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Cortical localisation of the visual and auditory word form areas: A reconsideration of the evidence

C.J. Price,* D. Winterburn, A.L. Giraud, C.J. Moore,
and U. Noppeney,

*Wellcome Department of Imaging Neuroscience, Institute of Neurology, 12 Queen Square,
London WC1N 3BG, UK*

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Abstract

In this paper we examine the evidence for human brain areas dedicated to visual or auditory word form processing by comparing cortical activation for auditory word repetition, reading, picture naming, and environmental sound naming. Both reading and auditory word repetition activated left lateralised regions in the frontal operculum (Broca's area), posterior superior temporal gyrus (Wernicke's area), posterior inferior temporal cortex, and a region in the mid superior temporal sulcus relative to baseline conditions that controlled for sensory input and motor output processing. In addition, auditory word repetition increased activation in a lateral region of the left mid superior temporal gyrus but critically, this area is not specific to auditory word processing, it is also activated in response to environmental sounds. There were no reading specific activations, even in the areas previously claimed as visual word form areas: activations were either common to reading and auditory word repetition or common to reading and picture naming. We conclude that there is no current evidence for cortical sites dedicated to visual or auditory word form processing.

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Keywords: Auditory; Visual; Word form areas; Repetition; Reading; Functional imaging

1. Introduction

In this paper, we review the evidence for human brain areas that are specialised for auditory and visual word form processing and then present a new functional imaging study that tests the various claims by comparing cortical activation for auditory word repetition and reading. The first anatomical models of word processing were based on data from post-mortem studies of patients with localised cortical lesions and specific language deficits (see Geschwind, 1965). The left posterior

* Corresponding author. Fax: +44-171-813-1420.

E-mail address: c.price@fil.ion.ucl.ac.uk (C.J. Price).

superior temporal cortex (Wernicke's area) was designated the site of "auditory images of speech" and the left angular gyrus was designated as a "visual memory center for words" (Dejerine, 1891, 1892). According to the neurological model (see Geschwind, 1965), reading involved visual processing in occipital cortices, followed by word identification in the left angular gyrus, conversion to auditory word forms in Wernicke's area, and speech output in the left posterior inferior frontal cortex (Broca's area). Thus, the neurological model presupposed areas that were specific to word form processing and separate from visual or auditory processing in general. Auditory word form processing was localised to Wernicke's area and visual word form processing was localised to the left angular gyrus. Some cognitive models of visual and auditory word form processing also propose word form modules (e.g., the auditory and visual input lexicons in the model by Patterson & Shewell, 1987). However, these models do not make any predictions as to how word form processing occurs at the neural level; they are consistent either with the existence of modular word form areas (as proposed by the neurological model) or the function of the word form lexicons arising from distributed neural processing.

The concept of modular word form areas has been pursued in several functional imaging studies (Cohen et al., 2000; Howard et al., 1992; Petersen, Fox, Posner, Mintum, & Raichle, 1989). Most functional neuroimaging studies of auditory word repetition (Giraud & Price, 2001; Howard et al., 1992; Petersen, Fox, Posner, Mintum, & Raichle, 1988a; Petersen, Fox, Posner, Mintum, & Raichle, 1988b; Price et al., 1996a) have reported reliable activation in the left posterior superior temporal cortex that is likely to correspond to Wernicke's area. However, activation in the left angular gyrus is not consistently seen during reading aloud as would be expected if this region corresponded to a visual word form area. This has led to three distinct and contrasting proposals regarding the cortical localisation of the visual word form area (Cohen et al., 2000; Howard et al., 1992; Petersen, Fox, Snyder, & Raichle, 1990). The evidence for each claim will be discussed in turn below.

The first imaging study of reading, reported by Petersen et al. (1990) proposed that the left medial extrastriate cortex housed the visual word form system because (i) this area was more active for viewing words and pseudowords relative to fixation but not for viewing consonant letter strings or falsefonts relative to fixation; and (ii) it is consistent with the left occipital lesions seen in alexia without agraphia. However, other studies have shown that the same left extrastriate region is activated by pictures of objects and other complex visual stimuli (e.g., Bookheimer, Zeffiro, Blaxton, Gaillard, & Theodore, 1995; Indefrey et al., 1997; Moore & Price, 1999). Therefore, left medial extrastriate activation is not specific to orthographic input and may reflect early visual processing that is modulated by the demands of the task (Mechelli, Humphreys, Mayall, Olson, & Price, 2000).

The second hypothetical visual word form area to be advocated on the basis of functional imaging data was proposed by Howard et al. (1992). They compared brain activation for (1) reading aloud relative to viewing falsefonts and saying "Crime"; and (2) auditory word repetition relative to hearing reversed words and saying "Crime." Reading activated a left posterior middle temporal area that was not observed for auditory word repetition. This area was linked to the visual input lexicon (another term for the visual word form system). However, the difference between reading and auditory word repetition in the Howard et al. (1992) study was not significant. Therefore there was no evidence to suggest that this area was more involved in visual word form processing than auditory word form processing.

The third area to be linked to the visual word form system is the left posterior inferior temporal cortex (Cohen et al., 2000). This group contrasted activation for reading words presented in the left and right visual hemi-fields and found that

irrespective of stimulus presentation, reading (relative to fixation) activated a left lateralised posterior inferior temporal area that is often damaged in patients with alexia without agraphia.¹ However, other imaging studies (Moore & Price, 1999; Price & Friston, 1997b) have found that the same left inferior temporal area is activated by picture, letter and colour naming which do not involve visual word form input. Lesion and electrical stimulation studies also indicate that the left posterior inferior temporal cortex is not specific to word form analysis. For instance, the linguistic role of the inferior temporal cortex was first noted in electrical stimulation studies (see Burnstine et al., 1990; Lüders et al., 1986, 1991) and the surrounding area was referred to as the “basal temporal language area.” Furthermore, although lesions that selectively damage the left posterior inferior temporal cortices are rare, Raymer, Foundas, and Maher (1997) describe a patient with acute damage to the left posterior inferior temporal lobe who suffered from anomia with impaired picture naming and naming to definition as well as reading. Thus, although the left posterior inferior temporal area is clearly involved in visual word processing, activation may reflect semantic and phonological processes that are not specific to reading.

In summary, three left lateralised regions (in the medial extrastriate, posterior middle temporal, and posterior inferior temporal cortices) have been linked to visual word form processing. However, other functional imaging studies show that the same areas also respond to non-lexical stimuli. Activation in the putative visual word form areas may therefore be evoked by (i) processes other than visual word form processing (e.g., early visual, semantic or phonological processes that are not specific to reading although they are required by reading); (ii) processes in addition to visual word form processing (i.e., the same area has different functions either because it has overlapping neural populations or because the function depends on activation in other distributed areas); or (iii) word form processing only but in close proximity to other regions that sustain other functions (i.e., segregation of word form areas will depend on techniques with higher spatial resolution).

Evaluating these hypotheses is not possible in a single imaging experiment. In this paper we attempt to replicate previous findings. In addition to comparing cortical activation for auditory word repetition and reading, the generalisability and specificity of the results was tested by including picture naming and environmental sound naming into the same design. Thirteen subjects were scanned during both auditory word repetition and reading; six subjects were scanned during auditory word repetition and environmental sound naming (full study reported in Giraud & Price, 2001); and eight subjects were scanned during reading and picture naming (full study reported in Moore & Price, 1999). The statistical analysis was then able to identify common areas for auditory word repetition and reading, and areas that were specific to auditory or visual word form processing.

We predicted that (1) both auditory word repetition and reading would activate the left posterior inferior frontal cortex (Broca’s area) and the left dorsal superior temporal gyrus (Wernicke’s area) and (2) auditory word repetition would specifically activate the superior temporal sulcus. With respect to reading, our regions of interest were the left medial extrastriate and posterior middle and inferior temporal cortices, as proposed by Petersen et al. (1990), Howard et al. (1992), and Cohen et al. (2000).

¹ Howard et al. (1992) did not measure activation in inferior temporal regions due to the limited field of view of the scanner.

2. Methods

The data from three different PET experiments were analysed with a single multi-study, multi-factorial statistical model.² All the subjects participated in 12 scans at the Wellcome Department of Cognitive Neurology on the same ECAT EXACT HR+ (model 962) PET scanner (Siemens/CTI, Knoxville, TN, USA) with collimating septa retracted; and all aspects of image processing were conducted using standardised procedures in SPM99 (from the Wellcome Department of Cognitive Neurology, www.fil.ion.ucl.ac.uk).

2.1. Design

2.1.1. Experiment 1: Auditory word repetition and reading

There were two activation conditions: auditory word repetition and reading; and two baseline conditions: hearing noise bursts and saying “OK” and seeing meaningless falsefonts and saying “OK.” Each subject participated in four scans per activation condition and two scans per baseline condition.

During each scan, 15 stimuli were presented for 300 ms at a rate of 1 every 4 s. There were a total of 120 different words (eight sets of 15) that were presented in either the auditory and visual domains with stimulus modality counterbalanced over subjects. Auditory words were spoken by a female voice, recorded, and digitised. Visual words were presented in lower case in Times New Roman font. For the baseline tasks, the auditory word lists were converted into frequency matched noise bursts that maintained the power spectrum and duration of auditory stimulation. Likewise, each list of visual words was converted into falsefonts, non-lingual symbols matched to the words for number and complexity of visual components.

2.1.2. Experiment 2: Auditory word repetition and sound naming

There were three activation conditions: auditory word repetition, environmental sound naming, and auditory repetition of syllables (e.g., “tata”); and three baseline conditions which all involved saying “OK” to auditory noise bursts matched to the corresponding activation stimuli for duration, temporal envelope, and average amplitude. Each subject participated in two scans per condition.

During each scan, 12 stimuli were presented at a rate of 1 every 4 s. The words were all names of objects with specific environmental sounds (e.g., animals, household objects, and vehicles). They were spoken in a male voice, recorded, and digitised as in Experiment 1. The environmental sound stimuli were recordings of the sounds made by the objects in the auditory word repetition condition (e.g., the word “dog” corresponded to the sound of a dog barking). The words were selected like this to match, as far as possible, the word condition to the sound condition with respect to the phonological output and semantic associations (although the semantic associations for words and sounds will not be identical). Thus, subjects were presented with the same objects in the word repetition and sound conditions but, over subjects, the initial presentation of each stimulus occurred an equal number of times in each domain. Thus priming effects (between word repetition and sound naming conditions) were counterbalanced across subjects. Syllable stimuli were generated so that they matched the words in terms of the number of syllables but no attempt was made to match the syllables to the words for phonemic content or complexity; even the bi- and tri- syllabic combinations were composed of repetitions of the same syllable/

² Differences between conditions were only computed within studies. Between studies we only looked for common effects.

phoneme (e.g., “ta,” “tata,” “tatata,”). They were recorded and digitised in the same male voice used to record the words. See Giraud and Price, 2001 for further details.

2.1.3. *Experiment 3: Reading and picture naming*

There were two activation conditions: reading and naming pictures of objects; and four baseline conditions: viewing meaningless falsefonts and saying “OK”; viewing pictures of meaningless objects and saying “OK”; viewing visual words and saying “OK”; and viewing pictures of objects and saying “OK”. Each subject participated in two scans per condition.

During each scan, 12 stimuli were presented for 625 ms at a rate of 1 every 1.9–2.5 s. There were a total of 96 object stimuli (8 sets of 12) and each subject saw half as written words and half as pictures with modality of presentation controlled across subjects. As in Experiment 1, the falsefont condition was matched to the word condition for number and complexity of visual components. The pictures of meaningless objects were also matched to the pictures of real objects for number and complexity of visual components. See Moore and Price, 1999 for further details.

2.1.4. *All experiments*

All subjects, in all conditions of each experiment, were instructed to articulate the response without generating any sound. Subjects’ responses were monitored using a video camera and lip reading. The silent response ensures that auditory processing from the sound of the subjects own response did not contribute to the activation patterns observed. Stimuli were presented visually on a monitor, or aurally through headphones. During auditory stimulation tasks, subjects were instructed to close their eyes to ensure no visual processing contributed to the observed activation.

2.2. *Subjects*

There were a total of 27 subjects; 13 males (mean age: 27.2 years) in Experiment 1; 4 males and 2 females (mean age: 36.6 years) in Experiment 2; and 8 males (mean age: 31 years) in Experiment 3. All were right handed, native English speakers, on no medication, free from any history of neurological or psychiatric illness, and gave written informed consent. The joint research ethics committee of the Institute of Neurology and National Hospital for Neurology and Neurosurgery approved the protocol.

2.3. *Imaging*

During each scan subjects received a 20 s intra-venous bolus of H_2^{15}O at a concentration of 55 Mbq/ml at a flow rate of 10 ml/min through a forearm cannula. The effective dose equivalent was <5.0 mSv as approved by the Administration of Radioactive Substances Advisory Committee of the Department of Health, UK. Correction for attenuation was made by a transmission scan with an exposed $^{68}\text{Ge}/^{68}\text{Ga}$ external source. Images were reconstructed by filtered back projection (Hanning filter, cut-off frequency 0.5 Hz). The voxels in the reconstructed images were $2.05 \times 2.05 \times 2$ mm.

2.4. *Data analysis*

Data from each subject in each Experiment were analysed with the same procedures in Statistical Parametric Mapping (using SPM99 www.fil.ion.ucl.ac.uk). Images from all subjects were realigned, normalised to a PET template, and smoothed

using a 16 mm gaussian filter using standardised routines (Friston et al., 1995, 1996). Statistical analysis tested for:

1. Areas commonly activated by both auditory word repetition and reading, identified by a conjunction analysis (see Price & Friston, 1997b) of contrasts:
 - (i) Auditory word repetition—“OK” to noise bursts (Experiment 1).
 - (ii) Reading—“OK” to falsefonts (Experiment 1).
 - (iii) Auditory word repetition—“OK” to noise bursts (Experiment 2).
 - (iv) Reading—“OK” to falsefonts (Experiment 3).
2. Areas more active for auditory word repetition than reading, identified by finding areas where there was:
 - (i) A main effect of auditory repetition (Experiments 1 and 2).
 - (ii) An interaction between stimulus modality (auditory or visual) and lexicality (the presence vs absence of words). We report the interaction score over studies and for Experiment 1 only.
3. Areas more active for reading than auditory word repetition, identified by finding areas where there was:
 - (i) A main effect of reading (Experiments 1 and 3).
 - (ii) An interaction between stimulus modality (auditory or visual) and lexicality (the presence vs absence of words). We report the interaction score over studies and for Experiment 1 only.

Threshold for significance Effects are reported at $p < .05$ corrected for multiple comparisons except in regions of interest (see Section 1) where we lowered the threshold to $p < .05$ uncorrected for multiple comparisons.

3. Results

3.1. Activation common to auditory word repetition and reading

As predicted, there was common activation for auditory word repetition and reading in the left posterior frontal cortex (Broca’s area) and the left posterior superior temporal cortex (Wernicke’s area). In addition, both auditory word repetition and reading activated the left posterior inferior temporal cortex (LPITC) and a central region of the left superior temporal sulcus. See part A of Table 1 for details of the anatomical localisation and Z scores. Fig. 1 illustrates the activations in Broca’s area, Wernicke’s area and the left posterior inferior temporal cortex. Fig. 2 illustrates the activation in the left superior temporal sulcus.

3.2. Areas more active for auditory word repetition than reading

In addition to the areas that were activated in common to auditory word repetition and reading, auditory word repetition increased activation in a central section of the left superior temporal gyrus (see part B of Table 1 for details). Fig. 2 illustrates that this activation is lateral to that reported in the superior temporal sulcus that was seen for both auditory word repetition and reading. However, as illustrated in Fig. 2, the area more active for auditory word repetition than reading is also activated during environmental sound naming and there is no significant difference ($p > .05$ even when uncorrected for multiple comparisons) between activation in this region for auditory word repetition and environmental sound naming (Experiment 2). The function of this area is therefore not specific to auditory word forms and may reflect high level acoustic processing that is engaged by both auditory repetition and sound naming more than saying “OK” to noise bursts.

Table 1
Details of activations

Anatomical region	Coordinates			Z-Score	<i>p</i> (corr)	<i>p</i> (uncorr)		
	<i>x</i>	<i>y</i>	<i>z</i>					
(A) Common to auditory word repetition and reading								
Left frontal operculum (Broca's area)	-42	22	8	4.1	.45	.000		
Left dorsal posterior temporal (Wernicke's area)	-66	-42	10	4.3	.27	.000		
Left posterior inferior temporal (LPITC)	-44	-56	-20	5.0	.01	.000		
Left central superior temporal sulcus	-50	-22	-6	4.9	.03	.000		
(B) Auditory word repetition > reading								
	Coordinates			Repeat > control	Repeat > control	Read > control	Interaction of stimulus modality by lexicality	
	<i>x</i>	<i>y</i>	<i>z</i>	Z-score	<i>p</i> (corr)	Z-score	Z-score	<i>p</i> (corr)
Left central superior temporal gyrus	-66	-22	4	6.9	.00	$Z < 1.6$	4.7(4.3)	.02(.09)

The anatomical names, coordinates (Talairach & Tournoux, 1988), Z-scores and corrected and uncorrected probabilities of the activations in common to auditory word repetition and reading (part A); and for auditory word repetition > reading (part B). For the common activations (part A), the minimal *T*-score is the smallest *T*-score in the contrasts entered into the conjunction. In part B, the interaction (of stimulus modality by lexicality) is reported twice: over studies and in brackets for Experiment 1 only, to confirm the effect is also seen within subjects.

3.3. Areas more active for reading than auditory word repetition

There were no areas that were significantly more active for visual than auditory word repetition. Nevertheless, we carefully examined the responses in the vicinity of the putative word form areas proposed by Petersen et al. (1990), Howard et al. (1992), and Cohen et al. (2000). We found activation in each region (see Fig. 3 for details) but activation in these areas was not specific to visual word processing. The left posterior middle temporal area reported by Howard et al. (1992) was activated by both auditory word repetition and reading with more activation in the auditory conditions than the visual conditions (see Fig. 3) and no interaction ($p > .05$ uncorrected) between lexicality (words more than controls) and stimulus modality (auditory more than visual). Thus, there appeared to be an additive effect of stimulus modality and lexicality.

The left posterior inferior temporal area reported by Cohen et al. (2000), was also activated by both auditory word repetition and reading and again there was an additive effect of stimulus modality and lexicality. However, in this case there was more activation for the visual than the auditory conditions. Thus, the left posterior inferior temporal cortex appears to be visually driven but modulated by the presence of meaningful visual stimuli such as words and pictures which need to be identified for naming.

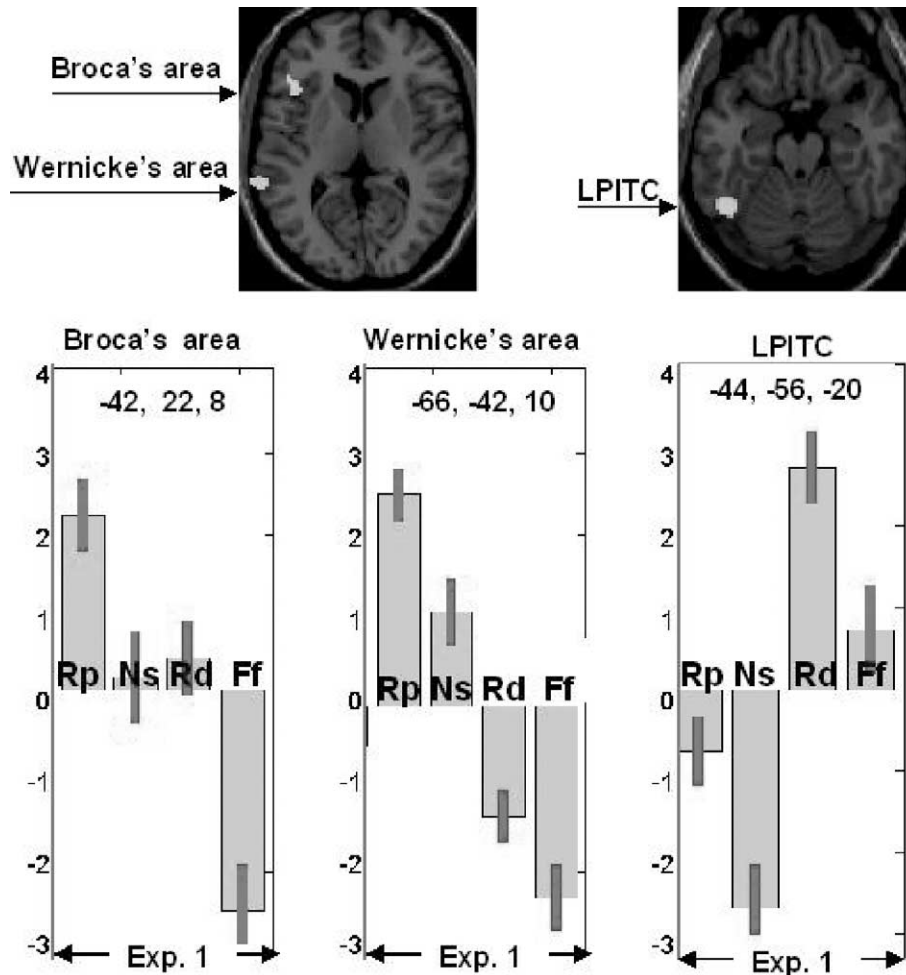


Fig. 1. Common activation for auditory word repetition and reading. Activations common to auditory word repetition and reading in Broca's area, Wernicke's area, and LPITC (see Table 1) are (i) localised and illustrated in yellow on transverse sections of a normal brain: 8 mm above (left) and 20 mm below (right) the ACPC line; and (ii) plotted for each condition (Rp, auditory repetition; Ns, noise bursts; Rd, read; Ff, falsefonts from Experiment 1 only)—0 on the y-axis corresponds to the mean activation for all conditions.

Finally, in the left medial extrastriate area reported by Petersen et al. (1990), there was no significant effect for either reading or auditory word repetition in Experiment 1 or over Experiments ($p > .05$ uncorrected for multiple comparisons). However, a left medial extrastriate area was activated for reading in Experiment 3 (Moore & Price, 1999). Critically this area was not specific to reading, it was also activated by picture naming (as previously reported by Bookheimer et al., 1995); and shows (see Fig. 3) a strong effect of stimulus modality (visual more than auditory).

In summary, our data are not consistent with any of the previous claims regarding the site a visual word form system but they do illustrate how such conclusions could arise when stimulus parameters and task demands are not fully controlled. For instance, differences between auditory and visual word form processing can be confounded by a main effect of stimulus modality—word form specificity can therefore

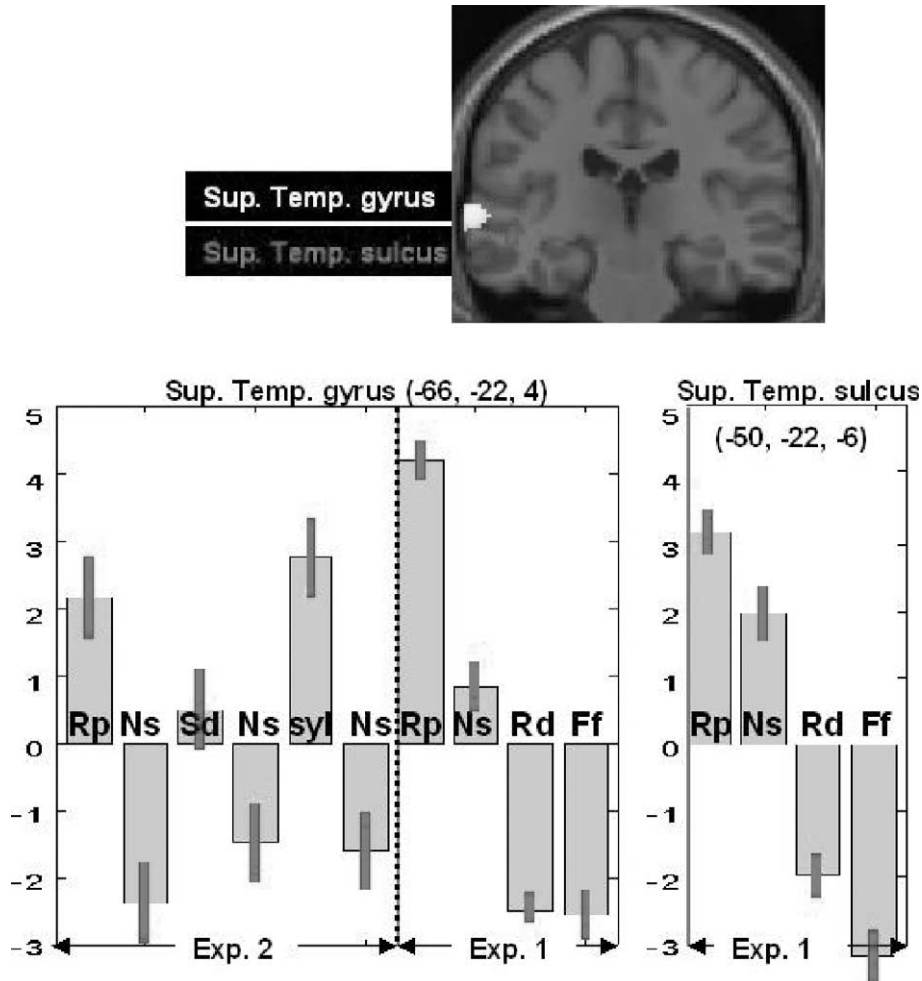


Fig. 2. Left superior temporal gyrus and sulcus activations. Activation in the left superior temporal gyrus (for repeat > read) is shown in yellow on a coronal slice of a normal brain 22 mm behind the ACPC line. It lies lateral to the superior temporal sulcus activation that is common to repeating and reading (shown in red). The plots illustrate (i) common activation in the superior temporal gyrus for auditory repetition of words (Rps), syllables (syl), and environmental sounds (Sd) relative to the stimulus specific noise control conditions (Ns) but no activation for reading (Rd) relative to falsefonts (Ff); and (ii) activation in the superior temporal sulcus for both repeating and reading. As in Fig. 1, 0 on the y-axis corresponds to the mean activation for all conditions.

only be implied when an interaction between stimulus modality and lexicality is present.

4. Discussion

The aim of this study was to evaluate the evidence for cortical sites associated with the auditory and visual word form systems. To this end, we compared activations elicited by reading and auditory word repetition and identified the neural regions (i) common to both reading and auditory word repetition, (ii) more active for auditory word repetition than reading, (iii) more active for reading than auditory word repetition. By including statistical comparisons between naming words, pictures, and

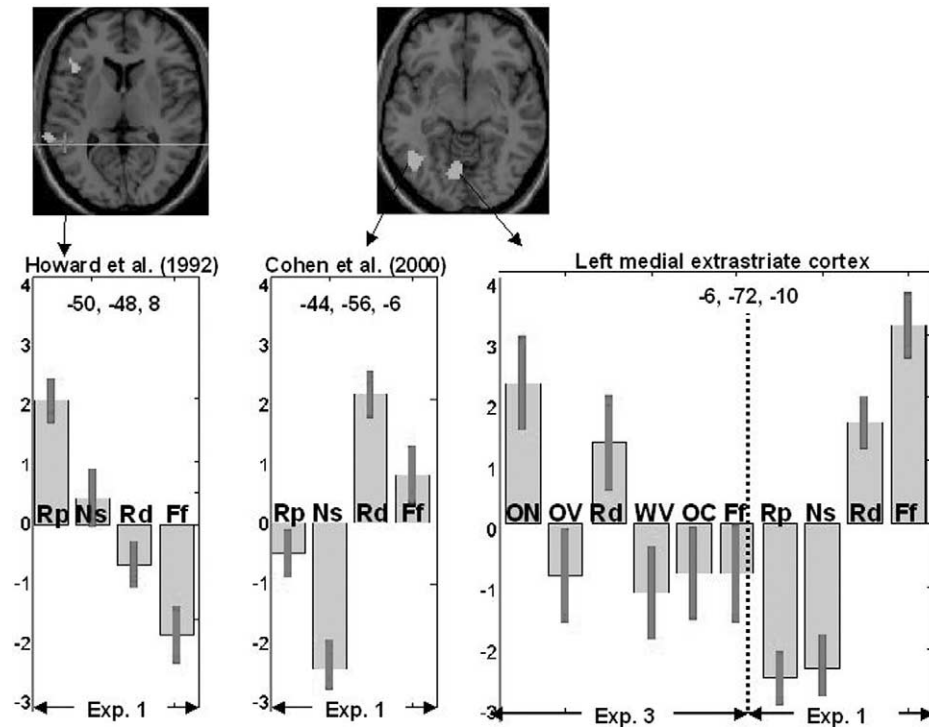


Fig. 3. Responses in the putative visual word form areas. Activation for reading and repetition (Experiments 1) at the peak co-ordinates of the visual word form areas proposed by Howard et al. (1992) and Cohen et al. (2000) are illustrated on transverse slices of a normal brain 8 mm above (left) and 8 mm below (right) the ACPC line. The corresponding plots of relative activity are shown below (as in Fig. 1). Also shown is the activation in the left medial extrastriate cortex seen for reading relative to falsefonts in Experiment 3 (Moore & Price, 1999) but not in Experiment 1. ON, object naming; OV, object viewing; WV, word viewing; OC, object control. There were no other effects ($p > .1$, uncorrected for multiple comparisons) in the medial extrastriate cortex that might correspond to the visual word form area proposed by Petersen et al. (1990).

environmental sounds, we were also able to ascertain the specificity of the observed effects.

4.1. Common effects for reading and auditory word repetition

As predicted by the neurological model, the left frontal operculum (Broca's area) and the left posterior superior temporal gyrus (Wernicke's area) were activated by both reading and auditory word repetition. The peak activation in Broca's area was located close to the anterior insula. This is consistent with a recent lesion study performed by Dronkers (1996) who identified the left anterior insula as a common site of damage in 25 patients with speech apraxia and noted that it was undamaged in patients without apraxia. Likewise, Wise, Greene, Büchel, and Scott (1999) have linked the anterior insula to *planning* speech articulation.

With respect to activation in Wernicke's area, our question concerns whether this corresponds to "auditory images of speech" that are involved in both auditory word repetition and reading, as proposed by the neurological model. Evidence in support of the neurological model comes from previous studies showing activation in Wernicke's area for hearing speech relative to nonspeech sounds (Binder et al., 2000; Mummery, Ashburner, Scott, & Wise, 1999; Scott, Blank, Rosen, & Wise, 2000) but

not for vocal sounds (e.g., laughing, sneezing) or environmental sound naming relative to amplitude modulated noise and scrambled voice stimuli (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Giraud & Price, 2001). However, other studies have shown activation in the same region during tasks that do not involve speech processing. For example, Celsis et al. (1999) report activation in Wernicke's area in response to unexpected (deviant) tones and Bischoff-Grethe, Proper, Mao, Daniels, and Berns (2000) report activation in the absence of speech input or output, when temporal predictability decreases in the spatial sequence of visually presented coloured squares. Thus, the responses in Wernicke's area do not simply correspond to the demands on auditory word form processing. It is possible that there may be several different areas within the posterior superior temporal region we are referring to as Wernicke's area. It is also possible that the same area may have different functions depending on the areas it interacts with. For example, Wernicke's area may have a role in auditory word form processing when it co-activates with Broca's area but different functions when it co-activates with other areas (see Price, Warburton, Moore, Frackowiak, & Friston, 2001 for similar hypotheses regarding the posterior inferior temporal lobe). Further studies are therefore required to explain these divergent findings before any definitive conclusions can be drawn.

In addition to activating Broca's and Wernicke's areas, both reading and auditory word repetition activated a left posterior inferior temporal region. Activation in this area has been observed in most previous functional imaging studies of reading and picture naming (see Bookheimer et al., 1995; Price & Friston, 1997b) but it is not consistently reported for studies of auditory word repetition (Price et al., 1996a; McCrory, Frith, Brunswick, & Price, 2000; Wise et al., 1999). Furthermore, lesions to the left posterior inferior temporal cortex impair reading and naming but not auditory word repetition (De Renzi, Zambolin, & Crisi, 1987; Foundas, Daniels, & Vasterling, 1998). This pattern of effects suggests that activation in the left posterior inferior temporal cortex is not necessary for auditory word repetition and is therefore unlikely to reflect auditory word form processing (which is necessary for auditory repetition). Possibly, left posterior inferior temporal activation reflects semantic processing of the words (which is not necessary for auditory word repetition) but we also need to consider whether it relates to visual word form processing (Cohen et al., 2000). This might occur if, during auditory word repetition, subjects automatically evoked a visual image of the heard word. However, we consider this to be unlikely for two reasons. One is that the left posterior inferior temporal area is necessary for picture naming (De Renzi et al., 1987; Foundas et al., 1998), a skill that is learnt prior to learning about visual word forms. The other is that subjects were not aware of generating a visual word form (demonstrating that "implicit" visual word form processing occurred during auditory word repetition would require sophisticated behavioral investigations). Therefore, although the function(s) of the left posterior inferior temporal cortex is/are still not clear, the pattern of activation is not consistent with an area that is specific to either auditory or visual word form processing.

Finally, a region deep in a central portion of the left superior temporal sulcus was activated by both reading and auditory word repetition (see Fig. 2). Again, although the function of this region is not clear, it is not specific to auditory or visual word form processing because it is also activated by environmental sound naming (Experiment 2, see Giraud & Price, 2001) and vocal sounds (Belin et al., 2000).

4.2. Areas more active for auditory word repetition than reading

The only area that was significantly more active for auditory word repetition than reading was located on the lateral surface of the left superior temporal gyrus.

Critically, this area also responds to environmental sound naming (see Fig. 2). Belin et al. (2000) have also reported activation (at $x = -62$, $y = -14$, $z = 0$) for hearing vocal sounds (coughing, sneezing, laughing, and sighing) relative to nonvocal sounds (finger snaps, footsteps, and bells) and demonstrated that filtering out either the high or low frequency components of voices significantly reduces neuronal activity. Activation in this area during auditory word form processing may therefore reflect acoustic processing elicited by a combination of frequency components that is involved in auditory word and environmental sound processing more than noise bursts.

4.3. Areas more active for reading than auditory word repetition

We found no areas that were more active for reading (relative to saying “OK” to falsefonts) than auditory word repetition (relative to saying “OK” to noise bursts). The absence of activation in the left angular gyrus (the visual word form area in the neurological model) was expected on the basis of previous functional imaging studies of reading aloud. The left angular gyrus usually activates only during reading tasks that specifically target semantic and phonological processing (Binder et al., 1997; Démonet, Price, Wise, & Frackowiak, 1994; Mummery, Patterson, Hodges, & Price, 1998; Pugh et al., 1996; Rumsey et al., 1997). It is also involved in semantic tasks on pictures of objects (Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996) and faces (Gorno-Tempini et al., 1998). Therefore, responses in the left angular gyrus are more consistent with semantic retrieval than visual word form processing.

The absence of activation in the left medial extrastriate area for reading relative to falsefonts in Experiment 1 is not consistent with previous studies of reading (see Mechelli et al., 2000 for a review) including Experiment 3 (Moore & Price, 1999). We have two possible explanations for these inconsistent results. One is that activation in the left medial extrastriate cortex depends on how subjects attend to the stimuli (see Mechelli et al., 2000). This in turn may depend on the size of the stimuli, the exposure duration and the rate of stimulation that were not held constant over experiments. The other explanation relates to the meaning of the words being read. In Experiment 3, the words referred to object names but in Experiment 1, the words referred to auditory features (e.g., “chime”), visual features (e.g., “yellow”) or movements (e.g., “jump”). Activation in this visually driven area may therefore be modulated by word meaning although further experiments are required to confirm this hypothesis. Irrespective of the precise function of the left medial extrastriate, it does not show greater responses to word than picture processing, therefore there is no evidence to suggest that it is dedicated to visual word form processing (see Bookheimer et al., 1995; Indefrey et al., 1997 for similar conclusions).

In the left middle and inferior temporal areas associated with visual word form processing by Howard et al. (1992) and Cohen et al. (2000), respectively, activation was observed for auditory word repetition as well as reading (see Fig. 3). Activation in the left middle temporal area (Howard et al., 1992) was greater for auditory words and noises than visual words and falsefonts; and activation in the left inferior temporal area (Cohen et al., 2000) was greater for visual words and falsefonts than auditory words and noises. Thus, direct comparisons between auditory word repetition and reading could be taken to imply that the left middle temporal area is specific to auditory word processing (contrary to the conclusions of Howard et al., 1992) and the left inferior temporal area is specific to visual word processing (consistent with the conclusions of Cohen et al., 2000). However, direct comparisons between auditory and visual word processing are confounded with sensory processing differences which are only controlled by including the baseline conditions.

Demonstrating modality specific word processing therefore rests on finding a significant interaction between stimulus modality (visual vs. auditory) and lexicality (words vs. noise/falsefonts). Instead, we demonstrated an additive effect of stimulus modality and lexicality in both posterior temporal areas which is not consistent with modality specific word form processing. The word form area hypothesis can only be verified if subjects evoke visual images of the words during auditory word form processing and naming. Although we believe this hypothesis is highly unlikely, it can only be rejected on the basis of behavioral investigations which are not at present available.

4.4. Summary and conclusions

At first glance, the functional imaging data appear to offer some evidence for cortical sites dedicated to auditory word form processing: (1) Wernicke's area was activated by both auditory word repetition and reading, as predicted by the neurological model; and (2) a region on the dorsal surface of the left superior temporal gyrus was more active for auditory word repetition than reading. However, although these areas may be necessary for auditory word form processing, they are not specific to auditory word form processing. Furthermore, on the basis of the current functional imaging data, we cannot distinguish whether these areas have one underlying function (e.g., high level acoustic processing); or more than one function determined either by spatially overlapping neural networks or task specific functional connectivity with other areas. Likewise, we have argued that there are no areas that specifically respond to visual word form processing and we have offered alternative explanations for the results that led to the proposals advocated by Petersen et al. (1990), Howard et al. (1992), and Cohen et al. (2000). Although we cannot exclude the possibility that visual word form processing is evoked during auditory word repetition, we can conclude that any previous claims regarding the cortical localisation of visual and auditory word form areas were premature.

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