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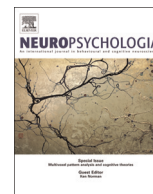
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## Representation of visual symbols in the visual word processing network

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## ABSTRACT

**Background:** Previous studies have shown that word processing involves a predominantly left-sided occipitotemporal network. Words are a form of symbolic representation, in that they are arbitrary perceptual stimuli that represent other objects, actions or concepts. Lesions of parts of the visual word processing network can cause alexia, which can be associated with difficulty processing other types of symbols such as musical notation or road signs.

**Objective:** We investigated whether components of the visual word processing network were also activated by other types of symbols.

**Method:** In 16 music-literate subjects, we defined the visual word network using fMRI and examined responses to four symbolic categories: visual words, musical notation, instructive symbols (e.g. traffic signs), and flags and logos. For each category we compared responses not only to scrambled stimuli, but also to similar stimuli that lacked symbolic meaning.

**Results:** The left visual word form area and a homologous right fusiform region responded similarly to all four categories, but equally to both symbolic and non-symbolic equivalents. Greater response to symbolic than non-symbolic stimuli occurred only in the left inferior frontal and middle temporal gyri, but only for words, and in the case of the left inferior frontal gyri, also for musical notation. A whole-brain analysis comparing symbolic versus non-symbolic stimuli revealed a distributed network of inferior tempor-occipital and parietal regions that differed for different symbols.

**Conclusion:** The fusiform gyri are involved in processing the form of many symbolic stimuli, but not specifically for stimuli with symbolic content. Selectivity for stimuli with symbolic content only emerges in the visual word network at the level of the middle temporal and inferior frontal gyri, but is specific for words and musical notation.

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## 1. Introduction

Neuroimaging studies have shown that perception of visual words is correlated with activation of a network of cortical regions, with a left hemisphere dominance (Barton et al., 2010; Reinke et al., 2008). This includes the middle temporal gyrus, inferior frontal gyrus, and in particular a region in the mid portion of the fusiform gyrus that has been named the ‘visual word form area’ (Cohen et al., 2000a, 2002b; McCandliss et al., 2003). Damage to the latter or its connections may be responsible for at least some cases of acquired alexia without agraphia, also known as pure

alexia (Epelbaum et al., 2008; Gaillard et al., 2006; Leff et al., 2006; Pflugshaupt et al., 2009; Sheldon et al., 2012).

As reading is an acquired visual expertise for an arbitrary set of stimuli specific to the culture and language to which the individual is exposed, the stimulus selectivity of this word processing network must develop through experience. Greater degrees of literacy are associated with greater responses to words in the visual word form area, and a decline in responses to other objects like faces (Dehaene et al., 2010). The ‘recycling hypothesis’ proposes that visual word perception exploits the competency of ventral occipitotemporal regions at analyzing line segments and junctions that make important contributions to processing of object contours (Dehaene and Cohen, 2011; Szwed et al., 2011). The dominance of left hemispheric regions may evolve through efficiency constraints that favour local intra-hemispheric connectivity between visual word processing regions and other language areas, which in most subjects are located in the left hemisphere (Plaut and Behrmann, 2011).

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Along with other studies showing that the left fusiform gyrus retains significant responsivity to stimuli other than words (Flowers et al., 2004; Price and Devlin, 2003; Starrfelt and Gerlach, 2007), these points suggest that the selectivity of regions of the visual word processing network for visual words over other types of objects is partial rather than absolute. Furthermore, one can also ask whether this partial selectivity is limited to visual words alone or favours certain other types of stimuli as well, a question that is prompted by several neuropsychological observations. A number of reports note that patients with pure alexia can also have difficulty with perception of written numbers, musical notation and other objects such as map symbols, road signs, and flags (Beversdorf and Heilman, 1998; Horikoshi et al., 1997; Kawamura et al., 2000; Starrfelt and Behrmann, 2011). Hence it may be that the expertise of this left visual cortical network may be not for words alone but also for certain other object classes.

One intriguing possibility is suggested by the fact that visual words, numbers, map symbols, musical notation and road signs are all types of visual symbols. That is, as stimuli they have an added semantic element, of signifying and communicating concepts or objects other than themselves. Musical notation is a unique category because it has an orthography that resembles written language. Flags and logos are symbols that represent entities, which also convey semantic meaning but lack a phonemic component, yet previous studies have suggested that logos can induce activity in the fusiform gyri (Bruce et al., 2014). There has been less study of instructive symbols such as traffic signs or other symbols used to indicate forms of action or behaviours, rather than representing entities in the manner flags and logos do. The neuropsychological reports in alexia raise the intriguing question as to whether the visual word processing network is involved in these other aspects of visual symbolic communication. This issue is further highlighted by several fMRI studies of the perception of musical notation, symbols, and logos that show activation of similar fusiform, middle temporal, and frontal regions (Bruce et al., 2014; Nakada et al., 1998; Reinke et al., 2008; Wong and Gauthier, 2010). Furthermore, a study of training with an unfamiliar language suggested that fusiform activity may be enhanced not just by visual familiarity but also by the semantic aspect of linking arbitrary meanings to the trained stimuli (Xue et al., 2006).

The goal of our study was to investigate the potential involvement of the visual word processing network in the perception of other types of visual symbols. We examined four classes of symbolic stimuli: visual words, musical notation, instructive symbols that indicate actions, and flags or logos that represent a national or corporate entity. For clarity, we focused upon emblematic symbols, for which the relation between the symbol's shape and the concept, item or event it signifies is arbitrary, in contrast to iconic symbols, which have a form that captures the defining physical aspects of the class of objects to which they refer (Shin et al., 2008). For each of the four classes we created an equivalent set of stimuli that did not have any symbolic content. Our hypothesis was that, if the word processing network is involved more generally in symbolic communication, then significant differences between the activity seen with symbolic versus non-symbolic stimuli would be found for some or all of these four classes.

## 2. Methods

### 2.1. Participants

16 healthy right-handed participants (11 males; mean age: 27.3 years, range: 21–39 years) with no history of neurological dysfunction, and visual acuity of 20/20, took part in the study. All

participants spoke English as a first language and did not know spoken or written Korean. Subjects who considered themselves literate in music were recruited via an online participation pool at the University of British Columbia. Music literacy was confirmed by an independent paper task in which subjects were presented with a music bar consisting of four to six notes, and, on a cartoon drawing of a piano, were instructed to write the order of notes the music would play. Only subjects who could correctly identify and locate 90% or more of the musical notes were included in the study. The protocol was approved by the institutional review boards of the University of British Columbia and Vancouver General Hospital, and written informed consent was obtained for all subjects in accordance with The Code of Ethics of the World Medical Association, Declaration of Helsinki.

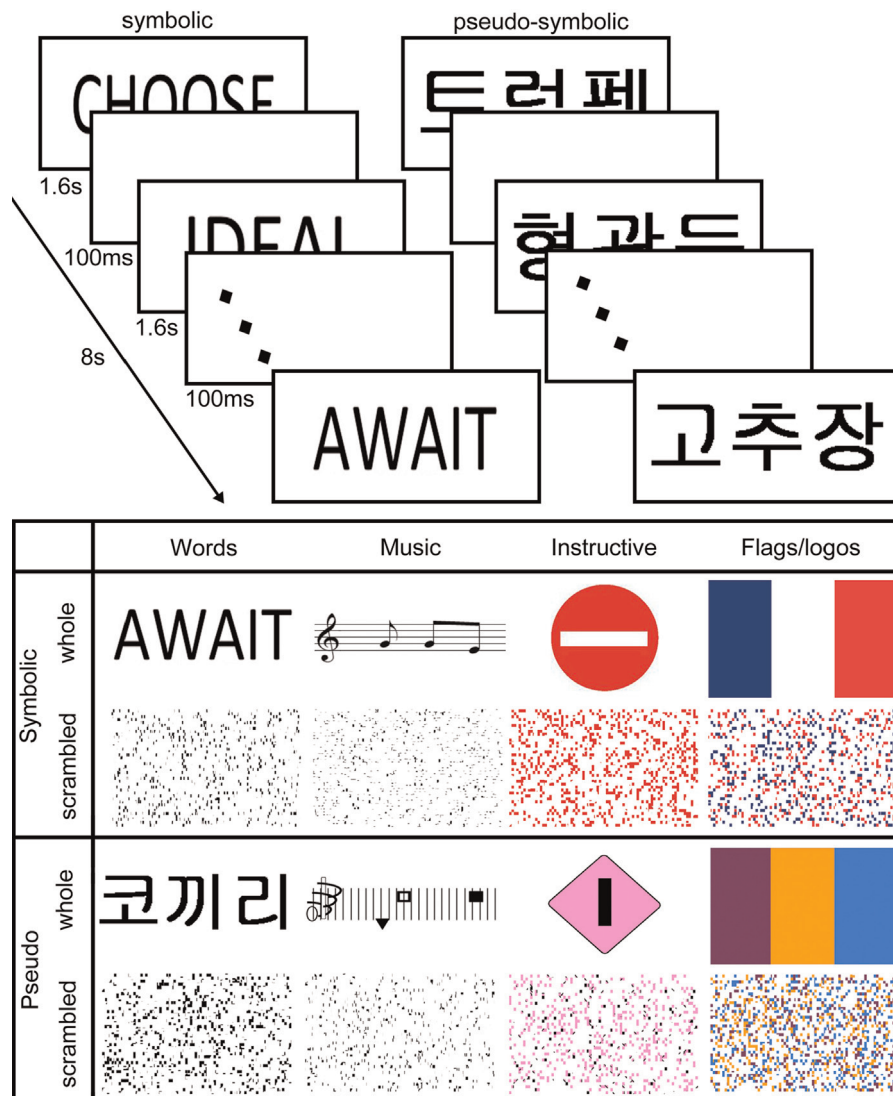
### 2.2. Stimuli

Fig. 1 shows the four stimulus categories participants viewed: (i) *visual words*, (ii) *musical notation*, (iii) *instructive symbols* (e.g. traffic signs), and (iv) *flags and logos*. *Visual words* were 4–6 letters long and were chosen to have minimal imageability, to minimize generation of visual imagery (average: 303; range: 233–338). Word criteria were obtained from the MRC Psycholinguistic Database ([http://websites.psychology.uwa.edu.au/school/MRCDataBase/uwa\\_mrc.htm](http://websites.psychology.uwa.edu.au/school/MRCDataBase/uwa_mrc.htm)). *Musical notation* were notes displayed on a staff that contained a common recognizable tune of three to five notes (e.g. Jingle Bells, London Bridge). *Instructive symbols* included symbols denoting actions, consisting mostly of traffic signs, and a limited number of device-operating symbols (e.g. play, rewind) or symbols indicating a warning or function (e.g. hazard sign, recycle). The latter were included to increase the variety of symbols, so that these were not confined to traffic situations. *Flags and logos* consisted of well-known country flags (e.g. United States, United Kingdom) and logos of popular brands (e.g. Pepsi, Nike). No text or depictions of living beings (animals or faces) were included in these non-word categories. Twelve individuals not involved in the study were shown various flags, logos and instructive symbols, and the most frequently recognized images were chosen for the experiment.

For each of the four symbolic categories, there was a non-symbolic equivalent that lacked a communicated meaning (Fig. 1). For *visual words*, Korean text was used as an equivalent. For *musical notation*, parallel vertical lines were used instead of horizontal lines as substitutes for staves, and miscellaneous shapes used to represent pseudo-notes. For *instructive*, and *flags and logos*, similar stimuli were created in Adobe Photoshop CS ([www.adobe.com](http://www.adobe.com)) and used as non-symbolic equivalents.

As images across the different categories naturally vary in size, stimuli were either sized at a fixed height of 300 pixels (*instructive symbols, flags and logos, and their pseudo-equivalents*) or a fixed width of 600 pixels (*visual words, musical notation, and their pseudo equivalents*), and mounted on a white background to produce a final image of about 600 × 300 pixels.

Finally, symbolic images and non-symbolic images had corresponding unidentifiable scrambled equivalents. Scrambled images were created using a Telegraphics add-on for Adobe Photoshop CS (<http://www.telegraphics.com.au/sw/info/scramble.html>) that randomizes pixel clusters across an image (cluster size: 8 × 8 pixels). This method was chosen over Fourier-transform scrambling as Fourier-transform images can often contain areas within the image resembling shapes. This resulted in a total of 16 stimulus groups: 4 conditions (*symbolic, non-symbolic, scrambled symbolic, scrambled non-symbolic*), for each of the 4 categories (*visual words, musical notation, instructive symbols, and flags and logos*).



**Fig. 1.** Examples of whole and scrambled stimuli used in the experiment. There were 4 stimulus categories: words, music, instructive, and flags and logos. Each category contained 4 conditions: symbolic, scrambled symbolic, non-symbolic, and scrambled non-symbolic. Each stimulus block contained images from a single condition (i.e. symbolic words), and a run included blocks from a single category (i.e. words).

### 2.3. Imaging parameters

Subjects were scanned in a Philips 3.0 T scanner at the UBC MRI Research Centre. T2\*-weighted scans using echo planar imaging were used to collect data from 36 interleaved axial slices (TR 2000 ms, TE 30 ms, FOV=240 × 216 mm<sup>2</sup>, 3 mm thickness with 1 mm<sup>2</sup> gap, voxel size 3 × 3 mm<sup>2</sup>, 128 mm<sup>2</sup> reconstruction matrix, reconstructed voxel size 1.88 × 1.6 mm<sup>2</sup>). These were co-registered onto a T1-weighted anatomical image (EPI) sequence, 170 axial slices, FOV=256 × 200 mm<sup>2</sup>, voxel size=1 × 1 mm<sup>2</sup>, slice thickness 1 mm, from each participant.

### 2.4. Protocol

Visual stimuli (13° × 6.3° visual angle) were back-projected onto a screen located inside the magnetic bore, approximately 57 cm from subjects' eyes. The experiment consisted of 4 functional runs, with a single run containing blocks of images from a single stimulus category; for example, the words run contained blocks of words, pseudo-words, scrambled words, and scrambled symbolic words. Each stimulus block included 5 images lasting 1.5 s separated by a 100 ms blank screen, resulting in 8 s stimulus

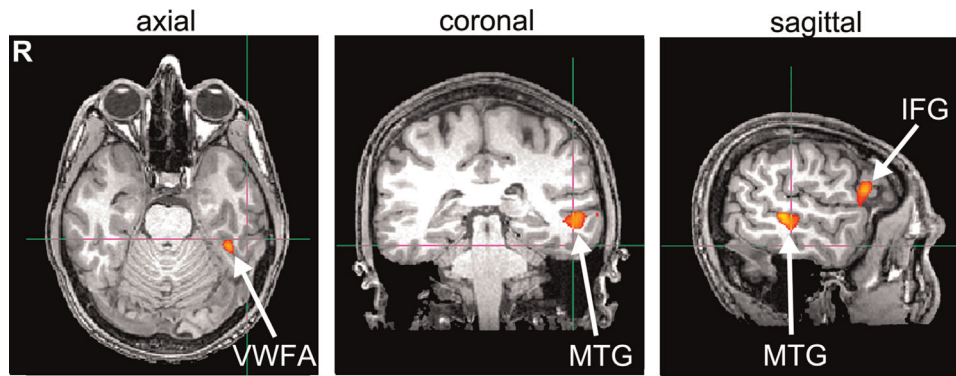
blocks. Stimulus blocks were separated by a 8 s fixation cross. Each of the 4 conditions was repeated 6 times, resulting in a total of 24 blocks per run. The order of functional runs (one for each stimulus category) was balanced across participants. Blocks were pseudo-randomised but were identical for each subject. To monitor attention, participants performed an irrelevant one-back task, whereby they indicate on an MRI-compatible button response pad if the same stimulus was displayed twice in a row.

### 2.5. fMRI analysis

Statistical analysis of the fMRI data was carried out using FEAT (<http://www.fmrib.ox.ac.uk/fsl>; (Smith et al., 2004). The initial 8 s of data from each scan were removed to minimize the effects of magnetic saturation. Motion correction was followed by spatial smoothing (Gaussian, FWHM 6 mm) and temporal high-pass filtering (cut-off of 0.01 Hz).

A region of interest (ROI) analysis was used to identify visually word-selective regions at the individual subject level. Fig. 2 and Table 1 show three regions that responded to *words* > *scrambled words* ( $p < 0.001$ , uncorrected) in more than half of the subjects: the lateral mid-portion of the fusiform gyrus (visual word form





**Fig. 2.** Visual word-selective regions in an individual subject. The visual word form area (VWFA), inferior frontal gyrus (IFG), and middle temporal gyrus (MTG) were identified in each subject using the contrast words > scrambled words.

**Table 1**

Average MNI coordinates of the regions of interest across participants, and the number of subjects ( $n=16$ ) in which each was identified.

Region		$n$	MNI Coordinates		
			$x$	$y$	$z$
Visual word form area	L	12	-42	-49	-22
	R	10	39	-47	-22
Middle temporal gyrus	L	13	-56	-40	-1
Inferior frontal gyrus	L	13	-48	25	8

area; left:  $n=12$ ; right:  $n=10$ ), the left inferior frontal gyrus (IFG;  $n=13$ ), and the left middle temporal gyrus (MTG;  $n=13$ ). Within these regions identified at the single subject level, we examined responses with a repeated-measures ANOVA, with factors of category (*visual word*, *musical notation*, *instructive symbol*, *flag/logo*), symbolic content (symbolic, non-symbolic) and image (intact, scrambled). For the fusiform gyrus, we also included an additional factor of hemisphere (left, right). We also report *a priori* planned comparisons between intact versus scrambled symbolic stimuli, intact versus scrambled non-symbolic stimuli, and symbolic versus non-symbolic intact stimuli. Note that as the contrast words > scrambled words was used to identify the regions of interest, differences between these two conditions are a foregone conclusion, and therefore statistics for this contrast are not included in the analysis.

Finally, to determine whether any areas outside the ROI's respond to symbolic visual representations, all 16 subjects were entered into a whole brain analysis ( $p < 0.05$ , corrected for multiple comparisons according to Gaussian random field theory (Worsley et al., 1992)), and areas of overlap were examined, using the contrast *symbolic > non-symbolic* for each of the 4 categories (words, music, instructive, flags and logos).

### 3. Results

#### 3.1. Region of interest analysis

##### 3.1.1. Visual word form area

In the visual word form area (Fig. 3), the omnibus repeated-measures ANOVA showed no main effects of Hemisphere ( $F(1,7)=0.04$ ,  $p=0.85$ ), Category ( $F(3,21)=1.70$ ,  $p=0.20$ ), or Symbolic content ( $F(1,7)=0.66$ ,  $p=0.44$ ). As the literature identifies a dominant visual word form area as being in the left hemisphere (at least in right-handed subjects), we also performed separate statistical analyses on the left and right visual word form areas. In neither was there a significant effect of Category (left:  $F(3,33)=$

1.27,  $p=0.30$ ; right:  $F(3,27)=0.51$ ,  $p=0.68$ ) or Symbolic content (left:  $F(1,11)=1.04$ ,  $p=0.33$ ; right:  $F(1,9)=1.33$ ,  $p=0.28$ ).

Next, paired-sampled  $t$ -tests were used to examine three planned comparisons for each category of stimuli: (1) intact versus scrambled symbolic stimuli, (2) intact versus scrambled non-symbolic, and (3) symbolic versus non-symbolic intact stimuli.

For *visual words*, there was a greater response to intact than scrambled versions of non-symbolic stimuli in the left ( $t(11)=5.16$ ,  $p < 0.001$ ), but not the right ( $t(9)=1.64$ ,  $p=0.14$ ), visual word form area ( $t(9)=5.25$ ,  $p < 0.001$ ). Neither the left nor right visual word form areas showed a difference in response to symbolic versus non-symbolic intact stimuli (left:  $t(11)=-0.24$ ,  $p=0.82$ ; right:  $t(9)=0.84$ ,  $p=0.43$ ).

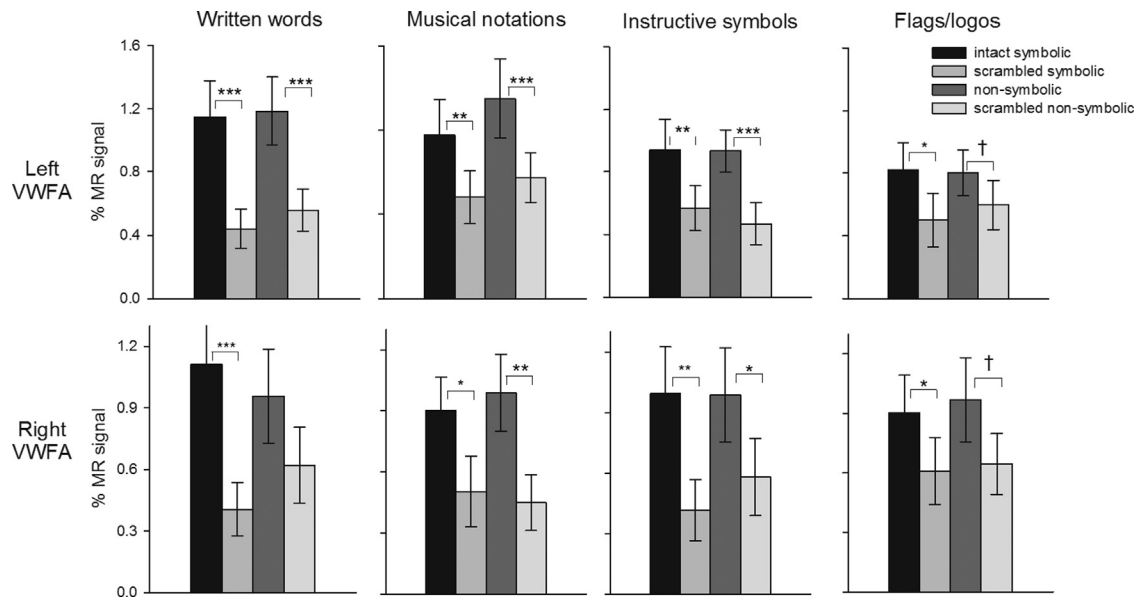
Similar results were observed for *musical notation* and *instructive symbols*. For *musical notation*, there was a greater response to intact than scrambled versions in both hemispheres, for both symbolic (left:  $t(11)=3.14$ ,  $p < 0.01$ ; right:  $t(9)=2.80$ ,  $p < 0.05$ ) and non-symbolic stimuli (left:  $t(11)=4.53$ ,  $p < 0.001$ ; right:  $t(9)=4.49$ ,  $p < 0.005$ ). Again, there was no difference in the response to symbolic versus non-symbolic intact stimuli (left:  $t(11)=-1.53$ ,  $p=0.16$ ; right:  $t(9)=-0.89$ ,  $p=0.40$ ). For *instructive symbols*, there was a greater response to intact than scrambled versions for both symbolic (left:  $t(11)=3.57$ ,  $p < 0.005$ ; right:  $t(9)=4.20$ ,  $p < 0.005$ ) and non-symbolic stimuli (left:  $t(11)=4.90$ ,  $p < 0.001$ ; right:  $t(9)=2.62$ ,  $p < 0.05$ ) and again, no difference in the response to symbolic versus non-symbolic intact stimuli (left:  $t(11)=0.03$ ,  $p=0.98$ ; right:  $t(9)=0.04$ ,  $p=0.97$ ).

*Flags and logos* showed a greater response bilaterally to intact than scrambled symbolic stimuli (left:  $t(11)=2.20$ ,  $p < 0.05$ ; right:  $t(9)=2.91$ ,  $p < 0.05$ ), but only a trend for a greater response to intact than scrambled non-symbolic stimuli (left:  $t(11)=2.05$ ,  $p=0.07$ ; right:  $t(9)=1.86$ ,  $p=0.10$ ). There was no difference in the response to symbolic versus non-symbolic stimuli (left:  $t(11)=0.16$ ,  $p=0.88$ ; right:  $t(9)=0.62$ ,  $p=0.62$ ).

In summary, both the left and right visual word form areas showed greater responses to intact than scrambled versions, with the single exception of non-symbolic *flags and logos*, but no difference between symbolic and non-symbolic stimuli for any category.

##### 3.1.2. Left middle temporal gyrus

The MTG (Fig. 4) showed a main effect of Category ( $F(3,36)=3.83$ ,  $p < 0.05$ ). This was due to larger responses for *visual words* compared to any of the other three categories (*musical notation*:  $F(1,47)=6.95$ ,  $p < 0.05$ ; *instructive symbols*:  $F(1,47)=12.43$ ,  $p < 0.001$ ; *flags and logos*:  $F(1,47)=10.51$ ,  $p < 0.005$ ). There was no effect of Symbolic content ( $F(1,12)=1.53$ ,  $p=0.24$ ), but there was a significant interaction between Category and Symbolic content ( $F(3,36)=4.13$ ,  $p < 0.05$ ). This was due to a difference between



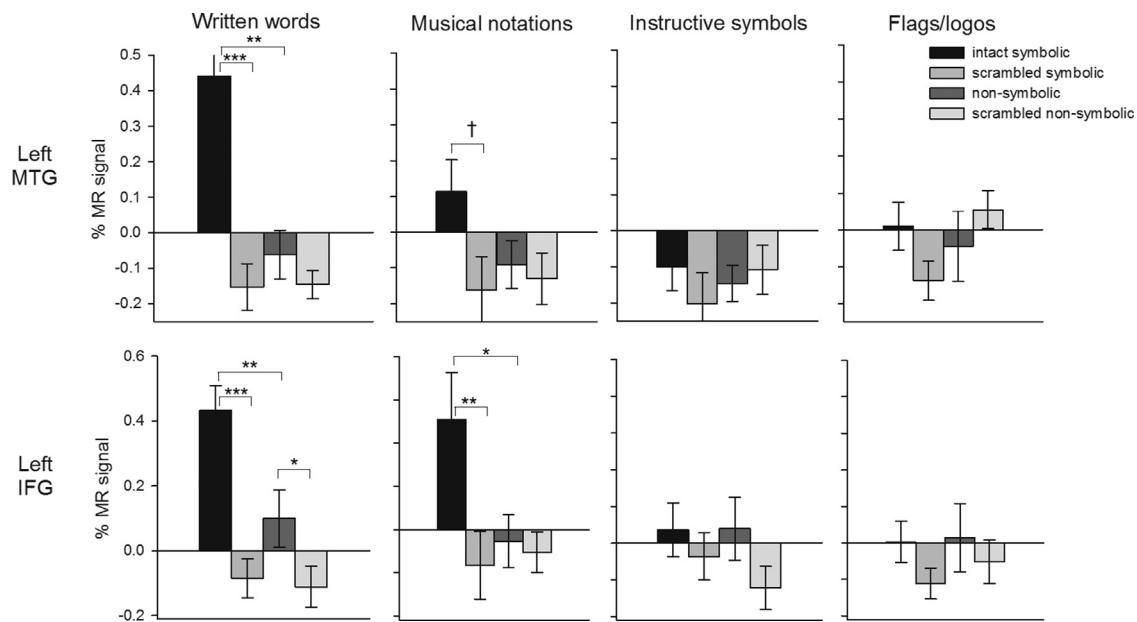
**Fig. 3.** Peak MR response in the left and right visual word form area to each of the 4 stimulus categories and conditions. Each intact condition was compared to the scrambled counterpart, and symbolic stimuli compared to non-symbolic stimuli, with stars indicating significant differences. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , †=trend. There was no difference in response between symbolic and non-symbolic for any category. Note that as word-selective regions were identified based on the contrast *intact symbolic words* > *scrambled symbolic words*, difference between these two conditions is, by definition, significant.

symbolic and non-symbolic stimuli for *visual words* ( $t(12)=3.80$ ,  $p < 0.005$ ), but not for *musical notation* ( $t(12)=1.61$ ,  $p=0.13$ ), *instructive symbols* ( $t(12)=0.63$ ,  $p=0.54$ ), or *flags and logos* ( $t(12)=0.46$ ,  $p=0.65$ ). Conversely, there was a difference among symbolic stimuli between *visual words* and *instructive symbols* ( $F(1,11)=15.74$ ,  $p < 0.005$ ) and *flags and logos* ( $F(1,11)=117.35$ ,  $p < 0.005$ ), with a trend for a difference between *visual words* and *musical notation* ( $F(1,11)=3.68$ ,  $p=0.08$ ), but no difference between any category for non-symbolic stimuli.

For *visual words*, there was no difference between intact and scrambled non-symbolic stimuli ( $t(12)=1.28$ ,  $p=0.23$ ). There was a greater response to symbolic than non-symbolic intact stimuli ( $t(12)=3.80$ ,  $p < 0.005$ ).

For *musical notation*, there was a trend for greater responses to intact than scrambled symbolic stimuli ( $t(12)=2.12$ ,  $p=0.06$ ), but no difference for non-symbolic stimuli ( $t(12)=0.51$ ,  $p=0.62$ ). There was no difference between symbolic and non-symbolic intact stimuli ( $t(12)=1.61$ ,  $p=0.13$ ).

For *instructive symbols*, there was no difference between intact and scrambled symbolic ( $t(12)=1.09$ ,  $p=0.30$ ) or non-symbolic stimuli ( $t(12)=-0.62$ ,  $p=0.54$ ), and no difference between symbolic and non-symbolic intact stimuli ( $t(12)=0.63$ ,  $p=0.54$ ). For *flags and logos* there was no difference between intact and scrambled symbolic ( $t(12)=1.91$ ,  $p=0.08$ ) or non-symbolic stimuli ( $t(12)=-1.14$ ,  $p=0.28$ ), and no difference between symbolic and non-symbolic intact stimuli ( $t(12)=0.46$ ,  $p=0.65$ ).



**Fig. 4.** Peak MR response in the left MTG (top row) and left IFG (bottom row) to each of the 4 stimulus categories and conditions. Each intact condition was compared to the scrambled counterpart, and symbolic stimuli compared to non-symbolic stimuli, with stars indicating significant differences \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , †=trend. This was found for words in the IFG and MTG, and for music in the IFG. Note that as word-selective regions were identified based on the contrast *intact symbolic words* > *scrambled symbolic words*, difference between these two conditions is, by definition, significant.

In summary, there was only a trend for the left MTG to respond more to intact than scrambled musical notation. The non-symbolic control stimuli did not show an advantage for intact over scrambled versions, unlike the results in the visual word form area. The difference between symbolic and non-symbolic stimuli was significant only for words.

3.1.3. *Left inferior frontal gyrus*

The left IFG (Fig. 4) showed a greater response to symbolic than non-symbolic stimuli ( $F(1,11)=5.80, p < 0.05$ ), with a trend to a main effect of Category ( $F(3,33)=2.72, p = 0.06$ ).

For *visual words*, there was a greater response to intact than scrambled versions of non-symbolic stimuli ( $t(11)=2.49, p < 0.05$ ). There was also a significantly greater response to symbolic than non-symbolic intact stimuli ( $t(11)=3.62, p < 0.005$ ).

For *musical notation*, there was a greater response to intact than scrambled versions of symbolic stimuli ( $t(11)=3.41, p < 0.01$ ) but no difference for non-symbolic stimuli ( $t(11)=0.29, p = 0.78$ ). There was a greater response for symbolic than non-symbolic intact stimuli ( $t(11)=2.86, p < 0.05$ ).

For *instructive symbols*, there was no difference between intact and scrambled versions of symbolic stimuli ( $t(11)=1.71, p = 0.12$ ) and only a trend for greater response to intact than scrambled versions of non-symbolic stimuli ( $t(11)=2.05, p = 0.07$ ). There was no difference between symbolic and non-symbolic stimuli ( $t(11) = -0.04, p = 0.97$ ). *Flags and logos* showed no difference between intact and scrambled versions of symbolic ( $t(11)=1.63, p = 0.13$ ) or non-symbolic stimuli ( $t(11)=0.99, p = 0.34$ ), or between symbolic and non-symbolic intact stimuli ( $t(11) = -0.04, p = 0.97$ ).

In summary, the left IFG showed a greater response to symbolic than non-symbolic intact stimuli for *visual words* and *musical notation*, but not for *instructive symbols* or *flags and logos*.

3.2. *Whole brain analysis*

A whole brain analysis compared the response to symbolic versus non-symbolic stimuli for each category to examine if there were any areas of overlap, particularly outside our defined ROIs. This revealed distributed activations within inferior tempor-occipital and parietal regions responding to the different categories (Fig. 5 and Table 2). Only an area in the left occipital pole showed overlap between any categories, showing overlap between

**Table 2**

Regions responding more to symbolic than non-symbolic stimuli for each category in the whole brain analysis.

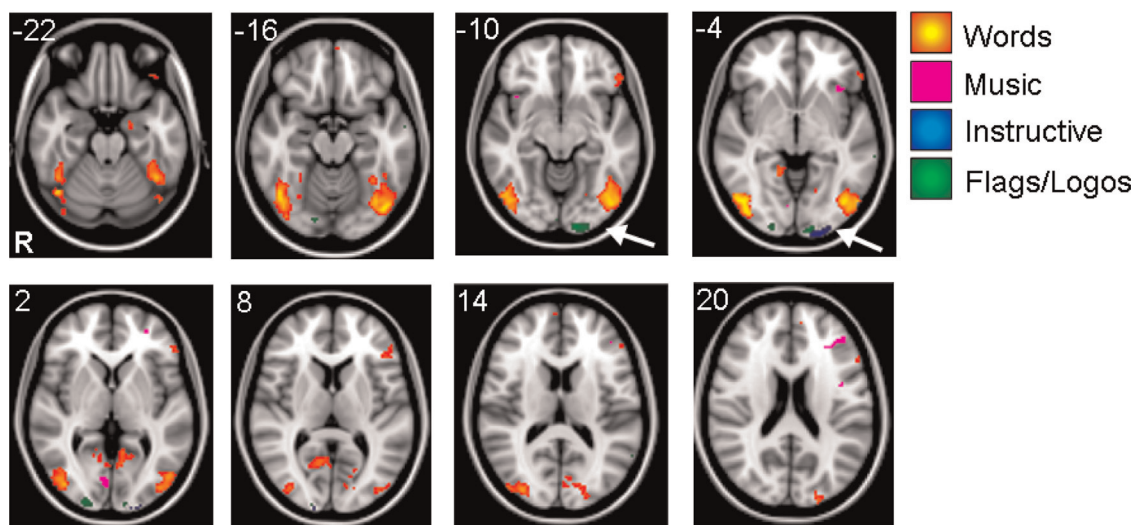
	Coordinates			Peak	
	x	y	z	z-score	
<i>Words &gt; pseudo words</i>					
Temporal occipital fusiform cortex	L	-42	-52	-22	4.9
	R	44	-54	-26	4.9
Lateral occipital cortex	L	-44	-74	-16	5.5
	R	46	-74	-4	5.6
Lingual gyrus	R	8	-58	6	4.1
	R	14	-50	-2	4.1
	L	-8	-64	2	4.0
Occipital pole	L	-22	-96	18	4.5
Inferior frontal gyrus	L	-44	28	10	4.1
Cuneal cortex	L	-4	-78	32	4.2
Temporal fusiform cortex	L	-38	-24	-26	4.0
Frontal orbital cortex	L	-36	34	-20	4.0
Amygdala	L	-20	-8	-20	3.9
<i>Music &gt; pseudo music</i>					
Lingual gyrus	R	8	-78	0	4.4
Inferior frontal gyrus	L	-56	14	24	4.0
Superior parietal lobule	L	-40	-42	44	4.4
Frontal pole	L	-42	38	18	3.9
Insular cortex	L	-38	22	-2	3.8
Superior frontal gyrus	L	-10	8	64	3.8
<i>Instructive &gt; pseudo instructive</i>					
Occipital pole**	L	-20	-102	-4	4.09
<i>Flags/logos &gt; pseudo flags/logos</i>					
Occipital pole**	L	-12	-98	-8	4.22
	R	26	-96	0	3.91

\*\* Signifies overlap.

*instructive symbols* and *flags and logos*.

4. **Discussion**

Our goal was to study the response of cortical components of a visual word processing network to a variety of visual stimuli that serve as emblematic symbols. We found that activation of the left and right visual word form areas occurred regardless of whether a stimulus had symbolic connotations, and responded to all four of our object classes when their shape and contour was intact rather than scrambled. These findings did not differ between the right



**Fig. 5.** Average statistical maps from the group analysis for symbolic > non-symbolic stimuli for each of the 4 stimulus categories. Only an area in the left occipital pole showed overlap between any of the 4 categories: instructive symbols and flags and logos. Maps are thresholded at  $p < 0.05$  (corrected for multiple comparisons).



and left fusiform gyri. A difference between visual words and a non-symbolic equivalent (Korean script) emerged only in the left middle temporal and left inferior frontal gyri. The left inferior frontal gyrus also showed a difference between musical notation and its non-symbolic equivalent. However, no regions showed a difference between symbolic and non-symbolic stimuli for instructive symbols or flags/logos.

#### 4.1. The visual word form area

The responsivity of the visual word form area to symbolic stimuli other than visual words has been documented in other studies. One study of iconic symbols of faces and houses compared to their scrambled counterparts found responses in bilateral fusiform gyri, including a region corresponding to the VWFA (Shin et al., 2008). Another study exploring task differences showed that attention to letters, line symbols or colours gave overlapping responses in the fusiform gyri bilaterally, as well as a region lateral to the left VWFA responding to letters (Flowers et al., 2004). A contrast between non-food logos and baseline images found activation in both fusiform gyri, with Talairach coordinates of  $x=39$ ,  $y=-70$ ,  $z=-11$  (Bruce et al., 2014). In pianists, reading words or reading music led to similar activation of visual and auditory association cortices, including the left middle temporal gyrus and the visual word form area (Nakada et al., 1998), and another report found that written music, word and math symbols had equivalent effects in the fusiform gyri (Talairach coordinates: left,  $x=-40$ ,  $y=-58$ ,  $z=-18$ ; right,  $x=36$ ,  $y=-55$ ,  $z=-20$ ), with no distinction between music experts or novices (Wong and Gauthier, 2010). Finally, one study examined the role of the visual word form area in symbolic communication, by comparing responses to words, black-and-white symbols, digits, and characters from an unfamiliar language, namely Hebrew (Reinke et al., 2008). In the left visual word form area, all stimuli gave responses greater than during a rest condition, the responses to words and symbols were equivalent, and the largest response was to the unfamiliar language. Responses were smaller and less differentiated in the right fusiform gyrus. The conclusion was that the left visual word form area was involved in processing both familiar and novel abstract visual stimuli.

While our results are consistent with the visual word form area responding to other stimuli as well as words, they also suggest that this responsivity is not related specifically to symbolic processing, given that equivalent responses were obtained from non-symbolic analogues. For word stimuli, the equivalent responses to a known language and to an unknown one would appear to run counter to proposals that the visual word form area is involved in processing abstract word identities (McCandliss et al., 2003). In part these were based on early findings of greater activation by written characters than other stimuli, such as non-word letter strings compared to faces (Puce et al., 1996), consonant letters compared to digits or simple linear shapes (Polk et al., 2002), words and pseudo-words compared to false fonts (Price et al., 1996) and an activation order of words more than consonant strings more than checkerboards (Cohen et al., 2002). However, other studies reported equivalent responses in the left fusiform gyrus for words and, pseudo-words (Dehaene et al., 2002; Petersen et al., 1990; Tagamets et al., 2000), or words and letter strings (Baker et al., 2007; Cohen et al., 2003; Vogel et al., 2012), even though the pseudo-words and letter strings lack the semantic associations of words. There are also studies that report the reverse, less response to words than pseudo-words (Mechelli et al., 2003) or pseudo-homophones (Bruno et al., 2008; Kronbichler et al., 2007), which has been attributed to differing demands on lexical retrieval or familiarity effects for orthographic representations. The reasons for these discrepancies are not clear.

Nevertheless, the fact that the left fusiform gyrus responds to letters or letter strings more than to other objects like faces, digits or geometric shapes (Baker et al., 2007; Cohen et al., 2003; Polk et al., 2002; Puce et al., 1996) would indicate that the semantic associations of words are not required to activate this region. In line with this, one study reported that, when presented with Chinese characters, the left fusiform gyrus was more sensitive to orthographic tasks involving the visual appearance of the word (i.e. is this a real character or not) than tasks related to the meaning of the word (Guo and Burgund, 2010).

Direct support for our finding of equivalent activation of the visual word form area by a known (English) and an unknown (Korean) language comes from other studies that also presented multiple language scripts. While some initial studies reported greater fusiform activity with familiar scripts than unfamiliar ones like Hebrew or Chinese (Baker et al., 2007), others have found either equal or greater responses to languages that their subjects did not read, such as Hebrew (Reinke et al., 2008), Korean (Xue and Poldrack, 2007), Amharic script (Vogel et al., 2012), or an artificial language (Xue et al., 2006). While two of these studies reported that activation declined as subjects learned the new language (Xue et al., 2006; Xue and Poldrack, 2007), it is not clear whether this is a familiarity effect or reflects acquisition of semantic associations.

Responsivity to unfamiliar language scripts would suggest that the visual word form area may be responsive to non-linguistic visual stimuli with similar structural properties. One study found no difference in the fusiform gyri between digits or letters and their scrambled versions (Price and Ansari, 2011). Unlike our scrambling process, theirs consisted of a rearrangement of line elements, thus preserving contour information: hence this is equivalent to our contrast between symbolic and non-symbolic stimuli. On the other hand, an fMRI study that compared words to line drawings of objects matched for contour length, features and luminance still found an advantage for words in the visual word form area (Szwed et al., 2011). However, a similar word advantage was found in areas V1/2 and V3v/V4, early visual areas that are not word-selective. This may be due to either residual low-level stimulus differences between the words and drawings used, or a top-down effect of familiarity or expertise for words. In either case, the finding of a word advantage in both the visual word form area and V1/2 means that this advantage cannot be taken as evidence of specificity for word forms. In a parametric study of stimuli embedded in noise, one study found that signal in the posterior occipitotemporal sulcus region was only about 15% less for line drawings than for words (Ben-Shachar et al., 2007).

There is also other evidence to suggest that the visual word form area may be involved more in processing structural properties of the visual word stimulus. Previous studies reporting that responses to words in the visual word form area are invariant to retinotopic location (Cohen et al., 2000a, 2002b) or letter case (Dehaene et al., 2004, 2001) were interpreted as supporting the view that this area is involved in an abstract analysis of visual words that is invariant to such stimulus properties (McCandliss et al., 2003). However, an fMRI-adaptation study showed sensitivity of both the right and left visual word form areas to handwriting style (Barton et al., 2010) and a recent study using pattern classification techniques found sensitivity to the hemifield location of words (Rauschecker et al., 2012).

Hence, as with our results, the majority of recent reports on the processing of words, letters, digits or line drawings do not indicate greater activation of the visual word form area by stimuli with either linguistic or other symbolic connotations. These results would be consistent with a pre-lexical role of the fusiform gyri and the visual word form area in particular in processing the visual attributes of both word and non-word stimuli. As others have



stated, this suggests a role in visual shape extraction that is not limited to words, but likely recruited to support word recognition, with a differential sensitivity to words emerging through experience (Ben-Shachar et al., 2007). This may indicate processing of aspects of object configuration that may be particularly useful in processing visual words (Starrfelt and Gerlach, 2007), as suggested by the recycling hypothesis (Dehaene and Cohen, 2011).

#### 4.2. *The inferior frontal and middle temporal gyri*

We found a heightened response to symbolic than non-symbolic objects only in the left inferior frontal and middle temporal gyri, mainly for words, but also for music in the inferior frontal gyrus. Our results for words are consistent with those of a study of perceptual learning, which found that prior to training with Korean, English speakers showed greater activation for English compared to the unfamiliar Korean script in the left inferior frontal and anterior temporal cortex, but not in the visual word form area (Xue and Poldrack, 2007). Also, a PET study found that, while both words and pseudo-words activated left medial extrastriate cortex, only words activated left prefrontal cortex, which they attributed to the fact that only words had semantic associations (Petersen et al., 1990).

Other studies have also suggested a specific response to visual symbols in similar regions. One study found that words and black-and-white symbols activated the bilateral inferior frontal gyri more than digits or words of an unfamiliar language (Reinke et al., 2008), while the study that contrasted digits or letters with their re-arranged counterparts found differences in the left angular gyrus (Price and Ansari, 2011). Although another study reported that the bilateral inferior frontal gyri responded more to letters than symbols (Flowers et al., 2004), their 'symbols' were a mix of items with symbolic connotations and other items that were mere random designs, intended to provide a match for the angularity and contour of letters: hence this study cannot be used to support a difference between words and other visual stimuli with symbolic content in these regions.

Regarding musical notation, in one early PET study the contrast between reading music and looking at single dots found a difference in the left occipitoparietal region (Sergent et al., 1992). In the study of bilingual pianists cited above, the contrast between reading music, English or Japanese versus looking at pictures showed similar activation for all three in the left middle temporal gyrus (Nakada et al., 1998). This study also suggested that the right transverse occipital sulcus was activated more by reading music than reading words, though this has not been replicated (Wong and Gauthier, 2010). Learning to read and play music was associated with increased activity in the left inferior frontal sulcus and left supramarginal gyrus when subjects were implicitly attending to written music (Stewart et al., 2003).

Little relevant work has been done with logos. A study of familiar versus unfamiliar car logos found a difference in the medial prefrontal gyrus (Schaefer et al., 2006), but this could be confounded by consumer connotations of the luxury brands used as well as the fact that both familiar and unfamiliar logos contained letters or words. Another study found that logos also activated the bilateral inferior frontal gyri and sometimes the left temporal cortex (Bruce et al., 2014), but the baseline condition was blurred images of the same objects, complicating interpretation of the findings.

Beyond words, music, and logos, gestures can also be a form of symbolic communication. One study that compared emblematic gestures with grasping movement suggested that both the right middle temporal and left inferior frontal gyri were active in processing meaning from either speech or gestures (Andric et al., 2013). Another suggested that semiotic gestures activate the right

inferior frontal gyrus, right superior parietal lobule and right temporoparietal junction (Villarreal et al., 2012), while another found a left hemispheric predominance for activity related to emblematic gestures in the inferior frontal gyrus and posterior temporal cortex (Lindenberg et al., 2012).

In our study, selectivity for symbolic versions of stimuli occurred in the inferior frontal and middle temporal gyri, but only for words and musical notation. This suggests that these two components of the visual word processing network do not have symbolic selectivity for all types of emblematic symbols, but are especially sensitive to the meaning of words and musical notation. One can speculate as to what it is about language and music that sets them apart from instructional symbols, flags and logos, in terms of symbolic processing. First, it may be that both language and music are forms of communication that consist of a temporal flow of ideas with syntax and grammatical structure, whereas this dynamic is not present with road signs, flags and logos, which merely represent things or actions in isolation. Second, the difference may also be related to the physical form of the symbols. Words and musical notation consist of monochromatic line segments, which, as others have noted, may capitalize on processes that analyze object contours (Dehaene and Cohen, 2011; Szwed et al., 2011) or stimuli with high-contrast and high-spatial frequency that stress the importance of grouping combinations (Vogel et al., 2012, 2014). In contrast, flags and logos tend to have coloured surfaces, and may emphasize different forms of visual processing. In this respect it may be of interest in future studies to perform region of interest analyses on frontal and temporal homologues in the right hemisphere with similar control of low-level visual properties.

#### 4.3. *Summary*

Our study focused on regions of interest identified as participating in a visual word processing network, and performed specific contrasts between symbolic and non-symbolic versions for each of our stimulus classes, to address the question as to whether this network was involved in other types of symbolic communication. We found similar responses in the fusiform components of the network to all types of visual symbols, but no special status for symbolic over non-symbolic versions. Rather, only the left inferior frontal and middle temporal gyri showed greater response to symbolic versions, but only for words, and in the case of the left inferior frontal gyrus, for musical notation as well. Our whole brain analysis showed that greater responses for symbolic variants occurred in different cortical regions for different classes of symbols, even if the visual word form area responded equally well to all symbols.

Our results are consistent with a growing body of recent evidence that the visual word form area is activated by many types of visual stimuli and is sensitive to visual more than semantic properties of such stimuli, as summarized above. Nevertheless, there is evidence that the visual word form area makes an important contribution to word recognition, even if it is not solely activated by words. Lesion studies show that loss or disconnection of the left visual word form area is associated with pure alexia, the loss of reading proficiency (Epelbaum et al., 2008; Gaillard et al., 2006; Molko et al., 2002; Sheldon et al., 2012). The involvement of this fusiform region in reading may have evolved because it is the visual area that is most interconnected with nearby language regions in the left hemisphere (Devlin et al., 2006; Plaut and Behrmann, 2011), or because it has a special sensitivity to high-contrast high spatial frequency line segments that comprise the characters in almost all writing systems (Szwed et al., 2009; Vogel et al., 2014), explanations which others point out are not mutually exclusive (Wandell et al., 2012). The latter is reflected in the

'recycling hypothesis', which proposes that the visual word form area has an intrinsic sensitivity to basic contours, which is recruited in the service of word recognition when literacy is acquired (Dehaene and Cohen, 2011).

However, word processing involves more than just the perception of the shape of the letters and words. Our studies suggest that the processing of these stimuli as components of a language, with symbolic and semantic connotations, may become apparent in left middle temporal and inferior frontal regions. Similar conclusions were reached by others about words (Petersen et al., 1990; Reinke et al., 2008) and we show that this may be true also for other forms of communication such as musical notation. Thus word processing involves a network of areas and, as others have proposed, word selectivity is not created by the activity in any one cortical region like the visual word form area, but from its connectivity with other components of a word network (Price and Devlin, 2003; Reinke et al., 2008). Similarly, while it may be that the fusiform gyrus is involved in visual processing of many types of symbols, thus explaining why alexic subjects can have difficulty with reading music, maps and road signs (Beversdorf and Heilman, 1998; Horikoshi et al., 1997), the specific processing of the meaning of these symbols may involve unique networks that differ for different types of symbols, as our whole-brain analysis indicates. This would be consistent with a recent 'many-to-many' hypothesis, that, any cortical visual region participates in processing many object types, and the processing of any object involves multiple visual regions (Behrmann and Plaut, 2013). In this view, object specification is not located within a single region, but is an emergent property of the pattern of network activation, a proposal which had already been advanced for visual word processing (Reinke et al., 2008).

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## Appendix A. Supplementary Information

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