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Comments and Controversies

The myth of the visual word form area

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Abstract

Recent functional imaging studies have referred to a posterior region of the left midfusiform gyrus as the "visual word form area" (VWFA). We review the evidence for this claim and argue that neither the neuropsychological nor neuroimaging data are consistent with a cortical region specialized for visual word form representations. Specifically, there are no reported cases of pure alexia who have deficits limited to visual word form processing and damage limited to the left midfusiform. In addition, we present functional imaging data to demonstrate that the so-called VWFA is activated by normal subjects during tasks that do not engage visual word form processing such as naming colors, naming pictures, reading Braille, repeating auditory words, and making manual action responses to pictures of meaningless objects. If the midfusiform region has a single function that underlies all these tasks, then it does not correspond to visual word form processing. On the other hand, if the region participates in several functions as defined by its interactions with other cortical areas, then identifying the neural system sustaining visual word form representations requires identification of the *set* of regions involved. We conclude that there is no evidence that visual word form representations are subtended by a single patch of neuronal cortex and it is misleading to label the left midfusiform region as the visual word form area.

Introduction

Reading involves access to prior knowledge about familiar letter combinations, their meanings and sounds. The visual word form is the combination of letters that make up the word. It is an abstract representation because it does not depend on the perceptual dimensions of the stimulus such as the location, color, size, or font of the letters. There are several ways that representations of visual word forms might be implemented at a cognitive or neural level. Some cognitive models of reading include a "visual word form system" or "orthographic input lexicon" as a specific functional module (Marshall and Newcombe, 1973; Patterson and Shewell, 1987), while others claim that knowledge of familiar letter combinations arises from interactions between orthographic, semantic, and phonological processing without explicit word form representations (Plaut et al., 1996; Seidenberg and McClelland, 1989). Thus it is of particular theoretical interest that Cohen and colleagues (2002) have recently claimed that visual word form representations: "are subtended by a restricted patch of left-hemispheric fusiform cortex [average Talarach coordinates $x = -43$, $y = -54$, $z = -12$] which is reproducibly activated by reading" (p. 1054).

In a series of functional neuroimaging experiments, Cohen and colleagues (2000, 2002) had subjects silently read visual words briefly presented to either the left or right visual hemifield. Written words relative to fixation activated many frontal, temporal, and parietal areas irrespective of the hemifield of presentation (Cohen et al., 2000). The authors, however, focused on a left lateralised midfusiform activation ($x = -42$, $y = -57$, $z = -6$; $Z = 8.49$) because it was the only area to lie in the occipitotemporal cortex where lesions give rise to pure alexia. Subsequently, Cohen et al. (2002) showed that the same area was more responsive to written words than consonant letter strings ($x = -43$, $y = -54$, $z = -12$; $t = 3.42$). Along with other evidence that

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the same area is activated irrespective of typographical case (Dehaene et al., 2001; see also Polk and Farah, 2002) and that it does not respond to same–different matching of auditory words or pseudowords (Dehaene et al., 2002), the authors have labeled this left midfusiform region the "visual word form area" (VWFA). Moreover, they claim it "therefore appears as a unimodal area, at least as far as word perception is concerned" (Cohen et al., 2002, p. 1055).

Potential objections to this hypothesis are considered by Cohen et al. (2002). Specifically, they note that:

> . . . in some studies, words in the auditory or tactile modality have been shown to induce left fusiform activation, which should not be expected if this region was purely devoted to visual processing (Binder, Frost, Hammeke, Rao, & Cox, 1996; Buchel, Price, & Friston, 1998; Buckner, Koustall, Schacter, & Rosen, 2000; Chee, O'Craven, Bergida, Rosen, & Savoy, 1999; Demonet, Price, Wise, & Frackowiak, 1994; Demonet et al., 1992; D'Esposito et al., 1997; Giraud & Price, 2001; Perani et al., 1998; Pihlajamaki et al., 2000; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Wise et al., 2000).

They go on to claim, however, that previous studies that demonstrated fusiform activation for stimuli other than visual words activated a fusiform region that was anterior to their proposed visual word form area. According to their review of the literature, fusiform activation for nonvisual stimuli had an average anterior–posterior coordinate of $y = -43$ (range -54 to -32). In contrast, studies of visual words activate a more posterior region with an average anterior–posterior coordinate of $y = -60$ (range -43 to -70). Cohen et al. (2002) therefore propose that there are several distinct areas in the left midfusiform gyrus and the "VWFA proper would occupy the middle portion of the left fusiform gyrus, with Talairach co-orindates (TC) close to $y = -60$, while increasingly more abstract and supramodal representations would occupy its more anterior sectors" (p. 1054). Even if nonvisual word stimuli do activate the "VWFA proper," Cohen et al. (2002) suggest that this could be due to "top-down" processing such as mental imagery activating visual word forms. As we argue below, however, these arguments are not consistent with either the neuropsychological nor functional imaging evidence.

Neuropsychological evidence

In support of their hypothesis, Cohen et al. (2002) claim that the left midfusiform area that they refer to as the VWFA "seems to be the critical lesion site for pure alexia, a unimodal deficit of word reading with sparing of writing and of auditory word comprehension (Beversdorf, Ratcliffe, Rhodes, & Reeves, 1997; Binder & Mohr, 1992; Damasio & Damasio, 1983; Dejerine, 1892; Leff et al., 2001)" (p. 1055). A closer inspection of this claim, however, reveals that there are no neuropsychological studies that have demonstrated a one-to-one mapping between damage to the left midfusiform region and a specific deficit with processing visual word forms. First, patients referred to as pure alexics usually have extensive left occipital lesions including the cuneus, calcarine sulcus, and lingual gyrus, in addition to the fusiform gyrus (see Damasio and Damasio, 1983). Consequently it is impossible to localize their word reading deficit to a particular area of damaged cortex. Second, although patients with pure alexia do not have agraphia, aphasia, dementia, or oral spelling deficits by definition (Benson and Geshwind, 1969), the term does not exclude the cooccurrence of other perceptual deficits. Thus, patients with pure alexia are often reported to have difficulties with color naming and picture processing (see Damasio and Damasio, 1983; De Renzi et al., 1987; Geshwind, 1965; Behrmann et al., 1998).

The classic neurological interpretation of pure alexia is a disconnection syndrome where the occipitotemporal lesion disconnects visual processing in the occipital cortices from language processing (i.e., phonological, syntactic, and semantic processing) in temporal and parietal regions of the left hemisphere (Damasio and Damasio, 1983; Dejerine, 1892; Geshwind, 1965). This explanation holds for patients with and without hemianopia and with and without callosal damage (Damasio and Damasio, 1983). It also accounts for the inconsistent cooccurrence of letter, number, picture, and color naming deficits which is explained by the extent of the lesion. For example, Kurachi et al. (1979) claim that object naming disturbances depend on the extent of damage to the left cuneus and Damasio and Damasio (1983) observed that color anomia is always accompanied by damage to the lingual gyrus that extends into the left hippocampal region. Conversely, picture, color, and letter naming can be spared while reading is impaired because reading is more complex and imposes greater demands on visual processing (see Benson and Geshwind, 1969; Friedman and Alexander, 1984; Geshwind, 1965; Behrmann et al., 1998). In other words, according to the disconnection account of pure alexia, the reading problem is the most salient manifestation of a more general visual problem.

The most quoted example of a word specific alexia is the study by Warrington and Shallice (1980). These authors dismissed the possibility that the reading impairment in pure alexia was due to visual or perceptual deficits because the patients they report showed no impairment with (1) complex picture interpretation; (2) recognition of pictures of objects in unconventional views; (3) selective attention; (4) visual short term memory, and that their patients were more impaired with tachistoscopic presentation of words than pictures. Warrington and Shallice (1980) therefore localized the deficit in their patients to the function of a word form system that "parses (multiple and in parallel) letter stings into ordered familiar units and categorises these units visually" (p. 109). The problem with this, and all neuropsychological studies that claim to have found deficits that are specific to alphabetic stimuli, is that there is no detailed task analysis of the visual processes involved in reading and other visual tasks such as complex picture interpretation. For instance, complex picture interpretation is a slow serial process whereas whole word reading requires fast parallel letter identification. Consequently, reading may be most affected by minor perceptual deficits. Furthermore, even if the patients reported by Warrington and Shallice (1980) did have deficits that were specific to visual word forms, they did *not* have lesions to the left midfusiform gyrus. One patient (R.A.V) had a left temporoparietal intracranial hematoma and the other patient (J.D.C.) had a glioma situated in the left temporoparietal region.

Finally, isolated lesions in the vicinity of the left midfusiform, that do not include occipital cortex, are rare because the blood supply comes from both the posterior and middle cerebral arteries thereby protecting it from ischemic damage. Nevertheless, rare reports of focal lesions in this area have been shown to result in picture naming and reading deficits in the absence of impaired object recognition, semantic impairment, or heard word repetition (Foundas et al., 1998; Raymer et al., 1997). This is consistent with reports that electrical stimulation in left basal temporal areas can selectively impair picture naming (see Burnstine et al., 1990; Luders et al., 1986, 1991). However, because lesions tend to be large and result in multiple disconnections, it is not possible to say whether the areas linked to naming correspond to the area that has been associated with the visual word form area.

In conclusion, to our knowledge, no previous lesion study (including those quoted by Cohen et al., 2002) has demonstrated a one-to-one mapping between visual word form recognition and a specific patch of cortex in the left midfusiform gyrus. Indeed Leff et al. (2001), who report a functional imaging study of a pure alexic who does not activate the left occipitotemporal junction when viewing written words, acknowledge: “As we only varied word rate and not word or symbol form, we cannot conclude from our study that this area is specific for word forms” (p. 518).

Functional imaging evidence

In the following section we report data from several previously published imaging studies to demonstrate that, in addition to reading, the precise region of the left mid fusiform gyrus identified by Cohen and colleagues as the VWFA is engaged in tasks without any visual word form component. We begin by illustrating activation for reading that identifies the left midfusiform area referred to by Cohen and colleagues. We then demonstrate that activation in this region is not specific to visual word forms but is also observed when subjects view and name pictures of familiar objects, make manipulation responses to pictures of unfamiliar nonobjects, name colors, and perform auditory and tactile word processing tasks.

Reading activation

The top row of Fig. 1 (see also Table 1) illustrates activation when normal subjects read visual words relative to rest (yellow) and relative to false fonts (red) as reported in Brunswick et al. (1999). The crosshairs indicate the peak coordinates for the VWFA ($x = -42$, $y = -57$, $z = -15$) according to Cohen et al. (2002). As can be seen, the only left lateralized region of the occipitotemporal cortex to be activated for words relative to false fonts corresponds exactly to the left midfusiform location that Cohen and colleagues have identified as the VWFA. This area clearly has a role in reading that is distinct from early visual processing and that was not appreciated in classic neurological accounts of language (see Price, 2000).

Object recognition/naming

The same area, however, is also engaged when subjects name, view, or generate verbs to pictures of objects (Bookheimer et al., 1995; Etard et al., 2000; Murtha et al., 1999) yet these tasks do not entail visual word form processing. Fig. 1 (row 2) illustrates the activation found when subjects named pictures of objects relative to saying “OK” to the same pictures (Moore and Price, 1999). This effect cannot be due to “implicit” activation of visual word forms when subjects name pictures because activation is *greater* for naming pictures than reading the written names of the same objects (Moore and Price, 1999, see Fig. 1, row 3) and we would not expect “implicit” word form activation (during picture naming) to exceed “explicit” word form activation (during reading). Furthermore, Chao et al. (1999, 2002) have reported activation in this region for pictures of animals more than pictures of tools (see Table 2). Even if picture naming does involve some degree of top-down, or “implicit,” activation of visual word forms, there is no reason to believe these effects should be greater for animals than tools. Similarly, van Turennout et al. (2000) have shown an effect of object learning in this area, with less activation when the picture is familiar (see Table 2). Thus, pictures of common objects activate the precise location of the putative VWFA and this activation can be enhanced by specific categories of object (Chao et al., 2002) or reduced by priming (van Turennout et al., 2000).

Visual form processing

Martin and Chao (2001) have suggested that midfusiform activation is driven by object form. Thus one possi-

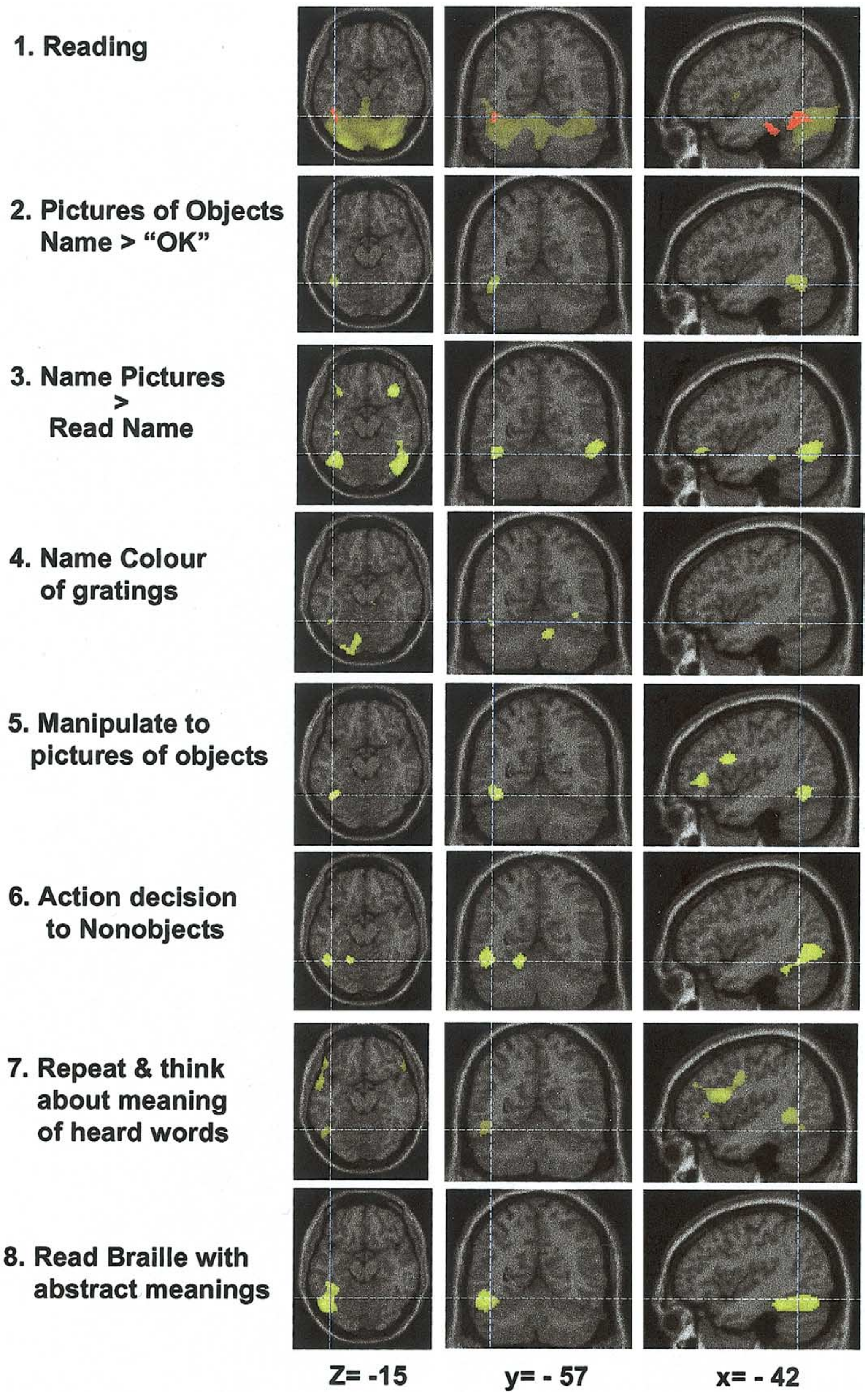

Fig. 1. Activation (in the posterior left midfusiform region) ($P < 0.001$ uncorrected) for words and pictures of objects in the area that Cohen et al., (2002) call the VWFA. The peak coordinates ($x = -42$, $y = -57$, $z = -15$) from Cohen et al. (2002) are indicated by the dashed white cross hairs. The transverse, coronal, and sagittal cuts are also at $x = -42$, $y = -57$, $z = -15$. Row 1: reading aloud words and pseudowords relative to rest (in yellow) and feature

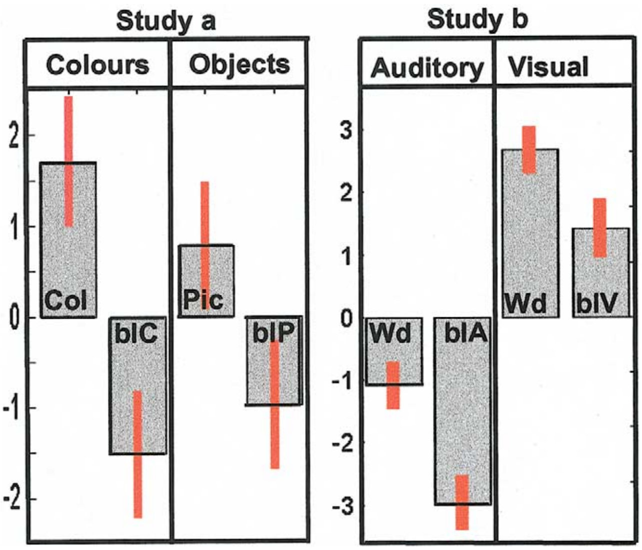

Fig. 2. Plots of relative blood flow values in percent change from the mean at $x = -42$, $y = -58$, $z = -16$. Study a involved (1) color naming (Col), (2) the corresponding baseline (B1C) which was saying "OK" to the same stimuli, (3) naming pictures of objects (Pic), and (4) saying "OK" to the same pictures (B1P). Data are from Price et al. (1996). Study b involved both auditory and visual conditions: (1) auditory word repetition; (2) saying "OK" to noise bursts (B1A); (3) reading visual words; and (4) saying "OK" to false font strings (B1V). Data are from Price et al. (2002).

bility is that the visual word form area is not specific to orthography but is also involved in processing object structure more generally. However, this "visual form" hypothesis cannot be the complete explanation. For instance, activation is also observed when subjects name the color of meaningless visual gratings relative to saying "OK" to the same gratings, where visual input is matched and the task does not require visual form processing (Price et al., 1996, see Fig. 1, row 6). Fig. 2 (study a) illustrates that the effect for color naming relative to saying "OK" to the same stimuli is as large as that observed for naming pictures relative to saying "OK" to the same pictures. These data therefore offer more support to an explanation in terms of "naming" than visual form processing, but see below.

Naming

The association of the left midfusiform area with naming has previously been noted in lesion and electrical stimulation studies (Burnstine et al., 1990; Foundas et al., 1998; Luders et al., 1986, 1991; Raymer et al., 1997). The problem with this account is that functional imaging activation in the left midfusiform area is not specific to naming. For instance, it is also seen when subjects use a manipulandum to make manual "twist" or "pour" action responses to pictures of familiar objects relative to perceptual judgements on the same stimuli (Phillips et al., 2002, see Fig. 1, row 4). Again, one might claim that simply viewing familiar objects implicitly engages naming but the same study showed that action decisions to unfamiliar nonobjects (with no names) activated the area relative to perceptual decisions (Phillips et al., 2002, see Fig. 1, row 5). Moreover, activation in the left midfusiform region is seen when subjects view pictures of unfamiliar nonobjects (with no name) relative to visual noise (van Turennout et al., 2000, see Table 2). Activation is even observed when subjects view simple shapes (circles and triangles) that move in a "socially interactive" way (e.g., chasing each other) relative to random motion of the same shapes (Castelli et al., 2002, see Table 2). These data are not consistent with an explanation of midfusiform activation in terms of naming.

Visual processing

Finally, activation in the left midfusiform area is not even limited to visual processing. It is also observed when subjects hear, repeat, and think about the meaning of auditory words (Price et al., 2002, see Fig. 1, row 8); hear words and make rhyming (e.g., soap-hope) judgments (Booth et al., 2002a, 2002b, see Table 2); hear definitions of objects and make semantic decisions (Thompson-Schill et al., 1999, see Table 2) or imagine the object (Mellet et al., 1998, see Table 2); and when congenitally blind subjects read tactile words with abstract meanings in Braille (Buchel et al., 1998, see Fig. 1, row 7). While it might be plausible that visual word forms were evoked when sighted subjects were engaged in the auditory tasks (although we know of no theory that posits this), mental imagery cannot account for activation in congenitally blind subjects who have never experienced visual word forms.

Fig. 2 (study b) illustrates the relative blood flow effects in the left midfusiform region when subjects read and repeat visual or heard words (Price et al., 2003). Although both reading and repeating activate this area relative to their corresponding baseline conditions, activation is greater for visual stimuli than auditory stimuli *irrespective of lexicality*. Thus, there was significantly

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decision on words and pseudowords relative to falsefonts (in red). Row 2: Naming pictures of objects relative to saying "OK" to the same pictures. Row 3: Naming pictures of objects relative to reading the written names of the same objects. Row 4: Naming color of grating relative to saying "OK" to same stimuli. Row 5: Moving a manipulandum in response to pictures of objects relative to scrambled pictures. Row 6: Key press "twist" or "pour" responses to pictures of nonobjects relative to screen size judgments (large or small) to the same stimuli. Row 7: Repeating and thinking about the meaning of auditory words. Row 8: Braille reading (single words with abstract meanings) relative to meaningless Braille. Details for all these activations are shown in Table 1.

Table 1
Details of studies and statistical results illustrated in Fig. 1

	Authors	Activation task	Activation stimuli	Baseline	Subjects	Total scans in contrast	Coordinates closest to ROI (−42, −57, −15)	Z score
1	Brunswick et al., 1999	Read	Words and pseudowords	Rest eyes closed	6	72	−42, −56, −16	3.9
2	Moore and Price, 1999	Name	Pictures of objects	Say OK to same pictures	8	32	−42, −54, −14	4.5
3	Moore and Price, 1999	Name	Pictures of objects	Read names of same objects	8	32	−42, −60, −14	4.5
4	Price and Friston, 1997	Name color	Colored gratings	Say "OK" to same stimuli	6	36	−42, −54, −14	3.1
5	Phillips et al., 2002	Manipulate	Pictures of objects	Manipulate to visual noise	6	24	−40, −58, −12	4.8
6	Phillips et al., 2002	Twist/pour decision	Pictures of nonobjects	Screen size dec. to same pictures	8	32	−46, −56, −14	4.4
7	Price et al., 2002	Repeat	Auditory words	Say "OK" to noise bursts	13	78	−44, −58, −12	3.0
8	Buechel et al., 1998	Feature decision	Braille words with abstract meanings	Braille nonwords, same task	6	24	−46, −56, −14	3.7

Note. Details of the paradigms and statistical effects illustrated in Fig. 1. The first column refers to row numbers used in Fig. 1, while the second indicates the reference where full study details can be found. The third, fourth, and fifth columns refer to tasks and stimuli used in activation and baseline conditions. The sixth column indicates the number of subjects in the study and the seventh column indicates the total number of scans in the contrast between the activation and baseline conditions that resulted in the activations detailed in the eighth and ninth columns. The coordinates in column 8 are in standard space (Talairach and Tournoux, 1988) and they correspond to the activation peak within 6 mm of the VWFA coordinates [$x = -42$, $y = -57$, $z = -15$] from Cohen et al. (2002). The final column provides the Z score at the given coordinate.

greater activation for viewing false font stimuli (i.e., the reading baseline) than listening to noise bursts (i.e., the repeating baseline, $Z = 5.4$, $P < 0.01$ corrected for multiple comparisons across the whole brain). Moreover, the absence of an interaction between stimulus modality (visual or auditory) and lexicality (words or baseline) illustrates that the difference between reading and auditory word repetition is not specific to visual word forms. Although the left midfusiform area is more strongly driven by visual input than auditory input, both auditory and visual words activate the region. These data illustrate how a direct comparison between visual and auditory word form processing (Dehaene et al., 2002) are confounded by the main effect of stimulus modality. Word form specificity can therefore only be implied when an interaction between stimulus modality and lexicality is present.

Functions of the left midfusiform gyrus

Overall, the results presented above indicate that the left midfusiform area is a polymodal area that is clearly driven by visual input, but also responds to tactile and auditory stimuli even during tasks that do not entail top-down activation of visual processes. If this left midfusiform area is not devoted to either visual form or visual word form

Table 2
Other paradigms activating the visual word form area (−42, −57, −15)

Reference	Task	Activation stimuli	Baseline	Coordinates
Bookheimer et al., 1995	Name/view	Pictures of objects	Random lines	−42, −58, −20
Murtha et al., 1999	Name/view	Pictures of objects	Plus signs	−44, −59, −21
Etard et al., 2000	Verb generation	Pictures of objects	Rest	−44, −60, −20
Chao et al., 1999	View pictures	Animals	Tools	−40, −59, −10
VanTurennout et al., 2000	Name pictures objects	Unprimed	Primed	−44, −54, −12
VanTurennout et al., 2000	View	Pictures of nonobjects	Visual noise	−38, −56, −20
Castelli et al., 2002	View simple moving shapes	With theory of mind interactions	Random movements	−46, −60, −10
Booth et al., 2002a, 2002b	Listen to words	Rhyming judgements	Pitch decision on noise bursts	−45, −60, −18
Thompson-Schill et al., 1999	Yes/no decisions to auditory stimuli	Heard questions about objects/animals	Same stimuli—digitally reversed	−41, −53, −11
Mellet et al., 1998	Heard definitions of objects	Mental imagery of object	Rest	−48, −60, −14

Note. Details from other studies showing activation within 5 mm of the putative visual word form area [$x = -42$, $y = -57$, $z = -15$] during paradigms that do not involve reading.

processing, what functional role does it play? There are three distinct possibilities:

1. Within the same anatomical area there may be different populations of cells that are involved in different functions, with one population of cells underlying visual word form processing while others are engaged by form processing, naming, etc. To test this hypothesis would presumably require spatial resolution sufficient to differentiate responses from adjacent neural columns, if not individual cells (i.e., single cell recordings). Theoretically, the presence of local excitation and surround inhibition makes such speculation unlikely as it means that neural columns are not locally independent (see Durbin and Mitchison, 1990). Even if such a population of cells does exist, however, it would still be misleading to label the macroanatomic region the "visual word form area" for the same reason that one doesn't refer to V1 as the "vertical bar area." Namely, the region as a whole is not responding in the same fashion as individual cells or columns.

2. The second possibility is that a single cognitive function underlies all responses (cf. Price and Friston, 1997). It should be clear from data presented above that if there is a such a function, it has yet to be identified. Clearly though, activation during tactile, auditory, and other nonreading tasks excludes a midfusiform function that is devoted exclusively to visual word form processing.

3. The final possibility is that the same population of cells can be assigned multiple functions that depend on their neuronal interactions with other cortical or subcortical areas. The hypothesis that the same population of cells can be assigned multiple functions that depend on its neuronal interactions is consistent with theories that advocate "one-to-many and many-to-one" mappings between functions and cortical areas (McIntosh, 2000; Mesulam, 1990; Passingham et al., 2002). As demonstrated above, the left midfusiform responds to visual, auditory, and tactile input, indicating polymodal interactions with the sensorimotor cortices. It is one of the areas that Damasio and Damasio (1994) refer to as a "convergence zone" where many feed forward and feed backward neural loops make contact. If its function depends on the interactions with other areas, then the neural correlates of that function can only be defined by specifying the *set of interacting regions*. The neural correlates of the visual word form system would therefore require identification of the set of interacting regions that is unique to visual word form processing.

Localization of the visual word form area

If the left midfusiform area does not correspond to the visual word form area, then which neural regions do sustain visual word form processing? As indicated above, there may be no neural area that is specific to visual word processing, rather, reading specific activation arises from unique interactions between visual and language regions that are each involved in many different functions. This proposal is consistent with the notion of parallel distributed processing (Rumelhart and McClelland, 1986) and the claim that our knowledge of familiar letter combinations arises from interactions between orthographic, semantic, and phonological processing without explicit word form representations (Plaut et al., 1996; Seidenberg and McClelland, 1989). Indeed, it is highly unlikely that a reading specific brain region would have developed in the human brain: From an evolutionary perspective, reading is a very recent skill; from a developmental perspective, it should be noted that reading can still be mastered in adulthood after the brain has fully matured.

In conclusion, although we are not disputing that the left midfusiform area is involved in visual word processing, we believe that it is misleading to label this region the "visual word form area." Reading evokes activation in a distributed set of regions (see Fiez and Petersen, 1998; Price, 2000 for reviews) and activation in one component of this system—the left midfusiform area—is not specific to visual word forms. In a broader context, this paper highlights a general problem with many functional imaging studies; we can infer that an area is involved in our function of interest but it is far more difficult to infer that the activated area is dedicated to that function without testing multiple competing hypotheses.

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References

Behrmann, M., Nelson, J., Sekuler, E.B., 1998. Visual complexity in letter-by-letter reading: "pure" alexia is not pure. Neuropsychologia 36, 1115–1132.

Benson, D.F., Geshwind, N., 1969. The alexias, in: Vinken, P.J., Bruyn, G.W., (Eds.), Handbook of Clinical Neurology, Vol. 4, Elsevier Science Ltd., Amsterdam, pp. 112–140.

Beversdorf, D., Ratcliffe, N., Rhodes, C., Reeves, A., 1997. Pure alexia: clinical-pathologic evidence for a lateralized visual language association cortex. Clinic. Neuropathol. 16, 328–331.

Binder, J., Mohr, J., 1992. The topography of callosal reading pathways. Brain 115, 1807–1826.

Binder, J., Frost, J., Hammeke, T., Rao, S., Cox, R., 1996. Function of the left planum temporale in auditory and linguistic processing. Brain 119, 1229–1247.

Bookheimer, S.Y., Zeffiro, T.A., Blaxton, T., Gaillard, W., Theodore, W., 1995. Regional cerebral blood flow during object naming and word reading. Hum. Brain Mapp. 3, 93–106.

Booth, J.R., Burman, D.D., Meyer, J.R., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., 2002a. Functional anatomy of intra- and cross-modal lexical tasks. Neuroimage 16, 7–22.

Booth, J.R., Burman, D.D., Meyer, J.R., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., 2002b. Modlaity independence of word comprehension. Hum. Brain Mapp. 16, 251–261.

Brunswick, N., McCrory, E., Price, C.J., Frith, C.D., Frith, U., 1999. Explicit and implicit processing of words and pseudowords by adult developmental dyslexics—a search for Wernicke's Wortschatz? Brain 122 (Pt10), 1901–1917.

Buchel, C., Price, C., Friston, K., 1998. A multimodal language region in the ventral visual pathway. Nature 394 (6690), 274–277.

Buckner, R., Koustall, W., Schacter, D., Rosen, B., 2000. Functional MRI evidence for a role of frontal and inferior temporal cortex in amodal components of priming. Brain 123, 620–640.

Burnstine, T.H., Lesser, R.P., Hart, J., Uematsu, S., Zinreich, S.J., Drauss, G.L., et al., 1990. Characterization of the basal temporal language area in patients with left temporal lobe epilepsy. Neurology 40, 966–970.

Castelli, F., Frith, C., Happe, F., Frith, U., 2002. Autism, asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. Brain 125, 1839–1849.

Chao, L., Haxby, J.V., Martin, A., 1999. Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. Nat. Neurosci. 2 (10), 913–919.

Chao, L., Weisberg, J., Martin, A., 2002. Experience dependent modulation of category-related cortical activity. Cereb. Cortex 12, 545–551.

Chee, M., O'Craven, K., Bergida, R., Rosen, B., Savoy, R., 1999. Auditory and visual word processing studied with fMRI. Hum. Brain Mapp. 7, 15–28.

Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, M., Michel, F., 2000. The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain 123, 291–307.

Cohen, L., Lehericy, S., Chochon, F., Lemer, C., Rivard, S., Dehaene, S., 2002. Language-specific tuning of visual cortex? Functional properties of the visual word form area. Brain 125, 1054–1069.

Damasio, A., Damasio, H., 1983. The anatomic basis of pure alexia. Neurology 33, 1573–1583.

Damasio, A.R., Damasio, H., 1994. Cortical systems for the retrieval of concrete knowledge: the convergence zone framework, in: Koch, C. (Ed.), Large Scale Neuronal Theories of the Brain, MIT Press, Cambridge, MA, pp. 61–74.

De Renzi, E., Zambolin, A., Crisi, G., 1987. The pattern of neuropsychological impairment associated with left posterior cerebral artery infarcts. Brain 110, 1099–1116.

Dehaene, S., Naccache, L., Cohen, L., Bihan, D.L., Mangin, J.F., Poline, J.B., Riviere, D., 2001. Cerebral mechannisms of word masking and unconscious repetition priming. Nat. Neurosci. 4, 752–758.

Dehaene, S., Le Clec'H, G., Poline, J.B., Bihan, D.L., Cohen, L., 2002. The visual word form area: a prelexical representation of visual words in the left fusiform gyrus. Neuroreport 13 (3), 321–325.

Dejerine, J., 1892. Contribution a l'etude anatomoclinique et clinique des differentes varietes de cecite verbal. CR Hebdomadaire Sceances Memories Soc. Biol. 4, 61–90.

Demonet, J.-F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J.-L., Wise, R., Rascol, A., Frackowiak, R., 1992. The anatomy of phonological and semantic processing in normal subjects. Brain 115, 1753–1768.

Demonet, J.F., Price, C.J., Wise, R., Frackowiak, R.S.J., 1994. Differential activation of right and left posterior sylvian regions by semantic and phonological tasks: a positron emission tomography study. Neurosci. Lett. 182, 25–28.

D'Esposito, M., Detre, J.A., Aguirre, G.K., Stallcup, M., Alsop, D.C., Tippett, L.J., Farah, M.J., 1997. A functional MRI study of mental image generation. Neuropsychologia 35 (2), 725–730.

Durbin, R., Mitchison, G., 1990. A dimension reduction framework for understanding cortical maps. Nature 343 (6259), 644–647.

Etard, O., Mellet, E., Papathanassiou, D., Benali, K., Houde, O., Mazoyer, B., Tzourio-Mazoyer, N., 2000. Picture naming without Broca's and Wernicke's area. Neuroreport 11 (3), 617–622.

Fiez, J.A., Petersen, S.E., 1998. Neuro-imaging studies of word reading. Proc. Natl. Acad. Sci. USA 95, 914–921.

Foundas, A., Daniels, S.K., Vasterling, J.J., 1998. Anomia: case studies with lesion localisation. Neurocase 4, 35–43.

Friedman, R.B., Alexander, M.P., 1984. Pictures, images and pure alexia; a case study. Cogn. Neuropsychol. 1, 9–23.

Geshwind, 1965. Disconnection syndromes in animals and man. Brain, 88, 237–294.

Giraud, A.L., Price, C.J., 2001. The constraints functional neuroimaging places on classical models of word processing. J. Cogn. Neurosci. 13 (6), 1–12.

Kurachi, M., Yamaguchi, N., Inasaka, T., Torii, H., 1979. Recovery from alexia without agraphia: report of an autopsy. Cortex 15, 297–312.

Leff, A.P., Crewes, H., Plant, G.T., Scott, S.K., Kennard, C., Wise, R.J., 2001. The functional anatomy of single word reading in patients with hemianopic and pure alexia. Brain 124, 510–521.

Luders, H., Lesser, R.P., Hahn, J., Dinner, D.S., Morris, H., Resor, S., et al., 1986. Basal temporal language area deomonstrated by electrical stimulation. Neurology 36, 505–510.

Luders, H., Lesser, R.P., Hahn, J., Dinner, D.S., Morris, H.H., Wyllie, E., et al., 1991. Basal temporal language area. Brain 114, 743–754.

Marshall, J.C., Newcombe, F., 1973. Patterns of paralexia: a psycholinguistic approach. J. Psycholinguistic Res. 2, 175–199.

Martin, A., Chao, L.L., 2001. Semantic memory and the brain: structure and processes. Curr. Opin. Neurobiol. 11, 194–201.

McIntosh, A.R., 2000. Towards a network theory of cognition. Neural Networks 13, 861–876.

Mellet, E., Tzourio, N., Denis, M., Mazoyer, B., 1998. Cortical anatomy of mental imagery of concrete nouns based on their dictionary definition. Neuroreport 9, 803–808.

Mesulam, M.M., 1990. Large scale neurocognitive networks and distributed processing for attention, language and memory. Ann. Neurol. 28, 597–613.

Moore, C.J., Price, C.J., 1999. Three distinct ventral occipitotemporal regions for reading and object naming. Neuroimage 10 (2), 181–192.

Murtha, S., Chertkow, H., Beauregard, M., Evans, A., 1999. The neural substrate of picture naming. J. Cogni. Neurosci. 11 (4), 399–423.

Passingham, R.E., Stephan, K.E., Kotter, R., 2002. The anatomical basis of functional localisation in the cortex. Nat. Rev. Neurosci. 3 (8), 606–616.

Patterson, K., Shewell, C., 1987. Speak and spell: dissociations and word class effects, in: Coltheart, M., Sartori, G., Job, R. (Eds.), The Cognitive Neuropsychology of Language, Erlbaum, London, pp. 273–294.

Perani, D., Paulesu, E., Galles, N.S., Dupoux, E., Dehaene, S., Bettinardi, V., Cappa, S., Fazio, F., Mehler, J., 1998. The bilingual brain: proficiency and age of acquisition of the second language. Brain 121, 1841–1852.

Phillips, J.A., Humphreys, G.W., Noppeney, U., Price, C.J., 2002. The neural substrates of action retrieval: an examination of semantic and visual routes to action. Vis. Cogn. 9 (4), 662–684.

Pihlajamaki, M., Tanila, H., Hanninen, T., Kononen, M., Laaskso, M., Partanen, K., Soininen, H., Aronen, H., 2000. Verbal fluency activates the left medial temporal lobe: a functional magnetic resonance imaging study. Ann. Neurol. 47, 470–476.

Plaut, D., McClelland, J., Seidenberg, M., Patterson, K., 1996. Understanding normal and impaired word reading: computational principles in quasi-regular domains. Psychol. Rev. 103, 56–115.

Polk, T.A., Farah, M.J., 2002. Functional MRI evidence for an abstract, not perceptual, word-form area. J. Exp. Psychol. Gen. 131, 65–72.

Price, C.J., 2000. The anatomy of language: contributions from fuctional neuroimaging. J. Anat. 197, 335–359.

Price, C.J., Friston, K.J., 1997. Cognitive conjunction: a new approach to brain activation experiments. Neuroimage 5 (4 Pt1), 261–270.

Price, C.J., Moore, C.J., Humphreys, G.W., Frackowiak, R.S.J., Friston, K.J., 1996. The neural regions sustaining object recognition and naming. Proc. R. Soc. Lond. B-Biol. Sci. 263 (1376), 1501–1507.

Price, C.J., Winterburn, D., Giraud, A.L., Moore, C.J., Noppeney, U., 2003. Cortical localisation of the visual and auditory word form areas: a reconsideration of the evidence. Brain Lang.

Raymer, A.M., Foundas, A., Maher, L.M., et al., 1997. Cognitive neuropsychological analysis and neuroanatomic correlates in a case of acute anomia. Brain Lang. 58, 137–156.

Rumelhart, D., McClelland, J., 1986. Parallel Distributed Processing, Vol. 1. MIT Press, Cambridge, MA.

Seidenberg, M., McClelland, J., 1989. A distributed, developmental model of word recognition and naming. Psychol. Rev. 96, 523–568.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme, Stuttgart.

Thompson-Schill, S.L., Aguirre, G.K., D'Esposito, M., Farah, M.J., 1999. A neural basis for category and modality specificity of semantic knowledge. Neuropsychologia 37, 671–676.

van Turennout, M., Ellmore, T., Martin, A., 2000. Long lasting cortical plasticity in the object naming system. Nat. Neurosci. 3 (12), 1329–1334.

Vandenberghe, R., Price, C.J., Wise, R., Josephs, O., Frackowiak, R.S.J., 1996. Functional anatomy of a common semantic system for words and pictures. Nature 383, 254–256.

Warrington, E.K., Shallice, T., 1980. Word form dyslexia. Brain 103, 99–112.

Wise, R.J., Howard, D., Mummery, C.J., Fletcher, P., Leff, A., Buchel, C., Scott, S.K., 2000. Noun imageability and the temporal lobes. Neuropsychologia 38, 985–994.