

Distinct unimodal and multimodal regions for word processing in the left temporal cortex

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How are word recognition circuits organized in the left temporal lobe? We used functional magnetic resonance imaging (fMRI) to dissect cortical word-processing circuits using three diagnostic criteria: the capacity of an area (1) to respond to words in a single modality (visual or auditory) or in both modalities, (2) to modulate its response in a top-down manner as a function of the graphemic or phonemic emphasis of the task, and (3) to show repetition suppression in response to the conscious repetition of the target word within the same sensory modality or across different modalities. The results clarify the organization of visual and auditory word-processing streams. In particular, the visual word form area (VWFA) in the left occipitotemporal sulcus appears strictly as a visual unimodal area. It is, however, bordered by a second lateral inferotemporal area which is multimodal [lateral inferotemporal multimodal area (LIMA)]. Both areas might have been confounded in past work. Our results also suggest a possible homolog of the VWFA in the auditory stream, the auditory word form area, located in the left anterior superior temporal sulcus.

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Introduction

In literate adults, the perception of a written word gives access, within half a second, to a wide variety of representations and processes ranging from orthography and phonology to semantics and articulation (Marinkovic et al., 2003). Accordingly, word reading is correlated with the activation of extensive bilateral cerebral networks, with left-sided predominance (for reviews, see for example, Fiez and Petersen, 1998; Jobard et al., 2003; Price et

al., 2003a). However, the efficacy of all those processing stages first depends on the fast and parallel identification of strings of letters by the visual system, which may be seen as the gateway into the reading network (Besner, 1989; Nazir, 2000; Paap et al., 1984; Pelli et al., 2003). Among the visual areas that are consistently activated during reading, we proposed that a region of the left inferotemporal cortex plays a crucial role in this perceptual expertise (Cohen et al., 2000). On the basis of imaging and neuropsychological data, we suggested that this region (the visual word form area or VWFA) computes a representation of abstract letter identities from visual input, a representation invariant for irrelevant parameters such as size, location, font, or case (for reviews, see Cohen and Dehaene, in press; McCandliss et al., 2003).

There are still ongoing controversies about the functional properties of the VWFA, and particularly about its involvement in the processing of auditory or even Braille words (Büchel et al., 1998; Cohen and Dehaene, in press; Price et al., 2003b). In a recent study using functional magnetic resonance imaging (fMRI), we contrasted the processing of written and spoken words while subjects performed a same–different task on consecutive words (Dehaene et al., 2002). In agreement with our hypotheses, the left inferotemporal cortex was activated by visual words in every subject, while there was no activation by spoken words. However, a number of other studies have demonstrated left inferotemporal activations during the perception of auditory words (e.g., see Binder et al., 1996; Büchel et al., 1998; Buckner et al., 2000; Chee et al., 1999; Démonet et al., 1992, 1994; D’Esposito et al., 1997; Giraud and Price, 2001; Perani et al., 1998; Pihlajamäki et al., 2000; Vandenberghe et al., 1996; Wise et al., 2000). As discussed in Cohen et al. (2002), this apparent discrepancy may result from at least two causes.

First, the left inferotemporal cortex may encompass several distinct areas involved in word processing, each area having distinctive patterns of activation to written or spoken words. Due to their close proximity, such regions may be difficult to distinguish, particularly when comparing the coordinates of activations across subjects and across studies, including group PET studies with a relatively low spatial resolution. Notwithstanding those methodological limitations, a review of ventral temporal activations suggests

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that words in nonvisual modalities yield activations more anterior (average $y = -43$) than the visual activations typical of the VWFA (average $y = -60$) (Cohen et al., 2002). Furthermore, the anterior activations are more sensitive to the semantic demands of the task, whereas posterior activations were observed even for visual pseudowords relative to random letter strings. Thus, the VWFA should possibly be distinguished from more anterior regions that are increasingly multimodal and engaged in semantic computations (for a convergent metaanalysis, see Jobard et al., 2003). Fine-grained spatial distinctions between inferotemporal regions with different modal selectivity have also been shown in studies of object perception (Amedi et al., 2001). To clarify this issue, one should resort to imaging techniques with a high spatial resolution and perform individual analyses to override the limitations due to interindividual anatomical variations (Sowell et al., 2002; Thompson et al., 1996).

A second source of difficulty in identifying the modality-dependent properties of inferotemporal cortex is that all visual regions, from area V1 to high-level inferotemporal cortex, can be activated in the absence of any visual input, depending on the requirements of the task (Pessoa et al., 2003; Somers et al., 1999). For instance, top-down activations have been evidenced in regions close to the VWFA during the mental imagery of faces or places (Ishai et al., 2000; O'Craven and Kanwisher, 2000). Similarly, the left inferotemporal cortex is activated when Japanese subjects write complex kanji ideograms or imagine doing so, a task with a strong visual component (Nakamura et al., 2000; Tokunaga et al., 1999). Such top-down influences may contribute to inferotemporal activations that are observed with auditory words, provided that the task involves some form of orthographic manipulation. For instance, Booth et al. (2002a, 2003) observed left inferotemporal activations when subjects performed a spelling task on auditory words, but not when they performed a rhyming task on the same stimuli (see also Burton et al., 2000). Thus, clarifying the role of task on the pattern of left inferotemporal activations requires that modality and task be independently manipulated.

We may now summarize the questions that are still open relative to the effect of word modality on left inferotemporal activations, distinguishing bottom-up from top-down influences. First, is there a unimodal visual area in the left inferotemporal region associated with visual word recognition (the VWFA)? Unimodality implies that this region should receive direct input from lower-level visual cortex, but not from equivalent auditory or tactile input systems. However this does not preclude some top-down activation by spoken words, but only when required by specific task demands. Second, if there is such a unimodal region, can it be distinguished from multimodal inferior temporal regions whose activation pattern would not crucially depend on input modality during word processing? Third, how are those areas affected by task demands, and particularly, can the VWFA be activated during auditory word processing if the task requires access to a visual or orthographic representation? Fourth, can equivalent areas be defined for spoken words?

To address those issues, we recorded brain activation with fMRI while manipulating stimulus modality (written vs. spoken words) and task demands (letter feature detection vs. phoneme detection). Letter feature detection (detecting whether a word contains a descending lowercase letter) was intended to activate visual or orthographic representations, even with auditory stimuli. Conversely, phoneme detection (detecting whether a word contains a specific phoneme) was intended to activate phonological representations even with written words.

We further combined this orthogonal task \times modality design with the priming method (Naccache and Dehaene, 2001), by asking which areas are sensitive to word repetition and, if so, whether they are sensitive to cross-modal as well as to within-modality repetitions. On half the trials, the target word was a repetition of the previous word, either in the same modality or in a different modality. We expected that many brain areas would show a reduced activation on such repeated trials (repetition suppression) and that the pattern of repetition suppression would provide further confirmation of modality specificity: unimodal regions would be sensitive exclusively to word repetition within the corresponding modality, while multimodal regions may show comparable repetition effects within and between modalities.

Note, however, that our design investigated conscious rather than subliminal repetition priming. One drawback of conscious priming is that, once subjects become aware of the repetition, they may strategically alter their response decisions. In that respect, priming may help distinguish bottom-up from top-down activations. On any given trial, repeated words must follow essentially the same path as nonrepeated words in the visual and auditory cortices, at least up to the point where repetition is consciously detected. Subjects may then bypass the detection of the target phoneme or letter and directly trigger the same response as on the previous trial. This model of conscious priming would predict that top-down activations reflecting task-dependent processes should be reduced by repetition more than bottom-up activations chiefly depending on stimulus modality.

Methods

Subjects

Seventeen subjects (10 females, 7 males), aged 20–30 years, with university education, fully right-handed according to the Edinburgh Inventory, participated in the study. All were drug-free, had no neurological or psychiatric history, and had normal anatomical MRIs. All gave their written informed consent. The experiment was approved by the Ethical Committee of the Hôpital de Bicêtre.

Tasks and stimuli

Subjects received lists of randomly mixed auditory and visual words. Before each list, they were instructed to perform either a phoneme detection task or a descender detection task (Fig. 1). The phoneme task and the auditory modality were a priori considered as “congruent,” as were the descender task and the visual modality. Nevertheless, subjects had to apply the specified task to all words in the current list irrespective of input modality. When words included a prespecified phoneme or a letter with a descender (g, j, p, q, y), depending on the task, subjects responded by pressing a key with their right hand. They responded with their left hand when words did not include the target. Subjects were asked to respond as fast as possible while minimizing errors. To induce processing of the descender task on an abstract graphemic level, visual words were printed in upper case, and subjects were asked to respond on the basis of a mentally generated image of the lower-case word. Moreover, on half the trials, the same target word as on the preceding trial was used again in the same or in a different modality.

Stimuli consisted of 384 French common nouns with a mean length of 6.90 letters (range: 4 to 8) and a mean log frequency of

Experimental design			
		stimulus modality	
		visual	auditory
orthographic task (target: descenders)	targets:	<u>p</u> inceau	/p \tilde{e} so/
		<u>pl</u> aine	/plen/
	non targets:	cr <u>a</u> inte	/kr \tilde{e} t/
		mine	/min/
phonological task (target: e.g. phoneme / \tilde{e} /)	targets:	<u>p</u> inceau	/p \tilde{e} so/
		cr <u>a</u> inte	/kr \tilde{e} t/
	non targets:	plaine	/plen/
		mine	/min/

Fig. 1. Experimental design. Subjects were presented with blocks of mixed visual and auditory words. Before each block, they were instructed to perform either a phoneme detection task or a descender detection task. Targets are underlined.

0.95 per million (range: -0.68 to 3.00). This corpus was divided into six sets of 64 words. Each set was associated with a target phoneme (three sets with phoneme / \tilde{a} /, two sets with phoneme / \tilde{o} /, one set with phoneme / \tilde{e} /). Half the words in each set comprised the target phoneme, and half did not. In each of those subsets of 32 stimuli, half the words included at least one letter with a descender (g, j, p, q, y), and half did not. To discourage subjects from performing the phoneme detection task on an orthographic basis, we selected target phonemes with multiple written equivalents, all requiring several letters. For instance, phoneme / \tilde{e} / is spelled out differently in pINceau, crAINte, fEINte, tYMpan, etc. Importantly, all letter groups used for the target phonemes can also be used to represent other phonemes. For instance, no phoneme / \tilde{e} / appears in the words mINe, chAINe, baEINe, or sYM \tilde{e} trie. Therefore, within each set of 64 words, care was taken to equate orthographically as closely as possible the two subsets of 32 words with and without the target phoneme. For instance, if a set included four words with the phoneme \tilde{e} written as an initial IN, four other words with an initial IN not pronounced as / \tilde{e} / were included in the set.

Procedure

Subjects received six fMRI sequences, with an alternation of phonological and orthographic sequences; half the subjects started with the phonological task and the other half with the orthographic task. Before each sequence, the task and the target were specified by spoken instructions. Each sequence included 120 trials in a pseudorandom order: 48 auditory trials, 48 visual trials, and 24 rest trials with no stimulus. On half of the nonrest trials, the stimulus was the same word as on the previous trial. For both repeated and nonrepeated trials, half of the stimuli were in the same modality as the previous word (AA or VV), and the other half were in a different modality (AV or VA). All trials had a total duration of 3000 ms. A central fixation point was continuously present except during the display of visual words. On auditory trials, the stimulus word was presented binaurally over headphones. On visual trials, the stimulus was displayed foveally for 200 ms. Additionally, the experiment was preceded by two short training sequences (one for each task) of 60 trials each.

Imaging parameters

Functional images sensitive to blood oxygen level-dependent (BOLD) contrast were obtained on a 3 T magnet (Bruker) with a T2*-weighted gradient echoplanar imaging sequence (TR = 3000 ms; TE = 30 ms; angle = 90° ; voxel size = 3.75×3.75 mm; matrix = 64×64). Covering the whole brain and the top of the cerebellum, 26 4.5-mm axial cuts were obtained every 3000 ms. Slice acquisitions were grouped at the end of each TR, thus leaving a 1300-ms initial silent period during which the target words were presented. A total of 124 brain volumes were acquired consecutively for each run (one image per trial, plus four initial images excluded from the analysis), for a total of 744 images per subject. High-resolution images (3D gradient, echo inversion-recovery sequence, TI = 700 ms, TR = 1600 ms, FOV = $192 \times 256 \times 256$ mm³, matrix = $256 \times 128 \times 256$, slice thickness = 1.2 mm) were also acquired for anatomical localization.

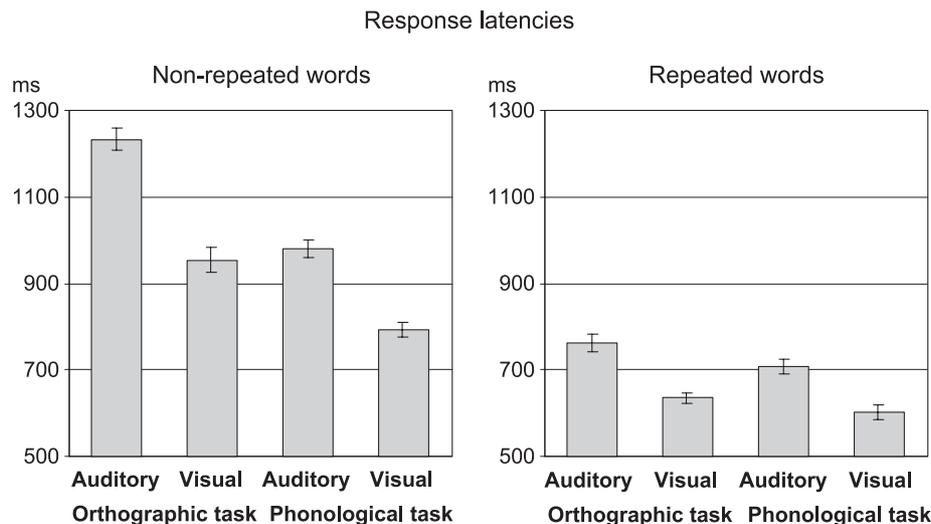


Fig. 2. Mean correct response latencies. In addition to main effects of modality, task, and word repetition, responses were faster when modality and task were congruent (phonological task with auditory stimuli or orthographic task with visual stimuli) than when they were incongruent. Error bars represent ± 1 SEM across subjects after subtraction of each subject's overall mean.

Statistical analysis of imaging data

fMRI data were processed using SPM99 software, starting with slice timing, correction for movements, spatial normalization, and smoothing with a 5-mm Gaussian kernel. We generated a linear model by defining 16 trial types: auditory or visual modality, orthographic or phonological task, repeated or nonrepeated word, repeated or nonrepeated modality. These categories were combined with indicator variables for the six sessions, yielding a total of 48

onset vectors, which were convolved with the standard SPM hemodynamic function and its derivative. Both individual analyses and group analyses were performed; the group analyses consisted in random-effect t tests using the individual contrast images smoothed at 5 mm (one image per subject). Unless otherwise indicated, in individual and in group analyses, contrast images were thresholded at a voxelwise $P < 0.01$. We evaluated the statistical significance of activation clusters on the basis of their size, applying a threshold of $P < 0.05$, corrected for multiple comparisons across the brain volume.

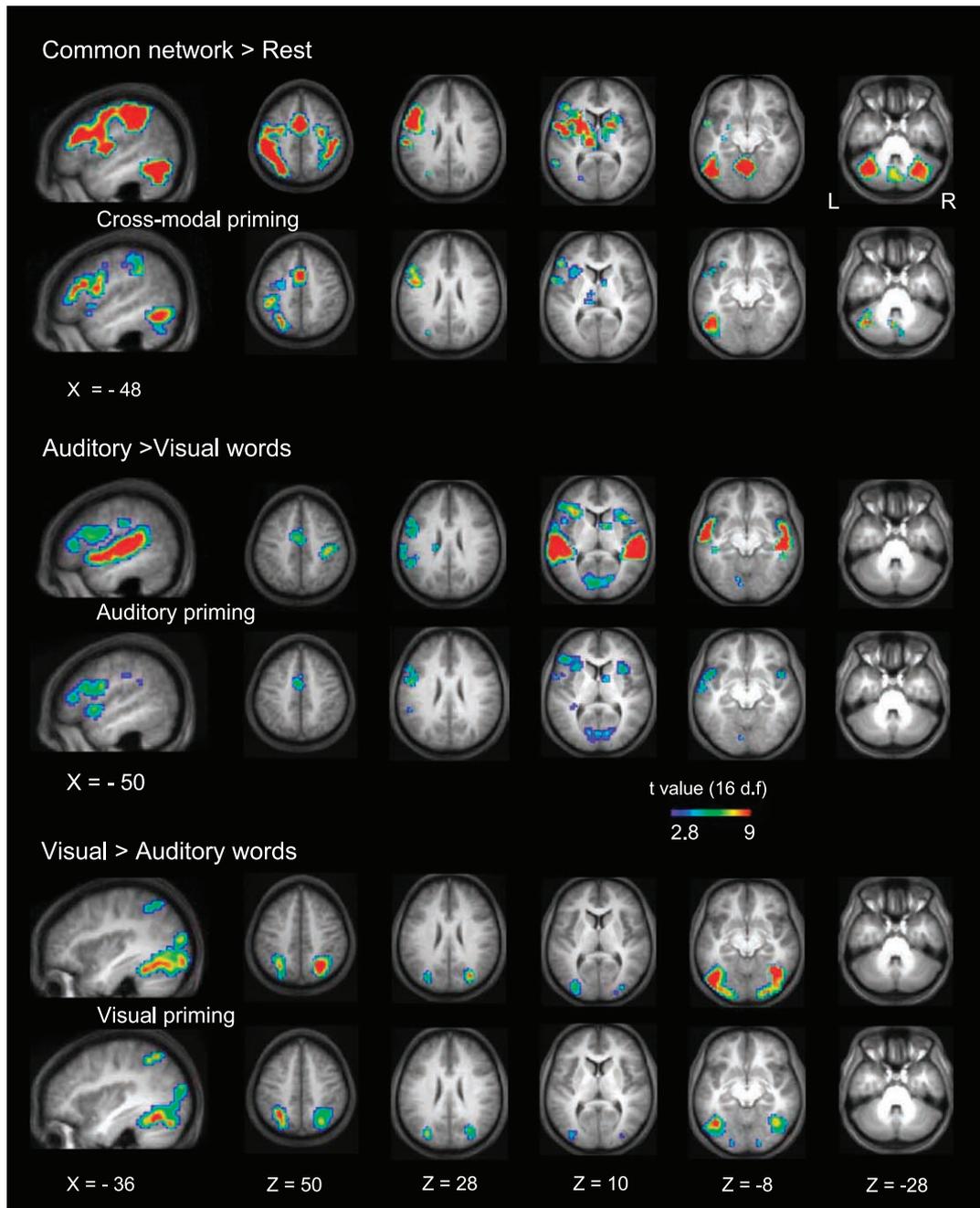


Fig. 3. (Top) Common network activated across both modalities and both tasks, including a left inferior temporal region (TC $-48, -60, -16$). (Middle) Activations by auditory versus visual words, irrespective of the task. (Bottom) Activations by visual versus auditory words, irrespective of the task, including left (TC $-44, -68, -4$) and right (TC $40, -60, -8$) inferior temporal regions. Odd rows show data from trials with nonrepeated words. Even rows show the subsets of those networks with significant word repetition suppression (top: suppression in AA, AV, VV, and VA pairs of trials; middle: suppression with AA pairs of trials; bottom: suppression with VV pairs of trials).

Behavioral results

Subjects made 3.8% errors overall. Error trials were excluded from the analysis of latencies.

Median latencies were computed for each subject and each condition and were entered in an ANOVA with subjects as random factor. Responses latencies depended in simple ways on the main experimental factors (Fig. 2). First, responses were faster to written than to spoken words (746 vs. 921 ms; $F(1,16) = 221, P < 10^{-6}$), a trivial consequence of the fact that, in both modalities, latencies were measured from the onset of stimuli. Second, the phonemic task was faster than the descender task (771 vs. 896 ms; $F(1,16) = 26.6, P < 10^{-3}$). Third, responses were faster when task and stimulus modality were congruent (i.e., phonemic task with auditory words, or descender task with visual words) than when they were incongruent (819 vs. 848 ms; $F(1,16) = 26, P < 10^{-3}$). Finally, trials with repeated words were much faster than nonrepeated trials (677 vs. 990 ms; $F(1,16) = 169, P < 10^{-6}$). Interactions indicated that this reduction of latencies with word repetition was larger for the more difficult conditions. There was more reduction for the descender task than for the phonemic task (effect size 82 ms; $F(1,16) = 103, P < 10^{-6}$) and for auditory than for visual stimuli (effect size 59 ms; $F(1,16) = 21, P < 10^{-3}$). Moreover, the repetition effect was larger when words were repeated within the same modality than across different modalities (effect size 61 ms; $F(1,16) = 47.5, P < 10^{-5}$).

Error rates showed a parallel pattern, with more errors (i) in the orthographic than in the phonological task, (ii) when task and modality were incongruent than when they were congruent, and (iii) with nonrepeated than with repeated words, particularly in the more difficult orthographic task and on incongruent trials (all P s < 0.05).

Behavioral data can be summarized as follows. First, there were straightforward effects of stimulus modality and of overall task difficulty. Second, there was an effect of the congruence of modality and task suggesting that phoneme detection was linked to auditory processing, and descender detection to visual processing. Third, word repetition reduced response latencies to fast values that were less dependent on task and on modality, thus suggesting that, whenever subjects detected a repetition, they merely replicated their previous response. Fourth, the effect of repetition was larger when words were repeated within the same modality, that is, were physically identical. This suggests that the overall repetition effect may be broken down into a modality-specific component and a cross-modal component, possibly depending on brain regions with different patterns of response to spoken and written words.

Imaging results

The analysis of response latencies suggested that the influence of modality and task was markedly reduced on repeated trials. Therefore, we first studied activations related to modality and task within the nonrepeated trials only and then considered the effect of word repetition.

Modality and task in nonrepeated trials

Network common to both tasks and both modalities

To identify regions commonly activated in all experimental conditions, we computed a main contrast pooling all tasks and modalities versus rest (voxelwise $P < 0.01$; corrected $P < 0.05$ for cluster extent) and masked it with the four restricted contrasts (modality \times task) versus rest (voxelwise $P < 0.01$ each) (Fig. 3).

This revealed bilateral rolandic, SMA/cingulate, parietal, lenticular and cerebellar activations, and left-hemispheric activations in the dorsolateral prefrontal cortex, Broca area/anterior insula, inferotemporal (TC $-48, -60, -16$; $Z = 5.5$), and thalamus.

Modality-related activations

We then studied regions that showed an effect of stimulus modality (Fig. 3 and Table 1). To identify auditory activations, we contrasted auditory versus visual stimuli (voxelwise $P < 0.01$; corrected $P < 0.05$ for cluster extent). To ensure that those activations did not result from deactivations by visual stimuli, the contrast was masked by both auditory tasks vs. rest (voxelwise $P < 0.01$ each). Visual activations were identified using the symmetrical procedure.

Auditory activations included bilateral superior temporal, inferior frontal/insular, inferior precentral, SMA/cingulate, calcarine, and right-hemispheric postcentral, and caudate activations. Visual activations included bilateral inferotemporal (left: TC $-44, -68, -4$; $Z = 5.08$; right: TC $40, -60, -8$; $Z = 5.33$) and posterior intraparietal activations. Note that the left inferotemporal peak was also significantly activated by spoken words relative to rest [$t(16) = 3.4$; $P < 0.005$], although more weakly than by written words. In contrast, the right inferotemporal peak showed strictly no activation by spoken words [$t(16) < 1$].

Single-subject analysis of modality effects in left inferotemporal cortex

These group results indicated the presence of left inferotemporal activations close to the visual word form area in two analyses. First, a left inferolateral temporal area was activated jointly by both tasks and both modalities (TC $-48, -60, -16$). Second, a slightly more mesial and posterior area was activated by written words more than by spoken words (TC $-44, -68, -4$). In the group analysis, those two regions were partially overlapping. However, this overlap might be due to intersubject averaging and smoothing. To clarify this, we examined both contrasts for each single subject (voxelwise $P < 0.01$; corrected $P < 0.05$ for cluster extent). In each subject, we

Table 1
Modality-related activations in trials with nonrepeated words

Area	Voxel Z score	TC		
		x	y	z
<i>Auditory > visual</i>				
L superior temporal	6.31	-64	-20	12
R superior temporal	6.56	56	-8	0
L inferior frontal/insular	3.80	-32	20	8
R inferior frontal/insular	4.71	44	16	0
L inferior precentral sulcus	3.75	-56	0	20
R inferior precentral sulcus	4.33	48	12	16
L supplementary motor/cingulate	3.16	-12	-8	40
R supplementary motor/cingulate	3.88	8	-12	44
L calcarine	3.22	-12	-92	16
R calcarine	3.21	8	-88	20
R postcentral gyrus	4.02	28	-28	64
R caudate	3.31	12	0	16
<i>Visual > auditory</i>				
L fusiform	5.08	-44	-68	-4
R fusiform	5.33	40	-60	-8
L posterior intraparietal	4.19	-24	-64	56
R posterior intraparietal	4.58	24	-60	48

Individual activations of the visual word form area (VWFA) and of a lateral inferotemporal multimodal area (LIMA)

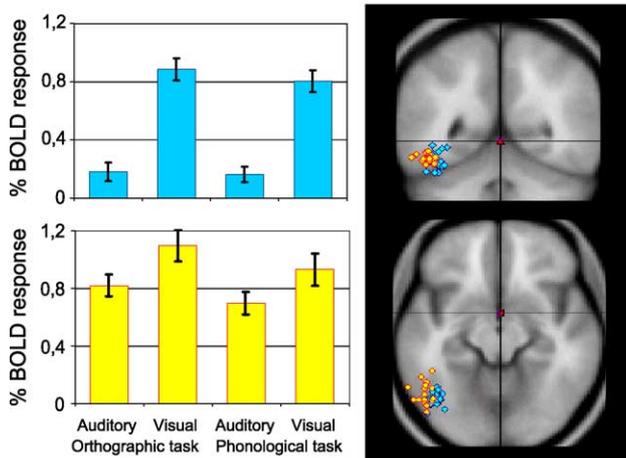


Fig. 4. Plot of individual peak activations showing joint activation to both tasks and modalities in the left lateral inferotemporal multimodal cortex (LIMA) (yellow dots) and modality-specific activation to visual words in the left occipitotemporal sulcus (VWFA) (blue dots). Activation was stronger for the orthographic than for the phonological task in the LIMA only.

identified the peak closest to the coordinates from the group analysis; in ambiguous cases, we report the peak with the highest Z score. This procedure isolated a multimodal peak in all but four subjects and a visual > auditory peak in all but two subjects. In the remaining cases, lower thresholds were applied ($P < 0.02$, unmasked, for the visual vs. auditory contrast; and $P < 0.02$, masked by the four restricted contrasts at $P < 0.05$ each, for the contrast of all activations vs. rest).

This within-subject analysis confirmed that the multimodal peak was significantly more lateral [$t(16) = 5.3$; $P < 0.0001$] and somewhat more anterior [$t(16) = 2.4$; $P = 0.027$] than the peak of visual activations (Fig. 4). In most subjects, multimodal and visual clusters showed little or no overlap. When there was some overlap, it was at the borders of the two clusters, restricted to less significant voxels.

We tried to determine whether those two activation foci had reproducible locations relative to sulcogyral landmarks. There was an important variability in regional sulcal organization. Nevertheless, the visual activation was consistently located in the depth of the lateral occipitotemporal sulcus, while the multimodal activation tended to follow the inferior temporal sulcus. As an example, Fig. 5 shows the brain of three subjects with an inferior temporal sulcus located respectively at an average, a markedly dorsal, and a markedly ventral position. In all cases, the multimodal activation focus was located in this sulcus. For the sake of

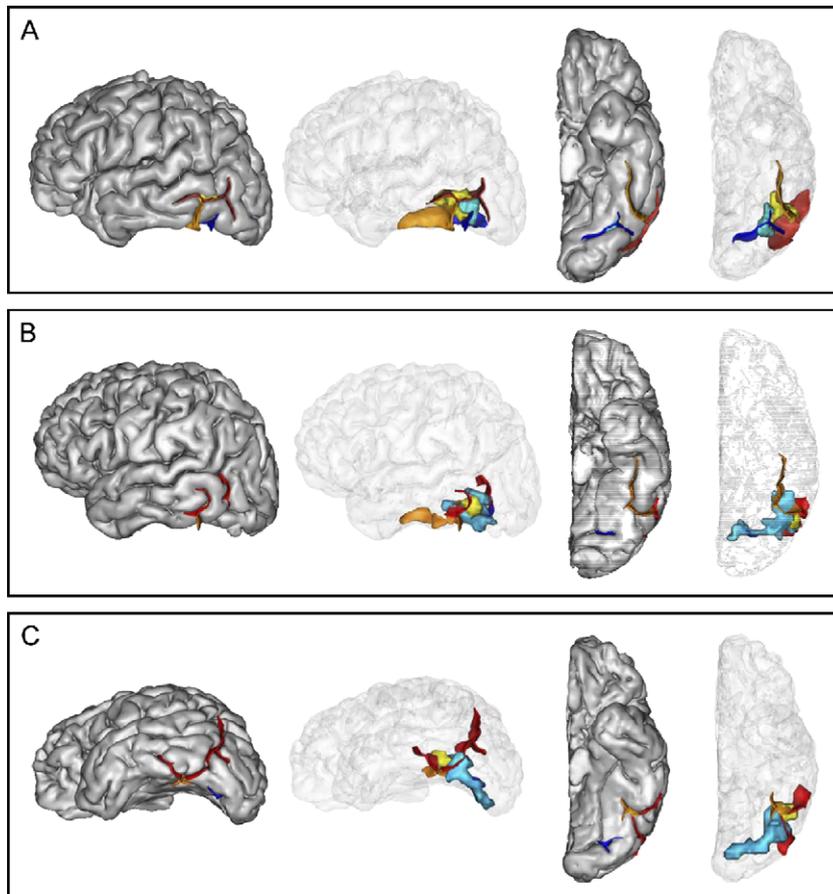


Fig. 5. The visual activation of the VWFA (light blue) was consistently located in the depth of the lateral occipitotemporal sulcus (dark blue), while the multimodal activation of the LIMA (yellow) tended to follow the inferior temporal sulcus (red), as illustrated by the brain of three subjects, with an inferior temporal sulcus located respectively at an average (A), a markedly dorsal (B), and a markedly ventral (C) position.

clarity, whenever it will be possible to distinguish clearly those two inferotemporal regions, we will refer to the visual area as the VWFA and to the multimodal area as the lateral inferotemporal multimodal area (LIMA). It should be clear that we use this acronym as a convenient label, without implying that it necessarily corresponds to a well-delimited cortical area with specific architectonic or connectivity properties. Fig. 4 shows the levels of activation of those areas as a function of task and modality.¹

Task-related activations within multimodal areas

We then studied regions that showed an effect of task (Table 2). To identify activations related to the orthographic task, we contrasted the orthographic versus the phonological conditions (voxelwise $P < 0.01$; corrected $P < 0.05$ for cluster extent). To ensure that those activations would not result from deactivations during the phonological task, the contrast was masked by orthographic activations versus rest in both modalities (voxelwise $P < 0.01$ each). Activations related to the phonological task were searched using the symmetrical procedure.

Multimodal orthographic activations included bilateral posterior intraparietal and collicular activations. In the left hemisphere, there was also a left calcarine activation. Finally, within the a priori left inferotemporal region, a cluster was found that did not reach the threshold for cluster extent corrected for whole-brain search (TC -44, -60, -8; $Z = 2.92$; 56 voxels). The opposite contrast (phonological > orthographic task) did not show significant activations.

Task-related activations within each modality

The behavioral data suggested that the orthographic descender task should be easier to perform with written than with spoken words and that, conversely, the phonological task should be easier with spoken than with written words. Analysis of this effect required examination of the influence of task on fMRI activations, separately for each stimulus modality. We therefore contrasted the orthographic versus the phonological conditions within each modality (voxelwise $P < 0.01$; corrected $P < 0.05$ for cluster extent), masked by the activation during the appropriate combination of task and modality relative to rest (e.g., visual orthographic activations vs. rest, voxelwise $P < 0.01$) (Table 2).

Within regions activated by written words, greater activations during the orthographic task than during the phonological task were found in essentially the same network as in the multimodal analysis, that is, bilateral intraparietal and left inferotemporal activations. There was also a right inferotemporal focus, below the threshold for cluster extent (TC 44, -60, -8; $Z = 3.88$; 27 voxels).

Within regions activated by spoken words, most of the multimodal task-related network was found again, although below the threshold for cluster extent. Moreover, there was stronger activation during the orthographic than during the phonological task bilaterally in the anterior cingulate gyrus, thalamus, caudate, and calcarine cortex. These latter activations, which were not part of the task-related activations within multimodal areas, are consistent with the idea that performing the orthographic task on spoken words imposes additional computations relative to perform-

Table 2

Task-related activations in trials with nonrepeated words

Area	Voxel Z score	TC		
		x	y	z
<i>Orthographic task > phonological task across both modalities</i>				
L posterior intraparietal	4.23	-16	-64	28
R posterior intraparietal	4.49	24	-60	56
R posterior intraparietal	3.92	20	-60	36
L calcarine	2.97	-12	72	12
Bilateral superior colliculi	3.09	0	-36	-4
L inferotemporal	2.92	-44	-60	-8
<i>Orthographic task > phonological task, visual modality</i>				
L posterior intraparietal	4.43	-28	-76	28
R posterior intraparietal	3.79	24	-56	52
R posterior intraparietal	3.64	20	-40	40
L inferotemporal	4.29	-32	-68	-16
L inferotemporal	3.02	-44	-64	-16
R inferotemporal	3.88	44	-60	-8
<i>Orthographic task > phonological task, auditory modality</i>				
L anterior cingulate	3.91	-12	28	28
R anterior cingulate	3.65	4	16	32
R precentral sulcus	3.31	20	0	68
L thalamus	3.84	-12	-20	28
R thalamus	3.47	12	-4	16
R calcarine	3.12	8	-76	12
L calcarine	2.72	-8	-88	4
L posterior parietal	4.02	-20	-76	40
R posterior parietal	3.45	28	-60	52
L inferotemporal	2.70	-44	-60	-4
<i>Phonological task > orthographic task across both modalities</i>				
No significant voxels				
<i>Phonological task > orthographic task, auditory modality</i>				
No significant voxels				
<i>Phonological task > orthographic task, visual modality</i>				
No significant voxels				
<i>Interaction orthographic > phonological task in auditory > visual modality</i>				
R thalamus	4.43	16	-4	4
R putamen	4.08	28	12	-4
R superior temporal gyrus	3.98	64	-32	8
R superior temporal gyrus	3.39	48	4	-4
R cingulate	3.51	4	8	28

ing the same task on written words. To verify this, we examined the interaction of task and modality. This interaction reached significance at the peak voxel of the bilateral thalamic ($P_s < 0.002$) and cingulate ($P_s < 0.02$) activations, the effect of task (orthographic > phonological) being significantly stronger in the auditory than in the visual modality.

Finally, the phonological task yielded no significantly greater activations relative to the orthographic task, even when restricting this contrast either to the auditory or to the visual modality.

Single-subject analysis of task effects in left inferotemporal cortex

In the group analysis, the effect of task on inferotemporal cortex was ambiguous, since it was found when we searched regions with multimodal activation, and also in the analysis of regions with activation to visual stimuli. In a previous section, we distinguished a visual occipitotemporal region (the VWFA) and a multimodal

¹ Note that, as visible on Fig. 4, an ANOVA on individual peak activations confirmed that the LIMA was activated more strongly by written than by spoken words and that there was a small activation of the VWFA by auditory words relative to rest ($P_s < 0.005$).

inferolateral temporal region (the LIMA). Were both regions affected by task, or was there a spread-out of task-related activation due to smearing of individual variability in the group analyses? To clarify this, individual peak responses were submitted to an ANOVA with task and anatomical region as within-subject factors (Fig. 4). In the VWFA, there was no effect of task [$F(1,16) < 1$], while this effect was significant in the LIMA [$F(1,16) = 8.5$; $P = 0.01$] for both spoken and written words ($P_s < 0.05$). This resulted in a significant interaction of task and anatomical region [$F(1,16) = 8.7$; $P < 0.01$], indicating that the two regions differed in relation to the task.

Effects of word repetition

We then studied the effects of word repetition, while manipulating the modality of the target and prime words. For simplicity, those analyses were collapsed across tasks. We expected activations to be reduced when the same target was repeated a second time (repetition suppression). Of particular interest was whether this reduction was present, not only when the same word was repeated physically in the same modality, but also when modality changed. Such a cross-modal effect can perhaps be expected within areas that respond multimodally to targets in both modalities; we also examined its presence in modality-dependent regions. This issue was particularly relevant for the two inferotemporal regions identified so far, the VWFA and the multimodal LIMA.

Effects of word repetition in multimodal areas

We first looked for cross-modal repetition suppression effects within the network activated in all tasks and modalities. To this end, we contrasted nonrepeated and repeated words (i.e., the main effect of repetition suppression; voxelwise $P < 0.01$; $P < 0.05$ corrected for cluster extent), masked by repetition suppression in the four combinations of consecutive modalities for the prime and target (AV, AA, VA, VV; voxelwise $P < 0.01$ each) and by the common network described in the preceding section. We observed cross-modal repetition suppression in essentially all of the left-hemispheric regions of the common multimodal network (see Fig. 3): the cerebellum (TC $-32, -60, -24$; $Z = 5.25$), the inferior temporal gyrus at the level of the LIMA (TC $-52, -56, -12$; $Z = 4.94$), Broca area/anterior insula (TC $-32, 20, 0$; $Z = 5.31$), the thalamus (TC $-12, -16, 12$; $Z = 4.15$), the precentral gyrus (TC $-60, 8, 16$; $Z = 4.86$; TC $-44, 0, 32$; $Z = 4.54$; and also TC $-32, -12, 64$; $Z = 4.91$, which could coincide with the frontal eye field), the dorsolateral prefrontal cortex (TC $-44, 20, 20$; $Z = 6.27$), the intraparietal sulcus (TC $-28, -72, 36$; $Z = 5.11$; TC $-44, -36, 44$; $Z = 4.85$), and bilateral SMA/cingulate (TC $0, 12, 48$; $Z = 5.53$). Note, however, that there was no repetition suppression in the bilateral caudate.

The behavioral analysis showed that the effect of word repetition was larger when words were repeated within the same modality. Accordingly, we examined whether regions of the common network would show greater repetition suppression on within-modality than on between-modality repetition. The corresponding interaction contrast was masked by the common network at the usual thresholds. This analysis showed that essentially all regions of the common network showed such an interaction, except the left anterior insula.

Finally, we performed symmetrical analyses to look for enhanced activations induced by word repetition within the

common network. We found no main effect of repetition enhancement and no greater repetition enhancement on within-modality than on between-modality repetition.

Effects of word repetition in modality-specific networks

Following a similar logic, we then studied the effect of word repetition separately for visual or auditory targets, restricting analyses to the corresponding modality-specific networks as identified before.

Auditory words. We contrasted nonrepeated versus repeated auditory words (voxelwise $P < 0.01$; $P < 0.05$ corrected for cluster extent), masking by the same contrast restricted to auditory and to visual primes (AA, VA; voxelwise $P < 0.01$ each) and by the modality-dependent auditory network described in the preceding section. This revealed repetition suppression in essentially all the auditory network, with the exception of the bilateral superior temporal cortex and the right postcentral region. Within the auditory network, no region showed stronger suppression for within-modality than for between-modality repetition.

As the absence of an overall repetition effect for auditory words in the superior temporal cortex was somewhat surprising, we searched specifically for within-modality suppression (i.e., with auditory primes and targets). In addition to the above network, we found a small cluster in the left STS (TC $-60, -8, -4$; $Z = 3.46$) with significant repetition suppression (Fig. 3).

Visual words. Symmetrical analyses were performed for visual words in the modality-dependent visual network. The left inferotemporal and parietal regions showed repetition suppression irrespective of the prime modality, including a peak that coincided with the VWFA (TC $-36, -60, -12$; $Z = 4.68$). In all of these regions, repetition suppression was significantly stronger for within-modality than for between-modality repetition.

There was no cross-modal repetition suppression in the most posterior occipitotemporal regions (posterior to TC $y = -76$). However, when searching specifically for within-modality suppression (i.e., with visual primes and targets), the entire visual network was activated, including bilateral occipital, inferotemporal, and parietal areas (Fig. 3).

Single-subject analysis of repetition effects in left inferotemporal cortex

Group analyses suggested that, in the left inferotemporal cortex, the same pattern of repetition effect prevailed in both the LIMA and the VWFA. To determine whether this similarity was due to intersubject averaging and smoothing, we performed an ANOVA on the individual BOLD response at the peaks of the two regions, with repetition, modality repetition, and anatomical region as within-subject factors. This analysis showed that there was a significant repetition effect in both the VWFA [$F(1,16) = 44.5$; $P < 10^{-5}$] and the LIMA [$F(1,16) = 79.5$; $P < 10^{-6}$], with a larger effect in the LIMA [$F(1,16) = 36.8$; $P < 10^{-4}$]. Furthermore, in both regions, the repetition effect was larger within the same modality than in different modalities [VWFA: $F(1,16) = 8.6$; $P < 0.01$; LIMA: $F(1,16) = 19.7$; $P < 0.001$].

Note that the VWFA, which showed some activation by nonrepeated spoken word relative to fixation, showed strictly no activation with repeated spoken words [$t(16) < 1$] (Fig. 6). In contrast, the LIMA was activated by repeated words both in the

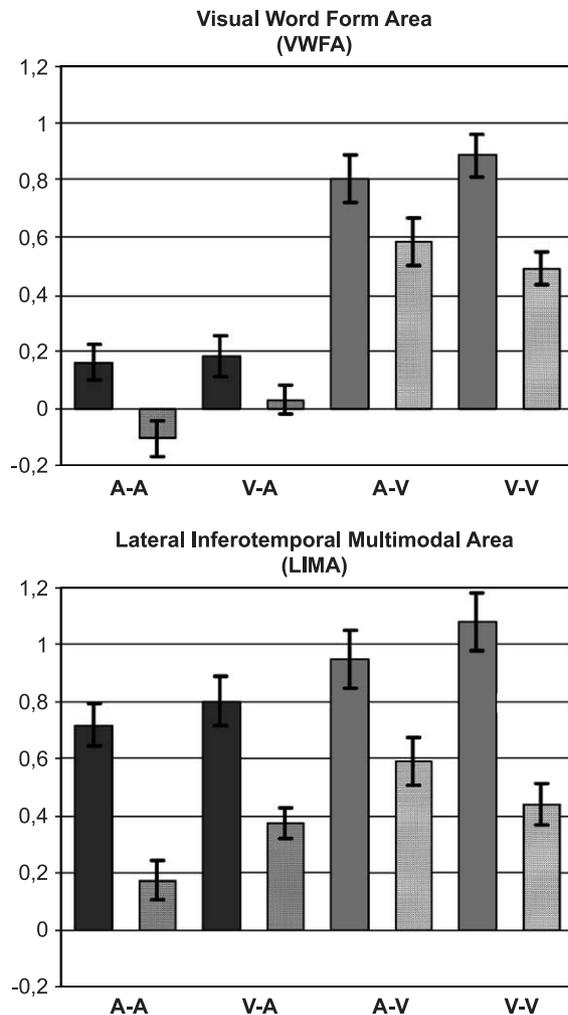


Fig. 6. Peak activation relative to rest of the VWFA and of the LIMA, as identified in individual subjects, for nonrepeated words (solid bars) and repeated words (hatched bars), broken down according to the modality of the preceding and of the target word (A, auditory; V, visual). The VWFA showed strictly no activation for repeated spoken words, while it was always strongly activated by written words. In contrast, the LIMA was activated by words in either modality. In both regions, the effect of word repetition was larger within than across modality.

visual [$t(16) = 7.4$; $P < 10^{-5}$] and in the auditory [$t(16) = 5.3$; $P < 10^{-4}$] modalities.

Discussion

We will first summarize and sort out the main patterns of activation observed across the whole brain, successively considering the effects of modality, task, and word repetition and highlighting the parallels between activations and behavioral data. We will then focus on a more detailed discussion of activations in the left inferotemporal cortex. Finally, we will discuss methodological issues raised by the present study.

Overall effects of modality, task, and repetition

As word repetition was expected to dampen down the influence of modality and task, their effects were studied on trials with

nonrepeated targets. Three distinct networks were identified on the basis of modality effects (Fig. 3). A large network, activated in all conditions, included left-hemispheric areas involved in supramodal language processing (Broca area, inferior lateral temporal cortex, etc.) and bilateral regions possibly involved in attentional control and response generation (SMA/cingulate, parietal, rolandic, basal ganglia). Beyond this network, some regions were more activated in one modality than in the other. Regions with an auditory preference included the bilateral superior temporal cortex involved in the processing of sound and speech (Binder et al., 2000; Griffiths and Warren, 2002), and also a set of areas whose role is less clear, including unexpected bilateral clusters in the calcarine cortex; these activations may relate to the fact subjects were not passively presented with the stimuli but were engaged in two difficult tasks that involve a substantial amount of top-down activity (see below). Regions with a visual preference were restricted to the classical ventral and dorsal visual streams bilaterally. On the basis of individual analyses, it appeared that the left inferotemporal activation identified in the multimodal network (the LIMA) was close to but more lateral than the activation identified in the contrast of written versus spoken words (the VWFA).

In the study of task effects, we found many regions with stronger activations during the orthographic than during the phonological task, while no areas showed the opposite effect. This asymmetry correlates with the behavioral effect of task difficulty, that is, longer RTs and higher error rates when subjects were detecting letters with a descender than when they were detecting a target phoneme. A set of regions showed an effect of task for both spoken and written words, including structures possibly involved in spatial attentional control (bilateral intraparietal and collicular) (Corbetta and Shulman, 1998; Kanwisher and Wojciulik, 2000; Mesulam, 1999) and in supramodal word processing (left lateral inferotemporal). Additional areas showed an effect of task for auditory words only (cingulate, thalamus, caudate, calcarine). This difference correlates with the behavioral effect of congruence of task and modality, namely, a greater difficulty for the orthographic task than for the phonological task when the words were spoken than when they were written. In the left inferior temporal cortex, individual analyses showed a significant effect of task in the LIMA but not in the VWFA.

Finally, we observed a pervasive reduction of activations induced by repeated words relative to novel words in essentially all activated areas. This reduction correlates with the large reduction of RTs and error rates on repeated versus nonrepeated trials, suggesting that many processing stages were facilitated or bypassed when word repetition was detected. This reduction was observed in most of the multimodal network identified initially and also in many of the regions with a preference for one modality over the other. In addition to the main effect of repetition, behavioral results showed that this effect was larger when words were repeated within than across modalities. We speculated that perhaps unimodal regions may be sensitive exclusively to word repetition within the corresponding modality, while multimodal regions may show comparable effects for word repetition within and between modalities. This was not the case, however, as almost the entire multimodal network showed larger repetition suppression within than between modalities. Most regions with a preference for one modality over the other also showed a larger modality-specific repetition effect. Only a few regions showed only within-modality suppression. Thus, we identified an STS cluster with only AA

repetition suppression, and occipital regions posterior to the VWFA with only VV suppression. Nevertheless, cross-modal priming was unexpectedly present in many areas, including unimodal ones, thus precluding using it as a diagnostic criterion. This may be a consequence of the conscious character of the repetition, as will be discussed below.

Functional properties of the visual word form area

Our first aim was to establish whether there is, in the left inferotemporal region, a unimodal visual area associated with word recognition. The activation observed in the left occipitotemporal sulcus, which coincided with the coordinates of the VWFA as identified in previous studies, showed properties compatible with this expectation. This region was activated whenever written words were presented with identical levels regardless of the task. It responded weakly to novel spoken words and showed no activation at all to repeated spoken words.

The finding of an activation whenever visual words are presented confirms the mandatory character of visual processing in this region. Indeed, previous research with subliminal stimuli indicates that the VWFA activates automatically whenever visual words are presented, even unbeknown to the subjects (Dehaene et al., 2001). The novel finding of the present study is that, although spoken words may activate the VWFA, they do not necessarily do so. In particular, the absence of any detectable activation of the VWFA by repeated auditory words indicates that this activation is not mandatory and, a contrario, that on nonrepeated trials, its activation probably resulted from task-induced top-down processing.

This interpretation fits with several previous data sets. We recently studied the activations to spoken and written words, using a repetition detection task (Dehaene et al., 2002). For written words, activations were observed in every subject in the left occipitotemporal sulcus, while there was no inferotemporal activation for spoken words. Similarly, in a detailed study of temporal activations during passive listening to speech and nonspeech sounds, Binder et al. (2000) found no left inferior temporal activations relative to baseline. In summary, it seems that written words yield a compulsory activation of the VWFA, while spoken words do not necessarily yield any left inferotemporal activations (see also Binder et al., 2000; Giraud and Price, 2001; Price et al., 1996b). Neuropsychological evidence also confirms the unimodal character of this region. Lesions restricted to the ventral aspect of the left midtemporal lobe and overlapping with the VWFA yield pure alexia, a severe disorder of reading with no impairment of auditory word processing (Cohen et al., 2003; Dejerine, 1892).

If the VWFA is involved in orthographic processing, why was it also (although modestly) activated by novel spoken words in both a graphemic and a phonemic task, without any difference between those two tasks? We designed the graphemic task so that it required subject to convert letters from uppercase to lowercase and attend to the resulting shapes, thus presumably requiring VWFA activation. However, the phonemic task might also have involved a considerable and undesired degree of top-down orthographic activation. Although we asked subjects to detect a specific phoneme, uncorrelated with orthography, many subjects reported introspectively an automatic intrusion of orthographic information in their decisions. Indeed, psycholin-

guistic experiments have often revealed that phoneme detection is heavily influenced by orthography (e.g., [Donnenwerth-Nolan et al., 1981](#); [Taft and Hambly, 1985](#); [Ziegler and Ferrand, 1998](#)) to the extent that English subjects may fail to detect the phoneme “v” in “of,” or French subjects the phoneme “p” in “subtil” ([Hallé et al., 2000](#)). Furthermore, some phoneme detection tasks are heavily influenced by acquisition of the alphabetic principle and may be out of reach of illiterate subjects ([Morais and Kolinsky, 1994](#)). Thus, the moderate activation of the VWFA by spoken words in the present tasks remains compatible with its role in orthographic processing, although further work will be needed to more clearly delimit its top-down activability as a function of task.

The contrast which allowed us to pick out the VWFA (i.e., written vs. spoken nonrepeated words) actually revealed two inferotemporal clusters. One was the VWFA, and the other was the right-hemispheric region symmetrical to the VWFA, an area which we recently proposed to label the R-VWFA ([Cohen et al., 2003](#)). Both the VWFA and the R-VWFA are activated by written words relative to rest, and more selective contrasts between alphabetic and other visual stimuli are required to evidence the specific tuning of the VWFA to written language. For instance, left-sided activations are emphasized when contrasting strings of consonants versus strings of pseudoletters ([Price et al., 1996a](#)), strings of letters versus checkerboards ([Cohen et al., 2002, 2003](#)), or foveal words versus pictures of faces, textures, or buildings ([Gauthier et al., 2000](#); [Hasson et al., 2002](#); [Puce et al., 1996](#)). No such contrasts were used in the present study. Nevertheless, one may note an interesting difference between the R-VWFA and the VWFA regarding the influence of modality. While the VWFA was perceptibly activated by novel auditory words, the R-VWFA showed no such activation and was exclusively activated by written words. This indicates that the R-VWFA is indeed a unimodal visual region and supports the idea that such is also the case of the contralateral VWFA. One difference, according to our interpretation, is that the VWFA can receive top-down influences from other downstream language areas, while the R-VWFA shows no top-down activation to spoken words, at least for the particular tasks that we used.

The lateral inferotemporal multimodal area

Our second goal was to determine whether the unimodal VWFA could be distinguished from multimodal inferior temporal activations during word processing. The lateral inferior temporal region which we proposed to call the LIMA shows such multimodal features. In the present study, this region, located lateral and slightly anterior to the VWFA, was always activated strongly by either spoken or written words, suggesting that it played a common processing role irrespective of modality. Comparison with other studies suggests that the occurrence of auditory activations is not systematic and depends on task requirements. Thus, as mentioned before, a number of studies showed no inferotemporal activations to spoken words, neither in the VWFA nor in the LIMA ([Binder et al., 2000](#); [Dehaene et al., 2002](#); [Giraud and Price, 2001](#); [Price et al., 1996b](#)). It is more difficult to determine whether the activation of the LIMA to written words is also sporadic, because this area is easily confounded with the VWFA. However, studies with individual localization of activations suggest that activations can be tightly restricted to the occipitotemporal sulcus (e.g., see [Dehaene et al., 2002](#); [Gauthier et](#)

al., 2000; Hasson et al., 2002, 2003; Puce et al., 1996). Thus, in the present state of knowledge, the LIMA appears as an optional component of both written and spoken word processing, which was probably emphasized by the present tasks.

Indeed, contrary to the VWFA, the LIMA was sensitive to task parameters. Activations were stronger during the alphabetic than during the phonological task. Task effects also appeared in previous studies, although it is often difficult to decide whether those effects affected the VWFA or the LIMA. Considering the weak-to-null activation of the VWFA by spoken words, task effects observed in the auditory modality more likely involve the LIMA. For instance, at coordinates close to the LIMA (TC $-58, -56, -8$), Burton et al. (2000) observed an activation when subjects performed same-different judgments on spoken syllables, but only when they had to extract the first phoneme of the syllable, not when they could base their decisions on the syllable as a whole. A recent study by Booth et al. (2002a) followed an approach similar to ours and obtained convergent results. Subjects performed a spelling or a rhyming task, with spoken or written words. Activations common to both modalities included a left inferior temporal region activated in all tasks and modalities (TC $-48, -57, -12$), and probably corresponding to the LIMA. Similarly to the present study, this exact region showed stronger activations for the spelling than for the rhyming task, irrespective of modality. It was distinct from slightly more mesial bilateral regions activated by visual more than by auditory words and probably corresponding to the VWFA (TC $-39, -60, -18$) and the R-VWFA (TC $39, -63, -21$), respectively. Other modality-specific activations broadly matched the unimodal visual and auditory networks that we observed here.²

Unfortunately, the available data do not allow specifying completely the functions of the LIMA. Its multimodal activation pattern fits the general role of the left lateral temporal cortex in providing a “convergence zone” supporting the linkage of orthographic, phonemic, and semantic information (Damasio, 1989). It is not clear, however, whether the LIMA establishes such links between lexical or sublexical entities. On the one hand, considering its activation in tasks with an emphasis on sublexical manipulations, one may speculate that the LIMA is important for the retrieval of graphemic information irrespective of the input mode (for activations induced by complex detection tasks, see also Démonet et al., 1992, 1994). In a recent study, Flowers et al. (2004) presented subjects with series of letters and meaningless symbols, printed in black or white. When subjects had to detect letters, rather than symbols or colors, there was a lateral inferotemporal activation peaking at TC $-62, -57, -6$. It was distinct from the VWFA, where no effect of task emerged. It is plausible that this lateral region corresponded to the LIMA, on the basis of its localization, its sensitivity to task demands, and its activation by a task requiring the explicit manipulation of sublexical units. On the other hand, Paulesu et al. (2000) observed an overactivation of the LIMA (TC $-58, -58, -14$) in English

readers relative to Italian readers, suggesting that this region plays a particular role in reading through a lexical route (see also lexical activations in Binder et al., 2003). Evidence from neuropsychology is also ambiguous, although it supports the hypothesis that the LIMA plays a common role in the processing of spoken and written words. A simple prediction is that its disruption should result in parallel symptoms in both modalities. Indeed, posterior inferior lesions of the lateral temporal cortex yield word-finding difficulties which may reflect impaired links between word forms and semantics. For instance, Raymer et al. (1997) and Foundas et al. (1998) described patients with circumscribed lesions of the posterior middle and inferior temporal gyri, including the ITS, who showed anomia irrespective of output modality (see also Chertkow et al., 1997). Note that, due to anatomical contiguity, anomia may be associated with pure alexia (De Renzi et al., 1987). In patients with semantic dementia, Mummery et al. (1999) found a peak of reduced activation in a semantic task relative to a visual task, at coordinates close to the LIMA (TC $-54, -52, -10$). As we try to maintain here a good level of anatomical precision, such clinical correlations should be considered with care. Nevertheless, it is likely that the LIMA belongs to the heteromodal cortex of the lateral temporal lobe, rather than to the ventral stream of the visual cortex, and it is plausible that it plays a more integrative and/or lexical role than the VWFA.

Finally, one should remember that, in discussing the features of the VWFA and LIMA, we consider only a subset of the left inferior temporal regions activated during language processing. Other more posterior visual region areas are activated by written words (see e.g., Cohen et al., 2002; Mechelli et al., 2000), while other multimodal activations dependent on semantic processing belong to more anterior regions of the inferotemporal cortex (for reviews, see Booth et al., 2002b; Giraud and Price, 2001).

An auditory equivalent of the VWFA?

While the present study focuses primarily on the processing of visual words, one may wonder whether similar principles of analysis also underlie the processing of spoken words. In particular, is there a unimodal auditory area involved in the analysis of the “auditory word form” and which would therefore be analogous to the VWFA in the visual modality? We observed a single left temporal area, in the left superior temporal sulcus (TC $-60, -8, -4$), which had two properties symmetrical to those of the VWFA: It showed a unimodal auditory response, and it was the only such area to exhibit repetition suppression when the same auditory word was presented twice, thus suggesting an implicit memory for auditory words across the 3-s intertrial interval. Furthermore, this is an area in which many studies have evidenced activation by speech (words, pseudowords, syllables) relative to nonspeech auditory stimuli, including vocal sounds (e.g., see Belin et al., 2002; Binder et al., 2000; Crinion et al., 2003; Scott et al., 2000), compatible with a phonological level of coding.

Several arguments support the hypothesis that this STS region may play in the perception of spoken words a role symmetrical to that of the VWFA in the perception of written words. (1) Both regions belong to unimodal association cortex. (2) Both show some selectivity for language, as they can be isolated by contrasting linguistic versus nonlinguistic stimuli (e.g., words vs. faces for the VWFA, and speech vs. noises or even nonspeech vocal sounds for the STS). (3) Both probably subtend prelexical representations (graphemic and possibly phonemic, respectively), as suggested by

² Note that Booth et al. (2002a,b) also found activations when contrasting the rhyming minus the spelling task, while we found no similar activations for the phonological minus the orthographic task. This difference and others are likely due to the differences between the two studies in terms of tasks and experimental design. Thus, the tasks used by Booth et al. (2002a,b) required the comparison of three successive words, inducing higher working memory demands.

comparable activations to real words and pseudowords. (4) Both regions seem to be tuned to culturally defined orthographic or phonological systems: the VWFA distinguishes real characters from false fonts (Brunswick et al., 1999; Price et al., 1996a) or legal letter strings from arrays of consonants (Cohen et al., 2002), while the left STS is sensitive to phonological changes in the subject's language (Jacquemot et al., 2003). (5) The VWFA and the left STS showed no effect of task in the present study. (6) Finally, lesions of those regions result in unimodal word comprehension deficits: pure alexia and verbal deafness (Barrett, 1910; Griffiths et al., 1999). Beyond those suggestive parallels, the functional properties of the left anterior STS should be further investigated to determine the precise representation format that it subtends. For instance, if abstract phoneme sequences are represented, one should expect invariance for irrelevant variations such as changes of speaker identity, voice pitch, intonation, or speech rate. Finally, Belin and Zatorre (2003) draw an interesting parallel between the right-hemispheric face fusiform area (FFA) involved in individual face recognition and the right anterior STS (TC 58, 2, -8) presumably involved in the representation of individual voices, as suggested by adaptation to voice repetition more than to syllable repetition. This idea is exactly symmetrical to the parallel that we propose between the VWFA and the left anterior STS, suggesting a symmetrical organization of the visual and auditory input systems for the recognition of specific persons and of specific words. Note, however, that Belin and Zatorre (2003) did not find stronger adaptation to syllable than to voice repetition in the left STS.

Points of method

We conclude by discussing several methodological consequences of the present work, which are likely to be valid for other fMRI studies that attempt to dissect a system composed of multiple, functionally distinct areas.

A first important conclusion is that, whenever an argument rests on the anatomical overlap of different effects in the same voxel, it is essential to perform those analyses at the single-subject level, as was done here for the left inferotemporal cortex. At the group level, smoothing and anatomical variability can lead to an artificial overlap between contrasts that are, in fact, anatomically separate in normal subjects (see e.g., Price and Devlin, 2003, and the reply by Cohen and Dehaene, 2004). Here, the group analysis was misleading in at least two ways: it created an artificial overlap between visual and auditory activations within the inferotemporal cortex, and it indicated that the effect of task was also widespread in this area. Both properties misleadingly suggested the presence of a single inferotemporal area of activation, whereas analysis of the same properties at the single-subject level clearly revealed the presence of two different areas, the VWFA and the LIMA, with sharply different responses and essentially no overlap.

Second, given this novel distinction between two ventral language areas, a careful reappraisal of past word-processing research will be required to estimate whether their properties have been confused in the past. Up to now, activations during reading in the ventral temporal cortex close to the appropriate coordinates were often attributed to a single region (see Tables 4 and 5 in Jobard et al., 2003), and their properties were all thought to characterize the VWFA. Those properties include modality specificity (Dehaene et al., 2002; Price et al., 2003b), response to words more than consonant strings (Cohen et al., 2002), case-independent subliminal priming (Dehaene et al., 2001), stronger

response to pseudowords than to real words (Mechelli et al., 2003; Paulesu et al., 2000; Xu et al., 2001), and stronger activations during word naming than during silent reading (Moore and Price, 1999). Those conclusions must now be reexamined, because most of them were based on group studies (although see Allison et al., 1994, 1999; Dehaene et al., 2002; Gauthier et al., 2000; Hasson et al., 2002, 2003; Nobre et al., 1994; Puce et al., 1996; Tarkiainen et al., 1999). Other studies also point to a fragmentation of left inferotemporal cortex, this time along the anteroposterior axis, on the basis of finding different properties of invariance in subliminal priming during visual word processing (Dehaene et al., 2004). More and more, careful studies of how those properties adhere together in the same voxel within a given subject will be needed to resolve the architecture of reading.

Perhaps the most important conclusion that may have to be revised following the VWFA/LIMA distinction is that the VWFA is the ventral site of reduced activation in developmental dyslexics (Brunswick et al., 1999; McCandliss and Noble, 2003; Paulesu et al., 2001; Pugh et al., 2000). In many studies (Paulesu et al., 2001; Shaywitz et al., 2002, 2003), although not all (Temple et al., 2003), the tasks were metalinguistic tasks comparable to those used in the present work (e.g., ascender detection in Paulesu et al., 2001), and the ventral temporal site of reduced activation in dyslexics appears to coincide with the LIMA. Whether as a cause or as a consequence of dyslexia, it is possible that both the basic expertise for invariant visual word recognition (in the VWFA) and the higher level cross-modal phonemic and lexical links (putatively involving the LIMA) do not develop normally in dyslexic children.

Finally, the present results also qualify the use of the priming method (Naccache and Dehaene, 2001) or habituation method (Grill-Spector and Malach, 2001) as a universal tool to determine the functional properties of brain areas in fMRI. Contrary to our expectations, we observed a clear decoupling of the modality properties of several areas, as identified directly by presenting visual or auditory stimuli, and the presence of within- and cross-modal fMRI repetition suppression. For instance, we expected the VWFA to show repetition suppression only when the prime and target were presented in the visual modality; and conversely, we expected higher level multimodal areas to show within- and cross-modal repetition effects of identical size. However, essentially all areas where repetition suppression was observed showed the same behavior: a large cross-modal effect and an even larger within-modality effect. Note that this behavior is parallel to what was observed in response times. Thus, our paradoxical fMRI repetition results can be explained by supposing that the fMRI signal reflects the reduced duration of activation on repeated trials, rather than local code of words. Our hypothesis is that the entire set of visual and multimodal areas is maintained in an active state while the response decision is being made, and when this decision is achieved faster on repeated trials, the entire network collapses earlier, thus showing a cross-modal effect even in modality-specific areas. In this manner, a repetition detected anywhere in the network can have a nonlocal effect on fMRI activation in many distant areas. If this interpretation is correct, then repetition suppression cannot be expected to faithfully reflect the local code within a given area—and our finding of strong cross-modal priming within a largely unimodal area strongly supports this conclusion.

This problem with habituation-based design may have been enhanced, in the present work, because we relied on trial-to-trial repetitions that could be consciously detected and could be strategically used to facilitate responding. During the intertrial

interval, subjects had the time to prepare for the next trial and could consciously translate the preceding word in written and spoken form, regardless of its original modality. Indeed, it has been argued that one of the functions of consciousness is to permit the globalization of information and its diffusion to many distant areas in a “global neuronal workspace” (Dehaene and Naccache, 2001; Dehaene et al., 1998). A contrario, this problem is much less likely to occur if word repetition is nonconscious or at least incidental and nonattended. In such cases, information about the prime word is thought to be extracted only in a bottom-up, feed-forward manner (Dehaene et al., 2003; Lamme et al., 1998, 2000) and not to be able to circulate and affect other areas through top-down interactions. Thus, both this theory and the present empirical results strongly support the use of subliminal or at least inconspicuous stimulus repetitions in fMRI designs using the priming or habituation method (Naccache and Dehaene, 2001).

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