Reading normal and degraded words: Contribution of the dorsal and ventral visual pathways

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Fast, parallel word recognition, in expert readers, relies on sectors of the left ventral occipito-temporal pathway collectively known as the visual word form area. This expertise is thought to arise from perceptual learning mechanisms that extract informative features from the input strings. The perceptual expertise hypothesis leads to two predictions: (1) parallel word recognition, based on the ventral visual system, should be limited to words displayed in a familiar format (foveal horizontal words with normally spaced letters); (2) words displayed in formats outside this field of expertise should be read serially, under supervision of dorsal parietal attention systems. 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 non-linearly, with the concomitant emergence of a word length effect on reading latencies reflecting serial reading strategies. fMRI activations were correlated with reading difficulty in bilateral occipito-temporal 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. 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. Those results clarify when and how the ventral parallel visual word form system needs to be supplemented by the deployment of dorsal serial reading strategies.
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Introduction

Whenever human adults read words, a cortical network is activated which involves left occipito-temporal cortex as a central node. This region, which has been termed the "Visual Word Form Area", is thought to house what psycholinguists and neuropsychologists have termed the "visual word form system" (Warrington and Shallice, 1980), a hierarchy of neural mechanisms for invariant visual word recognition (Cohen et al., 2000; Dehaene et al., 2005; McCandliss et al., 2003). The purpose of the present research is to further clarify the limits of this ventral reading system, and the conditions under which it needs to be supplemented by dorsal serial ("letter-by-letter") reading mechanisms.

We have proposed that the ability to read words stems from the more general ability of the ventral visual system to identify complex multipart objects. Encoding the abstract identity and the relative position of letters is loosely similar to recognizing the drawing of a car on the basis of its component parts and of their spatial relationships. Following this intuition, we recently proposed an attempt at modelling the neural processes of visual word perception, derived from general principles governing the organization of the primate visual system (the Local Combination Detector or LCD model, Dehaene et al., 2005). Neurophysiological observations in the macaque ventral visual regions have led to construe this system as a hierarchy of converging neural detectors with progressively larger receptor fields, tuned to increasingly complex objects (Booth and Rolls, 1998; Riesenhuber and Poggio, 1999; Rolls, 2000; Ullman, 2007). Encoding of complex shapes then results from the convergence of elementary contour detectors (Brincat and Connor, 2004; Tsunoda et al., 2001). The LCD model thus proposes that 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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This system reaches its optimal level of expertise only after years of practice. Children initially decipher words slowly and letter by letter, as indexed by a large effect of word length on reading latencies (Aghababian and Nazir, 2000). Over years of practice, speed increases and the length effect eventually disappears, at least for words of about 3 to 6 letters. Within the LCD framework, this adult pattern of performance is thought to reflect the parallel encoding of letters through the hierarchy of converging detectors. Through perceptual learning mechanisms, the ventral visual system progressively becomes attuned to the regularities of the writing system at all of the above hierarchical levels.

The goal of the present paper is to provide an empirical test of part of the LCD model using fMRI in adults. We propose to progressively degrade words in three different ways and to examine at which threshold of degradation the ventral reading hierarchy ceases to support parallel visual recognition. Perceptual learning mechanisms can only ensure that the visual system of the expert reader is attuned to the perception of normal print: horizontally aligned words presented in the foveal region in a usual font. When words depart from this standard format, reading becomes more difficult, as revealed by lower reading speed, and by the emergence of an effect of word length on reading latencies: response time becomes a linear function of the number of letters. For instance, reading low-contrast words (Legge et al., 1997), words printed in mIxEd case (Lavidor, 2002), vertically presented words (Bub and Lewine, 1988), or words displayed in the left visual field (Lavidor and Ellis, 2002), induces a word length effect.

We suggest that this length effect reflects a failure of parallel letter processing in the ventral pathway, and indicates the deployment of a serial mechanism based on a coordination of dorsal and ventral processes. Those strategies would generally involve the deployment of serial attention to letters or groups of letters within the target string, and therefore induce an effect of length. In terms of functional anatomy, such serial reading would involve both parietal structures driving spatial–attentional processes, and a modulation by this top-down attention of ventral occipito-temporal structures coding for word fragments such as single letters. Dorsal attention orienting (Gitelman et al., 1999; Husain and Rorden, 2003; Kanwisher and Wojciulik, 2000b; Mesulam, 1999) and ventral top-down modulation (Chawla et al., 1999; Kastner et al., 1998; Somers et al., 1999) have been previously observed in many visual tasks, but their contribution to reading remains understudied (Cohen et al., 2003; Henry et al., 2005; Mayall et al., 2001).

Understanding the mechanisms engaged in reading degraded words is thus instrumental in addressing two related questions. First, what are the limits of the perceptual expertise of the ventral visual system for reading? Second, what are the mechanisms of the interplay of the ventral and dorsal pathways during word reading?

In a first attempt to address those issues, we recently studied a simultanagnosic patient with bilateral parietal atrophy (Vinckier et al., 2006). The patient was excellent at reading normally printed foveal words, but she was severely impaired at reading words which 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. We proposed that above those critical thresholds, i.e. 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. This neuropsychological study thus provided a first estimate of the limits of the perceptual expertise of the ventral system, and pointed to the involvement of parietal cortex in reading

words exceeding such limits. Hall et al. (2001) found converging evidence of the deleterious influence of letter spacing and case alternation on reading performance in a patient with parietal (but also occipitotemporal) lesions.

Here we address those issues using behavioral measures and fMRI during word reading by normal subjects. We transformed stimulus words according to three modes of degradation: rotating words by 0° to 90° (rotation mode), separating letters with 0 to 3 blank spaces (spacing mode), or displacing words from 100% in the left hemifield to 100% in the right hemifield (position mode). Within each degradation mode, 5 successive levels of degradation were contrasted, from optimally displayed words (i.e. horizontal foveal words with contiguous letters) to heavily degraded words, thus allowing for a fine-grained assessment of a putative threshold effect on reading difficulty and brain activation (Fig. 1).

Some previous studies have addressed the influence of word degradation on brain activations, mostly showing modulation of the posterior ventral cortex by physical parameters such as visual contrast (Mechelli et al., 2000), visual noise (Helenius et al., 1999; Jernigan et al., 1998), stimulus rate and duration (Price and Friston, 1997; Price et al., 1996), and of the right parietal cortex by case alternation (Mayall et al., 2001). The LCD model, however, goes one step further by generating precise expectations concerning the degradation thresholds above which reading performance should be expected to deteriorate. Concerning rotation, behavioral measures suggest that for angles larger than 45–60° readers abandon the normal fast and parallel reading pattern (Koriat and Norman, 1985, 1989; Lavidor et al., 2001a). Accordingly, Vinckier et al.'s (2006) patient's reading performance dropped above a threshold angle larger than 50°. A tentative parallel might be drawn with IT neurons in macaques, which show an invariant response for object rotations up to about 45° (Logothetis and Pauls, 1995). There are thus converging indications that the ventral visual system cannot maintain rotation-invariant processing for angles above a limit of about 40–60°.

Concerning letter spacing, normal subjects begin to show a word length effect when reading words with letters separated by two spaces or more (Vinckier et al., in preparation). This value matches a prediction of the LCD framework, based on the principle that letter detector neurons with a local receptive field converge onto open bigram detector neurons (Dehaene et al., 2005). Given the increase of receptive fields in IT cortex by a factor of about 2.5 from one neural level to the next, the LCD model proposes that bigram detectors integrate letter information over a range of 2–3 letter positions, and should therefore fail to detect their preferred letter pairs whenever the component letters are separated by blank spaces of at least two letter widths. Indeed, in the above simultanagnosic patient, we observed a drop in reading performance whenever 2 or more spaces were inserted between letters (Vinckier et al., 2006). A similar threshold of about 2 spaces was expected in the present study.

Concerning the impact of word position in the visual field, it has been shown in normal subjects that while there is no length effect for words displayed in the right visual field, at least close to the fovea, such an effect emerges whenever words are displayed in the left visual field (for a review see Ellis, 2004). When words extend across central fixation, only their left part induces a length effect (Lavidor et al., 2001b). Within the LCD model, at least two factors may contribute to this effect: the left-hemispheric lateralization of the visual word form area, which implies that right visual field letters enjoy more direct and more numerous projections to invariant letter and word recognition processes than their left counterparts (Dehaene et al., 2005); and the left-to-right direction of
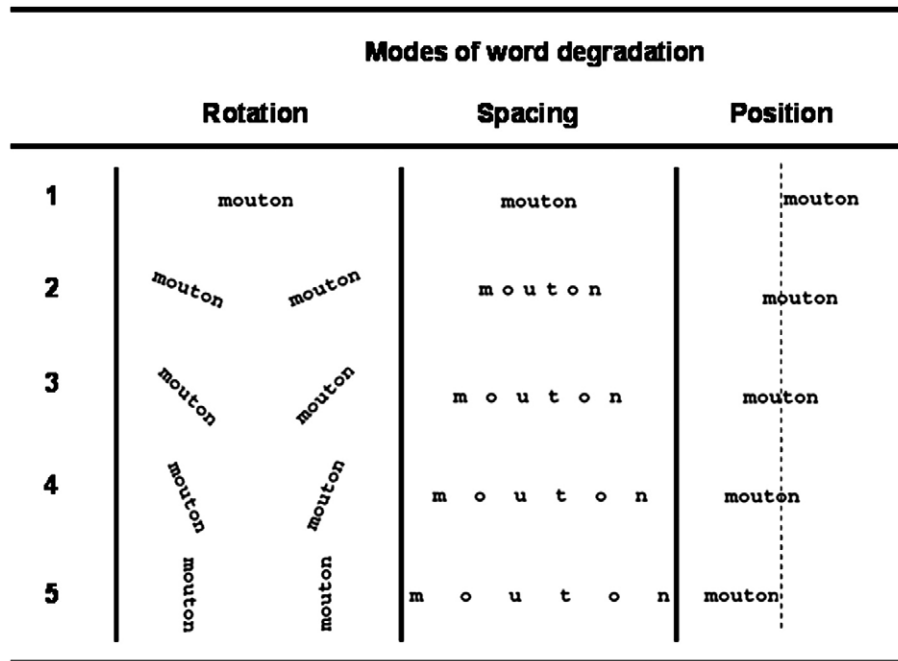
Modes of word degradation

Fig. 1. Schematic depiction of the stimuli. Words could be degraded according to three modes, each with 5 degradation levels including optimally displayed words. Degradation ranged by equal steps from 0° to 90° angles (rotation mode), from 0 to 3 blank spaces between letters (spacing mode), and from 100% in the left hemifield to 100% in the right hemifield (position mode). Rotations were applied randomly in a clockwise or anticlockwise direction.

reading which, combined with the leftward bias of the preferred eye landing, may induce greater perceptual learning in the right visual field (Nazir et al., 2004). We therefore expected that optimal fast and parallel reading would be disrupted as soon as the major part of words would be displayed in the left visual field.

For all three degradation modes, our behavioral and brain imaging predictions were similar. *First*, above a critical threshold of stimulus degradation, we expected the onset both of a slowing down of reading, and of a word length effect on response times, revealing the loss of parallel word identification and a switch to letter-by-letter reading. *Second*, we predicted the sudden onset of attention-related posterior parietal activations at the same critical threshold. *Third*, above this threshold we expected the parietal activation to drive an amplification of the posterior part of the ventral visual word form area, at a location devoted to letter-level coding. In addition to those specific predictions, we intended to explore whether some regions would be differently modulated by the three modes of degradation, and to investigate the neural bases of the word length effect.

Methods

Subjects

Twelve right-handed native French speakers with normal or corrected to normal vision participated in this experiment (4 men and 8 women, mean age 22 years). All subjects gave written informed consent and were naive about the aims of the experiment.

Stimuli

We selected 3 sets of 210 4-, 5- and 6-letter words, matched for frequency ($p = 0.83$). All were high-frequency nouns which did not refer to animals (frequency: 5–125 per million; mean: 29 per million) (http://www.lexique.org, New et al., 2004). To ensure constant attention and covert reading, three additional sets of 30 names of animals were used as infrequent targets for a semantic task (animal detection). These targets obeyed the same length and frequency criteria as non-animal words. Words were presented in lowercase Bold Courier New font, black on a white background, and were always within the central 10° of the visual field (letter height and maximum width: 0.45°). We degraded stimulus words according to 3 modes, each with 5 levels of degradation, including optimally displayed words (i.e. horizontal foveal words with contiguous letters) (Fig. 1).

In the Rotation mode, degradation was achieved by rotating the whole word (0, 22.5°, 45°, 67.5° or 90°), either clockwise or anticlockwise. In the Spacing mode, degradation was achieved by increasing the number of blank spaces between letters (0, 0.75, 1.5, 2.25 or 3 spaces). In the Position mode, degradation was achieved by translating words by various degrees: 100% or 75% into the left visual field, central (50% left, 50% right), or 75% or 100% into the right visual field (Fig. 1).

Experimental design

Each trial consisted of a 400 ms fixation dot, followed by a stimulus word (or by the fixation dot on baseline trials) displayed for 170 ms, followed by a 1816 ms fixation dot. Subjects were instructed to decide whether words referred to an animal or not, and to respond to each word by pressing a button with their right or left hand. Hand attribution was swapped at mid-experiment, and the initial hand attribution was counterbalanced across subjects.

The experiment consisted of 6 fMRI runs. Each run included 144 trials using the same mode of word degradation. Each run consisted of 24 baseline trials, 15 animal trials and 105 non-animal trials. Within each run and each semantic category, all combinations of

word length by degradation level were in equal proportions. Therefore, for a given subject, each word was presented only once, and was associated to a pseudo-randomly selected mode and degradation level. Stimuli were presented in a different pseudo-random order to each subject. In the rotation mode, clockwise and anticlockwise directions were pseudo-randomly chosen for each trial, so as to appear in equal proportions for all word lengths and all degradation levels.

fMRI acquisition and analysis

We used a 3-Tesla body system (Bruker, Germany) and a gradient-echo planar imaging sequence sensitive to brain oxygen-level dependent (BOLD) contrast (40 contiguous axial slices, 3 mm thickness; TR=2400 ms; angle=81,6°, TE=30 ms, in-plane resolution=3×3 mm, matrix=64×64). In each run, 144 functional volumes were acquired. The first 4 volumes were discarded to reach equilibrium. T1-weighted images were also acquired for anatomical localization.

Data processing, performed with SPM2 software, included corrections for EPI distortion, slice acquisition time, and motion; normalization; Gaussian smoothing (5 mm FWHM); fitting with a linear combination of functions derived by convolving a standard haemodynamic response function with the known time series of the stimulus types; and random effect group analysis. We only analyzed behavioral results and brain activations associated with the non-target words, which constituted the vast majority of data.

Behavioral results

Overall subjects made 1.7% errors and had a mean correct RT of 833 ms. For each subject, we computed the median RT for each cell of the crossed design Mode × Degradation level × Length, and those values were entered in an ANOVA with Subjects as random factor (Fig. 2). Error rates, which will not be discussed further, followed the same pattern as RTs, although only the main effects of Degradation level and Mode reached significance (Table 1).

Effects of the mode and degree of word degradation

There was a main effect of degradation level ($F(4,44)$=45.2, $p < 10^{-14}$), prevailing for the 3 modes of word transformation (all $p < 0.0001$). This effect was non-linear, as attested by significant linear ($t(11)$=7.9; $p < 10^{-5}$) and quadratic contrasts ($t(11)$= 6.8; $p < 10^{-4}$). The quadratic contrast was significant separately for the Rotation and Position modes (both $p < 0.001$) and marginal for the Spacing mode (p=0.06). There was a weaker main effect of degradation mode ($F(2,22)$=4.9; $p < 0.02$). Furthermore, degradation mode and degradation level interacted significantly ($F(8,88)$= 17.4, $p < 10^{-14}$), with a larger influence of degradation level for rotation than for either spacing or position manipulations (both interaction $p < 10^{-8}$), and also somewhat larger for spacing than for position manipulations ($p < 0.03$). We compared RTs between consecutive degradation levels, separately for the three modes of transformation. For rotation, there was a significant increase between levels 2–3, 3–4, and 4–5, corresponding to a sudden slowing down around 45° of rotation. For position and spacing, there was a significant increase only between levels 3–4 and 4–5, corresponding to a disproportionate slowing down of reading when letter spacing reached 2.25 spaces or when 75% of the word fell in the left hemifield (all $p < 0.05$).
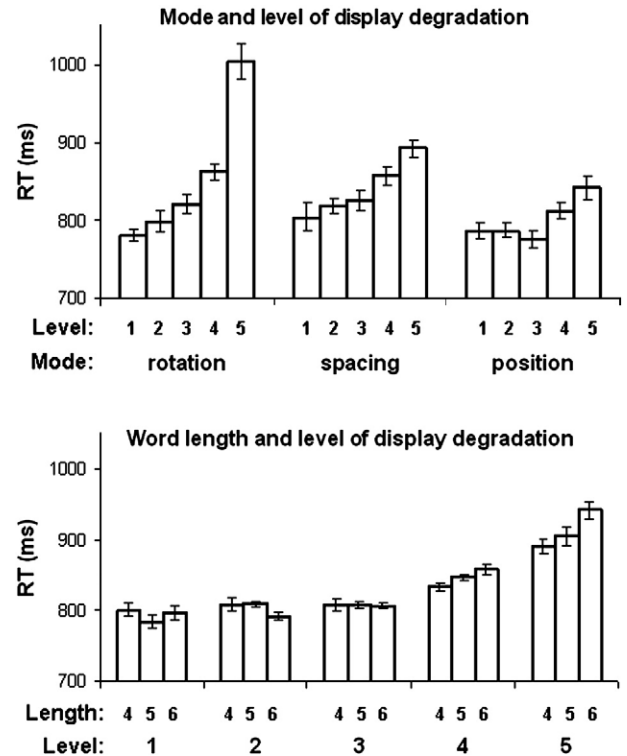

Fig. 2. Behavioral results. Top: Effect of display manipulations on reading latencies. Latencies increased non-linearly, starting from a Rotation of 45°, a Spacing of 2.25 blank spaces, and a Position of 75% in the left visual field. Bottom: Effect of word length on reading latencies, pooled over the three modes of word degradation. An effect of length appeared for degradation levels 4 and 5. Error bars represent ±1 S.E.M. across subjects after subtraction of each subject's overall mean.

Effect of word length

There was no main effect of word length (Fig. 2). However, as expected, there was a significant interaction of length and degradation level ($F(8,88)$=4.0, $p < 0.0005$), and no higher-level interaction with mode. An effect of length appeared for degradation levels 4 and 5 (both $p < 0.01$; average RT increase: 19 ms per letter), and was absent for words closer to an optimal display.

Summary

Behavioral data may be summarized as follows. *First*, reading difficulty increased non-linearly for all three modes of stimulus degradation, starting from a rotation of 45°, a spacing of 2.25 blank spaces, and a position of 75% in the left visual field. Moreover this increase was larger for Rotation than for the other modes of transformation. *Second*, the increase in reading difficulty was accompanied by the emergence, at about the same threshold of degradation, of an effect of word length on reading latencies.

Imaging results

Basic reading network

Within each fMRI run, one fifth of trials consisted of normal presentation of words (i.e. horizontal, foveal, and with normally

Table 1
Error rates for non-target words according to the mode and level of display degradation

Level	Mode of display degradation		
	Rotation (%)	Spacing (%)	Position (%)
1	4.2	3.5	3.1
2	4.0	3.5	2.4
3	3.1	4.5	1.9
4	6.4	5.2	2.1
5	8.0	4.9	3.6

spaced letters). Examination of the basic contrast of normal words versus the baseline resting trials (voxelwise threshold $p < 0.001$, threshold for cluster extent $p < 0.05$ corrected) replicated the usual network of activation observed during word reading (Fig. 3, top row). Activation was observed in bilateral occipital cortex (posterior to Montreal Neurological Institute (MNI) coordinate $y = -70$), unilateral left ventral temporal cortex with a sharp peak at the location of the Visual Word Form Area (MNI coordinates: -48, -60, -16; $Z = 5.20$) (Cohen et al., 2002), left inferior frontal cortex/insula, and left precentral sulcus with an extension into dorsolateral prefrontal cortex. In addition, bilateral rolandic, supplementary motor, cerebellar and putaminal/pallidal activations were presumably related to the generation of an overt motor response.

Whole-brain analyses of the impact of word degradation

We then examined in which areas word degradation had a significant influence. To optimally detect this effect, within each mode of degradation (i.e. Rotation, Spacing, and Position), we defined a degradation contrast by using the mean RT as an estimate of the reading difficulty at each degradation level, then subtracting the grand mean RT. We examined which voxels showed a profile of activation across the five levels of degradation which correlated with this profile of RTs. This contrast should be optimal for the detection of regions whose duration of activation matches the additional computation time reflected in RTs, because after convolution with the haemodynamic function, small changes in activation duration are mostly reflected by changes in the amplitude of the event-related BOLD signal (Sigman et al., 2007).

Overall effect of word degradation

We first examined this degradation contrast globally, pooling across the three modes of degradation (voxelwise threshold $p < 0.001$, threshold for cluster extent $p < 0.05$ corrected).

As predicted, word degradation impacted on both ventral and dorsal visual pathways (Table 2 and Fig. 3, second row). Dorsally, activation extended in the entire occipito-parietal pathway. It culminated in two symmetrical foci located in the left and right posterior intraparietal regions, an area which is known as an important source of top-down visuospatial attention (Gottlieb, 2007). Ventrally, bilateral occipito-temporal regions were seen. The left occipito-temporal region was more activated and peaked close to the coordinates expected from the LCD model to correspond to letter-level coding ($y = -70$). As shown in Fig. 4, this peak was about one centimetre posterior to the peak activation evoked by normal words ($y = -60$) and corresponding to the classical VWFA. Thus, the results suggest that a subpart of the visual system corresponding to letter-level coding was selectively amplified once the

words were degraded beyond the threshold where a word length effect was seen.

In addition to these regions, a degradation effect was also found in the bilateral calcarine cortex, bilateral SMA, left precentral cortex, and right inferior frontal cortex/insula (Table 2). At a lower threshold (voxelwise threshold $p < 0.01$, threshold for cluster extent 150 voxels), as depicted in Fig. 3, symmetrical activations were detected in the left inferior frontal cortex/insula and the right precentral cortex (Table 2).

Activations common to all modes of degradation

Within this network, we then examined which regions were showing a degradation effect common to rotation, spacing and position manipulations, by masking the pooled contrast (voxelwise threshold $p < 0.01$, threshold for cluster extent 150 voxels) by the three degradation contrasts restricted to the three modes of degradation (voxelwise $p < 0.01$ on three independent tests, for an overall voxelwise $p < 10^{-6}$). The only regions were the bilateral posterior intraparietal cortices (left: $-22\ -72\ 48$; $Z = 5.94$; right: $26\ -64\ 56$; $Z = 5.81$; Table 2).

Activation profiles in the dorsal and ventral pathways

In order to have a comparative view of the modulation of activation by word degradation in the dorsal and ventral pathways, we plotted activation profiles at the two dorsal parietal and the two occipitotemporal peaks identified by the overall correlation of activation with response latencies (Fig. 5). Several points of interest are visible on this figure, and were validated by additional ANOVAs performed on individual activation at the peak voxels within each region as dependent variable, with hemisphere (left or right), degradation level and mode as within-subject factors, and with subjects as random factor.

Parietal regions

In dorsal parietal cortex, the pattern of activation did not differ between the left and right hemispheres (all interactions involving the hemisphere factor with the degradation level or mode factors: $p > 0.10$). Activation increased with degradation level ($F(4,44) = 15.7$; $p < 10^{-7}$). Moreover, there was an effect of degradation mode ($F(2,22) = 6.9$; $p < 0.005$), with larger activations for rotation than spacing than position. Importantly, those two effects were additive, as the interaction of degradation level × mode was far from significance ($p = 0.53$). In summary, these analyses confirmed the global contribution of dorsal parietal cortex to reading all three types of degraded words.

Occipito-temporal regions

There was a main effect of degradation level in occipito-temporal regions ($F(4,44) = 10.2$; $p < 10^{-5}$), but a significant interaction with hemisphere ($F(4,44) = 3.3$; $p = 0.018$) indicated that this effect was larger in the left hemisphere than in the right (Fig. 5). In the left occipitotemporal cortex, activation increased with degradation level, but only for rotated ($F(4,44) = 10.3$; $p < 10^{-5}$) and spaced words ($F(4,44) = 6.3$; $p < 0.0005$), not for displaced words ($p = 0.61$), thus creating a significant degradation level × mode interaction ($F(8,88) = 2.8$; $p = 0.008$). There was no main effect of degradation mode ($p = 0.47$). In the right occipitotemporal region, only the main effect of degradation level was significant ($F(4,44) = 6.8$; $p = 0.0002$), with no significant effect of mode or interaction.
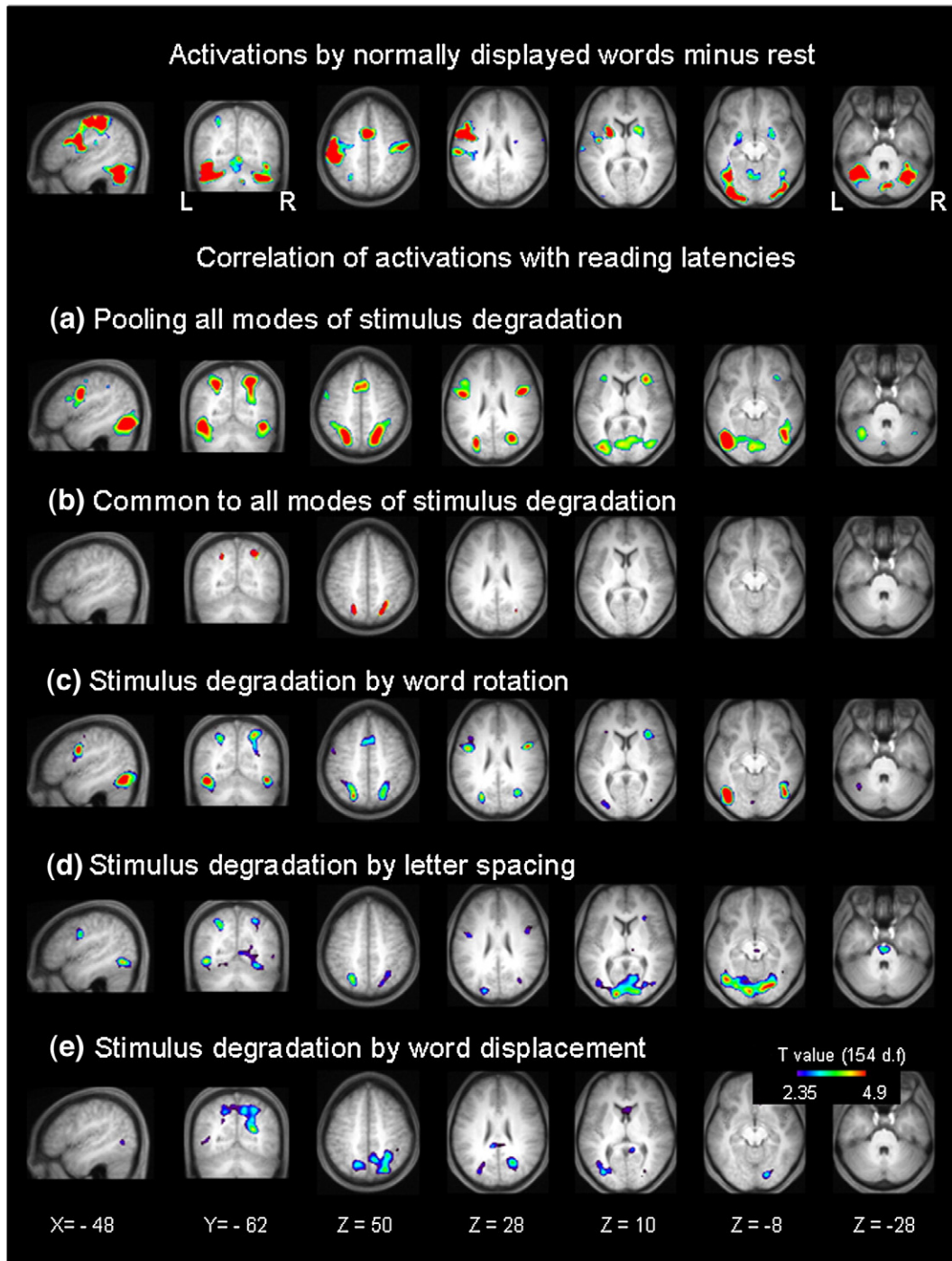
Fig. 3. Main fMRI results. The top row shows activations by normally displayed words relative to rest. All other rows show regions in which activation was correlated with word degradation, as indexed by reading latencies. From top to bottom: (a) Correlation pooled over the 3 modes of degradation; (b) pooled correlation masked by correlation for all three modes of degradation (voxelwise 10^{-2} each), showing common activations in the bilateral parietal lobes; (c–e) correlation computed separately fore each mode of word degradation. For illustration purposes we used a voxelwise threshold of $p < 10^{-2}$ and a threshold of 150 voxels for cluster extent.

In summary, the occipito-temporal regions were affected by rotation and spacing, but not by position. We verified that this constituted a significant difference with posterior parietal regions, whose activation increased with all three degradation modes. In an overall ANOVA with region (parietal or occipito-temporal) as an additional factor, within the position condition, there was a sig-

nificant region × degradation level interaction ($F(4,44)=4.2$; $p = 0.006$), while within the spacing or rotation conditions, no such interaction was found ($p=0.68$ and $p=0.92$).

There was a further interesting difference between dorsal and ventral regions. As visible in Fig. 5, the occipitotemporal cortex was always strongly activated by normally displayed words, and its

Table 2
Peaks of the network showing a significant modulation by word degradation, as indexed by the correlation of activation with response latencies (voxelwise threshold $p < 0.001$; threshold for cluster extent $p < 0.05$ corrected)

Structure	Hemisphere	MNI coordinates	Z-score
Occipitotemporal	Left	−42 −70 −10	7.09
	Right	44 −60 −12	5.45
Occipitoparietal	Left	−34 −82 8	4.23
		−26 −74 24	5.31
		−22 −72 48	5.94
	Right	40 −78 16	3.87
		30 −68 28	4.95
		26 −64 56	5.81
Calcarine	Left	−4 −84 −2	4.53
	Right	10 −82 −2	4.15
SMA	Left	−6 8 50	4.22
	Right	6 12 52	4.12
Precentral	Left	−48 0 34	5.78
	Right*	46 4 28	5.40
Inferior frontal	Left*	−32 22 2	3.61
	Right	32 22 6	4.56

*Voxelwise threshold $p < 0.01$; threshold for cluster extent 150 voxels.

activation was merely modulated by degradation. In contrast the parietal cortex was essentially inactive for optimal words, and activated only above a certain level of degradation. This was true for blocks in which position or spacing were varied (contrasts for activation to optimal words relative to rest: $p = 0.71$ for position, $p = 0.6$ for spacing). During blocks in which rotation was varied, there seemed to be an additional contextual effect whereby posterior parietal regions were activated even on the normal word trials ($t(11) = 3.8$; $p = 0.0029$), presumably due to an attentional set (preparation to rotate the word).

Differential effects of degradation modes

We also performed whole-brain searches for regions specific to a given mode of word degradation. Fig. 3 illustrates the 3 networks defined by their correlation with RTs, separately for the three modes of degradation. Outside of the common parietal areas, additional activation foci are discernible for rotation (left-predominant occipitotemporal cortex and SMA), for spacing (in the calcarine cortex), and for position (in mesial parietal regions). In order to formally identify significant differences, we examined which areas showed a significantly greater effect of degradation in one mode compared to another (voxelwise threshold $p < 0.001$, threshold for cluster extent $p < 0.05$ corrected).

Spacing

Regions with a larger modulation by spacing than by rotation included bilateral occipital clusters (left: −14 −92 12; $Z = 4.55$; right: 24 −78 −4; $Z = 5.34$). Those activations likely reflected the fact that as letter spacing increases, the spaced words stimulated increasingly peripheral locations in the left and right hemifields and hence activated a progressively larger extent of retinotopic cortex. Similarly, the comparison of spacing minus position showed a left occipital region (−12 −92 −2; $Z = 5.17$) overlapping with the one identified in the preceding contrast. The right occipital cortex did not appear in this difference contrast because its activation increased with degradation level both in the Position mode and in the

Spacing mode, as expected from a retinotopic region that responded to the left side of words.

Position

The comparison of Position minus Rotation showed a bilateral mesial parietal cluster with main peaks in the right precuneus (4 −56 44; $Z = 4.27$) and in the left retrospenial region (−8 −42 22; $Z = 4.16$). The right precuneus also appears in the Position minus Spacing contrast, although below the standard threshold for cluster extent ($Z = 3.35$, 32 voxels). The precuneus region is known to be deactivated during many cognitive tasks (McKiernan et al., 2003; Raichle et al., 2001), and indeed we found it to be increasingly deactivated with reading difficulty due to rotation or spacing. However, degradation by position led to an increase in activation of these regions, which culminated when words fell entirely in the LVF.

Rotation

The two remaining comparisons (rotation minus spacing and rotation minus position) did not show significant activations at the standard threshold. However, the influence of word rotation in the left occipitotemporal region mentioned before appeared in the comparison of rotation minus position, but below the threshold for cluster extent (−40 −70 −10; $Z = 4.30$; 180 voxels), together with a small symmetrical right-hemispheric cluster (44 −72 −6; $Z = 3.85$; 32 voxels).

The outcome of those pairwise comparisons may be summarized as follows: *First*, retinotopic occipital regions were modulated as a function of stimulus extension in the visual field. *Second*, mesial parietal regions were positively modulated by the difficulty
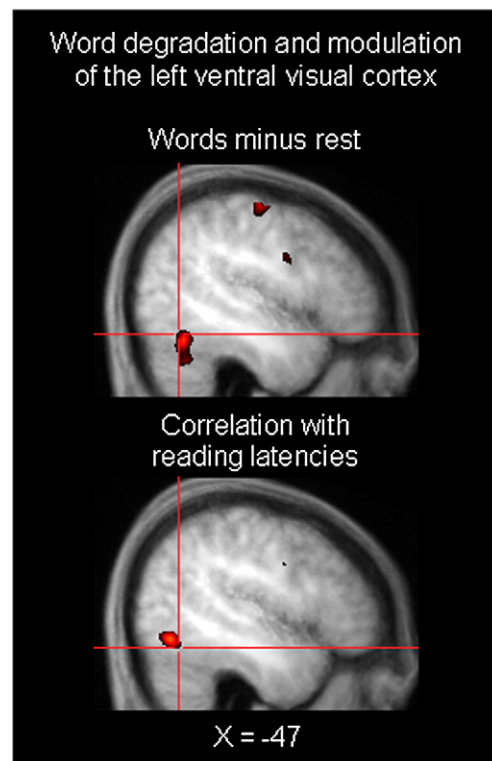

Fig. 4. Word degradation and modulation of the left ventral visual cortex. Thresholded activation images, showing that the modulation of the visual word form area by word degradation, as measured by the correlation with reading latencies, was maximum in a posterior segment ($Y = −70$; bottom), as compared to the more anterior peak activation by normal words ($Y = −60$; top).
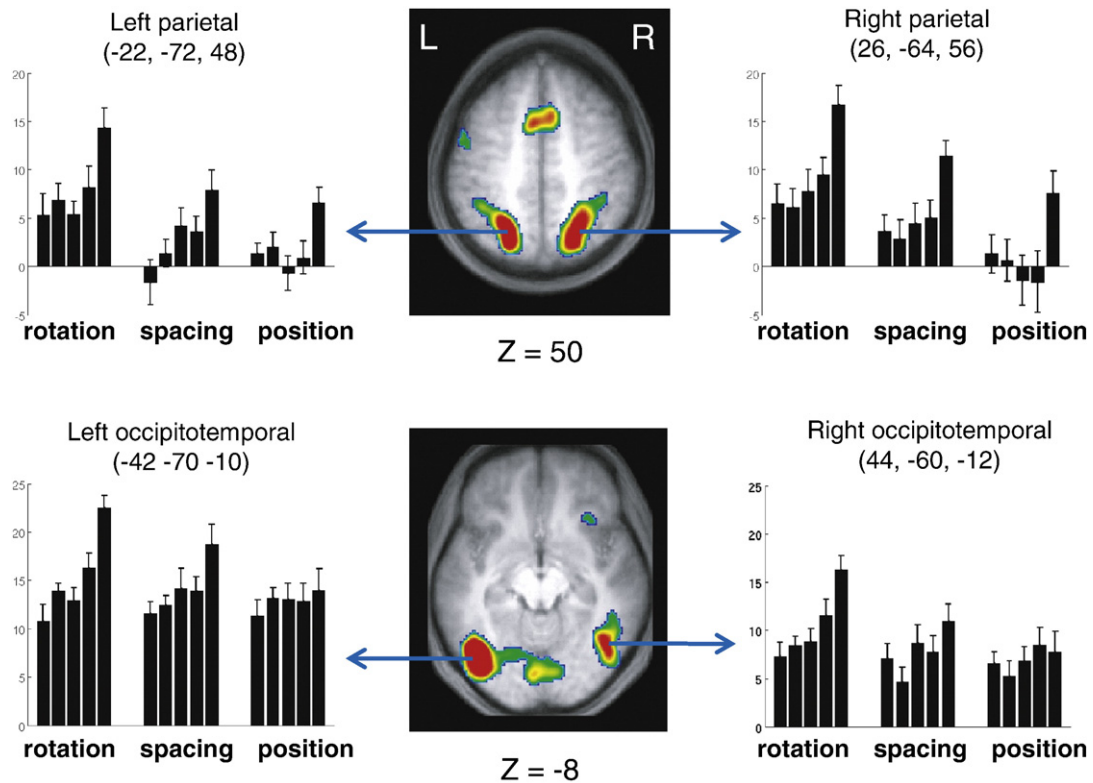
Fig. 5. Activation profiles showing the influence of word degradation at the main peak voxels of the dorsal and ventral pathways. The 5 bars in each group correspond to the 5 levels of increasing word degradation. Parietal activations increased with the amount of word degradation. There was also an additive effect of degradation mode, with larger activations for rotation than spacing than position. Occipitotemporal activations increased with the degree of word degradation for rotated and spaced words, but were insensitive to the displacement of words across the visual field. Activations are quantified using arbitrary units proportional to percent change in BOLD signal relative to rest.

specifically associated with words displayed in the left visual hemifield. *Third*, left-predominant occipitotemporal regions showed a stronger modulation by word rotation, and probably by letter spacing, than by word displacement.

Effect of word length

In order to study the cerebral correlates of the word length effect, we restricted the analysis to the larger degradation levels (4 and 5), as the length effect emerged behaviorally only for this amount of word degradation. We contrasted activations induced by 6-letter minus 4-letter words. Given the small size of the behavioral length effect, we lowered the threshold to voxelwise $p < 0.01$, still with a threshold for cluster extent of $p < 0.05$, corrected. We imposed an additional constraint of monotony by requiring that the activation induced by 5-letter words be intermediate between that of 4- and 6-letter words. We found a bilateral occipitoparietal cluster with two symmetrical peaks in the left and right hemispheres (left: -18 -84 18; $Z = 3.71$; right: 24 -76 18; $Z = 3.78$) (Fig. 6). Note that these regions were located about 1 cm posterior and 3 cm inferior to the bilateral dorsal parietal regions previously found to be jointly engaged by all three degradation modes.

Summary of the fMRI results

We showed that a number of regions were modulated by word degradation, reflecting the strategies required to identify rotated, spaced, or displaced words. A core region of the IPS, possibly including the human homolog of area LIP (Sereno, 2001; Simon et al., 2002), which did not belong to the normal reading network, was engaged by all modes of degradation. Other occipital and parietal regions were associated more specifically with one mode of degradation or the other. Furthermore, the activation of the ventral occipitotemporal cortex was also modulated, mostly by rotation and spacing. Finally, we found a moderate effect of word length restricted to highly degraded words in bilateral occipitoparietal regions.

Discussion

Word degradation and reading threshold

Our first prediction was that whenever word degradation does not allow the Visual Word Form system to encode words in a fast and parallel manner, reading performance should deteriorate, as

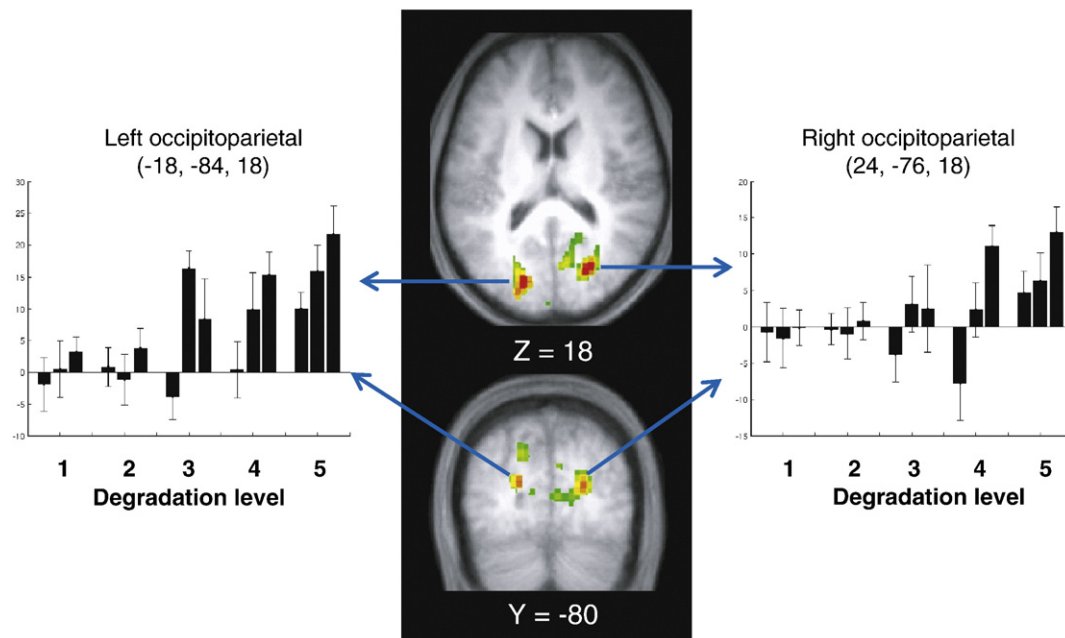# Effect of word length on activation profiles in occipitoparietal cortex

Fig. 6. Activation profiles showing the influence of word length in symmetrical occipitoparietal regions. The 3 bars in each group correspond to 4-, 5- and 6-letter words, respectively. There was a monotonous increase of activation with word length, whenever stimuli were sufficiently degraded (degradation levels 4 and 5).

indexed primarily by slower reading latencies. Moreover in such circumstances readers were expected to engage in effortful serial reading strategies, as revealed by the emergence of a word length effect. Behavioral data gathered during MRI scanning conformed to those expectations, as latencies increased non-linearly, starting from a Rotation of 45°, a Spacing of 2.25 blank spaces, and a Position of 75% in the left visual field. This slowing down was accompanied by the emergence, at about the same threshold of degradation, of a significant effect of word length. Moreover, those thresholds were in the expected quantitative range. As reviewed in the introduction, a critical angle of 40° to 60° was suggested by previous evidence of a shift to serial reading in normal readers (Koriat and Norman, 1989; Lavidor et al., 2001a), and by a dramatic inability to read words rotated by more than 50° in a patient with parietal damage (Vinckier et al., 2006). A critical spacing of 2.25 spaces between letters was also commensurate with the theoretical expectations of the LCD model (Dehaene et al., 2005) and the empirical findings in the parietal patient. According to the LCD model, and on the basis of neurophysiological evidence (Rolls, 2000), letters separated by more than 2 spaces cannot send converging activation to common bigram detectors, thus disrupting the parallel encoding of letter strings. Finally, moving words away from fixation in the left visual field decreased reading performance and triggered a length effect, again in agreement with previous behavioral and neuropsychological data (Cohen et al., 2003; Lavidor and Ellis, 2002). We propose that those behavioral thresholds reflect limits of the perceptual expertise of the Visual Form system which is tuned to process optimally words below definite levels of rotation, spacing, and displacement.

Reading strategies and modulation of parietal activations

Our second prediction was that fMRI data would support this interpretation of the reading thresholds by showing, above the thresholds of optimal reading, a non-linear increase in the activation of posterior parietal regions, associated with a switch from a largely automatic and parallel word identification process to an attention-based serial reading strategy. Indeed, the present fMRI data showed that a large extent of posterior parietal cortex was modulated by stimulus degradation. Two common spots were found in bilateral posterior parietal cortex, at a location coinciding with previous studies of visual attention (Gottlieb, 2007; Sereno, 2001; Simon et al., 2004, 2002; Wojciulik and Kanwisher, 1999). MEG activations were found in a similar posterior parietal region, particularly in the right hemisphere, when subjects were reading words degraded by shifting letters randomly above and below the midline, as compared to normal words (Pammer et al., 2006). Similarly Mayall et al. (2001) showed right parietal activations associated with reading MiXeD-cAsE as compared to normally printed words. Borowsky et al. (2006) found stronger parietal activations for pseudohomophones than for exception words. The causal role of the right parietal cortex in reading words in an unfamiliar format is further supported by evidence of impaired performance at reading mIxEd-CaSe words in normal subjects undergoing parietal inhibition with rTMS (Braet and Humphrey, 2006). Similarly, although with no discernible right-hemispheric predominance, parietal patients showed an increase in contralateral errors when reading mIxEd-CaSe words (Braet and Humphrey, 2007), pointing to a role of parietal regions in reading attention-demanding degraded words.

It is striking that those bilateral parietal regions are active during extremely different attention tasks, including peripheral attention shifting, sustained attention to parafoveal locations, and temporal attention to feature conjunctions (for reviews see Behrmann et al., 2004; Kanwisher and Wojciulik, 2000a; Pessoa et al., 2003). Thus, their exact involvement in reading remains to be clarified and could be attributed to a variety of spatial and attentional processes which readers may harness to read degraded words. We may speculate that these processes include the following components, for which posterior parietal involvement has been demonstrated: (i) A general function of selecting relevant objects for pending actions (Simon et al., 2002), which may concern particularly the common posterior parietal region which we found to be correlated with all three modes of word degradation; (ii) visual search and scanning of arrays of objects (Corbetta and Shulman, 1998); (iii) endogenous or exogenous orientation of attention to lateralized visual targets (e.g. Gitelman et al., 1999; Peelen et al., 2004); (iv) mental rotation (see review in Parsons, 2003), with activations correlated with rotation angle (Keehner et al., 2006); (v) supramodal executive control involved in strategy switching even with non-spatial tasks (Gurd et al., 2002), as required between easy and highly degraded trials; (vi) switch from global (word) to local (letters) attention (Wilkinson et al., 2001); (vii) attentional switch between object types (Serences et al., 2004), particularly top-down amplification, in the ventral stream, of letter detectors rather than of detectors of letter clusters. Considering this issue more broadly, it is likely that dorsal parietal cortex intervenes in word reading both early, for the initial orientation and shaping of the attention window, and at a later stage whenever a "second-pass" analysis is required for degraded or unfamiliar stimuli (Cohen et al., in press; Pammer et al., 2006; Vinckier et al., 2006).

The fact that all modes of word degradation entailed a slower reading and a length effect does not imply that those behavioral phenomena always reflected identical neural processes. It is likely that partly distinct strategies are appropriate for coping with modes of degradation as diverse as rotation, spacing, and displacement. Indeed, we found that while the dorsal posterior parietal cortex activation was shared by all three degradation mode, mesial posterior parietal regions (including right precuneus and left retrosplenial cortex) were selectively associated with the reading difficulty caused by word displacement. The precuneus is frequently seen in visual attention tasks (Corbetta and Shulman, 1998; Gitelman et al., 1999; Nobre et al., 1997) and has been reported to be selectively activated by an attention task as opposed to eye movement, hand grasping, pointing, arithmetic or language tasks (Simon et al., 2004, 2002). This region may play a role in attending to peripheral locations in the absence of eye movements, as the Position condition of the present experiment was the only one in which words were not centered on screen.

Word degradation and modulation of ventral visual cortex

According to our *third prediction*, we expected that the serial processing of degraded words should be accompanied by an amplification of posterior sectors of the occipitotemporal visual word form area. On the basis of fMRI priming data (Dehaene et al., 2004), the LCD model proposes that around Talairach coordinates $y = -64$, the occipito-temporal sulcus of both hemispheres contains a bank of location-specific letter detectors responsible for letter-level encoding of alphabetic strings. Indeed fMRI priming, at this level, was specific to the repetition of letters at a fixed location and

disappeared when the repeated letters were shifted by one location (Dehaene et al., 2005). We predicted that such low-level encoding of letters should be emphasized whenever readers have to rely on effortful serial letter-by-letter reading.

The results conformed to this prediction. We observed that activations were positively modulated by word degradation, peaking at the expected coordinates. This pattern was apparent in both hemispheres with a left-sided preponderance. As shown in Fig. 4, the modulation by word degradation was maximum in a posterior segment of the VWFA ($Y = -70$), as compared to the more anterior peak activation by normal words ($Y = -60$). Within the LCD model, which postulates that the VWFA houses a hierarchy of letter, bigram and morpheme detectors, this more posterior site fits with the idea that a smaller-grained representation of individual letters received selective attentional amplification once the degradation level exceeded the threshold associated with serial reading performance.

There was an intriguing difference between the ventral and dorsal regions in the modulation induced by the displacement of targets across the visual field. In the parietal regions, displacement of words in the left hemifield had an impact comparable to the other modes of degradation (i.e. rotation and spacing). In contrast in the ventral occipito-temporal cortex, moving words to the left hemifield did not yield increased activations, while rotation and spacing did. This may appear surprising, since there was still a significant word length effect for degraded words in the Position mode. Indeed, the slope of the length effect did not differ across the three degradation modes (19 ms/letter in the Position mode, as compared to 16 and 22 ms/letter for the rotation and spacing modes respectively). Shouldn't letter-by-letter reading, in the Position mode, have amplified the activation of the putative letter detectors just like in the other two conditions? The answer lies, once again, in the fact that the Position condition has a special status in that it is the only one in which words were not centered on screen. Rather, in this condition, reading difficulty was increased by shifting the word into the left hemifield. The LCD model predicts that in the posterior occipito-temporal sectors thought to be housing mostly location-specific letter detectors, activation should then shift to distinct neural populations coding for the new locations of letters, i.e. to the right posterior occipito-temporal cortex. This interpretation explains why only the Position condition did not cause any increase in the left occipito-temporal cortex, and predicts an increased activation in the right occipito-temporal cortex with word displacement into the left hemifield. This idea was supported by the comparison between words presented entirely in the right or in the left hemifield (voxelwise $p < 0.01$). As expected, the right minus left hemifield contrast showed only left posterior occipital activations ($-12 -94 -4$; $Z = 4.29$). The opposite contrast showed symmetrical right posterior occipital activations ($22 -88 -16$; $Z = 4.71$), but also right fusiform activations ($36 -74 -18$; $Z = 3.55$) extending anteriorily up to $y = -62$. This right fusiform activations is compatible with the notion that location-specific letter detectors are mostly expected at around $y = -64$ mm in both hemispheres (Dehaene et al., 2005).

Correlates of the word length effect

We also looked for the neural correlates of the length effect directly, by contrasting short and long words in the degraded conditions in which a length effect was found behaviorally. Unfortunately, the only correlates of the word length effect which we found were restricted to bilateral occipitoparietal regions. Although the role of those regions in word perception is difficult to specify at

present, they seem to correspond to areas V3A/V3B (Tootell et al., 1997), in which activations are positively correlated with the angular size of visual stimuli (Press et al., 2001).

We expected that longer words should have yielded stronger activations in the same regions that were modulated by word degradation, particularly the bilateral posterior parietal cortex. In retrospect, it seems likely that this effect was not detected because our experiment, which was mostly designed to study degradation effects, had little power to detect word length effects since we could only compare 4, 5 or 6 letter words. Furthermore, as illustrated in an extensive review (New et al., 2006), the literature is rather inconsistent regarding the existence of a word length effect with normally displayed words. New et al. (2006) re-analyzed a large empirical corpus from the English Lexicon Project (Balota et al., 2002), and concluded that when controlling for a number of other variables, there is no length effect for words with 5–8 letters, and that latencies then increase progressively for longer words. In contrast to real words, pseudowords yield a clear-cut and reproducible length effect (e.g. Weekes, 1997). It is thus obvious that the current design, which included only 4–6 letters real words was not appropriate for studying the mechanisms of the length effect prevailing with longer words or with pseudowords.

Valdois et al. (2006) recently addressed this issue, using a wider range of stimulus length (4 to 11 letters), with a full crossing of lexicality (words vs. pseudowords) and task (subvocal reading vs. lexical decision). Their theoretical approach, embodied in the ACV98 model (Ans et al., 1998), is related to ours in that it predicts that a length effect should prevail if and only if the parallel analysis of letter strings fails to yield a response appropriate to the task, thus requiring a second pass serial analysis. As expected, in addition to a small length effect with real words, they observed a large behavioral length effect and corresponding brain activations only when comparing long vs. short pseudowords during subvocal reading. Interestingly, those activations overlapped substantially with the network which we found to be associated with stimulus degradation: Bilateral parietal regions common to all degradation modes, and bilateral mesial occipital cortex associated with the extension of stimuli in the periphery of the visual field. Although only peak activations are reported by Valdois et al. (2006), the latter occipital clusters possibly extended up to the occipitoparietal region which we found to correlate with the length of degraded words. Valdois et al. (2006) also observed a length effect in the right mesial parietal lobe, slightly more ventral and posterior than our precuneus activation. In summary, the design of Valdois et al.'s (2006) study was more powerful than ours for the study of the length effect, plausibly explaining why they observed a dorsal parietal length effect. Their results support our main contentions, namely that the length effect is restricted to task- and stimulus-dependent conditions requiring serial processing; that it correlates with brain networks distinct from those subtending normal reading; and that the core of those networks may be located to the posterior parietal cortex.

Serial reading in other populations

It is interesting to compare the present results in normal adults with those of patients or children who also deploy effortful serial reading strategies. Following left occipitotemporal lesions, patients may develop pure alexia, an inability to identify words in parallel, due to the disruption of the Visual Word Form system. Most patients keep the ability to identify single letters and to slowly decipher words in a serial letter-by-letter reading strategy. We recently had the opportunity to compare brain activations during reading before and after the occurrence of alexia in a single patient with letter-by-letter reading (Gaillard et al., 2006). Relative to normal parallel reading, letter-by-letter reading was associated with an increase of activations in a bilateral network including the very same posterior parietal regions as in the present study. Similar results were also found in other pure alexic patients (see Cohen et al., 2004, 2003).

Serial reading also occurs early on in reading acquisition, as children have not yet reached the orthographic stage of fast word recognition and must still slowly decipher words letter after letter. A word length effect is very apparent in young readers, even when reading normal foveal words, and this influence of word length on reading latencies progressively decreases over the years of reading acquisition (Aghababian and Nazir, 2000). An abnormal length effect may persist in some dyslexic subjects (Valdois et al., 2003). Although it is still an open empirical issue, one may speculate that the attention-related regions identified in the present study should show a decreasing activation over time when children develop a higher reading expertise. In that respect, it is noteworthy that over a range of 6–22 years of age, Turkeltaub et al. (2003) found that activations in the right precuneus were negatively correlated with reading ability or with age.

Relations to models of the reading process

Ultimately, the coordination of ventral and dorsal systems should be incorporated into explicit models or computer simulations of the reading process. While space precludes a thorough review of the many existing models, our results and those of Valdois et al. (2006) seem incompatible with models that attempt to explain all the determinants of reading speed, including word length effects and their interaction with hemifield, as arising within a single word identification system (e.g. Whitney and Lavidor, 2004). It seems doubtful that the non-linear response time curves relating word length and word degradation can be explained within a single system, whether this system is thought to operate only in parallel, as postulated in most connectionist models (Seidenberg and McClelland, 1989) or only serially (Whitney and Lavidor, 2004). Indeed, our results directly show that, at the brain level, a second system is deployed for serial reading under degraded conditions. Although the relation between cognitive processes and brain areas need not be one-to-one, it seems likely this major cerebral division of labour also corresponds to the deployment of additional cognitive processes.

Our results therefore fit more easily with models that incorporate a mixture of parallel and serial processing routes that receive a differential weighting as a function of the input stimulus. One such model is Perry et al.'s (2007) dual route connectionist model CDP+, which represents the most recent attempt at a theoretical synthesis of reading and inherits features of three other prior models (Coltheart et al., 2001; Seidenberg and McClelland, 1989; Zorzi et al., 1998). According to CDP+, a parallel lexical reading route is supplemented by a serial grapheme–phoneme conversion route. The first step in reading through the sublexical route is the conversion of the string of letters into a string of graphemes through serial left-to-right scanning, presumably associated with dorsal parietal regions. Though Perry et al. (2007) do not simulate the types of word degradation used here, their model may account for our results by postulating an increased reliance on the sublexical route whenever words are too degraded to be processed by the

lexical route. Likewise, Vinckier et al.'s (2006) results would be explained by a greater engagement of the non-lexical serial route when reading pseudowords compared to real words.

We note, however, that the serial reading route is merely stipulated in CDP+, but is not modelled explicitly by actual connectionist mechanisms, even less related to actual brain architecture. In that respect, the ACV98 model proposed by Ans et al. (1998) represents an interesting alternative, as it comprises an explicit attention window and a mechanism to switch between parallel and serial reading modes. The model automatically detects when it is unable to identify the word by parallel reading, and then switches to a serial attention mode in which a window of attention slides serially across successive input syllables (while CDP+ is restricted to monosyllabic words). Although the ACV98 model has not yet received an implementation as detailed as CDP+, its architecture may accurately capture how the dorsal and ventral systems interact during reading (Cohen et al., in press).

Conclusion

On the basis of these converging results from adults, patients, and children, we propose that the bilateral posterior parietal regions play an essential role whenever serial reading strategies are deployed, either during normal reading (of words by young readers, or of pseudo-words by expert adults), or during compensatory reading when parallel word recognition is impossible (due to word degradation or to a ventral visual brain lesion). Our results confirm that the ventral visual word form system, alone, is limited in its invariance. It is tightly specialized for words presented under normal reading conditions, and does not resist to rotations above 45°, letter spacing above 2 spaces, or displacement of words to the left hemifield. Beyond those limits, readers quickly deploy a second system for serial reading, based largely on the posterior parietal cortex.

In light of those results, the narrow view that considers reading solely as a process of face-like expertise for recognizing visual words should give way to the emerging notion of "two reading systems", one ventral and one dorsal, which collaborate to identify the written string. While considerable efforts have been deployed to understand the internal organization of the ventral visual word form system, not much data is available yet on the exact contribution of the dorsal parietal system to reading. This relative neglect should be corrected, particularly in regard to the possibility that this dorsal system might play an important role in young readers and be a cause of specific reading impairments (Vinckier et al., 2006).

Acknowledgments

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