54 Ventral and Dorsal Contributions to Word Reading

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ABSTRACT   The core component of expert reading is the fast and accurate perception of single words by the visual system, an ability that results from years of intensive learning. We propose an integrated view of the contributions of the ventral and dorsal streams to this process, associating brain imaging in normal subjects and studies of brain-damaged patients. Together, these two sources of data indicate that fluent reading results from a tight collaboration of both pathways. In the left occipitotemporal cortex, the Visual Word Form system allows for the fast, invariant, and parallel encoding of well-formed letter strings. The occipitoparietal pathway makes an important contribution to reading through attention orienting, word selection, and within-word serial decoding under nonoptimal reading conditions.

The acquisition of reading by children rests on a delicate tuning of the visual system and of the verbal system, and on the elaboration of novel interactions between these two preexisting domains. As a result of this long and effortful process, adult readers are able to scan pages of text in a fast and orderly manner, identifying a flow of words that are each fixated only for a fraction of a second, immediately accessing their sound and meaning, and building up at the same time an integrated interpretation of the text. The core component of this remarkable process is the fast and accurate perception of single words by the visual system. A prerequisite for access to a word's sound and meaning is the identification of its component letters and of their order, an abstract representation that has been called the Visual Word Form (Besner, 1989; Paap, Newsome, & Noel, 1984; Warrington & Shallice, 1980).

In past years, research has concentrated on the contribution of the left ventral visual system to word-identification processes. However, like any complex visual task, reading is most likely achieved through a collaboration of the two components of the cerebral visual system—that is, the ventral occipitotemporal "what" stream and the dorsal occipitoparietal "where" stream (Ungerleider & Mishkin, 1982). In this chapter we propose an integrated view of the contributions of the ventral and dorsal streams to single-word reading. We systematically associate information from brain imaging in normal subjects and contributions from studies of brain-damaged patients with varieties of acquired "peripheral" dyslexias—that is, reading deficits resulting from impaired visual processing, as opposed to language-related "central" dyslexias. Together, these two sources of data indicate that fluent reading results from a tight collaboration of the ventral and dorsal visual pathways, with the occipitotemporal route dominating for expert reading of known words and the occipitoparietal pathway making an essential contribution to reading under dysfluent, unfamiliar, or degraded conditions.

Word processing in the ventral visual pathway

WORD PERCEPTION AS OBJECT PERCEPTION   Over the last decades, studies in monkeys and, more recently, functional imaging in humans have shown that object recognition is achieved through neuronal hierarchies located in the ventral occipitotemporal pathway. Moving from area V1 to inferotemporal (IT) cortex, converging neurons show an increasing invariance to position and scale, an increasing size of the receptive fields, and an increasing complexity of the neurons' optimal stimuli (M. Booth & Rolls, 1998; Riesenhuber & Poggio, 1999; Rolls, 2000; Serre, Oliva, & Poggio, 2007; Ullman, 2007). Connections include bottom-up and top-down projections within the ventral stream (Felleman & Van Essen, 1991), as well as projections to and from more remote frontal and parietal regions subserving attentional control (Kastner & Ungerleider, 2000).

We proposed that the ability to read words stems from this general ability of the ventral stream to identify complex multipart objects. According to the local combination detector, or LCD, model (Dehaene, Cohen, Sigman, & Vinckier, 2005), words are encoded through a posterior-to-anterior hierarchy of neurons tuned to increasingly larger and more complex word fragments, such as visual features, single letters, bigrams, quadrigrams, and possibly whole words.

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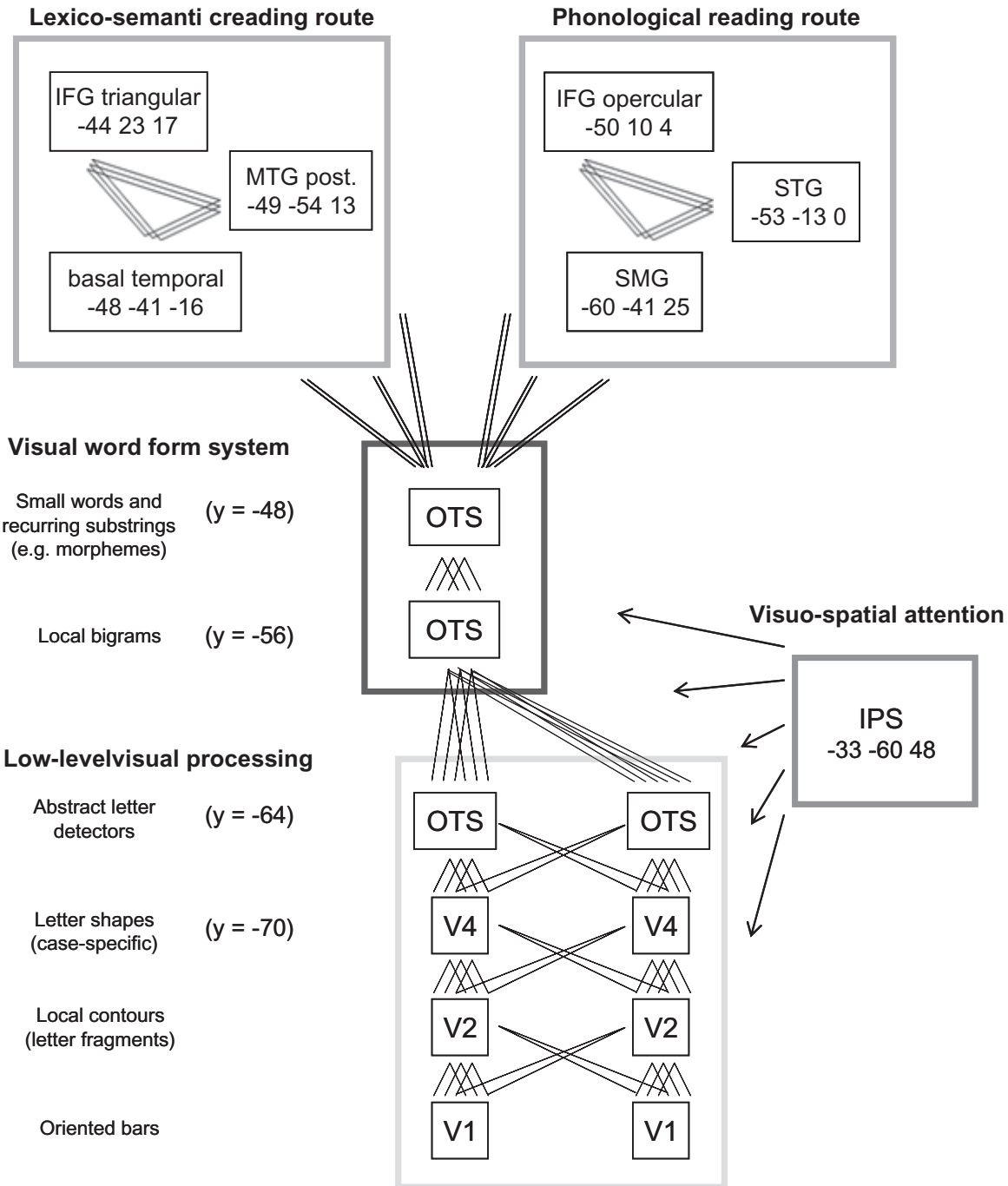
Lexico-semanti creading route

IFG triangular
-44 23 17

MTG post.
-49 -54 13

basal temporal
-48 -41 -16

Phonological reading route

IFG opercular
-50 10 4

STG
-53 -13 0

SMG
-60 -41 25

Visual word form system

Small words and recurring substrings (e.g. morphemes)   (y = -48)

OTS

Local bigrams   (y = -56)

OTS

Visuo-spatial attention

IPS
-33 -60 48

Low-levelvisual processing

Abstract letter detectors   (y = -64)

OTS   OTS

Letter shapes (case-specific)   (y = -70)

V4   V4

Local contours (letter fragments)

V2   V2

Oriented bars

V1   V1

FIGURE 54.1   Synthetic schema of the reading system, merging propositions from Dehaene, Cohen, Sigman, and Vinckier (2005) and Cohen and colleagues (2003). Low-level processing is achieved in each hemisphere for the contralateral half of the visual field (yellow). Information converges on the left-hemispheric Visual Word Form System where an invariant representation of letter strings is computed (red). The dorsal visual stream exerts a top-down attentional control on the hierarchy of ventral areas (blue). The ventral visual system then feeds the lexicosemantic and phonological reading routes (green). The proposed normalized coordinates for the lexicosemantic and phonological reading routes are from a meta-analysis of 35 PET and fMRI studies (Jobard, Crivello, & Tzourio-Mazoyer, 2003), and the coordinates of the visuospatial attention system are from Gitelman, Nobre, Sonty, Parrish, and Mesulam (2005). IFG: inferior frontal gyrus; MTG: middle temporal gyrus; SMG: supramarginal gyrus: OTS: occipitotemporal sulcus; IPS: intraparitetal sulcus.
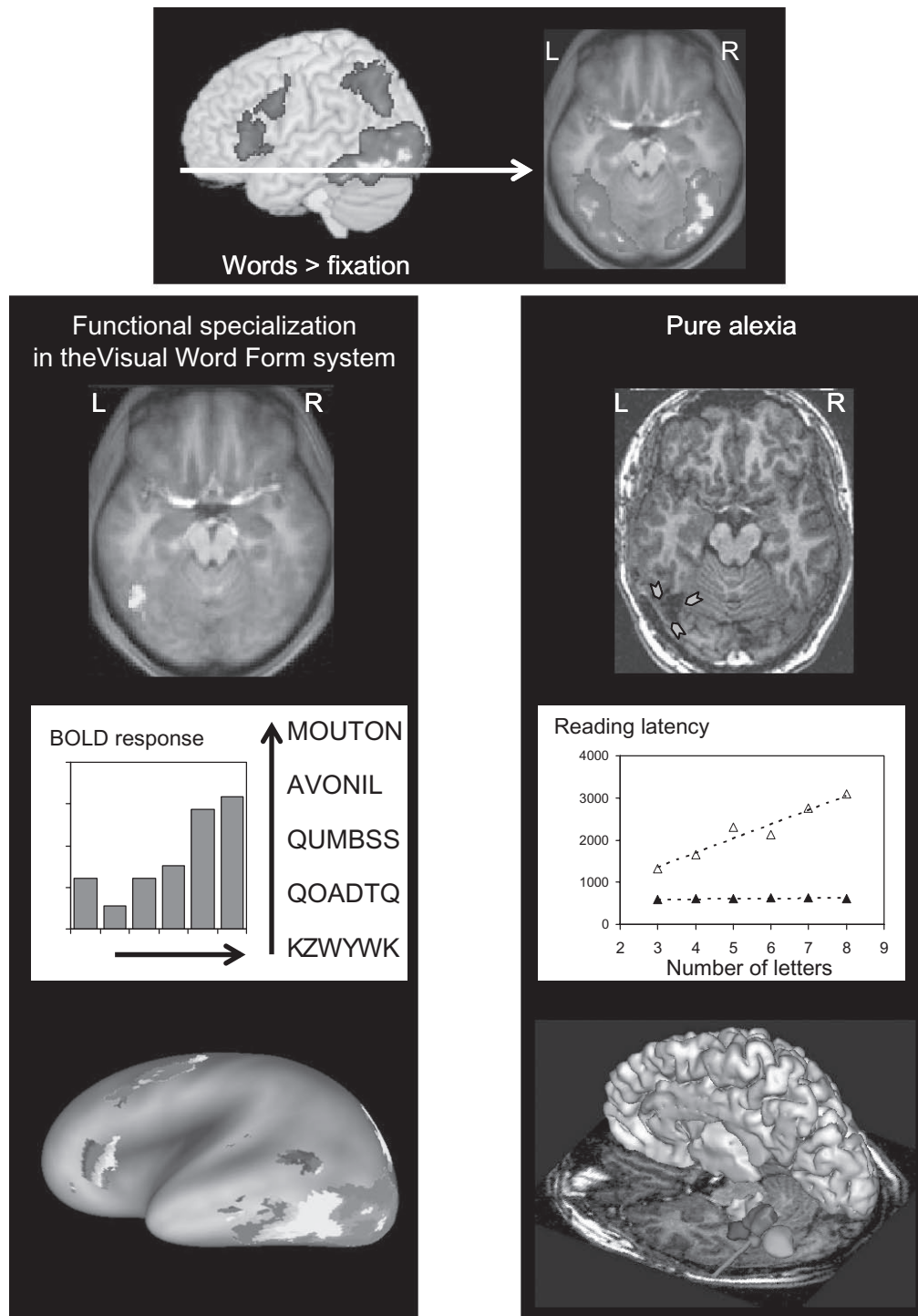
Figure 54.2 Word processing in the ventral pathway. *Top panel*: Activations induced by printed words relative to a fixation baseline in the left hemisphere (left) and in the bilateral ventral visual pathway (right). *Left panel* (adapted from Vinckier et al., 2007: The VWF system shows a linear increase of activation (top) by letter strings forming closer statistical approximations to orthographically legal strings (middle). This functional specialization increases progressively in ore anterior regions within the VWG system (bottom).

Right panel (adapted from Gaillard et al., 2006): Surgical lesion in the left ventral cortex responsible for pure alexia (top). Whereas before surgery word reading was fast and constant irrespective of word length, after surgery the patient showed slow letter-by-letter reading (middle). In the same patient, the 3D image shows te relative position of the VWFA (blue), of other category-dependent fMRI activation clusters before surgery, of the brain lesion (green), and of intracerebral electrodes (magenta).

This system reaches its optimal level of expertise only after years of practice. Through perceptual learning mechanisms, neurons within the ventral pathway become progressively attuned to the regularities of the writing system at all hierarchical levels. This hierarchy must also take into account the need to interact with downstream codes for phonological, morphological, and lexical knowledge of words (Goswami & Ziegler, 2006). Eventually, the adult pattern of performance—that is, fast and invariant word recognition with little influence of the number of letters—is thought to reflect the parallel encoding of letter strings through a fast bottom-up hierarchy of converging detectors.

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Early Visual Processing of Printed Words

Retinotopic processing   Letters are first processed in the hemisphere contralateral to their location in the visual field, probably in increasingly invariant format, through areas V1 to V4. Those areas, located approximately between Talairach coordinates (TC) $y = -90$ and $y = -70$, are modulated by physical parameters such as word length (Whiting et al., 2003) and visual contrast (Mechelli, Humphreys, Mayall, Olson, & Price, 2000), stimulus degradation (Helenius, Tarkiainen, Cornelissen, Hansen, & Salmelin, 1999; Jernigan et al., 1998), and stimulus rate and duration (Price & Friston, 1997; Price, Moore, & Frackowiak, 1996). Accordingly, the P150 wave evoked by word reading is only sensitive to the physical repetition of stimuli in a masked priming paradigm (Petit, Midgley, Holcomb, & Grainger, 2006).

Perceptual asymmetry   It has long been recognized that words are read more easily when they are displayed in the right visual field (RVF) than in the left visual field (LVF) (for reviews see Ducrot & Grainger, 2007; Ellis, 2004). By continuously varying fixation point inside and outside words, Brysbaert, Vitu, and Schroyens (1996) showed that the RVF advantage is closely related to another behavioral asymmetry, namely, that in the optimal reading position, gaze position falls left of word center (Nazir, 2000; O'Regan, Levy-Schoen, Pynte, & Brugaillere, 1984), so that most of the word falls in the RVF. Thus the visual reading span of about 10 letters (Rayner & Bertera, 1979) is not distributed equally across both hemifields, as letter-identification performance decreases more slowly with eccentricity in the RVF than in the LVF (Nazir, Jacobs, & O'Regan, 1998). In addition to higher accuracy and shorter latencies, the RVF advantage is characterized by parallel letter identification, as indexed by constant reading latencies irrespective of word length. The absence of a word-length effect is restricted to words displayed in the optimal viewing position, or fully within the sector of the RVF closest to the fovea. Outside of those conditions, a length effect emerges. Accordingly, when words extend across central fixation, only their left part

induces a length effect (Lavidor & Ellis, 2002; Lavidor, Ellis, Shillcock, & Bland, 2001).

The RVF advantage is a complex phenomenon, for which several compatible mechanisms have been put forward: degradation of information resulting from right-to-left interhemispheric transfer of LVF letters; better perceptual learning in the most stimulated sector of the visual field (Nazir, 2000; Nazir, Ben-Boutayab, Decoppet, Deutsch, & Frost, 2004); and rightward attentional bias. As to the ultimate causes of such perceptual or attentional asymmetries, they may involve left-hemispheric lateralization of language (M. Kinsbourne, 1972), left-to-right reading habits (Deutsch & Rayner, 1999; Lavidor & Whitney, 2005; Mishkin & Forgays, 1952), and the fact that the beginning of words is more informative than their end and should therefore be kept close to fixation, as acuity drops steeply away from the fovea (e.g. O'Regan et al., 1984).

Nazir and colleagues (Nazir, 2000; Nazir et al., 2004) emphasized the role of perceptual learning in the genesis of the RVF advantage, as a result of the most frequent perception of words in this sector of the visual field. Along those lines, it is plausible that expert word perception, like other instances of overpracticed perceptual abilities, is restricted to the trained region of the visual field and results from increased activation in retinotopic cortex, with increasing reliance on its more posterior sectors (Sigman et al., 2005). Congruent with this view, Cohen and colleagues (2002) found a left extrastriate region (TC -24 -78 -12) only responsive to RVF stimuli, which showed stronger activation by alphabetic strings than by checkerboards, while no such difference was observed in corresponding right extrastriate areas. Moreover, TMS inhibition of the left (but not of the right) occipital cortex induces a length effect for words displayed in the RVF (Skarratt & Lavidor, 2006). This effect occurs when TMS is applied 80 ms after word presentation, supporting the localization of the interference to the posterior visual cortex.

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Moreover, priming tasks with split-field stimuli suggest that alphabetic strings are encoded in a format less dependent on physical shape and case when they are viewed in the RVF than in the LVF (Burgund & Marsolek, 1997; Marsolek, Kosslyn, & Squire, 1992; Marsolek, Schacter, & Nicholas, 1996), possibly reflecting general processing asymmetries in the visual system (Burgund & Marsolek, 2000; Marsolek, 1995; Sawamura, Georgieva, Vogels, Vanduffel, & Orban, 2005). Accordingly, using a masked priming paradigm, Dehaene and colleagues (2001) have evidenced case-specific physical repetition priming in the right extrastriate cortex (though similar regions were also present in left extrastriate at a lower threshold) (for similar effects with object perception see Koutstaal et al., 2001).

Overall, such data support the idea that the posterior sector of the left ventral pathway develops superior percep-

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tual abilities for contralateral strings of letters (as indexed by measures of accuracy, speed, parallelism, and invariance), explaining at least the perceptual component of the RVF advantage.

Pathology: Reading with hemianopia or with apperceptive agnosia   The asymmetric role of posterior visual cortex in reading is supported by the pattern of reading impairments resulting from left versus right hemianopia. Reading is highly dependent on the integrity of the central visual field. As unilateral lesions affecting the retrochiasmatic visual tract up to primary visual cortex result in scotomas sparing at least half of the fovea, the ensuing reading impairments are relatively mild. Only right hemianopia without sparing of foveal vision induces noticeable reading difficulty (Zihl, 1995). First, the visual span of such patients is reduced, and they may require several fixations in order to perceive long words. Second, patients lose the reading advantage specific to the normal RVF. Accordingly, they show an influence of word length on reading latencies, as normal subjects do with words displayed in their LVF (Cohen et al., 2003). Third, perception in the right parafoveal field, in an area spanning about 15 letters (Rayner & McConkie, 1976), is important for preparing the accurate landing of the gaze on subsequent words (Sereno & Rayner, 2003). Therefore hemianopic patients make abnormally short and numerous saccades when reading word sequences (Leff et al., 2000; Zihl, 1995).

Finally, patients with so-called apperceptive agnosia (Humphreys & Riddoch, 1993; Lissauer, 1890) following (generally bilateral) lesions of intermediate visual areas such as V2 and V4 are impaired at word reading just as they are at identifying other types of shapes and objects (Heider, 2000; Michel, Henaff, & Bruckert, 1991; Rizzo, Nawrot, Blake, & Damasio, 1992).

Invariant Representation of Letters and the Visual Word Form Area   After percolating through retinotopic cortex, visual word information converges on the sector of ventral cortex anterior to V4, ranging approximately from TC $y = 60$ to $y = -40$, a region with larger receptive fields and greater capacity of invariance. This region receives afferences from both visual hemifields (Tootell, Mendola, Hadjikhani, Liu, & Dale, 1998) and shows repetition suppression by object images across changes in size, position, and orientation (Grill-Spector et al., 1999), and across a change of exemplar within a category (Koutstaal et al., 2001). Accordingly, we proposed that, during reading, part of this region (which we labeled as the Visual Word Form Area, or VWFA) is responsible for the computation of an invariant representation of letter identities (Cohen et al., 2000). Both this proposed labeling and the functional properties of this region have given rise to enduring controversies (Price & Devlin, 2003; Wright et al., 2007), which we tried to clarify by applying to the VWFA the distinctive notions of reproducible localization, partial regional selectivity, and functional specialization (for review and discussion see Cohen & Dehaene, 2004).

Specialization within the ventral stream

1. **Reproducible localization.** Reading-related activations are reproducibly located within the occipitotemporal sulcus lateral to the left fusiform gyrus (VWFA), with only a few millimeters of intersubject variability (Cohen et al., 2002; Jobard, Crivello, & Tzourio-Mazoyer, 2003). The VWFA is activated by visual words irrespective of their position in the visual field (Cohen et al., 2000). An associated electrical or magnetic signature is detected about 170–200 ms after stimulation (e.g., Cohen et al., 2000; Marinkovic et al., 2003; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999).

The remarkable topographical reproducibility of the VWFA may result from its optimal positioning within gradients biasing the a priori organization of the visual cortex, such as a posterior-to-anterior increase in perceptual invariance (Grill-Spector et al., 1998; Lerner, Hendler, Ben-Bashat, Harel, & Malach, 2001) and a mesial-to-lateral increase in preference for foveal versus peripheral stimuli (Hasson, Levy, Behrmann, Hendler, & Malach, 2002). A further reason for the localization of the VWFA, particularly for its usual left lateralization, may be the availability of more direct connections to other language-related sites involved in phonological or lexical processing (Cai, Lavidor, Brysbaert, Paulignan, & Nazir, 2008; Cohen, Jobert, Le [4] Bihan, & Dehaene, 2004; Epelbaum et al., in press; Mahon & Caramazza, in press).

2. **Partial regional selectivity.** The VWFA is activated by alphabetic strings relative to fixation but often also relative to complex nonalphabetic stimuli such as faces or geometrical patterns (e.g., Cohen et al., 2002; Puce, Allison, Asgari, Gore, & McCarthy, 1996). However, the difference in activation between words relative to visual objects is variable across studies, and may even be inverted, depending on a number of experimental parameters (e.g., Wright et al., 2007).This lack of absolute regional selectivity may be taken as a sensible argument against the use of the VWFA label, as this region may well be involved in processing nonalphabetic visual objects. However, selectivity may be detectable only at a higher spatial resolution. Thus intracranial recordings occasionally showed P150 or N200 waves elicited exclusively by letter strings, as compared to a variety of control stimuli such as phase-scrambled strings, flowers, faces, or geometrical shapes (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Allison, Puce, Spencer, & McCarthy, 1999). Moreover, some left inferotemporal lesions (see the [5] subsection "Pathology: Pure alexia") yield massive alexia

affecting even single letters, contrasting with the spared recognition of complex multipart objects, faces, or digit strings, demonstrating that the VWFA, even if activated by a wide range of stimuli, may evolve to be *necessary* only to word recognition.

3. **Functional specialization.** The issue of selectivity is independent of the hypothesis of a functional specialization of the VWFA. On top of their preexisting object coding properties, neurons in the VWFA develop elaborate functional specialization as they get attuned to arbitrary features of the subject's script. As the clearest instance of functional specialization, activation of the VWFA is stronger when the script is familiar than when it is unfamiliar (e.g., Hebrew versus alphabetic strings; Baker et al., 2007) or created de novo (Price, Wise, & Frackowiak, 1996). Moreover, using masked repetition priming, it was shown that the VWFA represents words in a format invariant for the upper- versus lowercase distinction (e.g., radio versus RADIO), another arbitrary culture-dependent feature of writing systems (Dehaene et al., 2004, 2001). Finally, within the subjects' familiar script, the VWFA is activated more strongly by letter strings forming closer statistical approximations to orthographically legal strings (including real words), showing that the VWFA incorporates constraints on letter combinations, which are specific to the familiar language (Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006; Cohen et al., 2002; Vinckier et al., 2007).

4. **Internal structure of the Visual Word Form system.** According to the LCD model, the anteroposterior extension of the VWFA (about 20 mm) should reflect its heterogeneous and hierarchically organized structure. Dehaene and colleagues (2004), using a subliminal priming design, showed that the type of prime-target similarity that causes fMRI priming varies according to the anterior-posterior location in left occipitotemporal cortex, with an increasing invariance for position and case change, and probably greater reliance on larger-size units such as bigrams or quadrigrams. More recently, Vinckier and colleagues (2007) tested whether a hierarchy of detectors of increasingly larger word fragments is present in the left occipitotemporal cortex. The frequency of letters, bigrams, and quadrigrams was manipulated, yielding a range of stimuli with an increasing structural similarity to real words. The more anterior an area was within the Visual Word Form region, the more sensitive it was to the frequency of complex components, revealing a gradient-like spatial organization *within* the VWFA (see Grainger and Holcomb, in press, for a review of ERP data relevant to the fragmentation of orthographic processing).

Pathology: Pure alexia Impairments affecting the Visual Word Form system correspond to the syndrome of pure alexia, as described in the 19th century (Binder & Mohr, 1992;

Damasio & Damasio, 1983; Dejerine, 1892). Pure alexia is an acquired and selective reading deficit occurring in previously literate patients. Patients typically have entirely preserved production and comprehension of oral language, and they can write normally either spontaneously or to dictation. However, they show various degrees of impairment of word reading. The critical cortical lesions generating pure alexia overlap with the VWFA as defined with functional imaging (Cohen et al., 2003; Gaillard et al., 2006). Pure alexia may also follow deafferentation of an intact VWFA following left-hemispheric white matter lesions (Cohen, Henry, et al., 2004; Epelbaum et al., in press). Posterior callosal lesions cause a selective deafferentation of the VWFA from the right occipital cortex, yielding alexia restricted to the LVF (Cohen et al., 2000, 2003; Molko et al., 2002; Suzuki et al., 1998).

In the most severe cases, known as global alexia, patients cannot identify single letters, let alone whole words (Dalmas & Dansilio, 2000; Dejerine, 1892). Such patients may or may not have access to abstract letter identities, as tested for instance in a cross-case letter-matching task (Miozzo & Caramazza, 1998; Mycroft, Hanley, & Kay, 2002). More often, patients show relatively preserved letter identification abilities and develop letter-by-letter reading strategies, as if only the most finely tuned mechanisms of word perception were affected, those allowing for rapid and parallel identification of letter strings. As an indication of this effortful reading strategy, patients show a large increase in the number and the duration of fixations per word relative to normals and even to patients with hemianopic dyslexia (Behrmann, Shomstein, Black, & Barton, 2001). There is some evidence that in letter-by-letter readers, residual letter identification can be subtended by right-hemispheric regions symmetrical to the VWFA or by spared patches of left-hemispheric ventral cortex (Bartolomeo, Bachoud-Levi, Degos, & Boller, 1998; Cohen, Henry, et al., 2004; Gaillard et al., 2006).

Finally, some patients show better-than-chance performance in purely implicit reading tasks such as lexical or semantic decision, contrasting with the apparent inability to identify printed words (Coslett & Saffran, 1989; Coslett, Saffran, Greenbaum, & Schwartz, 1993). Implicit reading has been most clearly evidenced with Arabic numerals, which can be compared accurately even when explicit reading is grossly impaired (Cohen & Dehaene, 1995, 2000), probably revealing effective right-hemispheric identification processes.

Contribution of the dorsal pathway

The operation of the ventral stream during word reading is modulated by attentional influences, originating from parietal regions, that may impinge on all processing levels from striate cortex (Chawla, Rees, & Friston, 1999; Somers, Dale, Seiffert, & Tootell, 1999) to ventral occipitotemporal areas

(Kastner, De Weerd, Desimone, & Ungerleider, 1998). In order to make sense of the variety of reading impairments that may follow parietal lesions, we will distinguish somewhat artificially three contributions of attentional control to single-word reading: orienting to the region of space where the target word is displayed, filtering out irrelevant words present in the vicinity of the target, and serially attending to letters or word fragments whenever letters cannot be effectively processed in parallel over the whole string.

8 ORIENTATION OF ATTENTION   Spatial attention modulates the efficiency of the visual processing of alphabetic stimuli. Thus words are better recognized when they appear in a region of the visual field to which attention has been directed by a previous cue (McCann, Folk, & Johnston, 1992), and subliminal letters have a priming effect on subsequent targets only when they are displayed at an attended location (Marzouki, Grainger, & Theeuwes, 2007). As mentioned before, the RVF advantage may partly result from a rightward bias of attention. Ducrot and Grainger (2007) showed that exogenous spatial cuing has no impact on the (asymmetrical) reading performance for words displayed only slightly off fixation, suggesting that in the central field, the RVF advantage is mostly perceptual. In contrast, cuing was very effective for more peripheral words and tended to reduce the RVF advantage. In a study of lateralized word reading, Cohen and colleagues (2002) found larger activations for RVF than for LVF words in the left precuneus and thalamus, with no activations for the opposite contrast, likely reflecting the attentional component of the RVF advantage.

Pathology: Neglect dyslexia   The defining feature of neglect dyslexia is the existence of a left-right spatial gradient in the rate of reading errors far exceeding the normal RVF advantage (for an overview and references see Riddoch, 1990). Following the general pattern of hemispatial neglect, it is much more common to observe left than right neglect dyslexia, although a number of right-sided cases have been reported. Neglect dyslexia is generally associated with signs of neglect outside the domain of reading, although patients with seemingly isolated neglect dyslexia have been reported. Neglect is thought to result from associated impairments of both nonlateralized and lateralized components of attentional/spatial processing (Husain & Rorden, 2003). The latter may depend on saliency maps of the opposite hemispace subtended by each posterior parietal lobe (Medendorp, Goltz, Vilis, & Crawford, 2003; M. Sereno, 2001). Assuming that those lateralized maps contribute to the top-down modulation of the ventral visual stream, one may expect that distinct varieties of neglect dyslexia may arise, depending on the side of the lesion, the affected parietal structure, the ventral regions that are deprived of attentional modulation, and so

on. Indeed, there are numerous clinical observations to illustrate this fractionation of neglect dyslexia (Riddoch, 1990).

Neglect errors typically affect the leftmost letters when patients read single words, and the leftmost side of the page when they read connected text. However, those two types of errors can be to some extent doubly dissociated, suggesting that neglect dyslexia is not a homogeneous syndrome (Costello & Warrington, 1987; Kartsounis & Warrington, 1989). This fractionation is best illustrated by the case of patient JR, who suffered from bilateral occipitoparietal lesions (Humphreys, 1998). When presented with words scattered on a page, he omitted the rightmost words, but his reading errors affected the leftmost letters of the words that he picked out. Likewise, he showed left neglect when he was asked to read single words, while he showed right neglect when trying to name the component letters of the same stimuli. This pattern suggests that JR's left lesion yielded right neglect in situations of competition between objects, while his right lesion yielded left neglect in situations of competitions between the parts of an object.

A clarifying framework was proposed by Hillis and Caramazza (1995), who suggested that the varieties of neglect dyslexia may be attributed to spatial attentional biases acting on one or more of progressively more abstract word representations derived from Marr's theory of object perception (Marr, 1982): a peripheral retinocentric feature representation, a stimulus-centered letter-shape level, and a word-centered graphemic representation akin to the Visual Word Form (for a review of supportive data see Haywood & Coltheart, 2000). Thus, in a deficit at the retinocentric level, error rate for a given letter should depend on its position in the visual field relative to central fixation and not on its rank within the target word. In contrast, in a deficit at the stimulus-centered level, error rate should depend on the distance from the center of the word irrespective of the position of the word in the visual field. Naturally, both parameters may be relevant in some if not in the majority of patients. More remote from neglect in its usual sense, neglect at the graphemic level yields errors affecting one end of words irrespective of their spatial position or orientation. Thus patient NG made errors with the last letters (e.g., hound → house) when reading standard words, but also vertical words and mirror-reversed words, as well as when naming orally spelled words and when performing other lexical tasks such as spelling (Caramazza & Hillis, 1990). Note, however, that there are alternative accounts of word-centered neglect dyslexia, in frameworks that refute the existence of object-centered neural representations (Deneve & Pouget, 2003; Mozer, 2002).

Finally, letter strings that are neglected in explicit reading tasks may nevertheless be processed to higher representation levels. This possibility is suggested by preserved performance in lexical decision (Arduino, Burani, & Vallar, 2003), by the
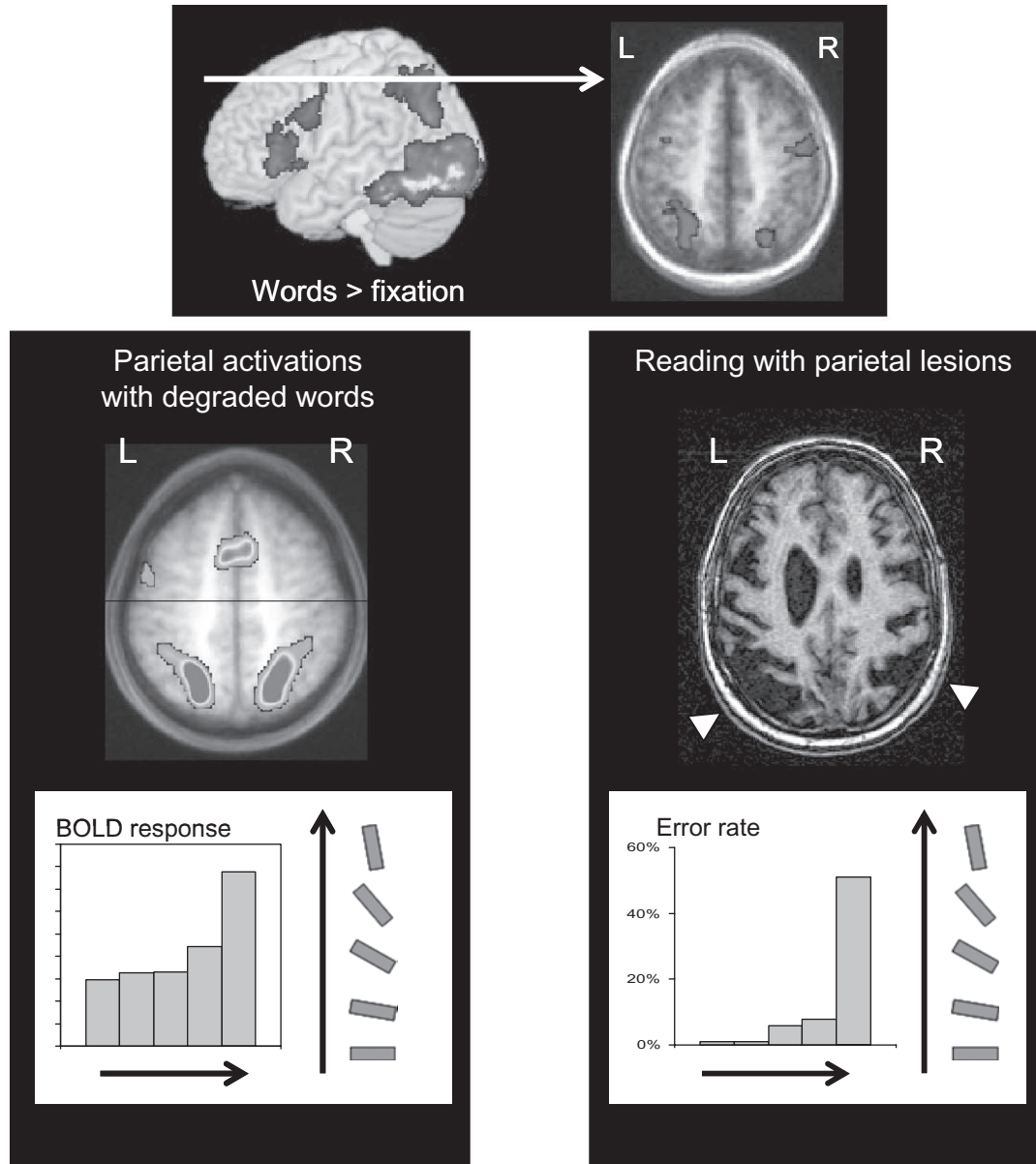
FIGURE 54.3   Contribution of the dorsal pathway to word reading. *Top panel*: Activations induced by printed words relative to a fixation baseline in te left hemisphere (left) and in the bilateral dorsal visual pathway (right). *Left panel* (adapted from Cohen, Dehaene, Vinckier, Jobert, & Montavont, 2008): The bilateral intraparietal cortex shows a nonlinear increase of activation with word degradation, correlated with reaction times (top). For instance, activations increased steeply for words rotated by more than 45° (bottom). *Right panel* (adapted from Vinckier et al., 2006): In a patient with bilateral parietal atrophy and spared ventral cortex (top), there was a severe reading impairment above a similar threshold of rotation angle, demonstrating the role of parietal cortex whenever display degradation exceeds the range of invariance in the ventral cortex.

fact that erroneous responses often tend to have the same length as the actual targets (K. Kinsbourne & Warrington, 1962), or by higher error rates observed with nonwords than with real words (Sieroff, Pollatsek, & Posner, 1988). The interpretation of such findings is still debated (Riddoch, 1990), but it is plausible that neglected words can be partially processed in the ventral visual pathway in the absence of conscious awareness, as has also been shown in normal subjects (Dehaene et al., 2001; Devlin et al., 2003) and with other types of visual stimuli such as faces or houses in neglect patients (Rees et al., 2000).

SELECTION OF ONE SINGLE WORD   For optimal reading, not only should the attention window encompass the target word, but it should also be narrow enough to exclude other neighboring words. In normal subjects it is possible to force a spread of attention over two words, by briefly presenting two words side by side, and specifying only

afterward which of the two should be reported (Davis & Bowers, 2004; Treisman & Souther, 1986). This procedure degrades performance and induces reading errors that are analogous to those observed in the pathological condition known as attentional dyslexia (for qualifications to this analogy see Davis & Bowers, 2004).

Pathology: Attentional dyslexia The hallmark of attentional dyslexia is the contrast between preserved reading of isolated words and high error rates when the target is surrounded by other words (for a review see Davis & Coltheart, 2002). It is generally attributed to an impaired attentional selection of one among several concurrent stimuli (Shallice, 1988). This induces (1) an inaccurate processing of the target (substitutions, additions or deletions of letters) as a result of the competition by surrounding words and (2) intrusion of distracters into later stages of processing (letter migrations from the flanking words into the response to the target).

Such ideas are in good agreement with imaging data in normals, showing that when multiple objects are presented simultaneously, they exert mutual inhibition, resulting in decreased ventral visual activations (Kastner et al., 1998). Directing attention toward one of the stimuli compensates this reduction of activity. Moreover, the activation induced by distracters in areas T4 and TEO is reduced in proportion to the attention that is paid to the target, and it is inversely correlated with frontoparietal activations (Pinsk, Doniger, & Kastner, 2004). It is thus plausible that in attentional dyslexics, impaired selection abilities, which are unmasked in the presence of flanker words, cause both visual errors due to a weakened representation of the target and letter migrations due to an excessive activation of distracters.

The phenomenon of flanker interference also prevails when patients are asked to read single letters surrounded by other letters. This finding leads to the paradoxical observation that patients may be good at reading isolated words but not at naming their component letters. More generally, interference seems to occur only between items of the same category. In their seminal article Shallice and Warrington (1977) showed that flanking letters but not flanking digits interfered with letter identification. Similarly, there is no mutual interference between letters and whole words (E. K. Warrington, Cipolotti, & McNeil, 1993). One may note that in some patients the interference between letters is the same whether the target and flankers are printed in the same case or not (Shallice & Warrington, 1977; E. K. Warrington et al.), suggesting that the impairment impinges on visual areas that already show high-level invariance, such as the VWFA. Still, the irrelevance of case changes for attentional selection is not absolute. Indeed, letter migrations between words may be reduced by using different typographic cases (Saffran & Coslett, 1996), suggesting that low-level visual features may help to focus the attention on the target word and to discard distracters.

In brief, attentional dyslexia may be due to insufficient attentional focusing on one among several concurrent letters or letter strings represented in the Visual Word Form system. Note that the few cases of attentional dyslexia with sufficient lesion data consistently point to a left parietal involvement (Friedmann & Gvion, 2001; Mayall & Humphreys, 2002; Shallice & Warrington, 1977; E. K. Warrington et al., 1993). Such asymmetry may relate to a left-hemispheric bias for object-oriented attention (Egly, Driver, & Rafal, 1994), or more generally to the left dominance for language.

Attending to Parts of Words and Serial Decoding As an outcome of perceptual learning, in expert readers the ventral visual pathway gets attuned to the perception of normal print: horizontally aligned words presented in the foveal region in a usual font are identified in a fast and parallel manner. There are, however, a number of circumstances in which this optimal encoding is either unavailable or inappropriate to the task at hand, as revealed by slower reading speed and by the emergence of a linear increase of reading latencies with word length. We suggest that this length effect reflects a failure of parallel letter processing in the ventral pathway and indicates the deployment of serial attention to letters or groups of letters (for an alternative account see Whitney, 2001; Whitney & Lavidor, 2004). Serial reading would involve parietal structures driving spatial-attentional processes (Gitelman et al., 1999; Husain & Rorden, 2003; Kanwisher & Wojciulik, 2000; Mesulam, 1999) and a modulation by this top-down attention of ventral occipitotemporal structures coding for word fragments (Chawla et al., 1999; Kastner et al., 1998; Somers et al., 1999).

Departure from parallel reading as indexed by the emergence of a length effect occurs in many conditions: (1) in children whose reading expertise is still incompletely developed, with an effect of word length persisting until about the age of 10 (Aghababian & Nazir, 2000); (2) in pure alexic patients who develop letter-by-letter reading following left ventral lesions, a strategy that is associated with parietal activations (Gaillard et al., 2006); (3) in normal subjects attempting to read words degraded by means of contrast reduction (Legge, Ahn, Klitz, & Luebker, 1997), of mIxEd case printing (Lavidor, 2002; Mayall, Humphreys, Mechelli, Olson, & Price, 2001), of vertical display (Bub & Lewine, 1988), and of lateral display in the LVF (Lavidor & Ellis, 2002); and (4) in normal subjects reading aloud pseudo-words, which probably requires the serial left-to-right conversion of graphemes into phonemes (Weekes, 1997). Interestingly, patients with semantic dementia who suffer from a progressive dissolution of lexical knowledge show a length effect even when reading real words (Cumming,

Patterson, Verfaellie, & Graham, 2006). This abnormal length effect is due to reduced top-down lexical support for word identification, compelling patients to process real words as pseudowords.

We recently studied the mechanisms involved in reading degraded words (Cohen, Dehaene, Vinckier, Jobert, & Montavont, 2008). We presented adult readers with words that were progressively degraded in three different ways (word rotation, letter spacing, and displacement to the visual periphery). Behaviorally, we identified degradation thresholds above which reading difficulty increased nonlinearly, with the concomitant emergence of a length effect. Functional MRI activations were correlated with reading difficulty in bilateral occipitotemporal and parietal regions, reflecting the strategies required to identify degraded words. A core region of the intraparietal cortex was engaged in all modes of degradation. Supporting the current interpretation, the same region is also activated, and its interactions with other parts of the reading network increase, when subjects are required to pay attention to letters within nondegraded words (Bitan et al., 2005; J. Booth et al., 2002). Furthermore, in the ventral pathway, word degradation led to an amplification of activation in the posterior Visual Word Form area at a level thought to encode single letters. We also found an effect of word length restricted to highly degraded words in bilateral occipitoparietal regions.

Pathology: Spatial dyslexia and Balint's syndrome Balint's syndrome, a consequence of bilateral dorsal parietal lesions, includes simultanagnosia, which prevents the binding of objects with a stable localization in space and the computation of their relative positions, and ocular apraxia, which precludes an accurate control of saccades toward peripheral targets (Rizzo & Vecera, 2002). The most salient impact of this disorder on reading is an inability to read connected text as a result of chaotic scanning of the display. The patients' gaze wanders randomly from word to word, and the relative position of words cannot be appreciated. However, patients can read accurately each of the disconnected words on which they land.

While the identification of optimally printed words is not substantially affected, patients may have major difficulties reading words presented in unusual formats, such as vertically arrayed or widely spaced letters. These difficulties disrupt the automatic binding of letters into single visual objects, and therefore require a scanning of component letters, which Balint patients cannot do. Due to impaired scanning, patients may also be unable to report one letter out of a string, even with optimally displayed real words (Baylis, Driver, Baylis, & Rafal, 1994). A similar account explains why Balint patients are impaired at reading pseu-dowords, for which grapheme-to-phoneme conversion requires the sequential inspection of graphemes. For instance, a patient could read accurately 29 out of 30 briefly presented words, while she identified only 4 out of 30 pseudowords (Coslett & Saffran, 1991).

We recently studied a simultanagnosic patient with bilateral parietal atrophy (Vinckier et al., 2006). She was excellent at reading normally printed foveal words, but she was severely impaired at reading words that were mirror reversed, or rotated by angles larger than 50°, or whose letters were separated by at least two blank spaces, or words displayed in her left hemifield. According to the present hypothesis, above those critical thresholds—that is, when stimulus degradation exceeds the perceptual tolerance of the ventral system—reading normally requires the intervention of the parietal lobes to pilot the attention-driven exploration of stimuli (for a congruent observation see Hall, Humphreys, & Cooper, 2001). Parietal lesions did not allow the patient to resort to such strategy. This study was congruent with an imaging study reviewed before (Cohen et al., 2008): overlapping parietal regions were activated in normal subjects and lesioned in the patient, and the same degree of word degradation boosted parietal activations in normals and caused a drop in the patient's performance.

Because of her parietal lesions, this patient also presented with orientation agnosia (e.g., Priftis, Rusconi, Umilta, & Zorzi, 2003). She was thus unable to discriminate normally oriented words or pictures of objects from the same rotated stimuli. However, while she was unable to discriminate pictures of objects from their mirror-reversed images, she could do so easily with reversible pseudowords. For instance, "boup" and "quod" appeared to her as distinct items, although they are mirror images of each other. The ventral pathway builds up a mirror-invariant representation of common objects (Logothetis & Pauls, 1995; Rollenhagen & Olson, 2000), which requires the intervention of explicit orientation analysis dependent on parietal cortex in order to discriminate mirror images. In contrast, the default invariance for mirror symmetry is "unlearned" by the ventral pathway in the particular case of reading, since reading requires the accurate discrimination of mirror-symmetric shapes (e.g., "p" versus "q").

Interfacing with the verbal system

As the result of a collaboration between ventral and dorsal routes, detailed visual information about letter strings is ultimately conveyed to downstream language areas. In this section, we briefly point out some open issues pertaining to the relationships of the visual system with the language-related components of word processing, including phonology and the lexicon.

10   LANGUAGE

MULTIPLE OUTLETS FROM THE VENTRAL STREAM   Assuming that word fragments of various sizes are identified in the ventral stream, one may expect that rich direct and indirect projections should exist toward areas involved in lexical, semantic, motor, or phonological processes. However, the pathways leading from the VWFA to all components of the reading network are not precisely defined. The macaque equivalent of the VWFA putatively falls within the IT complex, which projects to the inferior parietal lobule and the anterior temporal lobe, in addition to occipital and interhemispheric connections (Schmahmann & Pandya, 2006). Moreover, there may be a specifically human development of projections from the inferior temporal cortex to language-related superior temporal, parietal, and frontal regions, through the arcuate fasciculus (Catani, Jones, & ffytche, 2005; Epelbaum et al., in press) and the inferior fronto-occipital fasciculus (Catani, Howard, Pajevic, & Jones, 2002), respectively.

Following the observation of alexia with agraphia, Dejerine (1892) suggested that the next step following visual word processing should be the angular gyrus, which he postulated to be the "visual center of letters." Indeed, the angular gyrus is among the regions that are modulated during reading tasks, even if it often remains below the baseline level of activation (Binder et al., 2003; Binder, Medler, Desai, Conant, & Liebenthal, 2005), and there is functional connectivity between the angular gyrus and the left fusiform gyrus at coordinates matching the VWFA (Horwitz, Rumsey, & Donohue, 1998). There is also correlated activity in the VWFA and in left inferior frontal areas (Bokde, Tagamets, Friedman, & Horwitz, 2001). A further potential output pathway is to temporal regions anterior to the VWFA. These regions, which have been difficult to image with functional MRI because of magnetic susceptibility artifacts, are probably involved in supramodal semantic processing (for a review see Giraud & Price, 2001; Kreiman, Koch, & Fried, 2000; Lambon Ralph, McClelland, Patterson, Galton, & Hodges, 2001).

Finally, it is possible that different segments of the Visual Word Form system feed distinct language-related processes by projecting to distinct areas. Thus Mechelli and colleagues (2005) found that during reading the posterior fusiform cortex, which codes for single letters according to the LCD model, was coupled with the superior premotor cortex, possibly in relation to letter-to-articulation transcoding, while the anterior fusiform cortex, presumably coding for large word fragments, was coupled with Broca's pars triangularis, possibly in relation to lexicosemantic access. Accordingly, the former coupling increased during pseudoword reading, whereas the latter increased during exception word reading. In a similar vein, Grainger proposed on the basis of behavioral data that two types of orthographic code are computed: a coarse code used to rapidly access semantic information and a finer-grained code used to access phonology from orthography (Grainger & Holcomb, in press).

PHONOLOGICAL IMPACT ON VISUAL REPRESENTATIONS   One potential shortcoming of the LCD model is that it focuses primarily on the acquisition of visual expertise in reading—that is, how the ventral visual system eventually incorporates orthographic regularities. However, it is likely that word phonology also influences orthographic representations in the visual system. Early letter-to-sound mapping is thought to be crucial for reading acquisition, which may constrain the eventual structure of the orthographic code in adults (Goswami & Ziegler, 2006; Ziegler & Goswami, 2005).

The impact of phonology on visual processing emerges from the comparison between scripts that differ in terms of orthographic transparency—that is, the regularity of grapheme-phoneme conversion rules. According to the LCD model, transparency should be reflected in the size of the units encoded by occipitotemporal neurons. In "transparent" writing systems such as Italian or the Japanese kana script, the letter and bigram levels should suffice for grapheme-phoneme conversion. In an "opaque" script, however, such as English or kanji, a larger-size visual unit, more anterior along the visual hiearchy, should be used. Compatible with this idea, stronger and more anterior activation is observed in the left occipitotemporal region in English than in Italian readers (Paulesu et al., 2000), and, at a slightly more mesial location, during kanji than during kana reading in Japanese readers (Ha Duy Thuy et al., 2004; Nakamura, Dehaene, Jobert, Le Bihan, & Kouider, 2005).

However, evidence of an influence of phonology on visual processing within a given writing system is less clear. There are numerous behavioral demonstrations of an impact of phonology on the processing of printed words, as well as of cross-modal word activations in parietal and superior or lateral temporal regions (e.g., J. Booth et al., 2002; Cohen, Jobert, Le Bihan, & Dehaene, 2005; van Atteveldt, Formisano, Goebel, & Blomert, 2004). Still there is little evidence that some of those effects reflect the operation of the visual system per se, rather than of later speech-related processes. For instance, Grainger, Kiyonaga, & Holcomb (2006) showed that by 225 ms after the presentation of a target word preceded by a masked prime, ERPs distinguished homophone pseudoword primes, as compared to nonhomophone controls (e.g., bakon-BACON versus bafon-BACON). Although this time window is roughly compatible with processing in the Visual Word Form System, the anterior topography of this effect does not support an occipitotemporal source. The contribution of phonological structure to word encoding in the visual system is thus largely open to empirical research.

Conclusion

The present review emphasizes that fluent reading results from an intimate collaboration of multiple areas forming a distributed network. Although the VWFA clearly plays an essential role in expert reading, the recent literature has tended to forget that the dorsal spatial-attentional system also makes a major contribution through attention orienting, word selection, and within-word serial decoding. Adult readers probably rely on serial attentive reading under relatively rare conditions; but we speculate that young readers, in whom the word length effect is particularly large, rely heavily on the dorsal route early during the laying down of the grapheme-phoneme decoding stage. Although phonological sources of developmental reading impairments have received vast attention, our analysis suggests that occipito-parietal impairments are also very likely to have an impact on developmental dyslexia, as indeed suggested by recent research (Bosse, Tainturier, & Valdois, 2007; Lassus-Sangosse, N'Guyen-Morel, & Valdois, 2008; Valdois, Bosse, & Tainturier, 2004). In the future, developmental neuroimaging paradigms should be developed to directly image the ventral and dorsal routes as children learn to read.

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