

BRAIN ASYMMETRY AND VISUAL WORD RECOGNITION: DO WE HAVE A SPLIT FOVEA?

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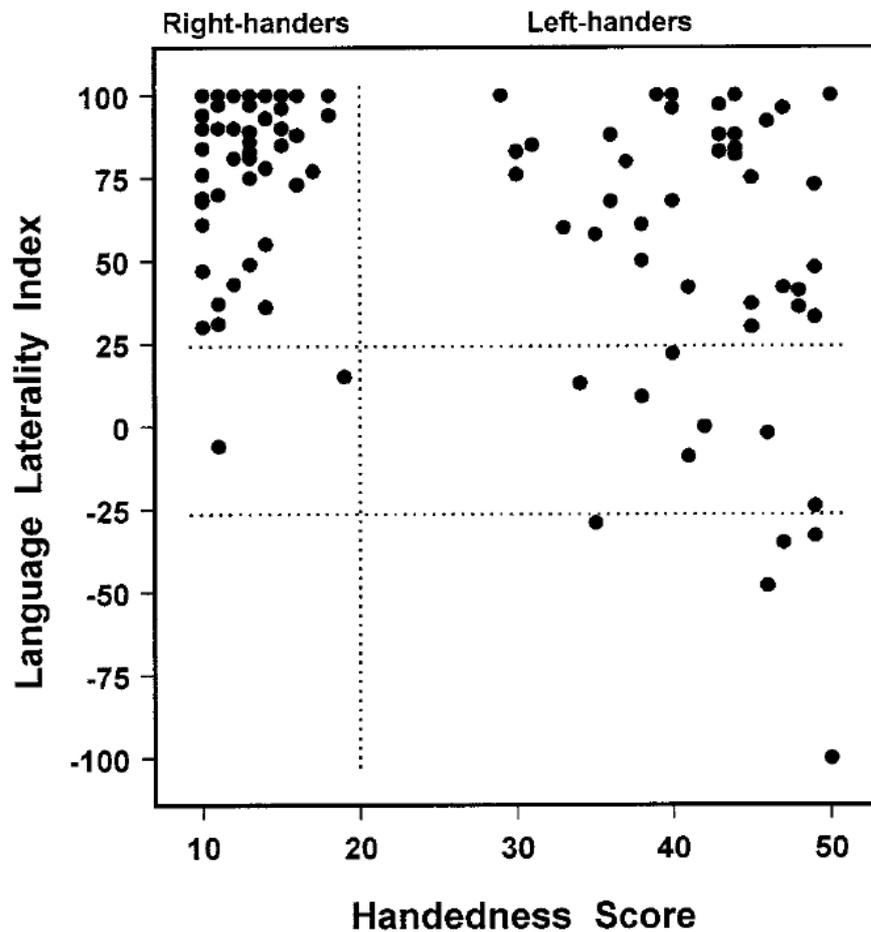
Do we have a split fovea?

Most people have left hemisphere dominance for spoken word production

The brain is divided in two halves, but both hemispheres do not process information exactly the same. One of the first findings about the consequences of brain damage was that speech problems were more likely after injuries to the frontal part of the left brain half than after injuries to the right brain half. This finding was first established in the 19th century by the French scientists Marc Dax and Paul Broca and remains a basic tenet of neuropsychology. For instance, after a review of a group of patients with unilateral brain damage, Bryden, Hecaen, and DeAgostini (1983) concluded that about half of the right-handed patients had speech problems after left hemisphere lesions (36 out of 70) against only 10% after right hemisphere lesions (5 out of 60).

Recent studies have extended the clinical findings to the healthy population. For instance, Pujol, Deus, Losilla, and Cadevila (1999) used brain imaging (fMRI) to determine the relative activity of the frontal lobes in the left and the right cerebral hemispheres of 50 right-handers and 50 left-handers, who took part in a word generation task. The participants were presented with a letter (e.g., F) and had to silently generate words starting with that letter. Pujol et al. used a laterality index defined as $100 * (L - R) / (L + R)$, L being the number of measurement units (voxels) active in the left hemisphere, and R being the number of voxels active in the right hemisphere. Figure 1 shows the results of the study, which are typical for all later studies examining brain dominance and can be summarised as follows: (i) the vast majority of participants show more activity in the left frontal cortex during word generation than in the right frontal cortex, (ii) the asymmetry is on average larger in right-handers than in left-handers, (iii) most participants show some activity in the right frontal cortex as well (i.e., the laterality index is not +100), and (iv) a small number of left-handers show a reversed dominance, with significantly more activity in the right hemisphere than in the left hemisphere. The percentages of people with reverse dominance usually quoted in the literature are 25% for left-handers and 5% for right-handers (Knecht et al., 2000; Loring et al., 1990). However, in our own work with university students we find that only about 10% of the lefthanders are clearly right-dominant for spoken language generation, a figure that seems to agree with Pujol et al.'s data in Figure 1 (Van der Haegen, Cai, Seurinck, & Brysbaert, 2011).

Figure 1: Correlation between handedness (measured from extreme right [score 10] to extreme left [score 50]) and activation laterality in the inferior frontal gyrus. The authors defined laterality scores larger than +25 as evidence for left hemisphere dominance, scores lower than -25 as evidence for right hemisphere dominance, and scores in-between as evidence for bilateral speech control. Source: Pujol et al., 1999.



Does speech dominance have implications for visual word recognition?

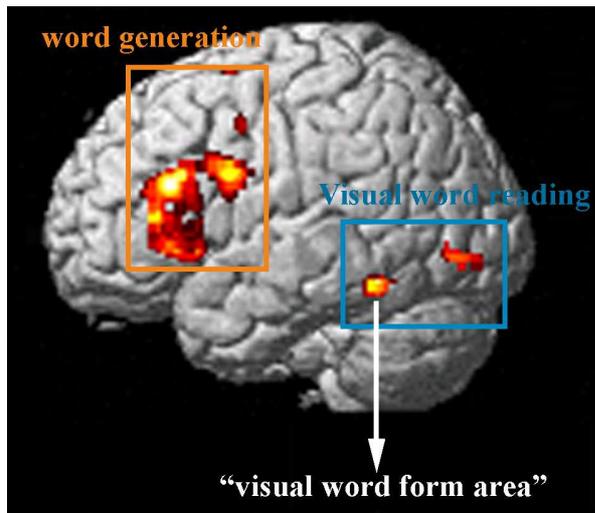
An important question is to what extent brain dominance for spoken language generation has implications for word reading. This need not be the case, as the former involves action control whereas the latter concerns visual perception. In addition, both activities depend on different parts of the brain. Visual word recognition predominantly makes use of the lower back part of the brain (i.e., the occipital and the temporal lobes) and not of the frontal lobes involved in speech production. So, there would be no anatomical contradiction between unilateral processing for spoken language production in the frontal lobes and bilateral processing for visual word recognition in the occipito-temporal part of the brain. As a matter of fact, some of the early evidence with split-brain patients suggested exactly this organisation.

Split-brain patients are patients who had their corpus callosum sectioned for the treatment of otherwise intractable epilepsy. This surgery disconnected the left and the right cerebral hemispheres and was used in those cases where an epileptic focus provoked uncontrolled activity in the opposite brain

half. By disconnecting the two hemispheres, it was possible to reduce the seizures. Gazzaniga (1983) presented a review of the research with these patients, which seemed to suggest quite extensive spoken and written language understanding in the isolated right hemisphere, but no speech output. For instance, split-brain patients seemed to understand visual words flashed to the right hemisphere (assessed by asking them to identify the corresponding object with the left hand), but were not able to name the words. In the same review, however, Gazzaniga (1983) criticised the studies and came to the conclusion that the evidence for right hemisphere language comprehension was not very strong, because it could be due to experimental flaws in the early studies and it was limited to very few participants. For instance, he argued that only 3 of the 28 patients from the East Coast sample demonstrated evidence of right hemisphere language. A different view was defended by Zaidel (1983), who took issue with Gazzaniga's conclusions and suggested that a better summary of the right hemisphere language capacities in split-brain patients was: "no speech, good auditory language comprehension, and moderate reading".

The question to what extent word reading is lateralised got a major impetus from modern neuroscience techniques. Two particularly interesting studies were published by Cohen and colleagues (Cohen, Dehaene, Naccache, Lehéricy, Dehaene-Lambertz, Hénaff, & Michel, 2000; Cohen, Lehéricy, Chochon, Lemer, Rivaud, & Dehaene, 2002). In these studies, Cohen et al. showed that a region in the left occipito-temporal junction was crucially involved in visual word recognition (Figure 2). This region was active independent of the position of the word in the visual field and, in particular, whether or not the word was initially projected to the left hemisphere. Cohen et al. called this area the "visual word form area" (VWFA) and claimed that information from written words had to pass through it to access the associated semantic and phonological memory representations.

Figure 2: Figure of the left hemisphere showing the frontal areas active in word generation and the visual word form area, as postulated by Cohen and colleagues. Posterior to the visual word form area is a part of the occipital cortex that is also particularly active in written word recognition (i.e., the red patch to the right of the visual word form area in the figure). It also tends to be left lateralized in typical healthy participants (e.g., Gold & Rastle, 2007), but was not correlated with the activity in the frontal language areas in Cai et al. (2010).



Cai and colleagues (Cai, Lavidor, Brysbaert, Paulignan, & Nazir, 2008; Cai, Paulignan, Brysbaert, Ibarrola, & Nazir, 2010) investigated whether the left lateralisation of the visual word form area was caused by the laterality of the frontal language processing areas or could be explained by other factors favouring the left hemisphere, such as left hemisphere dominance for detailed form perception or the left-right reading direction of the language tested. Cai et al. (2008) determined the laterality of spoken word production for a group of French-speaking right- and left-handers with a paradigm similar to Pujol et al. (1999) and selected four left-handers with clear right hemisphere dominance. All four of these participants had the visual word form area in the right hemisphere, suggesting that interactions between the anterior and the posterior language areas are indeed responsible for the lateralisation of the visual word form area. A person with speech control in one hemisphere is very likely to have the visual word form area in the same hemisphere (see Cornelissen et al., 2009, for evidence of rapid interactions between the occipito-temporal cortex and the left inferior frontal gyrus in visual word recognition).

Cai et al. (2010) repeated the Cai et al. (2008) study with 11 participants who were left dominant for language generation and 5 participants who were right dominant (participants were again French-speaking). Ten of the 11 left-dominant participants showed higher activation in the visual word form area of the left hemisphere; and 4 out of 5 right-dominant participants showed higher activation in the right hemisphere, suggesting that the correlation between the asymmetry of the language generation areas and the word reading areas may not be 100%. Another exception that was published involved a German-speaking person with left frontal dominance for speech production and right temporal dominance for spoken word recognition (Jansen, Deppe, Schwindt, Mohammadi, Sehlmeier, & Knecht, 2006).

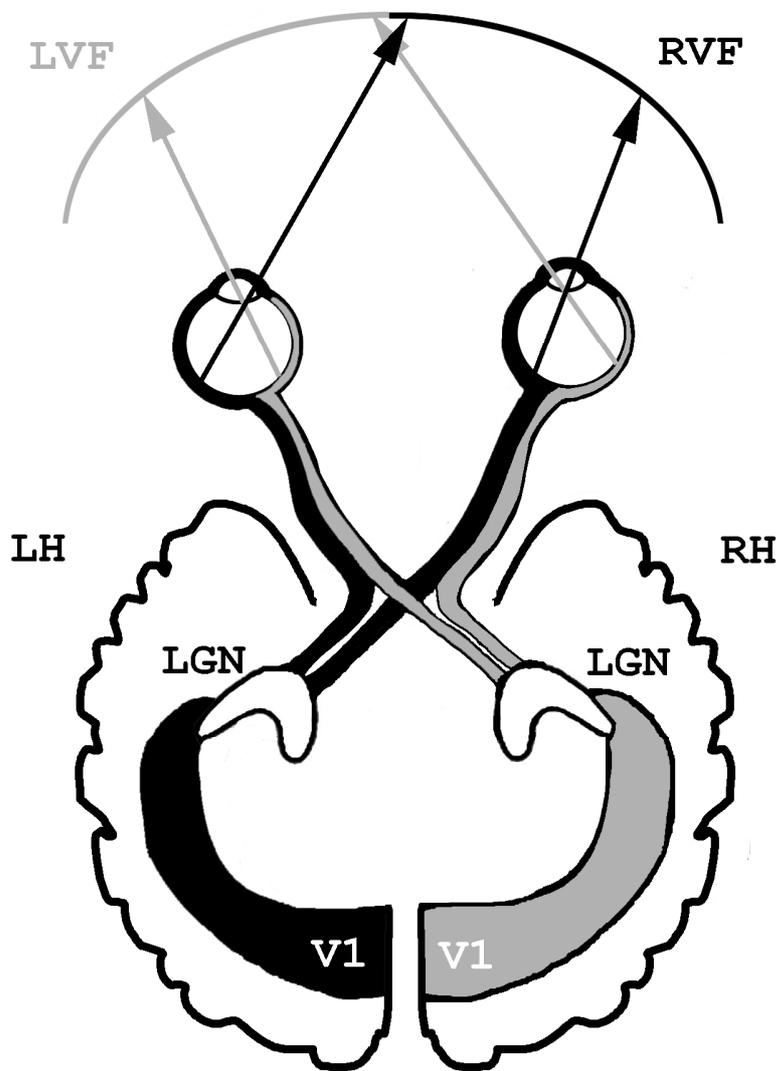
All in all, the evidence collected thus far indicates that the interactions between the frontal and occipito-temporal brain areas are so important for language processing that chances are very high that the visual word form area will be lateralized to the same side as the language production areas. This is particularly surprising for the right-dominant participants who read from left to right, because for these

participants most of the words are initially transmitted to the left hemisphere during reading, as we will see in the next section.

Brain asymmetry and parafoveal word recognition

The lateralisation of the visual word form area most likely has an impact on parafoveal word recognition. This is word recognition a few letter positions to the left or to the right of the fixation location (central vision is usually referred to as foveal vision). Indeed, the organisation of the visual system is such that stimuli in the left visual field (LVF) are initially sent to the right brain half, whereas stimuli in the right visual field (RVF) are sent to the left brain half. This is because the optic fibres from the nasal hemiretina (i.e., the side towards the nose) cross at the optic chiasm and project to the contralateral cerebral hemisphere (Figure 3).

Figure 3: Organisation of the visual system. Because the optic fibres coming from the nasal halves of the retina cross to the other hemisphere, all stimuli presented to the left of the fixation location are initially sent to the right cerebral hemisphere and all stimuli presented to the right of the fixation location are initially sent to the left cerebral hemisphere. This organisation is interesting for survival, because it allows humans to notice more rapidly whether an important moving stimulus (food or predator) is situated to the left or to the right. As a result, it presumably got selected by evolutionary pressure. As we will see later, psychologists disagree about whether the separation between LVF and RVF is sharp (i.e., a split fovea) or whether there is a small overlap of LVF and RVF in the middle of the visual field (i.e., a bilaterally projecting fovea)



The fact that words are recognised better in RVF than LVF was first documented in the 1950s, although the effect initially was not attributed to cerebral dominance but to reading-related attentional processes. Mishkin and Forgays (1952) investigated the left-right differences for English and Yiddish words (the latter is a language read from right to left), and reported a RVF advantage for English words, but a tendency towards an LVF advantage for Yiddish words (a finding shortly afterwards reported by Orbach, 1952 as well). Heron (1957, Experiment 5) also observed a RVF advantage in English readers when strings of letters were presented either to the left or to the right of the fixation location, but a LVF advantage when the letter strings were presented simultaneously in RVF and LVF or straddled each other in central vision. Heron attributed these findings to reading-related attentional biases in English. In his view, English-reading participants have a tendency to start reading at the leftmost word of a line of text

and to proceed from there to the end of the line. So, when two words are presented simultaneously in LVF and RVF, attention will first go to the word in LVF (the first word on the line) and then move to RVF. In contrast, when a word is presented either in LVF or in RVF, attention can immediately shift to the word that is presented and presumably this is easier from the fixation point to the word in RVF (in line with the normal left-to-right reading direction) than from the fixation point to the word in LVF (a movement which resembles the return-sweep needed to bring the eyes from the last word on one line of text to the first word of the next line).

Further research, however, established a genuine influence of brain dominance in the RVF advantage for words, even though other factors such as reading habits and the distribution of information within words play a role as well. The first important finding was that a significant RVF word advantage is observed for languages read from right to left, such as Hebrew and Arabic, when reaction times to the words are measured rather than recognition rates for very briefly presented stimuli (e.g., Faust, Kravetz, & Babkoff, 1993; Ibrahim & Eviatar, 2009; Lavidor, Ellis, & Pansky, 2002). Second, the RVF advantage has been found to be smaller for left-handers than for right-handers (e.g., Bryden, 1982, pp. 61-63), in line with the reduced left language dominance in this group. Finally, it was shown that people with right language production dominance, as measured with fMRI, have a LVF advantage for words rather than the typical RVF advantage (Hunter & Brysbaert, 2008; Van der Haegen et al., 2011).

Parafoveal word recognition plays a role in text reading, as can be concluded from studies in which the upcoming words are masked until the eyes land on them. Eye movements in reading are characterised by a sequence of fixations and short fast eye movements, called saccades (see the chapter by Schotter and Rayner in this volume). Verbal information is extracted during the fixations and mainly consists of the word being fixated, but also of the word next to it and sometimes the second next word. Rayner, Well, Pollatsek, and Bertera (1982, Experiment 1) concluded this from an English reading study in which three viewing conditions were compared: (1) a condition in which none of the upcoming words next to the currently fixated word was visible, (2) a condition in which one word was visible in the right parafovea, and (3) a condition in which two parafoveal words were visible. Reading rate in the condition with no parafoveal preview was 212 words per minute; in the condition with one parafoveal word visible it was 309 words per minute; and in the condition with two parafoveal words visible it was 339 words per minute, close to the reading speed when the full text was visible all the time (348 words per minute). The finding that reading is more efficient when participants have information of the words next to the one they are currently fixating is called the parafoveal preview benefit effect (e.g., Rayner, 1998).

The fact that word information can be extracted more efficiently from RVF than LVF may be one of the factors that have contributed to the predominance of the left-to-right reading direction in the world (another factor that has been proposed is that it may be easier to write from left to right with the dominant right hand; e.g., Bradshaw & Nettleton, 1983). Given the direct access of RVF parafoveal vision to the dominant left hemisphere, it makes more sense to have the upcoming word(s) in this visual field than in LVF. The languages read from right to left (such as Arabic, Farsi, Hebrew) require more interhemispheric information transfer to process the upcoming words in parafoveal vision in the dominant hemisphere. Interestingly, these languages tend to have a more compact writing system (e.g., vowels are omitted), so that the average saccade length can be reduced (5.5 characters instead of 7-9

characters in languages read from left to right; Pollatsek, Bolozky, Well, & Rayner, 1981). More information close to the fixation position makes sense if extra information needs to be transferred between hemispheres as callosal connections are better for central vision.

Brain asymmetry and foveal word recognition: the bilateral projection theory vs. the split-fovea theory

A more contentious issue is whether brain asymmetry also has consequences for the processing of centrally fixated words. The general assumption, both among psycholinguistics and among laterality researchers, has been that laterality is not involved in this case, that the LVF and RVF overlap in central vision, and that foveally presented words are transmitted simultaneously to the left and the right cerebral hemisphere. Surprisingly, this conclusion is not based on a lot of empirical evidence. Three arguments are usually put forward (for more extensive discussions, see Brysbaert, 1994, 2004; Ellis & Brysbaert, 2010; Lavidor & Walsh, 2004).

The first argument is the existence of macular sparing in hemianopia. Hemianopia refers to the loss of vision in LVF or RVF after a one-sided stroke or brain injury. In the majority of patients (but not in all) there is some preserved vision in the centre of the visual field, which can be interpreted as evidence for a bilaterally projecting fovea. Unfortunately, a review of the literature does not provide a compelling case for this interpretation. Two problems are mentioned. The first is that macular sparing often is due to spared tissue in the affected hemisphere. Because central vision occupies a large part of the visual cortex, which in addition is less susceptible to strokes, central vision has the highest chances of surviving brain injury. This explains why macular sparing is so variable, going from nearly 0 degrees to over 5 degrees (e.g., McFadzean, Hadley, & Condon, 2002; Trauzettel-Klosinski & Reinhard, 1998). The second problem concerns the precision with which spared vision has been measured in the cases of limited macular sparing. Eye movements are rarely controlled properly and researchers do not take into account the fact that the light flashes they use are likely to be visible over a wider area than the directly stimulated part of the retina (due to the light scatter). When Reinhard and Trauzettel-Klosinski (2003) controlled for both variables in patients without spared tissue in the affected hemisphere, they were unable to find evidence for macular sparing within the limits of their technique (.5° from the fixation location).

The second argument refers to five physiological studies published in the 1970s-1980s (Stone, Leicester, & Sherman, 1973; Bunt, Minckler, & Johanson, 1977; Bunt & Minckler, 1977; Leventhal, Ault, & Vitek, 1988; Fukuda, Sawai, Watanabe, Wakauwa, & Morigiwa, 1989). In these studies, one optic tract of various species of monkeys was sectioned or stained and the authors examined which ganglion cells of the retinas projected to this tract. By comparing the retinas of the left and the right eyes they could measure the amount of overlap between the nasal and the temporal hemiretina. From these studies it was concluded that there is a naso-temporal overlap of some 1-3° wide. In particular Bunt and Minckler (1977, p. 1445) made the explicit claim that "A 1°-wide strip centered on the vertical meridian has been found in which ipsilaterally and contralaterally projecting ganglion cells intermingle. This strip expands to a width of 3° at the fovea, ..." The claim of 3° overlap in central vision has been strongly contested in the physiological and ophthalmological literatures because (1) the overlap of foveal vision in Bunt and

Minckler's studies could not be measured directly but had to be inferred, and (2) because Bunt and Minckler's estimate does not agree with the conclusions drawn by the other researchers. As for the first problem, it is well known that the fovea does not contain ganglion cells. This part of the retina entirely consists of receptors (which is why visual acuity is so high in foveal vision). So, in all studies mentioned above the left and the right foveas did not contain any stained cells and the amount of overlap had to be inferred from stained ganglion cells around the fovea. From the observation of a limited number of stained ganglion cells in the "wrong" hemiretina Bunt and Minckler drew the sweeping conclusion that the entire fovea was bilaterally presented. This is surprising, given that the other authors proposed much smaller estimates (of at most 1°) and noticed that the amount of overlap was smaller towards the fovea than further in the periphery (suggesting an even smaller overlap in the fovea itself). Wyatt (1978) further questioned Bunt and Minckler's estimate because the number of "wrongly" stained ganglion cell was far too small to get projections from the entire fovea. Finally, Tootell, Switkes, Silverman, & Hamilton (1988) used a technique of neuronal staining in the visual primary cortex that did allow them to directly trace the naso-temporal overlap in foveal vision, and they concluded equally strongly (p. 1531) "We find neither a duplication nor an overrepresentation of the vertical meridian." Still, Bunt and Minckler's estimate of the foveal overlap is the one that made it into the psychological literature (Bourne, 2006; Jordan & Paterson, 2009; Lindell & Nicholls, 2003).

Finally, several researchers have pointed to null-effects as evidence for a bilaterally projecting fovea. For instance, Marzi, Mancini, Sperandio, and Savazzi (2009) asked participants to respond as fast as possible with their left or right hand to small light flashes presented in LVF or RVF. They reported that participants respond 6 ms faster when the stimulus and the responding hand were on the same side than when they were on opposite sides. However, this was only true when the stimuli were presented 6° from the fixation location, but not when they were presented 1° from the fixation location. From this finding, Marzi et al. concluded that (p. 3007) "This pattern of results is consistent with a nasotemporal overlap at 1° and a complete lateralization at 6°. Both hemiretinae contribute to the overlap area which can be considered as responsible for foveal sparing in hemianopic patients." Similarly, Jordan, Paterson, and Stachurski (2008) flashed words (such as *snow*) very briefly at various eccentricities and asked participants to choose from two alternatives (*snow-show*) which one had been presented. Jordan et al. reported a RVF advantage when the words were presented at an eccentricity of 2°, but not when they were presented at an eccentricity of less than 1°. They also interpreted this as evidence against the idea of a split fovea. As often happens in research, for each of these null effects there is a series of other studies reporting significant effects. So, Harvey (1978), Haun (1978), and Lines and Milner (1983) all reported significantly faster ipsilateral than contralateral responses for eccentricities well below 1° in the paradigm used by Marzi et al. (2009). Similarly, Fendrich and Gazzaniga (1989) and Hunter, Brysbaert, and Knecht (2007), among others, reported evidence incompatible with Jordan et al.'s (2008) conclusion. Some of this evidence will be summarised below (see also Ellis & Brysbaert, 2010, for a more detailed discussion).

The optimal viewing position in left and right dominant individuals

Brysbaert (1994) argued that the influence of brain asymmetry on foveal word recognition is easy to investigate. All one has to do is to compare a group of left-dominant participants with a group of right-dominant participants on the recognition of centrally presented short words. If there is a bilateral representation of the fovea, both groups should perform the same (as both hemispheres have immediate access to the information). In contrast, if the fovea is split, performance on foveally presented words should correlate with that of parafoveally presented words. More specifically, if participants show a RVF advantage for parafoveal word recognition, they should be faster at recognising words after fixation on the first letter (which makes the whole word fall in RVF) than after fixation on the last letter. Similarly, if they show a LVF advantage, they should be faster to recognise words after fixation on the last letter than after fixation on the first letter. Brysbaert (1994) presented some preliminary evidence in favour of the split fovea, but the research topic only really took off once it was possible to reliably assess cerebral dominance in healthy participants.

As indicated above, reliable and valid assessment of cerebral dominance for language production became available with the introduction of fMRI. Pujol et al. (1999), for instance, could have compared the performance of a group of 5 righthand dominant lefthanders to that of a control group on the basis of the data shown in Figure 1. Such a comparison was made by Hunter et al. (2007), who diagnosed a small group of left-handers with right speech dominance and a group of left-handers with left speech dominance. The authors made use of the Optimal Viewing Position paradigm (Figure 4, left panel; see also Brysbaert & Nazir, 2005, for a review of the task). Participants were asked to fixate the centre of a computer screen (indicated by two fixation lines) and words were presented in such a way that the participants looked on the first, the second, the third, ..., or the last letter of the stimulus word. They had to name the word as fast as possible.

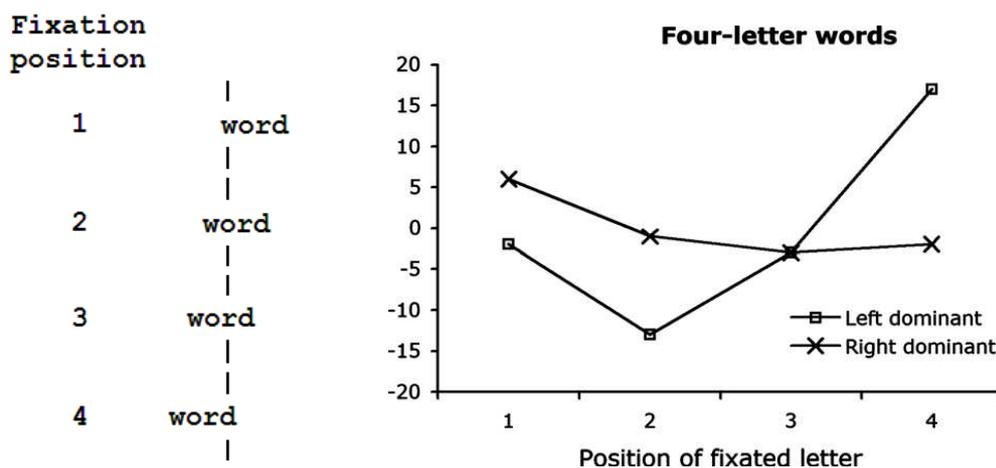


Figure 4. Left panel. Illustration of the Optimal Viewing Position paradigm with four-letter words. A trial starts with the appearance of two vertical lines slightly above and below the centre of the computer screen. Participants are asked to fixate between the two lines. After a brief interval a four-letter word is presented between the lines. Participants have to name the word as fast as possible. On different trials, the word is presented in such a way that participants look on the first, the second, the third, or the last letter. **Right panel.** Word naming times of four-letter words (relative to the group average) for left dominant and right-dominant participants as a function of the fixation position within the word. Participants with left

speech dominance named foveally presented four-letter words faster when they were presented in such a way that the participants were fixating on the first letter, whereas participants with right speech dominance had an advantage for words presented in such a way that participants were fixating on the last letter. Notice that the effect is gradual, not only present for fixations on the extreme letter positions but also for fixations on the second and the third letter. Source: [Hunter et al. \(2007\)](#).

The right panel of Figure 4 shows the speed with which the left and right dominant participants could name four-letter words as a function of the letter on which they fixated when the word appeared. As predicted by the split-fovea view, the left dominant participants were faster to name the word when it appeared in such a way that they were looking at the word beginning than when they were looking at the end. In contrast, the right dominant participants were faster to name the words when they fixated on the end than when they fixated on the beginning. The effect for right dominant participants was not completely the reverse of that of the left-dominant participants, in line with the finding that the asymmetry of the Optimal Viewing Position effect is not entirely due to cerebral dominance, but also influenced by the reading direction and the fact that word beginnings in general are more informative than word ends (Brysbart & Nazir, 2005). Because the stimuli were slightly more than 1.5° wide, the different OVP-curves for right and left dominant participants allow us to firmly reject the possibility of a 3° foveal overlap, although they may not completely rule out the possibility of a smaller overlap (e.g., smaller than 1°).

Other evidence for a split fovea

Ellis, Lavidor, and colleagues argued that the split fovea theory predicts more similarities between foveal and parafoveal word recognition. In principle, if the split fovea view is correct, every difference between RVF and LVF that has been documented should have its equivalent in foveal vision. For instance, it has been shown that word recognition suffers more from word length in LVF than in RVF. Lavidor, Ellis, Shillcock, and Bland (2001) examined whether the same was true for foveal vision, and indeed they observed that word recognition times depended strongly on the number of letters to the left of the fixation location but not on the number of letters to the right of the fixation location.

Ellis, Brooks, and Lavidor (2005) started from the finding that cAsE aLtErNaTiOn has a more detrimental effect in RVF than in LVF and again showed that foveal word processing was affected by case alternation in exactly the same way. That is, the detrimental effect of case alternation was stronger for letters to the right of the fixation location than for letters to the left. Lavidor, Hayes, Shillocock, and Ellis (2004) further showed that foveal word recognition speed depends on the number of words with a similar beginning but not on the number of words with a similar end, in line with the finding that a large number of orthographically similar words (so-called neighbours) speed up lexical decision more in LVF than in RVF.

Finally, Hsiao, Shillcock, and Lee (2007) measured the EEG-signals while Chinese-speaking participants silently named centrally presented Chinese two-character words. Hsiao found that the EEG-signal in the left hemisphere was more affected when the phonetic radical was the right character of the

word than when it was the left character; the reverse was observed in the right hemisphere. Apparently, the phonological information disclosed by the phonetic radical was initially picked up by the contralateral hemisphere only.

When does interhemispheric integration take place? The early vs. the late integration account

If one accepts that interhemispheric communication is needed for foveal word recognition, the logical next question is where in word processing the integration takes place. Two different views have been proposed.

The first view, called the early integration account, states that interhemispheric integration occurs before word processing proper starts. Word recognition does not begin until all letter information has arrived in the dominant hemisphere. An example of this approach is Whitney's (2001) SERIOL model of word recognition. In this model, words are processed serially from the first to the last letter. To make this possible, Whitney argued, it is necessary that the information from the word end (presented in RVF) is inhibited by the information from the word beginning (presented in LVF) until the latter information has arrived in the left hemisphere. Evidence for such an inhibition process was recently presented by Van der Haegen and Brysbaert (2011). They showed that the usual RVF advantage for word naming can be turned into a LVF advantage by presenting irrelevant letter information nearby in the opposite visual half field. Thus, a word presented to the right of fixation location is inhibited strongly by irrelevant letter information presented to the left, whereas irrelevant information presented to the right helps word recognition in LVF, at least when the two stimuli are in close proximity. This finding is similar to the one reported by Heron in 1957 (see above), but with a different interpretation (interhemispheric inhibition instead of reading-related attentional biases).

Shillcock, Ellison, and Monaghan (2000) proposed a late-integration theory. According to their computational model of word recognition, each hemisphere starts processing on the basis of the letters it received, and the two outputs are integrated at a later stage. As a result, word processing is different when a word is fixated on the first, the middle, or the last letter. When the word is fixated on the first letter, nearly all information falls in RVF and, hence, is projected to the left hemisphere, which takes care of the processing. In contrast, if the word is fixated on the last letter, nearly all information falls in LVF and is sent to the right hemisphere, which attempts to identify the word. Finally, in the case of central fixation, each hemisphere receives half of the information and starts to generate possible word candidates on the basis of the information it received and on the basis of an estimate of the total word length. According to Shillcock et al.'s (2000) model, the asymmetry of the OVP effect is not due to the extra time needed for interhemispheric transfer of information initially sent to the nondominant hemisphere but to differences in the efficiency of visual word recognition according to the amount of information received by each hemisphere and the effectiveness of the division of labour between both hemispheres.

To decide between both the early and the late integration account, Van der Haegen, Brysbaert, and Davis (2009) started from the finding that words are primed more when two of their letters are

transposed than when the corresponding letters are replaced by different letters (Perea & Lupker, 2003, 2004). So, participants are faster to recognise the target word *JUDGE* when it is preceded by the prime *jugde* than when it is preceded by the prime *junpe*, arguably because letter positions are not encoded very strictly (see the chapter by Davis in this book). Van der Haegen et al. (2009) reasoned that for a late integration theory it would be more detrimental when the two transposed letters are sent to different hemispheres (i.e., *jug*de*, where the * indicates the position of fixation) than when they are projected to the same hemisphere (e.g., *ju*gde*). The input *jug** to the right hemisphere is as incompatible with the target word *judge* as the input *jun**; similarly, the input **de* to the left hemisphere is not more informative than the input **pe*. In contrast, the input *ju** is compatible with the target word *judge*, and the input **gde* is more informative than the input **npe* if letter positions are not coded in a strict manner (as suggested by the transposed letter priming effect). Contrary to the predictions of the late integration account but in line with the early integration account, Van der Haegen et al. (2009) found no extra drop in the priming when the participants were viewing between the two transposed letters compared to when they were viewing to the left or to the right of the transposed letters. There was an increase of priming as the distance between the transposed letters and the viewing position grew (arguably because letter position coding is less precise away from the viewing position), but there was no effect specific to the split of the transposed letters across the hemispheres.

Another attempt to test the late-integration account was made by McCormick, Davis, and Brysbaert (2010). Their starting point was the semantic competition effect for embedded subset words reported by Bowers, Davis, and Hanley (2005). Bowers et al. found that participants needed more time to indicate that the word *warm* did not refer to a body part than to indicate that the word *gaunt* did not refer to a body part, whereas the reverse pattern was obtained when participants were asked to indicate whether these words referred to a family relative. Bowers et al. (2005) had predicted this pattern of results on the basis of the semantic properties of the words embedded within the target stimuli. The meaning of the embedded word *arm* in *warm* was incongruent with the “no” response to the question “is this a body part?” Similarly, there was an incongruence between the meaning of the embedded word *ant* in *gaunt* and the “no” response to the question “is this a relative?” The incongruence resulted in longer reaction times and more mistakes. McCormick et al. hypothesized that a late integration account would predict less interference from the embedded word when the embedded word was divided over the hemispheres (as in *wa*rm* and *gau*nt*) than when the embedded word was sent entirely to one hemisphere (as in *w*arm* and *g*aunt*). Again, however, they found no evidence for such a difference.

All in all, the evidence strongly points towards the early integration account of interhemispheric communication. This agrees with the critical role of the visual word form area as the gateway to visual word perception.

What contribution does the non-dominant hemisphere make?

Although the evidence reviewed thus far strongly points to a model of visual word recognition in which the visual information is rapidly funnelled to the visual word form area from which further processing is initiated through interactions with the frontal language areas, there are some indications that the

nondominant hemisphere is not completely left out of consideration. First, there usually is some concurrent activity in the homologue brain areas of the nondominant hemisphere each time the visual word form area or the frontal language areas are active (see Figure 1). Second, Cai et al. (2010) noticed that the nondominant homologue of the visual word form area became more active when words were presented vertically than when they were presented horizontally, as if assistance from the nondominant hemisphere was called upon to deal with the higher processing load. Third, Mohr, Pulvermuller, and Zaidel (1994) and Mohr, Endrass, Hauk, and Pulvermuller (2007) reported that word processing improved if the same word was presented simultaneously in LVF and RVF than when the word was presented in RVF only. They interpreted this as evidence for cooperative interactions between word representations in the nondominant and the dominant hemisphere, possibly as the outcome of neural summation. The cooperation critically depends on interhemispheric transmission, as the gain of bilateral word presentation was not observed in a split-brain patient (Mohr, Pulvermuller, Rayman, & Zaidel, 1994).

Other evidence for a contribution of the nondominant hemisphere came from Hillis et al. (2005) who examined patients with acute injuries to the left visual word form area as a result of a stroke. They administered lexical tasks with spoken and written input and output, and identified the extent of brain damage with diffusion- and perfusion-weighted imaging. To their surprise, they did not find that damage to the visual word form area induced impairment of written word comprehension but led to problems with naming or writing words, very similar to what has been observed in the nondominant hemisphere of split-brain patients. To account for their findings, Hillis et al. proposed that the visual word form area has two roles in reading: First, the computation of input-independent letter-sequences needed for visual word recognition and, second, the transfer of the input to output representations. They hypothesised that the nondominant homologue of the visual word form area can easily take over the first role, but not the second. Again, this points to a more dynamic organisation of the reading system than a simple unilateral stream of information processing.

Federmeier (2007) made a proposal along the same lines as Hillis et al. (2005). In her PARLO framework both hemispheres are capable of understanding words, but only the left hemisphere is able to predict upcoming words in sentences on the basis of interactions with the language production system. Because the right hemisphere comprehension system lacks cross-talk between the word comprehension system and language production, it is more bottom-up, limited to the veridical maintenance of information processed thus far.

Suggestions that the nondominant hemisphere may be kept “informed” along the stream of processing (and may occasionally be called to help in case of processing difficulties; e.g., Lindell, 2006) reminds of Corballis and Beale’s (1976) claim that the cerebral hemispheres keep each other up to date in order to maintain coherence. In Corballis and Beale’s view, each time a hemisphere acquires new information, a copy of the memory trace is sent to the other brain half. It will be interesting to see whether further evidence for this idea can be found in language processing.

The importance of interhemispheric communication

The massive information exchange between the cerebral hemispheres involved in reading is likely to put demands on interhemispheric communication, certainly if all information is not initially sent to both brain halves in parallel as was believed by the traditional bilateral projection view. A highly relevant finding in this respect was published by Carreiras, Seghier, Baquero, Estévez, Lozano, Devlin, & Price (2009). These authors showed that learning to read results in a massive increase of white matter in the posterior part of the corpus callosum, the part related to visual information transfer from one hemisphere to the other. This was also true for illiterates learning to read at adult age, in line with the finding that the degree of myelination of axons is not fixed but depends on the use of the connections.

The need for interhemispheric communication also raises the question what happens when the communication is compromised. Indeed, the corpus callosum has been claimed to be part of the latest maturing network of the brain (Pujol, Vendrell, Junque, Martivilalta, & Cardevila, 1993) and a malfunctioning corpus callosum has been proposed as one of the factors that may contribute to difficulties in reading acquisition (Monaghan & Shillcock, 2008). Furthermore, the corpus callosum is not impervious to the deterioration of white matter in old age (Salat, Tuch, Greve, van der Kouwe, Hevelone, et al., 2005) and is known to be compromised in a number of diseases, such as HIV-1 infection (Wohlschlaeger, Wenger, Mehraein, P., & Weis, 2009). It will be interesting to see whether this has any consequences for reading speed.

Finally, there is evidence that the mechanisms of interhemispheric integration may differ between individuals. Chiarello, Welcome, Halderman, and Leonard (2009) examined the relationship between visual field asymmetries for lexical tasks and reading performance in a sample of 200 young adults. They found that participants with strong and consistent hand preferences performed better on word recognition tasks when they had large visual field asymmetries. The same relationship was not observed for mixed handers, suggesting that the information integration across hemispheres in these participants may be achieved differently.

Conclusion

In this chapter we have seen that the anatomical divide between the left and the right brain half has implications for visual word recognition. In particular, it introduces the need for massive interhemispheric communication. Unlike what was believed in the traditional view, it looks increasingly likely that interhemispheric integration is already needed from the very first stages of word processing, when the letter information is combined to activate stored word representations. Taking into account these insights not only improves our understanding of the neurophysiological and cognitive mechanisms of reading, it also gives us new ideas to look at individual differences in reading.

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