan de meeste letters rechtstreeks naar de RH gezonden worden.

Ook de SFT-studies werden echter bekritiseerd omwille van hun gebruikte methodologie. Recent wezen Jordan en Paterson (2009) op vier tekortkomingen: (1) Fixatielocaties werden niet gecontroleerd door middel van een eye-tracker, waardoor het onzeker is dat de participaten de woorden benoemden terwijl ze op de letter tussen de fixatielijnen focusten; (2) Stimuli werden vaak te groot aangeboden, waardoor ze buiten het foveale gebied vielen waardoor een gekruiste visuele organisatie niet ter discussie staat; (3) De resultaten werden beïnvloed door binoculaire dispariteit, i.e. spatiale verschillen tussen onze twee ogen; (4) Benoeming versterkt de nood aan interhemisferische transfer aangezien het de meest gelateraliseerde functie is.

De huidige studies onderzochten de BPT en de SFT onder strikt methodologische omstandigheden. In wat volgt worden vijf hoofdstukken samengevat die nagingen of centraal gepresenteerde woorden inderdaad opgesplitst worden en wat de gevolgen hiervan zijn voor het leesproces. Tot slot worden nog enkele implicaties van de gevonden resultaten en mogelijk toekomstig onderzoek besproken.
Huidige studies en discussie


Duidelijke evidentie voor de SFT kan echter pas gevonden worden wanneer de OVP-curves voor LH en RH dominante participanten vergeleken worden in een voldoende grote steekproef. Hoofdstuk 3 beschreef een gedrags- en een fMRI-taak die de spraakdominantie van de links- en rechtshandige participanten uit Hoofdstukken 5 en 6 testte. In Hoofdstuk 3 werden de resultaten van de linkshandigen besproken. 250 linkshandigen namen deel aan een visuele half veld (VHF) taak, waarin twee verschillende figuren of woorden in LVV en RVV werden aangeboden. Een pijl in het midden van het scherm duidde aan welke stimulus zo snel mogelijk luidop benoemd of gelezen moest worden. Snellere reactietijden in RVV werden beschouwd als
een eerste indicatie voor LH dominante, een LVV voordeel wees op een RH dominante. In fMRI werd de spraakdominantie in een gestandaardiseerde taak getest voor een subgroep van 50 participanten. Ze werden gevraagd om gedurende 15 s zoveel mogelijk woorden in stilte te bedenken die begonnen met de letter die centraal op het scherm aangeboden werd. Hun hersenactiviteit tijdens de woordgeneratietaak werd vergeleken met die tijdens een controleconditie, waarin het niet-woord *baba* op het scherm kwam en gedurende 15 s mentaal herhaald moest worden. Vervolgens werd een lateralisatie-index per persoon berekend op basis van LH en RH activiteit in Broca’s area. Een waarde lager dan -0.60 betekende een sterke RH spraakdominantie; Waarden boven +0.60 werden geclassificeerd als LH spraakdominantie. De LVV-RVV benoemingsstijdverschillen en lateralisatie-indexen correleerden significant, vooral wanneer enkel participanten met eenzelfde VHF voordeel voor figuren en woorden werden opgenomen (respectievelijk $r = 0.76$, $p < 0.001$ en $r = 0.74$, $p < .001$). Van der Haegen, Cai, Seurinck en Brysbaert (2011) recruteerden hierdoor niet alleen de steekproef die nodig is om de aanwezigheid van interhemisferische transfer tijdens woordherkenning te onderzoeken, maar toonden ook aan dat de VHF taken als een eerste snelle en goedkope screening methode voor (a)typische spraakdominantie kunnen gebruikt worden (zie ook Hunter & Brysbaert, 2008). Meer gedetailleerde informatie over de taallateralisatie van een individu kan daarna bekomen worden aan de hand van beeldvormingstechnieken als fMRI of de meer invasieve Wada-test (Wada & Rasmussen, 1960), waarbij één hemisfeer tijdelijk geanesthezedert wordt en daarna de mogelijke productie door LH en RH nagegaan wordt.

**Hoofdstuk 4** testte dezelfde linkshandige participanten in een lexicale decisietaak in fMRI. De verschillende subprocessen van taalverwerking (e.g. spraakproductie, spraakperceptie, lezen, prosodie etc.) kunnen elk in een verschillende mate gelateraliseerd zijn. Een globale taallateralisatie-index zou dan ook een vertekend beeld geven over de dominantie van een individu (Seghier, Kherif, Josse & Price, 2011). In de lexicale decisietaak werden de participanten gevraagd om met hun dominante hand op een knop te drukken indien de letterreeks op het scherm een bestaand woord vormde, en om met hun niet-dominante hand te drukken indien het een niet-woord was. De activatie in de linker- en rechter- VWFA werd vergeleken door woordactivatie te contrasteren met willekeurige patronen van zwarte pixels op een witte achtergrond ter grootte van een woord. Zevenenvijftig linkshandigen namen deel aan deze studie: Dertig onder hen werden voordien geclassificeerd als LH spraakdominant, 20 waren RH
sprakedominant, en zeven vertoonden geen duidelijk activatieverschil tussen LH en RH in de mentale woordgeneratietak uit Hoofdstuk 3. De sprakedominantie-indexen correlerden significant met de leesdominantie-indexen ($r = 0.76, p < .001$). De sprakedominante hersenhelft was voor de meeste participanten dus eveneens de hersenhelft waar de meeste neurale activiteit werd geobserveerd tijdens de lexicale decisies. Lezen was echter opvallend minder gelateraliseerd dan spraak: Achtten personen hadden een leesindex boven 0.60, zes hadden een waarde onder -0.60, maar niet minder dan 31 linkshandigen (i.e. 54.4%) vertoonden overwegend bilaterale activiteit. Drie participanten bleken spraak en lezen in een verschillende hersenhelft te verwerken (bijvoorbeeld spraak in LH en lezen in RH of vice versa). Van der Haegen, Cai en Brysbaert (2012) verzamelden hierdoor naast sprakilateralisatie-indexen ook indexen voor lezen die een verschil in leesgedrag tussen LH en RH dominanten kunnen voorspellen (zie Hoofdstuk 6). Bovendien toont deze studie aan dat spraakproductie en lezen nauw gerelateerd zijn, ondanks een minder uitgesproken lateralisatie van lezen. In de gedragsliteratuur werd veelvuldig gevonden dat de fonologie van een woord de orthografische herkenning beïnvloedt (bijvoorbeeld aan de hand van priming waarbij woorden in een lexicale decisietaak voorafgegaan worden door kort gepresenteerde fonologisch of orthografisch gerelateerde woorden; Dimitropoulou, Duniabeitia & Carreiras, 2011). Hoewel top-down invloed van fonologie op orthografie nog niet in alle neurocognitieve modellen opgenomen werd, wijst ook Hoofdstuk 4 in deze richting: Doordat spraak en lezen meestal in dezelfde hemisfeer worden verwerkt, kunnen tijdkosten om informatie uit te wisselen tussen deze twee processen beperkt worden.


Nederlandstalige samenvatting
enkel verklaard kan worden door het verschil in lateralisatie, en niet door de kwadratische component wat zou impliceren dat LH en RH dominanten verschillen in visuele scherpte vertonen. Deze data duidden voor het eerst overtuigend aan dat niet alleen het lezen van parafoveaal gepresenteerde woorden interhemisferische communicatie vereist, maar ook foveale stimuli initieel gesplitst worden. De letters die eerst naar de niet-dominante hemisfeer gezonden worden moeten bijgevolg overgedragen worden naar de dominante hemisfeer, wat een tijdskost veroorzaakt. Hoewel de data uit Hoofdstuk 2 reeds suggereerden dat de studies van Brysbaert (1994) en Hunter et al. (2007) valide waren, werd in Hoofdstuk 5 evidentie gevonden voor de SFT onder de voorwaarden die gesteld werden door onder andere Jordan en Paterson (2009). We kunnen op basis van deze data niet bewijzen dat de fovea precies op de verticale middellijn van het visuele veld wordt gesplitst, aangezien de kortste woordlengte drie letters bedroeg. Twee-letter woorden maken echter slechts 0.5% deel uit van de Nederlandse taal (Keuleers, Brysbaert & New, 2010), waardoor een eventueel afwijkend mechanisme voor de centrale twee letters een minimale impact op het leesgedrag zou hebben.

Tot slot werd in Hoofdstuk 6 nagegaan of spraaklateralisatie ook de positie en de duur van fixaties tijdens het lezen van teksten beïnvloedt. De LH en RH spraakdominanten namen hiervoor deel aan twee taken: (1) Ze werden gevraagd om in stilte teksten (i.e. vier krantenartikelen, twee kortverhalen en een beschrijving van twee landen) te lezen terwijl hun ogen werden gemeten door een oogbewegingsapparaat, waarna ze deze teksten moesten samenvatten; (2) In een tweede taak werden 250 reeksen van tien zes- of acht-letterwoorden gepresenteerd op het scherm, waarvan 50 reeksen een woord uit een bepaalde semantische categorie (e.g. groenten) bevatten. De participants moesten de linkerknop indrukken zodra ze een targetwoord lazen, of op de rechterknop drukken indien geen woord uit de vooraf bepaalde categorie voorkwam. Enkel de reeksen zonder targetwoord werden opgenomen in de analyses om de resultaten niet te beïnvloeden door het vinden van het targetwoord. Opnieuw werden verschillen in het leesgedrag van LH en RH spraakdominanten gevonden: De initiële landingspositie in een woord lag gemiddeld meer naar rechts toe voor de RH dominanten, met verschillen van 0.23 letters in de teksten en 0.41 letters in de woordreeksen. Het verschil was groter voor langere dan voor kortere woorden: van 0.05 letters voor vier-letterwoorden tot 0.40 letters voor acht-letterwoorden (teksten) en 0.24 letters ten opzichte van 0.59 letters voor respectievelijk zes- en acht-letterwoorden (woordreeksen). De verschuiving van gemiddelde
landingspositie was beperkt, maar een stabiele observatie die significant was. Wellicht landden de ogen van RH dominanten niet verder naar het woordeinde toe omdat de eerste letters ook voor hen de meeste informatie bevatten om een woord te identificeren (Brysbaert & Nazir, 2005). Net zoals in de OVP-resultaten werd het effect zowel bij links- als rechtshandige LH dominanten teruggevonden wanneer zij afzonderlijk werden vergeleken met de RH dominanten. De lexicale decisie lateralisatie-indexen uit Hoofdstuk 4 konden geen verschil in landingspositie voorspellen, hoewel de taken uit stillezen bestonden. Wellicht is lezen té bilateraal geregiseerd in de cortex waardoor lateralisatiewaarden niet uitgesproken genoeg waren om een verschil in fixatiediagramen te veroorzaken. Zoals Hoofdstuk 4 aangaf, zijn spraak- en lexicale decisie indexen onderling wel gecorrleerd. Er werden evenmin duidelijke resultaten gevonden wanneer fixatieduur als afhankelijke variabele werd opgenomen in het statistisch model: Zowel de LH als RH dominanten vertoonden een omgekeerde U-curve met de langste fixaties op het midden van een woord; Een effect dat in de literatuur bekend staat als de Inverted OVP effect. Dat spraaklateralisatie een verwaarloosbare invloed heeft op de duur van fixaties komt overeen met de eerder gevonden opsplitsing van (1) enerzijds hogere-orde linguïstische factoren zoals de voorspelbaarheid van de context en woordfrequentie die bepalen wanneer ogen bewegen en (2) anderzijds factoren zoals woordlengte en afstand tot de vorige fixatie die sturen waar ogen landen. Op basis van de resultaten uit Hoofdstuk 6 is spraaklateralisatie een bijkomende variabele die landingsposities tijdens lezen beïnvloedt.

**Implicaties en toekomstig onderzoek**

Uit de bespreking van de huidige studies blijkt dat de LH en RH moeten communiceren tijdens foveale woordherkenning, en dat dit een invloed heeft op de fixaties tijdens lezen. Een rolende onderzoeksvraag die hieruit voortvloeit is hoe de transfer van letters snel genoeg verloopt om vlot lezen te garanderen. Tot nu toe werden twee visies hierover gepubliceerd in de literatuur: De late integratievisie voorgesteld in het split fovea model van Shillcock, Ellison en Monaghan (2000) en de vroege integratievisie opgenomen in het Sequential Encoding Regulated by Inputs to Oscillations within Letter units of SERIOL model van Withney (2001).
Shillcock et al. (2000) gaan ervan uit dat letters van een gesplitst woord geïntegreerd worden tijdens het woordherkenningsproces zelf. Zodra letters geprojecteerdd worden naar een hemisfeer, zal die hemisfeer woorden genereren die de ontvangen letters bevatten. De letters worden pas in een later stadium samengebracht. Deze visie impliceert dat woordherkenning sterk beïnvloed wordt door de letterpositie waarop gefixeerd wordt: Een verschuiving van de fixatie zal de hemisferen andere woordkandidaten doen genereren. Van der Haegen, Brysbaert en Davis (2009; zie ook McCormick, Davis & Brysbaert, 2010) testten dit door gebruik te maken van het *transposed letter priming* effect. Pereia en Lupker (2003) vonden meer facilitatie op de reactietijden van een lexicale decisie wanneer het targetwoord voorafgegaan werd door een prime met getransponeerde letters dan met vervangen letters. Van der Haegen et al. manipuleerden de letters van zes-letterwoorden op posities 2-3 (e.g. mrogen – MORGEN) of 4-5 (e.g. moregn – MORGEN), en lieten bovendien hun participanten fixeren tussen de posities 1-2, 2-3, 3-4, 4-5 of 5-6 tijdens de lexicale decisies. Ze vonden echter geen verminderde priming met de getransponeerde of vervangen letters bij fixaties op de cruciale posities 2-3 of 4-5 (e.g. mrogen versus ms-agen voor posities 2-3 en more-gn versus mori-pn voor posities 4-5). Dit zou wel verwacht worden door Shillcock et al.: Op andere posities wordt woordherkenning nog steeds gehinderd door letters op een foutieve positie, maar beide hemisferen ontvangen wel de juiste letteridentiteiten en er zou dus meer priming verwacht worden op de niet-cruciale posities. De grootte van het priming effect op de verschillende posities uit Van der Haegen et al. konden beter verklaard worden door de afstand tussen de fixatie en de getransponeerde letters dan door de factor of de getransponeerde letters al dan niet naar verschillende hemisferen werden geprojecteerd.

De tweede visie over letterintegratie na een initiële foveale split werd voorgesteld in het SERIOL model door Whitney (2001; zie ook Whitney, 2008; Whitney & Berndt, 1999; Whitney & Cornelissen, 2008). Dit model bestaat uit meerdere niveaus. Op het *retinale* niveau bevindt zich een \( \Lambda \) - vormige visuele scherpe curve, met de meeste scherpte in het midden bij centrale fixatie. Op het tweede niveau worden *features* herkend (e.g. een schuine lijn / uit de letter W). Hier is een strikte scheiding tussen LVV en RVV. Features die in LH worden herkend hebben andere eigenschappen dan features in RH. De helling van de scherpte-curve wordt hier omgekeerd voor LVV, maar niet voor RVV, zodat de eerste letters de meeste activatie krijgen in een schrift dat van links naar rechts gelezen wordt (zie Hoofdstuk 1, Figuur 7A). Bovendien

Naast de mechanismen hoe letters opnieuw geïntegreerd worden, stelt zich de vraag wat de mogelijke gevolgen zijn voor woordherkenning indien interhemisferische transfer niet optimaal verloopt. Een vertraagde uitwisseling van informatie tussen de hemisferen is een van de factoren die zouden kunnen bijdragen tot het verklaren van dyslexie, een leesstoornis waarbij de moeilijkheden niet verwacht worden op basis van de leeftijd, intelligentie, sensorische capaciteiten of educatieve kansen van een persoon (World Health Organization, 2007). Ondanks onduidelijkheid over de replicaerbaarheid en onderliggende mechanismen, vonden studies...

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Tot slot kan een gesplitte fovea gevolgen hebben voor de herkenning van andere visueel gepresenteerde stimuli dan woorden. De tijd die nodig is om informatie uit te wisselen tussen de hemisferen kan afhankelijk zijn van de informatie die verwerkt moet worden, maar indien een split fovea vooral invloed heeft op de processen vóór het eigenlijke herkenningsproces is het niet ondenkbaar dat dit gegeneraliseerd kan worden naar andere taken, zoals object- of gezichtsherkenning. Luo, Shan, Zhu, Wang en He (2011) vonden bijvoorbeeld evidentie voor de SFT in zowel woord- als gezichtsherkenning bij een Chinese patiënt met een laesie aan het splenium van het corpus callosum en in het linker mediale occipitotemporale gebied. Wanneer de patiënt samengestelde woorden moest lezen met één karakter in LVV en één in RVV werd zijn lage herkenningscore duidelijk beïnvloed door leesproblemen in LVV. Aangezien hij geen informatie kon doorgeven van de RH naar LH kan dit verklaard worden door de SFT. In de gezichtsherkenningstaak moest de patiënt het geslacht van gezichten beoordelen, waarbij de ene helft van een vrouwelijk gezicht afkomstig was en de andere helft van een mannelijk gezicht. De beoordelingen waren duidelijk gebaseerd op de linkerkant van de stimuli, die geprojecteerd konden worden naar het intacte gezichtsherkenningsgebied in de RH. Evidentie dat
interhemisferische communicatie nodig is om een stimulus te herkennen werd dus zowel voor de woorden als voor gezichten teruggevonden.

Een belangrijk verschil tussen woorden en objecten/gezichten is dat de laatste categorie bijna altijd symmetrisch is of symmetrie benadert, terwijl woorden zelden uit symmetrische letters opgebouwd zijn. Intuïtief kan verondersteld worden dat meer communicatie nodig is bij asymmetrische stimuli dan bij symmetrische, aangezien daar beide hemisferen bijna identieke informatie ontvangen. Een vroege integratie die voor de herkenning plaatsvindt zoals in het SERIOL model (Whitney, 2001) is dan nog steeds mogelijk: Treder (2010) besluit in zijn review over symmetriedetectie dat symmetrie snel en automatisch geëvalueerd wordt en in twee stappen kan verlopen: Spatiale filters maken een eerste beoordeling over de (a)symmetrie van een object, waarna de eigenlijke symmetriedetectie plaatsvindt gebaseerd op een eerste indruk van de spatiale filters. De interhemisferische transfer tijd kan dus bepaald worden door de spatiale filters, hoewel deze visie tot op heden speculatief blijft.

**Conclusie**

De studies uit deze doctoraatsverhandeling testten de hypothese van de BPT en SFT. De recente kritieken op de methodologie van voorgaande SFT studies bleken de evidentie dat foveale informatie initieel gesplitst worden niet ongeldig te maken. Ook onder strikt methodologische voorwaarden werden verschillen gevonden in de *optimal viewing position*-curves van LH en RH spraak/leesdominanten. Zoals verwacht door de SFT, konden LH dominanten woorden snelst benoemen wanneer ze in het begin van het woord fixeerden, waardoor het aantal letters dat getransfereerd moest worden beperkt bleef. RH dominanten waren snelst bij fixaties op het woordeinde, zodat de meeste letters rechtstreeks naar hun dominante RH gezonden werden. Een splitsing van foveale woorden bleek zelfs het leesgedrag te beïnvloeden, hoewel de verschillen in initiële fixatiepositie beperkt bleven bij het lezen van woorden in een context. Toekomstig onderzoek zal moeten uitwijzen hoe en wanneer letters opnieuw worden geïntegreerd en of de SFT gegeneraliseerd kan worden naar andere visuele herkenningsprocessen.
Referenties


