

Brain activations during letter-by-letter reading: A follow-up study

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Abstract

Lesions affecting the ventral cortex of the left temporal lobe commonly yield a selective reading impairment known as pure alexia. It is thought to result from the disruption or deafferentation of the Visual Word Form Area (VWFA), a region in the left lateral occipitotemporal sulcus activated whenever normal subjects are viewing alphabetic strings. Most pure alexic patients retain the ability to identify single letters, and develop a strategy of letter-by-letter (LBL) reading. We recently studied fMRI activations in LBL readers and clarified the underlying mechanisms. However, LBL reading is a dynamic process which may improve over months or years of practice, although the cerebral bases of this continuing improvement are currently unknown. We had the opportunity to run the same behavioural testing and fMRI experiment a second time in an alexic patient, 8 months after collecting the data reported by Cohen et al. [Cohen, L., Henry, C., Dehaene, S., Molko, N., Lehericy, S., Martinaud, O., Lemer, C., & Ferrieux, S. (2004). The pathophysiology of letter-by-letter reading. *Neuropsychologia*, 42, 1768–1780]. We analyze the changes that occurred over this period in the pattern of reading-related activations, while the patient's LBL reading improved. The activation level decreased in most of the overall network between the two sessions. This general trend contrasted with a focal increase restricted to specific left frontal and parietal areas. When studying the contrast between words and consonant strings, which may be taken as a correlate of LBL reading, we also found a general decrease, except for similar left frontal and parietal regions, which showed a significant increase. We suggest that the pattern of evolution fits with the minimal hypothesis of normal strategic abilities and skill learning, associated with perceptual tuning in right-hemispheric structures able to substitute the disrupted VWFA.

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1. Introduction

Acquired lesions affecting the ventral cortex of the left temporal lobe commonly yield a selective reading impairment known as Pure Alexia, as speech processing, spelling abilities, and the visual recognition of other classes of objects may be spared (Damasio & Damasio, 1983; Binder & Mohr, 1992). The critical site of lesions responsible for Pure Alexia overlaps with activations observed in the lateral

occipitotemporal sulcus whenever normal subjects are viewing alphabetic strings (Cohen et al., 2003). In some patients this area is spared but deafferented by callosal or left-hemispheric lesions (Cohen et al., 2004a, 2004b). This area, which we proposed to label as the Visual Word Form Area (VWFA) is thought to subtend a representation of abstract letter identities, invariant for irrelevant perceptual parameters such as position, size, font or case (Cohen et al., 2000; Dehaene et al., 2001). The core deficit in Pure Alexia is the loss of the rapid and parallel identification of strings of several letters. In normals, this ability is revealed by constant reading latencies irrespective of word length, at least in optimal viewing conditions (Lavidor, Ellis, Shillcock, & Bland, 2001; Weekes, 1997). Most pure alexic patients retain the ability

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to identify single letters, even if more slowly than normals, allowing them to develop a strategy of letter-by-letter (LBL) reading. A strong correlation of reading latencies with word length is diagnostic of the LBL strategy, with a slope in the order of hundreds of ms per letter (Behrmann, Black, & Bub, 1990a).

A classical account of LBL reading is that letters are identified in the intact right hemisphere, then serially transferred to the left-hemisphere through callosal connections, and eventually combined by verbal working memory processes, allowing to retrieve word identity in the lexicon or compute the pronunciation of pseudowords (Binder & Mohr, 1992; Speedie, Rothi, & Heilman, 1982). Note that while the topography of some of the callosal connections involved in normal reading are fairly well defined, the precise location of the interhemispheric connection which can be usefully recruited for letter-by-letter reading is not precisely identified, although they may be anterior to the splenium (Binder & Mohr, 1992; Cohen et al., 2004a; Molko et al., 2002; Sidtis, Volpe, Holtzman, Wilson, & Gazzaniga, 1981). We recently provided support to this general interpretation by studying fMRI activations in two LBL readers (Cohen et al., 2003, 2004a). In summary, we showed that the right-hemispheric region symmetrical to the impaired VWFA (the R-VWFA) displays functional properties normally specific to the VWFA itself, namely stronger activations to alphabetic stimuli than to chequerboards, suggesting that it subtends letter identification. Furthermore, LBL reading is correlated with increased activation in the right occipital cortex, which subtends letter input in right hemianopic patients, and in a left-hemispheric working memory network including Broca's area, and in bilateral prefrontal regions.

LBL reading is a dynamic process which may improve over months or years of practice (Behrmann, Black, & Bub, 1990b). Indeed, this potential progress is the basis of most rehabilitation techniques (Greenwald & Gonzalez Rothi, 1998). However, the cerebral bases of this continuing improvement are currently unknown. We had the opportunity to run the same behavioural testing and fMRI experiment a second time in an alexic patient, 8 months after collecting the data reported by Cohen et al. (2004a). In the present note, we analyze the changes that occurred over this period in the pattern of reading-related activations, while the patient's LBL reading improved.

2. Methods

The medical history, brain lesion, behavioural methods, and functional imaging procedure were fully described by Cohen et al. (2003, 2004a) and will be only summarized here. The patient was a 20-year-old right-handed woman, who underwent the resection of a left occipital tumor. The left occipital lobe, the left side of the splenium of the corpus callosum and the mesial ventral temporal lobe

were removed. The patient suffered from Pure Alexia with LBL reading, a deficit which was attributed to the deafferentation of her VWFA. During the 8 months since the first fMRI session, the patient's tumor showed no clinical or radiological signs of relapse, while reading improved.

To assess her reading abilities, the patient was presented with two lists of frequent nouns of various lengths. Words were presented for an unlimited duration, while reading latencies were measured. The patient had been tested already with one of the lists at the time of the first fMRI session, i.e. 8 months earlier, and with the other list 1 year earlier.

During the fMRI session, the patient was visually presented with short alternating blocks of words, consonant strings, chequerboards, or fixation. She was asked to pay attention to all stimuli, and to read covertly real words. We showed that she could very rapidly distinguish real words from consonant strings, and that she engaged in LBL reading with real words only. In the following analyses we used a voxelwise threshold of $P < 0.005$, with a clusterwise threshold of $P < 0.05$ corrected. The $P < 0.005$ threshold was also used for contrasts used as statistical masks.

3. Results

3.1. Behaviour

The patient was flawless but abnormally slow when reading words. Fig. 1 shows the reading latencies for 3–8-letter words, with an overall drop from the initial testing session (mean: 8316 ms) to the time of the first (mean: 5677 ms) and the second fMRI sessions (mean: 3483 ms). Despite this improvement, there was still a typical pattern of LBL reading, with increasing latencies for longer words (slope: 328 ms per letter).

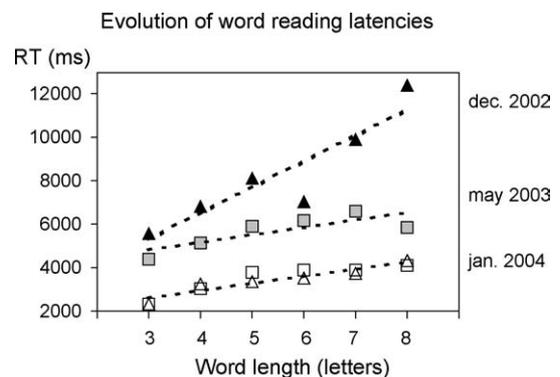


Fig. 1. There was a continuing reduction in reading latencies from the initial testing session (black symbols) to the time of first (grey symbols) and of the second (white symbols) fMRI sessions. Despite this relative improvement, there was still a typical pattern of letter-by-letter reading, with longer latencies for longer words. Triangles and squares correspond to two distinct lists of words.

3.2. Imaging

3.2.1. Overall activation network

The overall reading network was delineated by contrasting alphabetic stimuli (i.e. words and consonants) minus chequerboards, masking by alphabetic stimuli minus fixation (Fig. 2). During Session 1, this showed an extensive fronto-parieto-temporal network, with left-predominance, except in

the occipito-temporal region where this predominance was reversed due to the left-hemispheric lesion (Cohen et al., 2004a). During Session 2, this analysis showed activations in essentially the same areas (Fig. 2), including the VWFA and the R-VWFA.

We then looked for significant changes between sessions. Decreases were identified by subtracting alphabetic stimuli minus chequerboards in Session 1 minus Session 2, masking

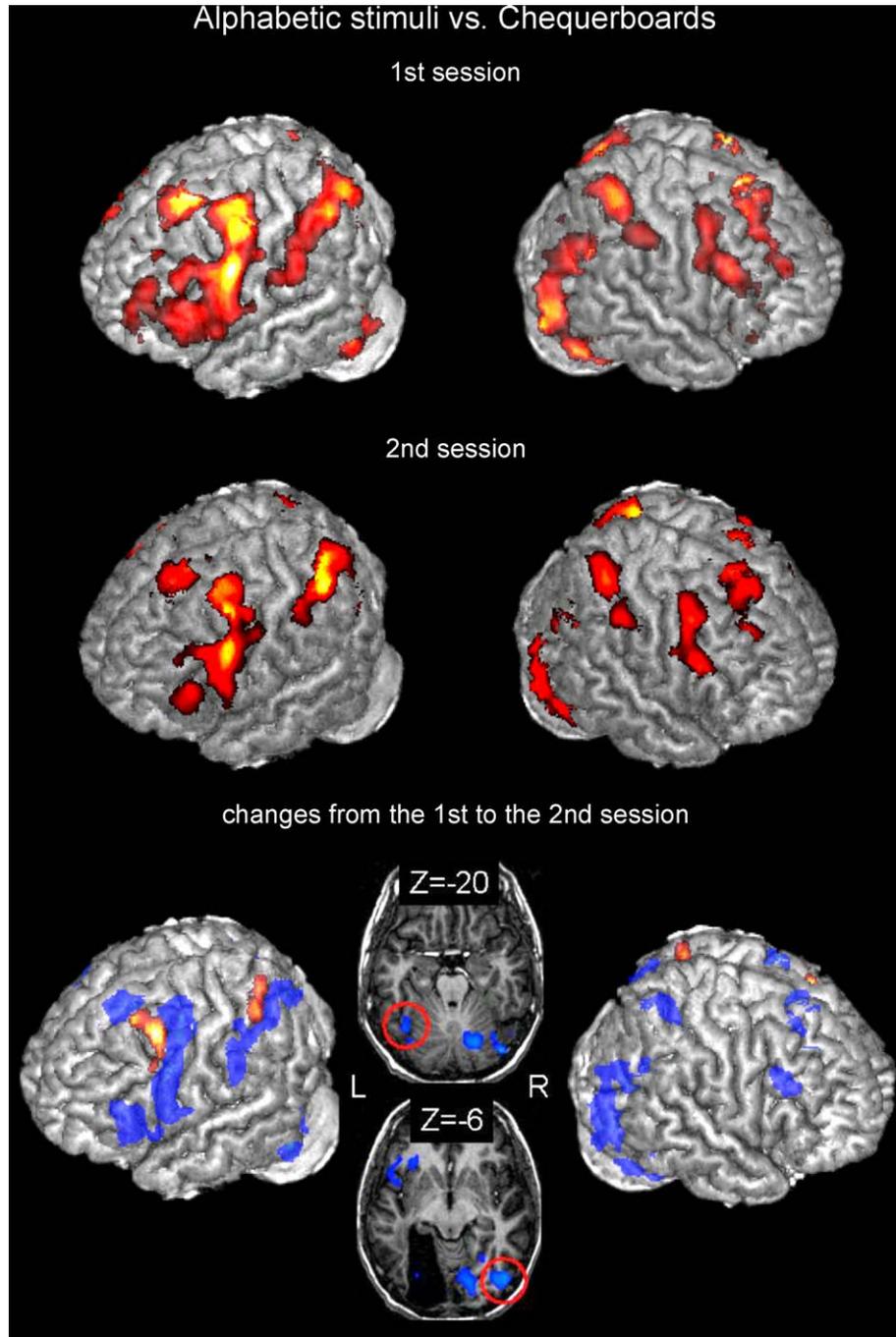


Fig. 2. Anterolateral views of the patient's brain. Functional overlays show areas activated by alphabetic stimuli vs. chequerboards. Top: Activations during the first fMRI session. Middle: Activations during the second fMRI session. Bottom: The contrast decreased in most of the network from the first to the second fMRI session (blue); restricted left-hemispheric frontal and parietal regions showed increased activations (hot). The decrease in the VWFA and R-VWFA are illustrated on the bottom central slices.

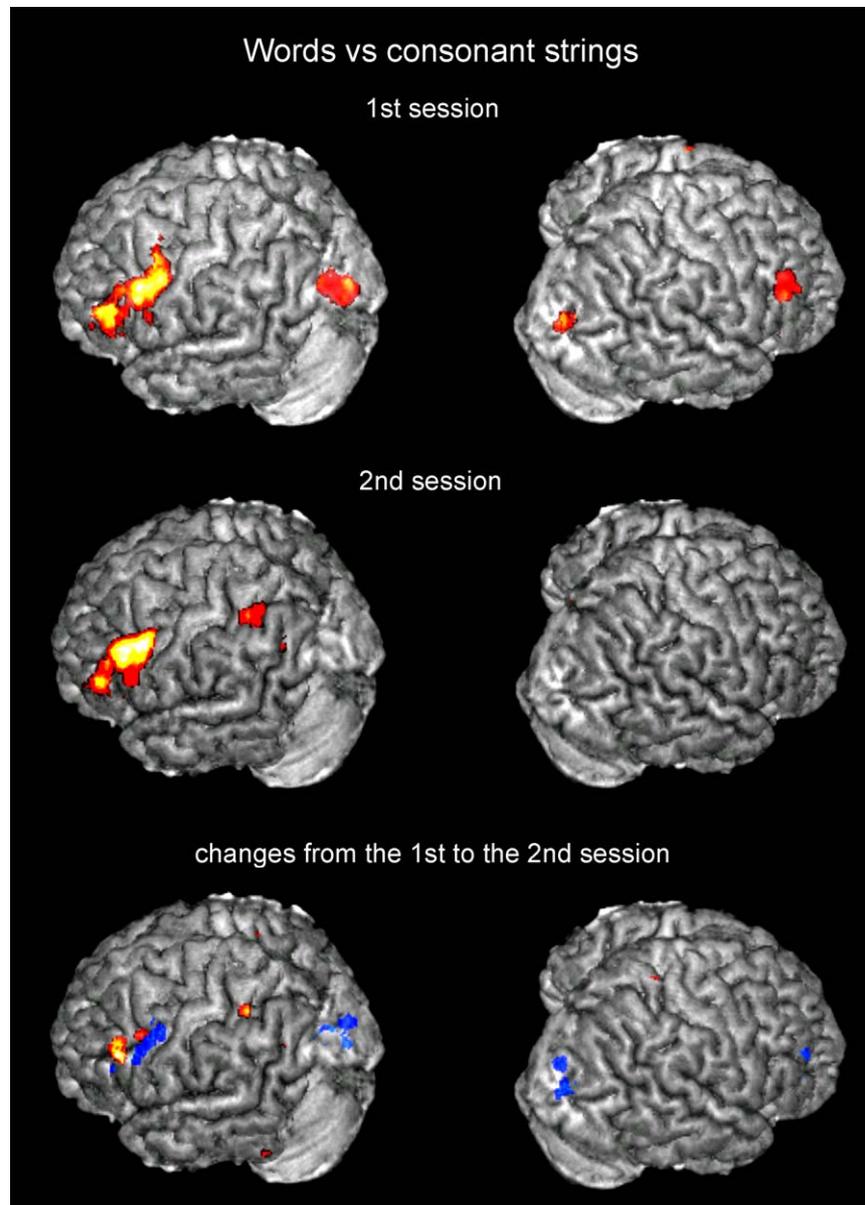


Fig. 3. Posterolateral views of the patient's brain. Functional overlays show areas activated by LBL reading of real words, as compared to viewing consonant strings. Note that the right occipital activations are visible on left lateral views due to the resection of the left occipital pole. Top: Activations during the first fMRI session. Middle: Activations during the second fMRI session. Bottom: The contrast generally decreased between sessions (blue), except for increases in left-hemispheric frontal and parietal regions (hot).

by the contrast in Session 1. Increases were identified by the symmetrical procedure. Almost the entire network showed a significant decrease from Session 1 to Session 2 (Fig. 2). This decrease affected, among other regions, the bilateral ventral occipitotemporal stream, including the VWFA (TC $-42 -66 -29$; $Z = 7.60$) and the R-VWFA (TC $39 -51 -30$; $Z = 4.45$) (at the peaks observed in Session 1: $Z = 2.94$ for the VWFA; $Z = 4.01$ for the R-VWFA).

Only two left-hemispheric regions showed a significant increase: the posterior part of the middle frontal gyrus (TC $-36 6 48$; $Z > 8.0$), and the anterior part of the superior parietal lobule (TC $-24 -54 60$; $Z = 6.67$).

In order to determine whether, due to the general activation decrease, the regions that showed an excess of activation during the first session returned to a normal level, we compared the patient's second session to a group of nine controls. Like in the initial study (Cohen et al., 2004a), we used a voxelwise $P < 0.02$, with a clusterwise $P < 0.05$ corrected within the patient's overall reading network, i.e. the volume activated by alphabetic stimuli minus fixation. Among the regions that initially showed an excess of activation, the right ventral temporal cortex returned to a normal level, while the right occipitoparietal cluster was still significantly above normal level (TC $33 -63 15$; $Z = 3.82$). Conversely, the frontal (TC $-24 -9 54$;

$Z = 3.58$) and parietal (TC $-42 -51 57$; $Z = 2.64$; below clusterwise threshold) regions which increased across sessions were eventually activated more strongly than in normals.

3.2.2. Letter-by-letter reading

As the patient engaged in LBL reading only with real words, we tried to isolate more specifically the activations related to this strategy by contrasting words minus consonant strings, masking by words minus fixation (Fig. 3). During Session 1, this procedure showed a network mainly including left precentral cortex and Broca's area, and right occipital and prefrontal cortex (Cohen et al., 2004a). During Session 2, similar left frontal areas were activated (TC $-48 15 27$; $Z = 6.93$; TC $-39 30 0$; $Z = 5.46$). However there were no more right occipital activations, while a left parietal focus appeared (TC $-21 45 42$; $Z = 4.84$). Note that there was no difference between words and consonants in the VWFA or the R-VWFA in either sessions.

In order to identify decreases from Session 1 to Session 2, we compared the contrast of words minus consonants in Session 1 minus Session 2, masking by the contrast in Session 1. The statistic for cluster extent was corrected within the volume activated by words minus consonants over both sessions ($P < 0.05$). Increases were identified using the symmetrical procedure. There was a decrease in a large portion of the network: left precentral (TC $-60 6 30$; $Z = 4.93$), right occipital (TC $21 -87 3$; $Z = 3.84$) and right prefrontal (TC $30 33 -12$; $Z = 3.92$). There was also a small but strong cluster in the anterior cingulate cluster below the extent threshold (TC $3 39 30$; $Z = 5.55$).¹ Conversely, there was an increase in two left-hemispheric regions: the posterior inferior frontal sulcus (TC $-54 18 24$; $Z = 5$; TC $-36 9 27$; $Z = 3.40$) and the anterior intraparietal sulcus (TC $-39 -48 54$; $Z = 4.05$).

Following the same logic as before, we compared the patient's activations to the group of nine controls. Among the regions that initially showed an excess of activation for words relative to consonants, the right occipital cortex returned to a normal level, while the left frontal, which increased between sessions, remained above the normal level (TC $-36 3 33$; $Z = 2.68$).

4. Discussion

The main findings of this follow-up study can be summarized as follows. When considering the overall reading network identified by contrasting alphabetic stimuli minus chequerboards, we found that the topography of activations was mostly unchanged as compared to the first fMRI session, including left-predominant frontoparietal and right-predominant temporal areas. However, the activation level decreased in most of this network between the two sessions. This general trend contrasted with a focal increase restricted

to specific left frontal and parietal areas. When studying the contrast between words and consonant strings, which may be taken as a correlate of LBL reading, we also found a general decrease, except for left frontal and parietal regions similar to those just mentioned, which showed a significant increase. In order to understand this pattern of evolution, one may distinguish two simultaneous requirements for the emergence and improvement of LBL reading. First, the specific visual function of the removed VWFA should be substituted by some intact structures with roughly equivalent computational properties. It may be expected that such structures should remain active whatever the level of proficiency reached by the patient, although possibly with different activation levels or changes in functional tuning across time. Second, the patient should elaborate and train the overall LBL reading strategy, which requires the coordination of visuospatial, attentional, working memory, and lexical processes. This situation is largely similar to the skill learning involved in mirror reading in normal subjects, a task that also involves the tuning of the visual system to novel shapes (i.e. mirror-reversed letters). These two aspects of the follow-up pattern will be discussed in turn.

We showed that following disruption of the VWFA, the recognition of letters was probably achieved in the symmetrical right-hemispheric R-VWFA (Cohen et al., 2003, 2004a). Accordingly, the R-VWFA was activated in both sessions with a comparable profile, namely a larger activation for alphabetic strings than for chequerboards, with no difference between words and consonant strings. It is thus likely that it retained the same functional role in LBL reading, i.e. the visual identification of letters. Concerning the deafferented VWFA itself, we previously argued, mostly on the basis of anatomical data, that it probably played no causal role in the patient's behaviour. Follow-up data are neutral relative to this hypothesis, as activity decreased without disappearing, while reading performance improved. As to the more posterior right occipital regions implementing visual input in right-hemianopic patients, they initially showed stronger activation for words than for consonants. This effect may be attributed to attentional enhancement during LBL reading (Muller, Bartelt, Donner, Villringer, & Brandt, 2003; Somers, Dale, Seiffert, & Tootell, 1999), or simply to a longer-lasting visual processing of real words than of consonant strings (Price & Friston, 1997). At any rate, this difference was not observed in Session 2, suggesting either that the tuning of the LBL reading network did not require such enhancement any more, or that word processing had become substantially faster. An hypothetical tuning of the visual system may be understood in the framework of the reverse hierarchy theory (Ahissar & Hochstein, 2004). In the early post-lesion period, accurate letter identification would require amplification of low-level visual levels representing the component features of letters, due to the coarse tuning of the right-hemispheric visual system, as compared to the expert left-hemisphere. After extensive practice, the improved tuning of the visual cortex to letters would allow the task to be performed on the

¹ When raising the voxelwise threshold to $P < 0.0001$, the cluster was significant for extent ($P = 0.013$, corrected within the whole brain).

basis of higher-level letter representations, no longer requiring a strong amplification of occipital cortex. Finally, it is interesting to note that a longitudinal pattern of occipitotemporal activation similar to the present one was observed during mirror-reading (Poldrack, Desmond, Glover, & Gabrieli, 1998; Poldrack & Gabrieli, 2001): (1) An initial occipital enhancement for mirror words relative to normal stimuli, followed by a decrease following skill learning. (2) A stable or increased activation in the mid-fusiform cortex close to the VWFA.

Beyond the areas involved in visual input, most of the network subtending alphabetic processing showed a decrease of activation from Session 1 to Session 2. As mentioned before, reduced processing time may contribute to decreased activations during learning. However, this is unlikely to play an important role in the present case. As mentioned in the study of Session 1 (Cohen et al., 2004a), the patient attempted to identify all words through LBL reading, but the rate of stimulus presentation (SOA = 2500 ms) was often shorter than the time required for an accurate identification. Thus, blocks of word reading were “saturated” by the LBL reading procedure. Despite the reduction of reading latencies, the situation was comparable during Session 2, as reading latencies fell somewhat below 2500 ms for three-letter words only. Activation decreases may also be linked to a reduced need for executive control as tasks become more automatic, and there was indeed a decrease in bilateral prefrontal regions (Figs. 2 and 3). Similarly, improved expertise may require less monitoring of errors, which might account for the reduced difference between words and consonants in the anterior cingulate cortex (Botvinick, Cohen, & Carter, 2004).

Other accounts of activation decreases during learning have been reviewed by Poldrack (2000). Experience may bring about a reduction in initially active regions, in parallel with a sharpening of responses in a better-tuned or more task-specific network. Accordingly, we observed increases in restricted frontal and parietal areas surrounded by activation decreases. Interestingly, a subset of those areas showed an increase in the contrast between words and consonant strings, suggestive of an improved tuning to the LBL reading task.

The left posterior frontal region where we observed an increase also showed an increase associated with the learning of mirror-reading (Poldrack & Gabrieli, 2001). It is involved in verbal/phonological working memory processes (Gruber & von Cramon, 2003), and its activation may reflect a more efficient lexical search or retrieval during LBL reading. As to the region of anterior intraparietal/SPL increase, it is activated by tasks of spatial working memory (Gruber & von Cramon, 2003) and is involved in spatial attention (Gitelman et al., 1999). It may be associated with a more efficient scanning of letters, although a contribution to phonological working memory cannot be excluded.

In conclusion, we should acknowledge that any detailed account of the evolution of brain activations in this patient can only be tentative. However, the overall pattern fits well with the minimal hypothesis of normal strategic abilities

and skill learning, associated with perceptual tuning in right-hemispheric structures able to substitute the disrupted VWFA. The same view probably applies more generally to functional compensation following brain lesions, and may explain the heterogeneity of post-lesional activation patterns, depending on the potential of substitution for the damaged modules, and on the development of compensation strategies (Demonet, Thierry, & Cardebat, 2004; Rijntjes & Weiller, 2002).

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