"What" and "Where" in Word Reading: Ventral Coding of Written Words Revealed by Parietal Atrophy

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Abstract

■ The visual system of literate adults develops a remarkable perceptual expertise for printed words. To delineate the aspects of this competence intrinsic to the occipitotemporal "what" pathway, we studied a patient with bilateral lesions of the occipitoparietal "where" pathway. Depending on critical geometric features of the display (rotation angle, letter spacing, mirror reversal, etc.), she switched from a good performance, when her intact ventral pathway was sufficient to encode words, to severely impaired reading, when her parietal lesions prevented the use of alternative reading strategies as a result of spatial and attentional impairments. In particular, reading was disrupted (a) by rotating word by more than 50°, providing an approximation of the invariance range for words encoding in the ventral pathway; (b) by separating letters with double spaces, revealing the limits of letter grouping into perceptual wholes; (c) by mirror-reversing words, showing that words escape the default mirror-invariant representation of visual objects in the ventral pathway. Moreover, because of her parietal lesions, she was unable to discriminate mirror images of common objects, although she was excellent with reversible pseudowords, confirming that the breaking of mirror symmetry was intrinsic to the occipitotemporal cortex. Thus, charting the display conditions associated with preserved or impaired performance allowed us to infer properties of word coding in the normal ventral pathway and to delineate the roles of the parietal lobes in single-word recognition. ■

INTRODUCTION

Young literate adults generally have read over 10^8 words (Geisler & Murray, 2003), thereby developing in their visual system a remarkable perceptual expertise for the parallel recognition of printed words (Aghababian & Nazir, 2000). To delineate the aspects of this competence intrinsic to the *occipitotemporal* visual "what" pathway, we followed the paradoxical approach of studying a female patient with bilateral lesions of her *occipitoparietal* "where" pathway, responsible for a severe visuospatial impairment. We reasoned that depending on critical geometric features of printed words (rotation angle, letter spacing, mirror reversal, etc.), the patient may switch from good performance, when her intact ventral pathway would be sufficient to encode words, to impaired reading, when her parietal lesions would prevent the use of alternative serial reading strategies. We expected that charting the display conditions associated with preserved or impaired performance would allow us to infer properties of word coding in the normal ventral pathway and to delineate the roles of the parietal lobes in single-word recognition.

Important features of the reading expertise are parallel letter processing, perceptual invariance, and effective letter discrimination. Parallel letter encoding is illustrated by the fairly constant reading latencies that are observed irrespective of word length, at least within a range of about three to six letters (Lavidor & Ellis, 2002; Weekes, 1997). Perceptual invariance allows one to identify letter strings irrespective of irrelevant parameters such as color, size, font, case, or position. As to effective letter discrimination, it is required to identify letters differing by minute but important visual details (e.g., "e" vs. "c"), or by mirror symmetry (e.g., "p" vs. "q"). There is functional imaging, neuropsychological, and electrophysiological evidence suggesting that the ventral occipitotemporal pathway is crucial to this expertise (review in Cohen & Dehaene, 2004). Functional magnetic resonance imaging (fMRI) evidence indicates that letters are encoded in the ventral temporal lobe in a format invariant for changes in case (Dehaene et al., 2004; Dehaene et al., 2001) or position (Cohen et al., 2002). The central role of the ventral cortex in the expert perception of words is also supported by the reading impairments observed in patients with (mostly left) occipitotemporal lesions, who have lost the ability to read letters in parallel or even to identify single letters (Cohen et al., 2003). In monkeys, recordings of

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inferotemporal (IT) neurons reveal properties that might prefigure the properties of parallelism, invariance, and discrimination required by reading (Riesenhuber & Poggio, 1999). For instance, IT neurons detect complex multipart objects by pooling information from neurons activated by their component parts (Baker, Behrmann, & Olson, 2002; Tsunoda, Yamane, Nishizaki, & Tanifuji, 2001), which may be akin to the parallel encoding of short familiar strings on the basis of their component letters. This idea was incorporated in a neural framework that we recently proposed to account for word processing in the ventral visual system (the local combination detector [LCD] model; Dehaene, Cohen, Sigman, & Vinckier, 2005). In this framework, parallel letter recognition is a natural consequence of general principles that govern the visual system, namely, increasing complexity and size of the receptive fields. At higher levels of this hierarchy, neurons tuned to short familiar strings of letters are thought to collect activation from simultaneously firing letter detectors. As to invariance, some IT neurons activated by specific shapes or objects show responses invariant for color, size, rotation, or position (Booth & Rolls, 1998; Ito, Tamura, Fujita, & Tanaka, 1995; Logothetis & Pauls, 1995). These properties of invariance, which were also studied in humans (Grill-Spector & Malach, 2001; Grill-Spector et al., 1999), may be likened to the insensitivity of readers to these same parameters, at least within limits commensurate with familiar display conditions (e.g., Lavidor, Ellis, & Pansky, 2002; Lavidor, Babkoff, & Faust, 2001). However, the default perceptual invariance of the ventral stream may also be detrimental to reading, by hampering the discrimination of letters with a similar shape. Particularly, some IT neurons are invariant for mirror symmetry, an obvious advantage with common objects, as the two mirror images of, for example, a bicycle are equally good tokens of the same object (Rollenhagen & Olson, 2000; Logothetis & Pauls, 1995). This invariance for mirror symmetry at the neural level has behavioral counterparts in macaques and humans (Fiser & Biederman, 2001; Biederman & Cooper, 1991). In contrast, reading requires the accurate discrimination of mirror-symmetric shapes (e.g., "p" vs. "q"), and the mirror image of a word is generally not a readable item. In the LCD framework, we hypothesize that the default invariance for mirror symmetry must be "unlearned" by the ventral pathway in the particular case of reading, but the cerebral bases of this process have not been subject to empirical study (Dehaene et al., 2005).

Here we propose to test this speculative model of the contribution of ventral occipitotemporal cortex to reading by studying the pattern of impaired and preserved word recognition in a patient with parietal lesions. Although parietal activations may be observed during normal reading (e.g., Cohen et al., 2003), they are not among the most reproducible foci in large metanalyses (Bolger, Perfetti, & Schneider, 2005; Jobard, Crivello, &

Tzourio-Mazoyer, 2003). In contrast, studies using mirror-reversed (Kassubek, Schmidtke, Kimmig, Lucking, & Greenlee, 2001; Poldrack & Gabrieli, 2001) or mixed-case (Mayall, Humphreys, Mechelli, Olson, & Price, 2001) words suggest that whenever words are displayed in unusual formats that elude the expertise of the ventral pathway, the parietal lobes are strongly engaged, presumably in order to deploy attention-demanding reading strategies. Those may involve serial letter scanning, mental rotation, and working memory processes. In normal subjects, this may be reflected by the loss of parallel letter processing and the emergence of an effect of word length on reading latencies when using a variety of nonoptimal displays (see review in Cohen, Vinckier, & Dehaene, in press). Hence, we reasoned that patients with selective lesions to the dorsal pathway would be unable to engage in such strategies and would therefore be impaired at reading those stimuli that escape the competence of the ventral pathway. Charting the conditions in which a reading deficit occurs should clarify the role of the dorsal stream in single-word reading and thereby delineate the limits of the intrinsic processing abilities of an isolated ventral stream.

We studied a patient with bilateral parietal dysfunction and tested specific predictions relative to parallelism, invariance, and letter discrimination in the ventral visual stream. We manipulated word rotation, letter spacing, and mirror symmetry, and formulated the following hypotheses. First, a general expectation was that the patient would adequately process dimensions coded in the ventral cortex such as color or object identity. Second, behavioral measures show that for rotations larger than 45°–60°, readers abandon the normal fast and parallel reading pattern (Lavidor et al., 2001; Koriat & Norman, 1985). A parallel might be drawn with IT neurons in macaques, which show an invariant response for object rotations up to about 45° (Logothetis & Pauls, 1995). Hence, we expected that the patient would be impaired at reading words rotated by an angle above a threshold of about 45°–60°, naturally including vertical words. Third, IT neurons that detect complex multipart objects combine information from neurons activated by the contiguous components of those objects (Tsunoda et al., 2001). Assuming that the parallel encoding of letter strings follows a similar principle (Dehaene et al., 2005; Grainger & Whitney, 2004), we expected that separating letters should disrupt parallel encoding in the ventral pathway. Above some spacing threshold, the difficulty could be circumvented only through serial letter processing, a strategy presumably impaired in parietal patients. Fourth, in the case of reading, a default invariance for mirror reversal should not prevail, as "p" and "q" must be identified as distinct objects. If this selective restriction to mirror generalization is implemented in the ventral pathway, we expect the patient to discriminate mirror images of letter strings better than mirror images of common objects.

Moreover, if the ventral system is tuned to recognize only normally oriented letters, the patient should be unable to read mirror images of words. We will first summarize the patient's history and cognitive status, and then turn to the results of specific reading tests.

COGNITIVE STATUS AND BRAIN LESIONS

The patient, a 63-year-old right-handed woman, developed progressive gestural and visual difficulties over the three years preceding this study. Anatomical MRI showed brain atrophy predominating in dorsal regions, with a sharp contrast between preserved ventral occipitotemporal cortex and severely shrunk dorsal occipitoparietal cortex, with a dramatic enlargement of the intraparietal sulcus (Figure 1). Complete neuropsychological data are provided in the Appendix. The patient showed cognitive impairments congruent with bilateral parietal involvement, including left neglect and severe simultanagnosia, an inability to explore and locate objects scattered in space. She was, for instance, unable to grasp the meaning of complex pictures or to count sets of dots. In contrast, visual functions subtended by the occipitotemporal pathway (object and color identification) were spared. Reading abilities followed this dissociated visual pattern. On the one hand, text reading was impossible.
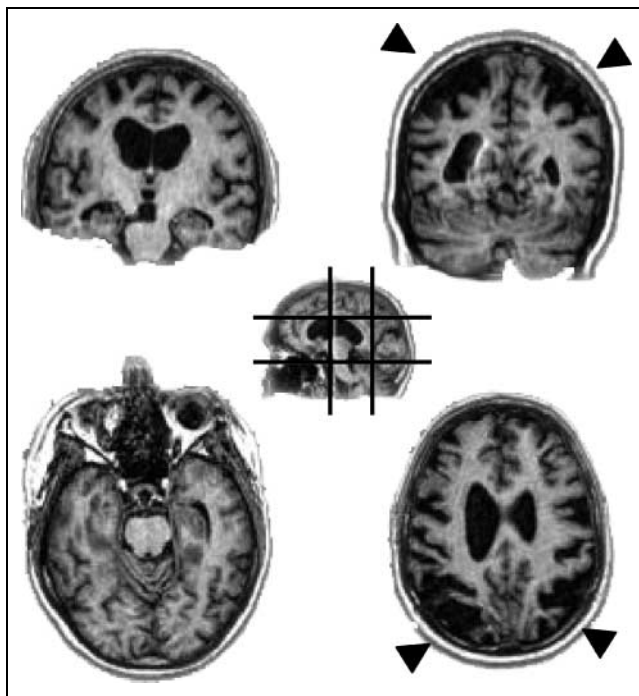

Figure 1. T1-weighted MRI showing brain atrophy predominating in dorsal regions, mostly visible in the parietal cortex. There is a clear-cut contrast between the preserved ventral occipitotemporal cortex (bottom left) and the severely shrunk dorsal occipitoparietal cortex, with a dramatic enlargement of the intraparietal sulcus (arrows).

From pages of text, the patient read only scattered words, mostly picked out on the right side. On the other hand, words that she selected were generally read correctly. She could also read isolated words presented foveally, and even words flashed for only 170 msec in her nonneglected right visual hemifield. Note, however, that she made 70% errors when reading pseudowords. There was thus a dissociation between impaired dorsal and preserved ventral visual processing, both with general visual tasks and during reading. In the following experiments, we identified conditions that induced a drop in reading performance, revealing a defective contribution of the dorsal pathway, hence the limits of the ventral perceptual expertise.
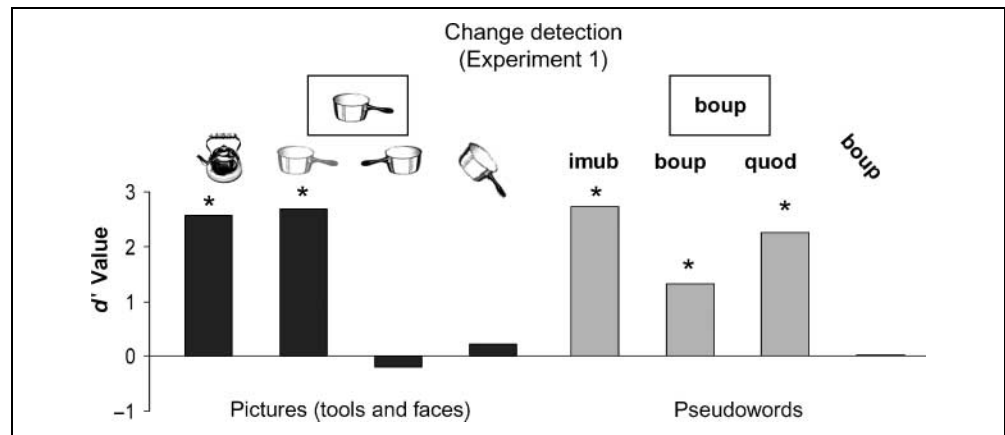
EXPERIMENT 1: CHANGE DETECTION

In this experiment, we checked whether the coding of ventral visual parameters would be spared, and the coding of dorsal parameters impaired. Moreover, this dissociation served as a reference to establish whether the ability to distinguish mirror images of letter strings segregates with dorsal or ventral parameters. To this end, the patient was asked to detect changes in pairs of successive stimuli (reversible pseudowords, pictures of faces, tools, or Chinese characters). The two images in a pair were either identical or different in terms of identity, color, rotation, or mirror reversal (Figure 2).

Methods

We prepared 12 original stimuli from each of four categories: faces, Chinese characters, tools, and reversible pseudowords (Figure 2). Pseudowords were readable four-letter strings whose mirror images were also readable pseudowords (e.g., ''boup'' and ''quod''). Four modified versions were derived from each original item by (1) 30° rotation, (2) 60° rotation, (3) left–right flip, and (4) color change (shades of red instead of levels of gray). In the first session, the patient was presented with 480 pairs of successive stimuli. Pairs comprised either two occurrences of one of the original stimuli or one original stimulus and one of its four modified versions in equal proportions (20% each). In ''different'' pairs, the original image was equally often the first or the second to be presented. Stimuli were displayed within the central 6° of the visual field. Each trial consisted of a fixation point (200 msec), the first image (800 msec), a fixation point (1000 msec), and the second image (800 msec). The patient was asked to detect any perceptible change between the two pictures. In the second session, the same change-detection task was performed using only original nonmodified stimuli. Each pair comprised either two identical stimuli or two different stimuli from the same category (10 same and 10 different trials for each category). The patient's performance did not differ

between 30° and 60° rotation angles, and the two conditions were pooled. Finally, in a distinct session, the patient was asked to read aloud the pseudowords.

Results

Results are presented in Figure 2 and Table 1. First, the patient discriminated accurately stimuli differing by parameters coded in the ventral pathway (object identity and color). This was true for pseudowords [identity: $d' = $ inf., $\chi^2(1) = 13$, $p < .001$; color: $d' = 1.47$, $\chi^2(1) = 10$, $p = .001$], as well as for the different classes of nonalphabetic pictures pooled together [identity: $d' = 1.5$, $\chi^2(1) = 15$, $p < .001$; color: $d' = 2.6$, $\chi^2(1) = 90$, $p < 10^{-15}$]. The different types of nonalphabetic pictures considered separately followed the same pattern, except for the Chinese characters, which the patient could not distinguish from one another better than chance ($d' = 0$). Second, for both pseudowords and pictures, she responded at chance for rotation changes, a dimension presumably coded in the dorsal pathway [pseudowords: $d' = 0$; pictures: $d' = 0.08$; $\chi^2(1) < 1$].

Again, this was true for all types of pictures considered separately. Finally, for the critical condition of mirror reversal, she responded at chance with pictures, $d' = -0.18$; $\chi^2(1) < 1$, whereas she was accurate with pseudowords, $d' = 2.5$, $\chi^2(1) = 27$, $p < .001$. In a distinct session, the patient was asked to read aloud the pseudowords. As usual, with pseudowords, the patient made numerous errors (41% errors). She never read an item as its mirror image.

In summary, this experiment confirmed the dissociation between preserved ventral and impaired dorsal coding of stimuli for both words and pictures.[1] Moreover, the dissociation between preserved pseudowords and impaired pictures in the detection of mirror reversal suggests that the ventral pathway computes a mirror-invariant coding for common objects, left/right discrimination then requiring parietal intervention. More importantly, it reveals that letters escape this default invariance for symmetry. The patient's intact ventral pathway allowed her to discriminate ''boup'' and ''quod'' despite their mirror symmetry, demonstrating that it encodes them as distinct items.

Table 1. Experiment 1: Error Rates in the Change Detection Task

	Chinese Letters	Tools	Faces	Pseudowords
First session				
Repetition	16.7 (4/24)	12.5 (3/24)	0 (0/24)	12.5 (3/24)
Color change	4.2 (1/24)	20.8 (5/24)	4.2 (1/24)	37.5 (9/24)
30° Rotation	95.8 (23/24)	95.8 (23/24)	100 (24/24)	87.5 (21/24)
60° Rotation	75 (18/24)	83.3 (20/24)	83.3 (20/24)	87.5 (21/24)
Mirror reversal	87.5 (21/24)	95.8 (23/24)	95.8 (23/24)	8.3 (2/24)
Second session				
Repetition	30 (3/10)	10 (1/10)	10 (1/10)	10 (1/10)
Identity change	70 (7/10)	0 (0/10)	20 (2/10)	0 (0/10)

Values are presented as percentages.

One could argue that the patient performed the mirror discrimination task on the basis of a nonvisual (e.g., phonological) representation of stimuli. For instance observing that ''boup'' and ''quod'' do not sound the same, she would answer ''different'' without paying attention to their visual structure. Similarly, she would respond ''same'' to the two mirror images of a bicycle because both images activate the same name ''bicycle'' or the same semantic content. It is indeed possible that the patient applied such a strategy, although (1) it would not correspond to the instructions, which strongly emphasized the detection of any visual change, (2) it would be effortful and inefficient considering the patient's severe difficulties in sounding out pseudowords, and (3) it would not account for her good performance in discriminating color changes. However, whatever the level on which the patient based her decision, the fact that she performed accurately suggests that mirror-symmetric letter strings were represented as distinct visual objects at those higher levels of the object-recognition system that provide an input to the verbal system. Indeed such distinct visual representations are required for the subsequent encoding of ''boup'' and ''quod,'' for example, as distinct phonological strings. The same was not true for other pictures, for which the patient's performance was random.

EXPERIMENT 2: READING MIRROR-REVERSED AND VERTICAL WORDS

Assuming that the ventral pathway is tuned to represent words only in their usual orientation, but not their mirror images, one predicts that the patient should be impaired at reading mirror-reversed words. In this experiment, the patient was asked to name normal and mirror-reversed words. We also used vertical words to test the further prediction that large rotation angles should disrupt word reading (Figure 3).

Methods

We prepared three lists of 20 familiar words, each including an equal proportion of three- to six-letter words. The three lists were matched in frequency ($p = .5$), number of syllables ($p = .12$), neighborhood size ($p = .65$), and neighborhood frequency ($p = .36$). Words from Lists 1 and 2 were presented one at a time (1) in a normal horizontal left-to-right fashion and (2) in vertical orientation, with their component letters in upright position. Words from List 3 were presented horizontally but in mirror-reversed configuration (Figure 3). Stimuli were presented centrally on a computer screen for an unlimited duration. In order to help the patient to direct her attention to the stimuli, each word was preceded by a spatial cue consisting of an array of dots rapidly converging from the periphery to the center of the screen.
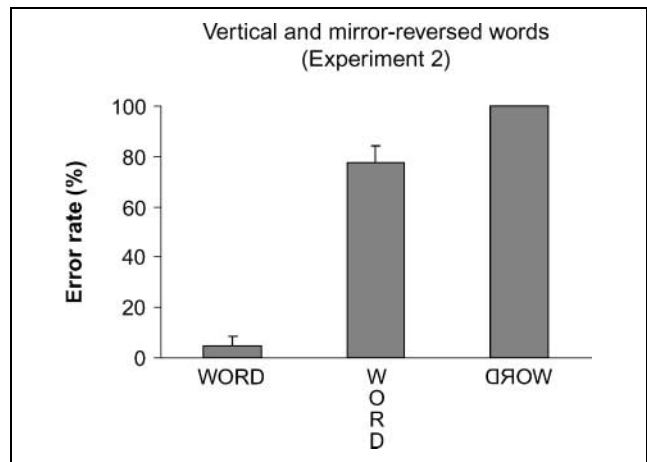

Figure 3. Experiment 2 (error rates and *SD*). The patient could accurately read normally oriented words, whereas she was severely impaired with vertical and mirror-reversed words.

The different types of display were explained to the patient, who was asked to read each word aloud.

Results

Although the patient was accurate with normal words (5% errors), she was unable to read a single mirror-reversed word (100% errors), generally producing no response at all. This major impairment confirmed the orientation-specific coding of letter strings in the ventral pathway, which is unable to process by itself mirror-reversed alphabetic strings.

The patient was also severely impaired with vertical words (77.5% errors). Error rate increased with word length, from 50% with three-letter words to 100% with six-letter words. Errors mostly consisted of an absence of response and, occasionally, of visually related words. The impact of rotation on reading performance will be studied in greater detail in the next experiment.

EXPERIMENT 3: READING ROTATED WORDS

In Experiment 2, we observed that the patient was unable to read vertical words, whereas she read horizontal words accurately. In Experiment 3, we studied the degradation of her performance over a continuum of rotation angles ranging from horizontal to 80°. We used either clockwise or counterclockwise rotation, and words were rotated either globally or in a staircase fashion (Figure 4).

Methods

A list comprising 50 five-letter and 50 seven-letter high-frequency words was constructed (frequency, 20–45 per million). Five- and seven-letter words were matched for
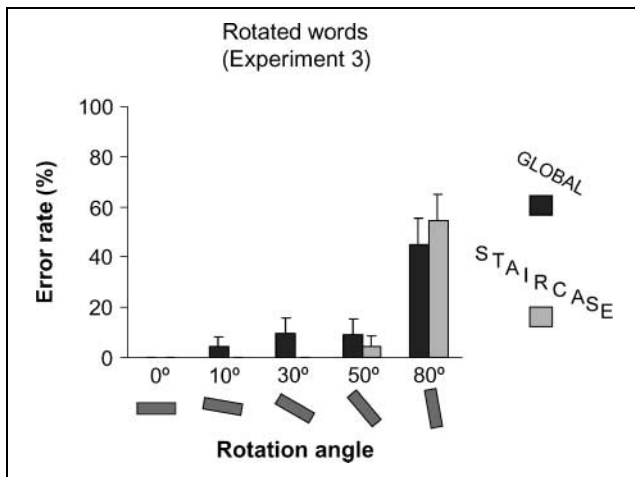
Figure 4. Experiment 3 (error rates and *SD*). When the patient was reading rotated words, her performance deteriorated steeply above a critical angle between 50° and 80°. Clockwise and counterclockwise rotations are pooled.

frequency (p = .78). We used two modes of display rotation: Words were either rotated globally or rotated in a staircase fashion (i.e., with upright letters) (Figure 4). For each rotation mode, we used nine angles of rotation (0°, 10°, 30°, 50°, 80°, each clockwise and counterclockwise). All words were presented once in the global and once in the staircase mode, in random order, with a randomly selected rotation angle. Words were presented centrally on a computer screen for an unlimited duration, preceded by the same spatial cueing as in Experiment 2, and the patient was asked to read them aloud. In addition, half of the experimental set was run a second time, asking the patient simply to indicate whether stimuli had a normal horizontal orientation or whether they were abnormally slanted, without requiring the patient to read them aloud.

Results

The distinctions of clockwise versus counterclockwise and of staircase versus global rotation had no substantial

impact on the patient's performance and were pooled unless stated otherwise (Table 2). Error rates differed greatly depending on rotation angle, $\chi^2(4) > 20, p < .001$. The patient responded with good accuracy for rotations less than or equal to 50° (3.4% errors). In this range, performance was stable irrespective of rotation amplitude, $\chi^2(3) = 2.72, p = .52$. Error rates then increased steeply from 50° to 80°, reaching 50% errors, yielding a highly significant difference between 0° and 50° and 80° angles, $\chi^2(1) = 65, p < .001$. The only difference between clockwise and counterclockwise rotation was a somewhat higher error rate, with 80° rotation, for the clockwise than the counterclockwise direction: 68% and 32%, respectively; $\chi^2(1) = 4.45, p = .03$. Interestingly, the patient was never aware of the slanted orientation of stimuli. Even for large angles, and irrespective of her own reading performance, she always claimed that she observed no abnormality in display orientation.

In summary, the patient's dramatic impairment in reading vertical words actually resulted from a drop at a critical rotation angle between 50° and 80°. This discontinuity suggests that the ventral pathway ensured perceptual invariance up to rotations of 50°, larger angles requiring a parietal engagement, which was impossible to the patient. This pattern fits our hypothesis that performance should drop whenever stimulus distortion exceeds the capacity of the ventral pathway to achieve invariance. Moreover, we now have indications regarding the value of the critical threshold for word rotation.

EXPERIMENT 4: READING WORDS WITH SPACED LETTERS

In Experiments 1 to 3, we manipulated the overall orientation of letter strings. In Experiments 4a and 4b, we used horizontal stimuli, but tried to disrupt word processing by introducing blank spaces between consecutive letters. We expected that beyond some degree of spacing, parallel letter processing in the ventral stream should break down. This would induce a reading deficit due to the patient's inability to compensate

Table 2. Experiment 3: Error Rates when Reading Rotated Words

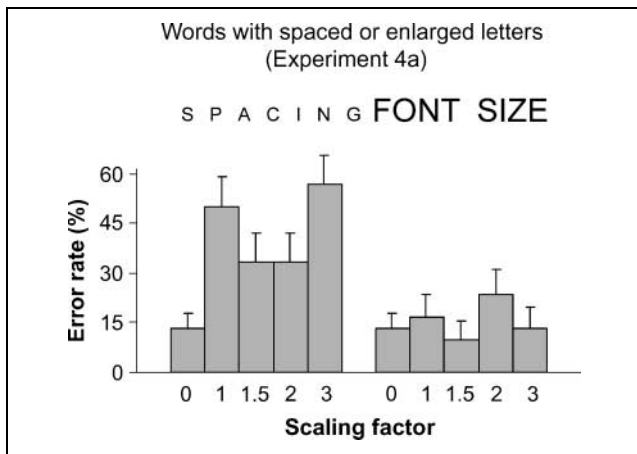| Rotation Mode	0°	10°	30°	50°	80°
Clockwise					
Global	0 (0/22)	0 (0/12)	18.2 (2/11)	9.1 (1/11)	72.7 (8/11)
Staircase	0 (0/22)	0 (0/11)	0 (0/12)	9.1 (1/11)	63.6 (7/11)
Counterclockwise					
Global		8.3 (1/12)	0 (0/10)	9.1 (1/11)	18.2 (2/11)
Staircase		0 (0/11)	0 (0/10)	0 (0/12)	45.5 (5/11)

Values are presented as percentages.

Figure 5. Experiment 4a (error rates and *SD*). Increasing the size of letters did not modify the patient's reading performance (font size condition). In contrast, introducing one or more spaces between letters induced high error rates (spacing condition).

through orderly letter scanning. The patient was asked to name words whose letters were separated by various blank spaces (spacing condition). Moreover, we wished to determine whether a disruptive influence of spacing would actually result from letter separation or from words with spaced letters occupying a larger extent of space. Therefore, we also asked the patient to name words that were enlarged to the same overall size as in the spacing condition by using larger but contiguous letters (font size condition) (Figure 5 and Table 3).

Methods

A list comprising 50 four-, six-, and eight-letter high-frequency words was constructed (frequency, 20–50 per million). Four-, six-, and eight-letter words were matched for frequency ($p = .28$). Targets were presented in uppercase Arial, white on a black background, and were always within the central $10°$ of the visual field. Stimuli were presented in two possible modes (spacing and font size), with five possible values of the scaling factor (Figure 5). At scaling 0, font size and spacing condition were identical, consisting of strings of contiguous 9 pt letters (letter height and maximum width, $0.36°$). In the spacing mode, increasing the scaling factor was achieved by increasing the number of blank spaces (0, 1, 1.5, 2, or 3) between letters, while keeping letter size constant. In the font size mode, letters were always spaced normally, and increasing the scaling factor was achieved by increasing the size of letters to match the width of letter strings at the same scaling factor in the spacing mode. Stimuli were presented centrally on a computer screen for an unlimited duration, and the patient was asked to read them aloud.

In Experiment 4a, each stimulus was presented once in the font size and once in the spacing mode in random order. In Experiment 4b, the same material was used again, but (1) stimuli were preceded by the same converging array as in Experiments 2 and 3, and (2) words were not presented in the font size mode, but were presented twice in the spacing mode.

Results

Influence of Spacing on Error Rates

In Experiment 4a, the patient made 13.3% errors at scaling 0, that is, standard words made up of small contiguous letters. Error rates increased when space was inserted between letters: 43.3% errors for scaling 1–3 in the spacing condition; $\chi^2(1) = 14.9, p < .001$. The difference between spacing 0 and 1 was highly significant, $\chi^2(1) = 11.8, p < .001$, whereas there was no difference between values of spacing 1 to 3, $\chi^2(3) = 5.2, p > .1$. In contrast, there was no difference between standard words and words printed with larger letters: 15.8% errors for scaling 1–3 in the font size condition; $\chi^2(1) < 1$. More generally, performance did not change with increasingly larger letters (i.e., font size mode), $\chi^2(4) = 2.5, p = .64$.

In Experiment 4b, we used the spacing condition again, but also tried to help the patient focus her

Table 3. Experiment 4: Error Rates when Reading Words with Spaced or Enlarged Letters

| | Scaling Factor | | | | |
	0	*1*	*1.5*	*2*	*3*
Experiment 4a					
Spacing	13.3 (8/60)	50 (15/30)	33.3 (10/30)	33.3 (10/30)	56.7 (17/30)
Font size	13.3 (8/60)	17 (5/30)	10 (3/30)	23 (7/30)	13 (4/30)
Experiment 4b					
Spacing	16.7 (10/60)	21.7 (13/60)	18.3 (11/60)	36.7 (22/60)	35 (21/60)

Values are presented as percentages.

attention on stimuli by preceding words with the same converging array of dots as in previous experiments (Figure 6). As before, increasing the space between letters induced an increase in error rate from 20% for contiguous letters to 41.7% for spacing 3, $\chi^2(4) = 17.2$, $p < .01$. However, the profile of errors differed from Experiment 4a, as the insertion of two spaces rather than one was needed to degrade the patient's performance: There was a significant difference between spacing 1.5 and 2, $\chi^2(1) = 7.9$, $p < .01$, but neither between the smaller values of spacing 0 to 1.5, $\chi^2(2) < 1$, nor between the larger values 2 and 3, $\chi^2(1) < 1$.

Qualitative Analysis of Errors with Optimal Displays

In Experiments 4a and 4b, the patient made relatively few errors with optimal stimuli, that is, horizontally printed words with contiguous letters. However, her performance was below the normal level (37/240 errors, 15%). We analyzed the qualitative features of this small corpus of errors, which may be informative on the contribution of parietal structures to reading. Two errors were lost from the recording and could not be analyzed. All errors consisted of real words (except for two non-responses and one nonword), generally with an obvious visual similarity to the targets. Errors generally preserved the number of letters (24 out of 33 errors had a correct length ± 1 letter, 73%). Most errors resulted from letter substitutions (e.g., PAGE → RAGE; SOIE → SOIF), often combined with letter deletions or insertions (e.g., VISION → VERSION; INSTINCT → DISTINCT). Because of the patient's spatial neglect, most errors affected the leftmost part of words (e.g., PANTALON → TALON; ILLUSION → INFUSION). In 23 out of 33 errors (70%), the right half of targets was intact in the error, whereas in only 1 error (3%), the left half was intact.[2]
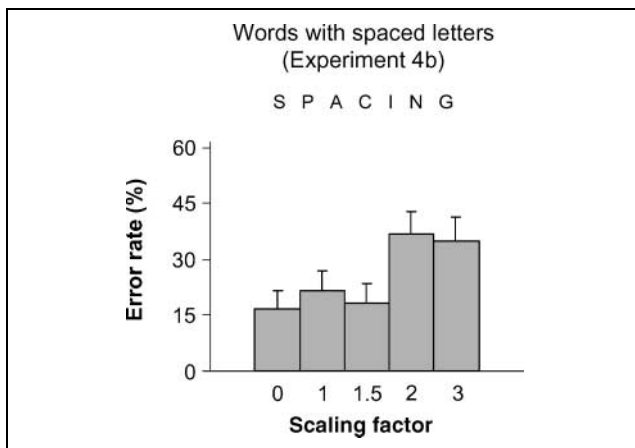
We noted that the patient produced a single, perfect anagram response (ONZE → ZONE) and a few other errors that might be construed as anagrams combined with the addition or substitution of one or a few letters (e.g., PROBABLE → PORTABLE). Such errors could be of great potential interest, as they may reveal the impact of parietal lesions on the computation of letter order. However, their paucity precluded any substantial study. This limitation possibly reflected lexical constraints in the experimental material. Even assuming that she had some mild impairment in computing letter order, it would be unlikely for the patient to reach an error response fulfilling the conditions of being a real word, having its rightmost letters in common with the target, and being an anagram of the target. In such conditions, it was not even possible to establish whether the few putative anagram errors were more than coincidental. Overall, the rareness of anagram errors rather suggests that the severe parietal deficit did not substantially affect the computation of letter order. Moreover, on scrutiny of the corpus of errors, we found no convincing instances of migration of visual features between letters (e.g., E I → F L as a possible migration of a horizontal bar from E to I).

Finally, we checked whether error rates were modulated by lexical frequency. Target words below or above the median frequency did not yield different error rates ($p = .71$), and the frequency of targets and of the corresponding error responses did not differ either ($p = .32$). There was also no difference in error rates between targets below or above the median for he cumulated frequency of neighbors (i.e., words differing from the target by one letter).

In summary, inserting a minimum of one or two spaces between letters induced a sudden increase of errors, whereas increasing letter size had no impact whatsoever. This showed that spacing was indeed the critical parameter, but also suggested that perceptual invariance for size was spared.

Figure 6. Experiment 4b (error rates and *SD*). When stimuli were preceded by a spatial cue, two or more spaces between letters were necessary to induce high error rates.

DISCUSSION

On the basis of a hypothetical link between the computational requirements of word reading and some physiological properties of IT neurons in primates, we formulated a set of predictions on the residual and impaired reading abilities in a patient with bilateral parietal damage. We assumed that parietal intervention is mandatory whenever words are displayed in unfamiliar formats that elude the perceptual expertise of the ventral pathway. The rationale of our approach was that such displays should induce high error rates in parietal patients, thereby revealing the limits of the ventral expertise.

In the following, we will consider in turn the main parameters that we manipulated (rotation, letter spacing,

mirror reversal), as well as parameters of visual hemifield and lexical status. In each case we will discuss the mechanisms of the patient's deficit and the information gained on word coding in the ventral pathway, trying to clarify the answers to the hypotheses formulated in the Introduction.

Invariance for Rotation and Perception of Rotation

Why was the Patient Impaired at Reading Words Rotated Close to the Vertical?

In Experiments 2 and 3, we observed that the patient was almost entirely unable to read words rotated by 80° or 90°. A first hypothesis is that reading such unusual displays may require mental rotation in order to bring a representation of single letters or of whole strings to a standard orientation (Jordan, Heinze, Lutz, Kanowski, & Jancke, 2001; Corballis & McLaren, 1984; Cooper & Shepard, 1973). As mental rotation is dependent on the parietal cortex (see reviews in Parsons, 2003; Gauthier et al., 2002), including when using letter stimuli (Jordan et al., 2001), one may expect parietal lesions to interfere with the processing of rotated words. However, contrary to handedness judgments used in most mental rotation tasks, simply identifying single alphanumeric characters is almost unaffected by the angular orientation of stimuli (e.g., Corballis, Zbrodoff, Shetzer, & Butler, 1978), suggesting that reading rotated letters does not require mental rotation (for a review, see Koriat & Norman, 1989). It is thus unlikely that the patient's deficit resulted from an impaired mental rotation of single letters. Accordingly, there was no difference in her performance between the staircase and global rotation modes, although only the latter would require mental letter rotation.

In contrast to single letters, reading whole words is substantially more difficult with rotated than with standard stimuli. In Hebrew readers, Koriat and Norman (1985) have shown, using lexical decision, that rotating words by up to 40° does not alter the normal response pattern. At 60°, latencies start to increase; for greater angles, a strong influence of word length appears, with longer latencies for larger numbers of letters. Using a split-field lexical decision task, Lavidor et al. (2001) observed that for angles of 45° or more, response latencies increase, whereas the right hemifield loses its perceptual advantage over the left hemifield. There are thus converging indications that normal readers cannot maintain optimal processing for angles above a limit of about 40°–60°. This complex nonlinear pattern does not fit a simple hypothesis that reading tilted words would always require mental rotation, with a difficulty directly proportional to the rotation angle. It rather suggests that small angles induce no measurable cost, whereas angles greater than about 60° require letter-by-letter reading

(maybe in combination with mental rotation), as revealed by the length effect. By using ambiguous stimuli that could be considered either as single characters or as pairs of characters (e.g., as B or as 13), Koriat and Norman (1989) confirmed that the serial processing of tilted strings of characters is necessary to encode the order of letters as required during word reading.

Thus, impaired mental rotation, although possibly present in the patient, was probably not the only cause of her inability to read words close to the vertical. More important could be an inability to scan letters sequentially, a by-product of Bálint's syndrome. Letter-by-letter reading requires selective attention to each letter within stimulus strings, accurate control of attention and gaze movements, and trans-saccadic memory of previously attended locations, all functions dependent on parietal integrity (Husain & Rorden, 2003; Kanwisher & Wojciulik, 2000; Gitelman et al., 1999; Mesulam, 1999).

Why was the Patient Impaired at Judging Stimulus Rotation?

Experiment 3, in addition to showing the patient's inability to read words close to a vertical orientation, also showed her striking inability to explicitly appreciate the orientation of stimuli. More importantly, this was true irrespective of her reading performance, that is, both for small angles that did not hinder her performance and for angles close to the vertical. The same was observed in Experiment 1 with a change detection task, as the patient was unable to discriminate stimuli rotated by 30° or 60° from the original version. This phenomenon falls in the scope of object orientation agnosia, a (mostly right) parietal deficit whose core symptom is an inability to discriminate between images differing in orientation, contrasting with preserved object identification (see review in Priftis, Rusconi, Umilta, & Zorzi, 2003). As a special case of orientation agnosia, the contrast between preserved reading of rotated words and lack of awareness of their orientation may be reduced to the dichotomy between ventral and dorsal visual streams (Davidoff & Warrington, 2001). Goodale and Milner (1992), among others, proposed that the dorsal pathway computes view-dependent visual descriptions primarily aimed at guiding motor reactions, whereas the ventral pathway computes view-independent descriptions to support recognition of object identity. The patient's deficit in estimating object orientation would then result from an impairment of parietal orientation-dependent representations.

Why was the Patient Good at Reading Moderately Rotated Stimuli?

Considering the patient's complete inability to read words close to the vertical, her excellent performance

with words rotated by up to 50° may seem paradoxical. It suggests that the spatial/attentional processes subtended by the parietal lobes are not required for moderately disoriented stimuli. Indeed, there is independent evidence that the coding of visual objects in the ventral pathway is invariant to some degree for depth and in-plane rotation. Note that as depth rotation is equivalent to a change in point of view, it has received more attention than in-plane rotation, the parameter that we manipulated here. At the single-neuron level, most IT neurons selective for meaningful patterns show sensitivity to orientation in the image plane (Tanaka, Saito, Fukada, & Moriya, 1991). Logothetis and Pauls (1995) and Logothetis, Pauls, and Poggio (1995) showed that Gaussians fitting the tuning curves had a standard deviation of 30°, on average, for depth rotation and were somewhat wider for in-plane rotation. Similarly, the responses of face-detecting neurons decrease by half for rotations of about 60°, both in depth and in plane (Perrett & Oram, 1998). Thus, putative neurons optimally tuned to alphabetic characters in a standard upright orientation would efficiently detect those stimuli even if rotated by about 50°. A link may be proposed between the neuronal and the behavioral level. For instance, Logothetis and Pauls (1995) have drawn a precise parallel between single-neuron tuning curves for depth or in-plane rotation and the performance profile of the same macaque in a detection task with rotated variants of a trained image. Related results were obtained in humans by James, Humphrey, Gati, Menon, and Goodale (2002), who showed priming for rotated images of objects in the ventral occipitotemporal cortex, suggesting that this region computes a representation invariant for rotation (see also Grill-Spector et al., 1999). In summary, the patient's preserved ability to read words rotated by up to 50° probably reflect the coding invariance intrinsic to her intact ventral visual pathway.

Parallel Perception and Letter Spacing

In Experiment 4, the patient was impaired at reading words with spaced letters. This deficit probably resulted from the same causes as the impairment for words rotated close to the vertical, that is, that beyond some degree of spacing, letters behave as distinct objects, and that the patient's simultanagnosia prevents her from scanning them properly. In Experiment 4b, the patient's performance declined when letters were separated by at least a double space. This value matches an explicit prediction of the LCD framework (Dehaene et al., 2005). According to this model, letter detectors with a local receptive field converge on open bigram detectors. Based on the increase of receptive fields in the IT cortex by a factor of about 2.5 from one neural level to the next (Rolls, 2000), the LCD model proposes that bigram detectors should be disrupted by separating the component letters by blank spaces of at least two letter widths (Dehaene et al., 2005), precluding their parallel encoding into larger units. Accordingly, normal subjects begin to show a word length effect when reading words with letters separated by two spaces or more (Vinckier, Forget, Dehaene, & Cohen, in preparation). This value is thus a plausible estimate of the limits of the letter-grouping ability of the ventral pathway.

Why then, in Experiment 4a, was a single space sufficient to disrupt reading? In Experiment 4b, targets were preceded by a cue helping the patient to direct her attention to the appropriate region of space. The whole letter string could then be processed optimally in the ventral stream, a process disrupted by a minimum of two spaces between letters. We speculate that in Experiment 4a, in the absence of spatial cues, the patient was unable to adjust her attention window to the whole region encompassing the set of letters. As a result, letters were processed as independent objects even when separated by a single space, a task out of the patient's reach.

Word Coding and Mirror Reversal

Why was the Patient Impaired at Reading Mirror-reversed Words?

In Experiment 2, the patient was unable to read a single mirror-reversed word. The reasons of this deficit are probably the same as those discussed about the deficits for vertical words and words with spaced letters, namely, impaired selective attention, control of attention and gaze movements, and possibly mental rotation of letters, which are normally required to scan letters from right to left and to identify flipped letters. Functional imaging shows strong parietal activations during mirror reading (Kassubek et al., 2001; Poldrack & Gabrieli, 2001; Dong et al., 2000), in good agreement with the patient's deficit.

Why was the Patient Good at Discriminating Words from Their Mirror Images?

The patient's disrupted mirror reading directly illustrates the inability of her intact ventral pathway to encode mirror-reversed letter strings. This asymmetric coding may not appear as a surprise considering that reversing a word generally results in a nonreadable item or, at best, in a different word. However, in this respect, words appear as an exception to the principle of invariance for mirror symmetry that is pervasive in the domain of object recognition. Thus, after exposure to an image in a given orientation, humans and animals spontaneously treat the mirror-symmetrical version as equivalent to the original. For instance, in a picture-naming task, Fiser and Biederman (2001) and Biederman and Cooper (1991) observed an equivalent priming for the original stimuli

and their mirror images. They also showed that subjects were only 60% correct when explicitly judging whether the first and second occurrence of stimuli had the same left/right orientation. Monkeys trained to a specific view of wirelike objects spontaneously generalized recognition to mirror-reversed images (Logothetis & Pauls, 1995), although a set of IT neurons responded equally to both images (Rollenhagen & Olson, 2000). Similarly, a substantial proportion of cells tuned to profile images show two peaks of responsiveness, one for each of two mirror-symmetric views (Perrett et al., 1991). In the case of reading, generalization for mirror reflection is frequent during the early stages of reading acquisition. At that period, children often read and write indifferently in both directions, and confuse mirror-image letters such as b and d, a phenomenon that may persist up to adulthood in dyslexic subjects (Walsh & Butler, 1996; McMonnies, 1992). The LCD framework proposes that this default mirror generalization must be unlearned when children are learning to read (Dehaene et al., 2005).

Putting aside the special case of letters, a consequence of invariant coding in the ventral cortex is that dorsal processes are required for tasks emphasizing the discrimination between mirror images. Indeed, most studies of mental rotation that show parietal activations resort to classical same–different handedness decision tasks with pairs of images (Parsons, 2003). Moreover, Gauthier et al. (2002) showed that activity increases in the superior parietal lobe in proportion to viewpoint disparity only when subjects are comparing the handedness of the two images but not their shape. Accordingly parietal patients may be unable to discriminate mirror images (e.g., Priftis et al., 2003), possibly due to an inability to achieve ''the explicit coding of object parts relative to a view-specific frame'' (Humphrey & Riddoch, 2006). This was precisely the case of our patient, who was at chance level in Experiment 1 for discriminating mirror images of tools, faces, or Chinese characters. Assuming that letters are an exception to the default mirror-invariant coding in the ventral cortex, it results that parietal processes are not required to discriminate mirror-image alphabetic stimuli. Accordingly, in Experiment 1, the patient was excellent at discriminating pairs of reversible pseudowords such as boup versus quod. In this respect, she was similar to previous patients with mirror agnosia, whose discrimination between mirror images was preserved for alphabetic stimuli. However, in all those studies, mirror reversal resulted in illegal stimuli such as reversed asymmetrical letters or nonwords compared with real letters or words (Priftis et al., 2003; Davidoff & Warrington, 2001; Turnbull & McCarthy, 1996). There was thus a confound between the ability to discriminate mirror images and the ability to discriminate legal and familiar from novel and illegal items. We do not face this problem here, as our stimuli were designed to be equally legible pseudowords in both

orientations. In summary, the patient's pattern of behavior demonstrates that in literate adults, the breaking of symmetry in the coding of printed words is intrinsic to the ventral visual cortex.

Word Reading in the Left and Right Hemifields

We showed that the patient was generally good at reading horizontal words with contiguous letters. However, the split-field reading task suggests a slightly more complex picture. This task was interesting in two respects. On the one hand, the patient's good performance with right-hemifield stimuli confirmed that for optimal displays, parallel letter encoding was possible even with displays too short to allow for letter-by-letter scanning. On the other hand, the severe deficit with left-hemifield words suggests that this sparing did not apply to the entire visual field. Two distinct but compatible accounts may be proposed. First, we argued that selective attention to single characters is not required to group contiguous letters into perceptual wholes. Nevertheless, selective attention is required to select the appropriate spatial window in which word reading should proceed. Thus, in normal subjects, forcing a spread of attention over several simultaneous words interferes with the identification of each individual word (Davis & Bowers, 2004; Treisman & Souther, 1986). Considering the patient's neglect as a spatially biased impairment of selective attention (Husain & Rorden, 2003), her impairment with left-sided words is a natural consequence of her parietal lesions. A second more subtle factor may explain why a lateralized reading deficit should affect the left hemifield. In normal subjects, split-field studies show that although there is no length effect for words displayed in the right visual field (RVF), at least close to the fovea, such an effect emerges whenever words are displayed in the left visual field (LVF) (Lavidor & Ellis, 2002). Accordingly, when words extend across central fixation, only their left part induces a length effect (Lavidor, Ellis, Shillcock, & Bland, 2001). One account of this asymmetry is that the optimal gaze position for reading is slightly left of word center, and that perceptual expertise, including parallel letter processing, develops mostly as a property of the RVF (Nazir, 2000). Thus, even in normal subjects, reading in the LVF would require serial letter processing, as revealed by the lateralized length effect (for a different account, see Whitney & Lavidor, 2004). As usual, such a requirement for serial letter processing cannot be met by our patient, explaining her lateralized reading deficit.

Reading Pseudowords

As shown in the clinical assessment and in Experiment 1, the patient was severely impaired at reading aloud pseudowords. At first sight, this deficit may seem unexpected,

as the visual encoding of legible pseudowords should involve the same processes as the visual encoding of real words, both obeying the regularities of French orthography at the prelexical level. Indeed, the activations induced in the occipitotemporal cortex by pseudowords are comparable to or stronger than those induced by real words (Mechelli, Gorno-Tempini, & Price, 2003; Dehaene, Le Clec'H, Poline, Le Bihan, & Cohen, 2002). Moreover, the patient's flawless performance in discriminating pseudowords supports the hypothesis of a spared visual coding. Still, impaired pseudoword reading has been repeatedly reported in patients with Bálint's syndrome (Baylis, Driver, Baylis, & Rafal, 1994; Coslett & Saffran, 1991). One possibility is that pseudowords require the serial left-to-right conversion of graphemes into phonemes for the progressive buildup of a phonological string, as revealed by the word length effect observed in normal readers (Weekes, 1997). The corresponding letter scanning may be disrupted by parietal lesions, impeding the overt reading of pseudowords. As a further illustration of an impaired processing of individual letters within strings, patients with Bálint's syndrome (Baylis et al., 1994) and patients with so-called attentional dyslexia following (generally left) parietal lesions may be good at reading isolated words, but impaired at naming their component letters (Mayall & Humphreys, 2002; Friedmann & Gvion, 2001; Shallice & Warrington, 1977; Warrington, Cipolotti, & McNeil, 1993).

The Length Effect in Normal Subjects

In the above discussion we mentioned on several occasions that the patient was impaired at reading stimuli that in normal subjects would induce an influence of length on naming latencies: rotated words (Koriat & Norman, 1985), words with spaced letters (Vinckier et al., in preparation), words presented in the left visual hemifield (Lavidor & Ellis, 2002), and pseudowords (Weekes, 1997). In normal subjects, a length effect also emerges with low-contrast words (Legge, Ahn, Klitz, & Luebker, 1997), words printed in mIxEd case (Lavidor, 2002), vertically presented words (Bub & Lewine, 1988), or low-frequency words (Weekes, 1997). We suggest that this variety of circumstances may be reduced to the general hypothesis that whenever a response cannot be generated after a first pass in the ventral stream, some more information must be gathered by way of appropriate attentional strategies (Cohen et al., in press; Ans, Carbonnel, & Valdois, 1998; Grainger & Jacobs, 1996). Those strategies would generally involve attention to letters or groups of letters within the target string and, therefore, induce an effect of length. The reasons why parallel letter analysis in the ventral stream should not be sufficient to respond may include (1) acquired ventral lesions as in letter-by-letter readers (Cohen et al., 2004; Cohen et al., 2003), (2) incomplete development of

perceptual expertise as in young children (Zoccolotti et al., 2005; Aghababian & Nazir, 2000), (3) degraded or unfamiliar displays incompatible with an optimal operation of the ventral pathway, for example, low contrast or vertical words, and (4) tasks or stimuli specifically requiring serial letter processing, such as pseudoword reading or letter-detection tasks. This general proposal about the interplay of the ventral and dorsal visual pathways in the perception of printed words should generate empirical testing, both with neuropsychological and brain imaging methods. In particular, one should study activation patterns during reading, manipulating the same parameters as those that generated high error rates in our patient.

APPENDIX: NEUROPSYCHOLOGICAL BACKGROUND

On clinical testing, the patient showed a variety of cognitive impairments suggestive of bilateral parietal involvement. First, she had all components of Gerstmann's syndrome:

Agraphia: She was severely impaired at writing to dictation even single letters, often producing distorted scribbles. In addition to this apraxic agraphia, she also showed central agraphia, as evidenced by the numerous errors she made when spelling out words orally, including her own name (e.g., "voiture" → V, R, E).

Acalculia: When presented orally with simple arithmetic problems, she was generally correct with familiar multiplication problems (e.g., $3 \times 4 \to 12$; $9 \times 9 \to 81$), although she was unable to solve most elementary subtraction problems (e.g., $11 - 3 \to ?$; $5 - 2 \to 7$).

Finger agnosia: She made errors when naming fingers on designation (e.g., index → middle finger).

Left–right confusion: When pointing to a specified body part, she made occasional side errors, mostly when she was asked to point to the examiner, and she was generally not confident in her own answers.

Second, she had limb apraxia, making frequent errors or approximations when imitating arbitrary hand postures, producing symbolic gestures, or simulating the use of common tools. She was unable to dress by herself. Third, she had left spatial neglect, as evidenced in line cancellation and dot counting tasks, in which she picked out only the rightmost items. She also had some degree of left motor neglect, for instance, leaving out her left upper limb in awkward positions or omitting to use it when eating. Fourth, in the visual domain she showed a dissociation between functions subtended by the ventral and dorsal pathways. She had simultanagnosia, as evidenced for instance by her piecemeal description of the Cookie Theft picture (Goodglass & Kaplan, 1972). In the dot counting test from the Visual Object

and Space Perception (VOSP) Battery (Warrington & James, 1991), she always answered 3, although five to nine points were actually presented. When asked to point to the dots while counting them, she selected the rightmost items and often counted several times a given dot. She was essentially unable to complete the other tests for spatial processing from the VOSP Battery. In contrast to those deficits, she could flawlessly identify familiar real objects on visual presentation. She was also excellent with drawings of tools (0/14 errors) and with the short picture naming test from the Birmingham Object Recognition Battery (BORB) (2/15 minor errors: spider → bee; celery → zucchini) (Riddoch & Humphreys, 1993). Finally, she had normal anterograde memory on a short five-word learning test (Dubois et al., 2002).

The patient's reading abilities reflected her dissociated pattern of visual impairment. On the one hand, text reading was severely impeded by simultanagnosia and neglect. When presented with a page of text, the patient read randomly scattered words, mostly picked out of the right half of the page. She could not consistently follow a given line nor jump to the beginning of the next one. When presented with large letters made up of smaller letters (''Navon stimuli''), she only identified the small component letters, as has been shown in other patients with Bálint's syndrome (Jackson, Swainson, Mort, Husain, & Jackson, 2004). On the other hand, and in agreement with her preserved object naming, words that she selected were almost always read correctly. The patient was asked to read aloud a list of 20 familiar three- to six-letter words and a list of 20 pseudowords, matched one by one in terms of phonological and graphemic consonant–vowel structure. She made 10% errors with real words, and 70% errors with pseudowords. Almost all erroneous responses to pseudowords consisted of real words with some visual similarity to the target (e.g., gof → golf). The patient was asked to read aloud 40 words flashed for 170 msec, randomly displayed in her left or her right hemifield (maximum lateral extension 4°), while she was fixating a central cross. She made 11% errors with RVF words, but as much as 78% errors with LVF words. Four trials were discarded because the patient did not maintain central fixation. This test illustrated both the preservation of the patient's ability to effectively read even briefly flashed words, and a marked deficit in her LVF.

In brief, in addition to other parietal deficits, the patient showed a clear-cut dissociation between impaired dorsal and preserved ventral visual processing, apparent both with general visual tasks and during reading.

Notes

1. The only exception was her poor performance in discriminating same from different Chinese characters. It is likely that for readers unfamiliar with the Chinese script, such stimuli are treated as combinations of independent strokes. Encoding Chinese characters would therefore require accurate localization of strokes relative to one another, a task obviously out of reach of a simultanagnosic patient with parietal lesions. Accordingly, even in Chinese readers, low-frequency characters induce greater left parietal activations, at coordinates almost identical to those observed with spatial/attentional tasks (Kuo et al., 2003; Gitelman et al., 1999).
2. Introducing blank spaces between letters increased the error rate, but the qualitative features of errors remained basically the same as with normal words: production of real words, visual similarity with targets, and a strong left bias.

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