Task by stimulus interactions in brain responses during Chinese character processing ☆

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ABSTRACT

In the visual word recognition literature, it is well understood that various stimulus effects interact with behavioral task. For example, effects of word frequency are exaggerated and effects of spelling-to-sound regularity are reduced in the lexical decision task, relative to reading aloud. Neuroimaging studies of reading often examine effects of task and stimulus properties on brain activity independently, but potential interactions between task demands and stimulus effects have not been extensively explored. To address this issue, we conducted lexical decision and symbol detection tasks using stimuli that varied parametrically in their word-likeness, and tested for task by stimulus class interactions. Interactions were found throughout the reading system, such that stimulus selectivity was observed during the lexical decision task, but not during the symbol detection task. Further, the pattern of stimulus selectivity was directly related to task difficulty, so that the strongest brain activity was observed to the most word-like stimuli that required "no" responses, whereas brain activity to words, which elicit rapid and accurate "yes" responses were relatively weak. This is in line with models that argue for task-dependent specialization of brain regions, and contrasts with the notion of task-independent stimulus selectivity in the reading system.

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Introduction

Behavioral studies of reading have consistently revealed the task-specificity of various effects defined in terms of stimulus properties. Indeed, at least one phenomenon that is central to model evaluation—the interaction of consistency and frequency in reading aloud (Seidenberg et al., 1984)—is weak or non-existent in the lexical decision task (Andrews, 1982). The notion that stimulus properties have highly distinct effects across tasks is further demonstrated by item-level analyses of the variance accounted for by factors such as frequency, consistency, and neighborhood density demonstrating that they are ordered differently under different task demands (e.g., Balota et al., 2004).

Task manipulations in fMRI are often relatively coarse-grained, and designed to reveal the relative specialization of regions engaged by reading with respect to orthographic, phonological and semantic processing. For example, Frost et al. (2009) individually assessed these pathways by using different versions of a task in which participants were asked to detect matches between pictures and spoken or written words; they then related activity across modalities (auditory vs. visually presented words) to variability in phonemic awareness, a predictor of reading ability (see also Landi et al., 2010). A similar approach to varying the input modality in order to tap different subcomponents of the reading system over the course of development has also been widely pursued (Booth et al., 2004; Cone et al., 2008). All of these studies use different forms of rhyming or matching tasks to explicitly enforce the task-relevance of specific stimulus dimensions.

In contrast to studies that manipulate task to study different subprocesses of reading, studies designed to explore how different stimulus properties are processed throughout the reading system tend to use tasks whose demands are intentionally unrelated to reading, such as detecting a row of non-text symbols in a rapidly presented stream of stimuli (Vinckier et al., 2007), detecting repeated stimuli from trial to trial (Wang et al., 2011; Yang et al., 2011) or detecting the nonlinguistic feature (ascenders, color, size, etc.) of the stimuli (Binder et al., 2006; Liu et al., 2008; Starrfelt and Gerlach, 2007).

The possibility that stimulus selectivity might interact with task demands has been suggested largely by indirect comparisons across

task. Studies of processing in the putative "visual word form area" (VWFA) using rapid presentation of stimuli, and requiring relatively minimal processing (e.g., Vinckier et al., 2007) have shown a graded pattern of selectivity in this region, with the greatest activity to words, and successively less activity to pseudowords, letter strings of varying statistical probability, and so on, down to non-text stimuli. In other tasks, the selectivity of this region has been less clear (Dehaene and Cohen, 2011; Price and Devlin, 2011). For example, we recently observed a finely graded, but *reversed* pattern of selectivity to word-likeness throughout the fusiform gyrus in a one-back task (Wang et al., 2011).

Despite their potential implications for understanding the organization of the brain basis of reading, relatively few studies have directly addressed stimulus by task interactions. In one example of such a study, Carreiras et al. (2007) tested for task by stimulus interactions by looking for regions in which the difference between word and pseudoword stimuli varied between naming and lexical decision. Their results revealed effects of lexicality in a small set of regions not typically considered in the "reading network"—pre- and supplementary motor regions, pre-central gyrus, and right inferior frontal gyrus (IFG)—and found an interaction between task and lexicality only in the right IFG. It may not be surprising that these interactions were so limited—despite the fact that lexical decision and naming clearly impose such different task demands with respect to these stimulus classes—when we consider that differences between words and pronounceable pseudowords are often quite subtle in neuroimaging studies using a variety of tasks (Dehaene et al., 2005; Kronbichler et al., 2004, 2007; Vigneau et al., 2005).

In the current study, we examine task by stimulus interactions between an active word recognition task (lexical decision) and a passive reading task (symbol detection), while varying the word-likeness of stimuli parametrically from random arrangements of strokes up to real Chinese characters, in order to have a wide "dynamic range" to observe stimulus-driven effects. We also pursued an analysis strategy in which candidate functional regions are identified via data-driven techniques (Beckmann and Smith, 2004), and their response properties tested in fully factorial ANOVAs, which is potentially more sensitive than previously used methods. The data provide a novel characterization of task by stimulus interactions, which are critical to understand, because they raise important questions about how the apparent tuning or sensitivity of particular regions to particular stimulus properties might contribute to function across a variety of behavioral contexts.

Method

Participants

Sixteen university students (10 female) participated in both Lexical Decision (LD) and Symbol Detection (SD) tasks in the fMRI experiment. All participants were students at Beijing Normal University, native speakers of Mandarin Chinese with normal or corrected-to-normal vision, aged between 18 and 25, and no history of neurological disease or learning disability. They provided written informed consent and were paid an hourly stipend for participation.

Materials

Stimuli comprised real Chinese characters, pseudo-characters and "artificial" characters, with 30 stimuli in each of six conditions designed to manipulate wordlikeness parametrically (Wang et al., 2011; Yang et al., 2011). Real characters were selected to be "phonograms," comprising a combination of a phonetic component (that provides probabilistic information about pronunciation) and a semantic component (that provides probabilistic information about meaning). Three types of pseudo-characters were constructed, reflecting

a parametric manipulation of wordlikeness: 1) pseudo-characters containing both Phonetic and Semantic components (PS), 2) pseudo-characters containing Only Semantic components (OS) and 3) an Only Orthographic (OO) condition, in which neither phonetic nor semantic components were present. Artificial stimuli were constructed by arranging subcomponents of real characters into combinations that are orthotactically illegal (analogous to the use of consonant strings in alphabetic writing systems). Two types of orthotactic violation were used, although they are considered together in the context of the current analysis: the reversed radical (RR) condition was composed by reversing the position of components in the OO pseudo-characters. The NN condition was composed by randomizing the individual strokes that made up the RR stimuli. Ninety additional real character stimuli were included in order to balance the number of "word" responses in LD task. Filler frequency, alignment (left–right), number of radicals and strokes were matched to the target stimuli.

Procedure

Symbol detection (SD) and lexical decision (LD) tasks

Participants were familiarized with the symbol detection (SD) and lexical decision (LD) tasks, then lay comfortably in the scanner and viewed stimuli via rear projection during the tasks. Participants performed SD task first. Both tasks were run using fast random-interval event-related designs. On each trial, a 200 ms fixation cross was presented, followed by a stimulus presented for 500 ms, followed by a randomly jittered ITI (mean of 5.3 s, range from 1 to 14 s). Stimulus presentation was controlled, and response time and accuracy were recorded using E-Prime software.

For the SD task, participants were asked only to respond to symbols (a pair of pound signs: "##") by pressing a button with their right index finger. The task was completed in two consecutive runs of 120 trials, 15 for each of the six critical stimulus conditions and 30 for symbol targets.

In the LD task, participants viewed the same critical stimuli as in the SD task (not including the symbol targets) along with 90 filler characters included to balance the number of "yes" and "no" responses. Their task was to respond by button press with their right index finger to real characters and with their middle finger to all non-character stimuli. This task was completed in two consecutive runs of 135 trials, 15 for each of the six critical conditions and 45 for fillers.

MRI acquisition

Functional and anatomical images were collected using a 3 T Siemens Magnetom TrioTim syngo MR system, with a 12-channel head coil in the State Key Laboratory of Cognitive Neuroscience and Learning of Beijing Normal University. Functional images were collected using a gradient-recalled-echo echo-planar imaging sequence sensitive to the BOLD signal. Forty-one axial slices were collected with the following parameters: $TR = 2500$ ms, $TE = 30$ ms, flip angle $= 90°$, $FOV = 20$ cm, matrix $= 64 \times 64$, 3 mm thickness, yielding a voxel size of $3.125 \times 3.125 \times 3$ mm, interleaved slices with no gap. The SD task was completed in two runs of 296 TRs (12 m, 20s), and the LD task was completed in two runs of 332 scans (13 m, 50s) including four TRs of rest at the beginning and end of each run.

Following the acquisition of functional data, high resolution T1-weighted anatomical reference images were obtained using a 3D magnetization prepared rapid acquisition gradient echo (MPRAGE) sequence, $TR = 2530$ ms, $TE = 3.45$ ms, flip angle $= 7°$, $FoV = 25.6$ cm, matrix $= 256 \times 256$ with 1 mm thick sagittal slices.

Data analysis

MRI data analysis

Functional data were analyzed using AFNI (Cox, 1996, program names appearing in parentheses below are part of the AFNI suite).

Cortical surface models were created with FreeSurfer (available at http://surfer.nmr.mgh.harvard.edu/), and functional data projected into anatomical space using SUMA (Argall et al., 2006; Saad et al., 2004, AFNI and SUMA are available at http://afni.nimh.nih.gov/afni).

Preprocessing

After reconstructing 3D AFNI datasets from 2D images (to3d), the anatomical and functional datasets for each participant were co-registered using positioning information from the scanner. The first 3 volumes were discarded, and functional datasets preprocessed to correct slice timing (3dTshift) and head movements (3dvolreg), reduce extreme values (3dDespike) and detrend linear and quadratic drifts (3dDetrend) from the time series of each run, with no smoothing or filtering.

The two runs of the each task were concatenated (3dTcat) for input to the general linear model analysis to estimate percent signal change for each condition in each task. In addition, all four runs were concatenated (3dTcat) for each participant, and the averaged dataset for all 16 participants' time series was computed (3dMean) as the input for independent component analysis.

Surface-based spatial normalization of anatomical and functional data was accomplished using Freesurfer (Fischl et al., 1999) and SUMA (Argall et al., 2006). Anatomical data were reconstructed (to3d), and a surface model for each participant was made with Freesurfer: cortical meshes were extracted from the structural volumes, then inflated to a sphere and registered anatomically (Fischl et al., 1999). Using the surface atlas, an averaged subject was created by averaging surfaces, curvatures, and volumes from all subjects. The averaged surface was converted into SUMA (Argall et al., 2006) and was then put a standard mesh on the SUMA surfaces. The standard mesh was then converted to a volume and transformed to Talairach space (Talairach and Tournoux, 1988, using @auto_tlrc, to the N27 template) for visualization and reference purposes. Functional data were normalized by transforming volumes resulting from AFNI or MELODIC analyses into surface representations using the standardized surfaces, and computing averages over surfaces.

Independent component analysis (ICA) followed by simple correlations to identify candidate regions for further analysis

In order to identify coherent patterns of BOLD response over the course of the experiment, a data-driven approach was applied to the preprocessed time series. This analysis was carried out using Probabilistic ICA (Beckmann and Smith, 2004) as implemented in MELODIC (Multivariate Exploratory Linear Decomposition into Independent Components) Version 3.09, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Schmithorst and Holland (2004) determined that using ICA with group-averaged data was largely equivalent to group ICA, except for components that are found in relatively small numbers of participants. Because our focus here is in characterizing the data at the group level, we took this approach (which is also computationally much more efficient).

The following data pre-processing was applied to the averaged data: masking of non-brain voxels; voxel-wise de-meaning of the data and normalization of the voxel-wise variance. Pre-processed data were then whitened and projected into a 483-dimensional subspace using probabilistic principal component analysis where the number of dimensions was estimated using the Laplace approximation to the Bayesian evidence of the model order (Beckmann and Smith, 2004; Minka, 2000). The whitened observations were decomposed into sets of vectors, which describe signal variation across the temporal domain (time-courses) and across the spatial domain (maps) by optimizing for non-Gaussian spatial source distributions using a fixed-point iteration technique (Hyvarinen, 1999). Estimated component maps were divided by the standard deviation of the residual noise and thresholded ($p > 0.5$) by fitting a Gaussian/gamma mixture model to the histogram of intensity values (Beckmann and Smith, 2004).

In order to identify spatial components whose activity is related to task demands, the temporal modes of all ICs arrived at by MELODIC were submitted to a simple correlation analysis. The time series of stimulus presentation (task > rest) was convolved with a hypothetical hemodynamic response function (waver), and its correlation with each IC's temporal mode was computed. Only ICs significantly correlated ($p \leq 0.0001$, equivalent to a Bonferroni corrected p<.05 for 483 tests) were considered as task-related and included for further analysis. The spatial components observed in ICA can be widely distributed across anatomical regions, making it difficult to compare results of this analysis to the more common region-of-interest based approach. To obtain spatially discrete regions of interest for further analyses, we selected thresholded spatial patterns obtained by MELODIC, using both magnitude ($Z > 2.58$, p<.005, uncorrected) and extent (cluster size > 50, $2 \times 2 \times 2$ voxels) to achieve a corrected threshold of p<.005. The spatially thresholded IC was then used as a mask to extract the beta mean value from the GLM results for each condition in two tasks (3dmaskave).

Analyses of task × stimulus interactions

We first computed voxel-by-voxel estimates of percent signal change for all stimulus classes in both tasks using a standard GLM approach. Preprocessed data for two runs in each task were analyzed in general linear model (3dDeconvolve) including seven regressors of no interest (six estimates of head movement from motion correction from 3dVolreg, and one regressor for "filler" trials). The six experimental regressors were hypothetical hemodynamic response functions (HRFs) constructed by convolving the time series of stimuli presentation in each condition (Real, PS, OS, OO, RR and NN) with a model HRF (waver). The peak value of the estimated HRF curve was considered as the percent signal change of each condition.

Mean percent signal change was then extracted for each ROI identified by the ICA/correlation method by simple averaging (3dMaskave) for each participant. This resulted in a data set for each ROI that could be submitted to a 2 (task: SD vs. LD) × 6 (stimulus) repeated-measures ANOVA, with participant as the random variable using the |STAT package (Perlman and Horan, 1986). Because of the large number of tests, a strict (p<.001, roughly equivalent to p<.01 for 103 tests) threshold for significance was selected.

The main advantage of testing for interactions after first identifying candidate functional ROIs as we have here is that it identifies a set of voxels that are hypothesized to have similar activity without reference to the experimental design. Voxel-wise tests for significant interactions are prone to reveal contiguous voxels that have very different interactions, so that averaging across an ROI does not accurately represent the pattern observed in any of its constituents. Here we identify the ROIs without consideration for task, providing a basis for averaging those data together before testing for interactions. In practice, many contiguous regions had very similar patterns of interaction. To simplify presentation, we tested for higher-order interactions with region (in a Region × Task × Stimulus ANOVA on the same data) and collapsed sets of contiguous regions together into larger ROIs where no interactions with Region were found. Data from all regions in which significant main effects or interactions were found are presented in supplementary materials, with representative regions discussed in the Results.

Functional connectivity analysis

To test for functional connectivity, voxel-wise correlations were computed based on the mean time series from a seed volume selected by conjunction of task related ICs overlapping by at least 20% with left fusiform gyrus. For each task, drift effects, head motion and repeat trials were removed from the original time series (3dSynthesize). These cleaned data were used to compute an average time series for the seed volume, which was then tested for correlation with activity in every voxel in the data set (3dDeconvolve).

In order to determine r values from the results of 3dDeconvolve (which returns R^2), results were squared and assigned the sign of the corresponding beta value. For group analyses of correlations, Fisher's Z transformation formula was used to reduce skewness and make the sampling distribution more normal: $z = (1/2)*\ln((1 + r)/(1 - r))$, where z is approximately normally distributed with mean r, and standard error $1/(n - 3)0.5$ (n is sample size). Group analysis was conducted for each task by comparing the mean correlation coefficients Z from all participants to zero (3dttest). The contrast of LD > SD correlation map was created via paired t-test on each Z values of LD and SD task. Activation maps and regions reported as active were obtained by first thresholding individual voxels at $p < 0.005$ (uncorrected), and then applying a subsequent cluster-size threshold (at least 41 voxels) based on Monte Carlo simulations (3dClustSim), resulting in a corrected threshold of $p < 0.05$.

Results

Online behavioral performance of lexical decision task in the scanner

As shown in Fig. 1, a significant effect of Stimulus was observed both for response latency, F (5, 75) = 83.17, p < 0.01, and for response accuracy, F (5, 75) = 18.54, p < 0.01 across all conditions. When "no" responses are considered independently, a graded effect of word-likeness was observed both for response latency, F (4, 60) = 125.22, p < 0.01, and for response accuracy, F (4, 60) = 22.64, p < 0.01. The responses to the artificial stimuli were faster (t (15) = 14.84, p < 0.01) and more accurate (t (15) = 5.98, p < 0.01) than response to pseudo-characters constructed to be similar to real Chinese characters. Among pseudo-characters, there was a monotonic effect of sublexical information for response latency, F (2, 30) = 41.18, p < 0.01, and accuracy, F (2, 30) = 11.35, p < 0.01, such that items containing both semantic and phonological cues were the most difficult to reject, and stimuli containing neither were the easiest. Response on PS (995 ms) condition was slower than OS (944 ms) condition (p = 0.06), which was in turn slower than OO (838 ms) condition (p < 0.01). The OO (90.1%) condition was more accurate than the OS (79.6%) and PS (79.4%) conditions (Ps < 0.01), and there was no difference between OS and PS condition (p = 1.00). Artificial stimuli were most accurate (97%) and fastest (689 ms) to reject. The RR (700 ms) condition was slower than the NN (677 ms) condition (p < 0.01), but these conditions did not differ in accuracy (p = 0.66).

Overall network for task > rest

The MELODIC analysis yielded 483 independent components (ICs), explaining 64.24% of the variance in the data. Of these, 103 were identified as task-related based on the correlation between their temporal mode and a task > rest regressor including all critical stimuli (fillers and symbol targets were included as a regressor of

no interest). As shown in Fig. 2, the network of regions correlated with the task > rest regressor is widely distributed throughout visual and motor regions in addition to parietal regions associated with spatial processing and frontal regions associated with language processing, reading, and particularly Chinese character recognition. Task by stimulus ANOVAs revealed that 77 of these regions had significant main effects of stimulus, task, or interactions between these factors. Interactions between stimulus and task were observed in 33 regions, a main effect of task was observed in 21, a main effect of stimulus was observed in 13, and ten regions had main effects of both task and stimulus but no interaction between them. In an additional 26 regions, no main effects or interactions involving Stimulus or Task were observed; these are mapped in white in Fig. 2.

One advantage of using a data-driven approach to identify spatial patterns of interest before testing their response patterns, is clear from Fig. 2. Many spatially contiguous regions that are all strongly correlated with a task > rest regressor differ with respect to the Task × Stimulus analysis. For example, one large, contiguous "blob" of activity includes much of the visual system, but the different regions identified within it include portions that are differentially impacted by task, stimulus, or their interaction. In a GLM analysis, a voxel-by-voxel test of the task > rest contrast would likely have revealed a very similar overall pattern, but would have provided no guidance in how to select ROIs to test for more subtle effects (see also Yang et al., 2011, for a direct comparison of whole-brain GLM contrasts with this approach).

Task by stimulus interactions

As shown in Fig. 3, Task × Stimulus interactions were observed widely throughout regions typical of the reading network for Chinese (Bolger et al., 2005; Tan et al., 2005), including fusiform and superior parietal lobe regions thought to be engaged in orthographic processing, inferior frontal and insular regions associated with phonological and semantic processing and middle frontal gyrus, which appears to be specifically engaged by written forms with complex spatial arrangements (Bolger et al., 2005; Siok et al., 2004; Tan et al., 2003; Yoon et al., 2006). Interestingly, a similar Stimulus × Task interaction was found bilaterally in all of these regions. In addition, this interaction was observed in midline areas associated with task difficulty, and some visual areas not typically understood to have a specific role in word or character recognition (Table 1).

The form of this interaction was remarkably consistent across regions, with the effect of stimulus class present only—or more strongly—under the demands of the lexical decision task (see Supplementary Fig. 1 for graphs of the interaction in all regions identified by the ICA and ANOVA analysis). Further, the effect of stimulus class in LD generally followed the behavioral results, in that there was a direct relationship between percent signal change and behavioral measures of task difficulty.
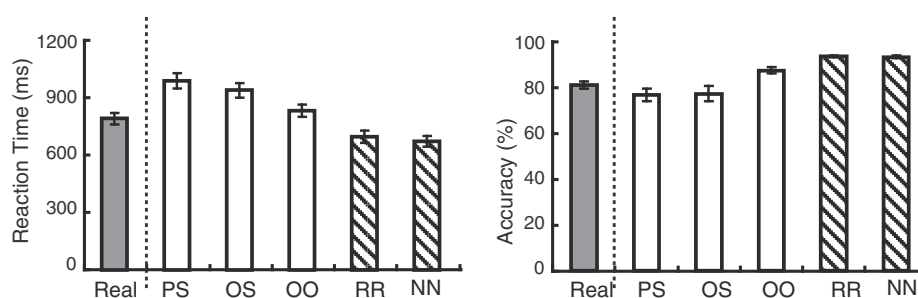

Fig. 1. Response time (left) and accuracy (right) in the lexical decision task. The dashed line separates real words (requiring "yes" responses) from non-word stimuli, which decrease in word-likeness from left to right: PS = pseudocharacters with phonetic and semantic components; OS = pseudocharacters with semantic components only; OO = pseudocharacters with orthographically legal components, but no phonetic or semantic information; RR = artificial stimuli created by reversing the canonical position of orthographic components from the OO stimuli; NN = artificial stimuli produced by randomizing the position of individual strokes that make up the other stimuli.
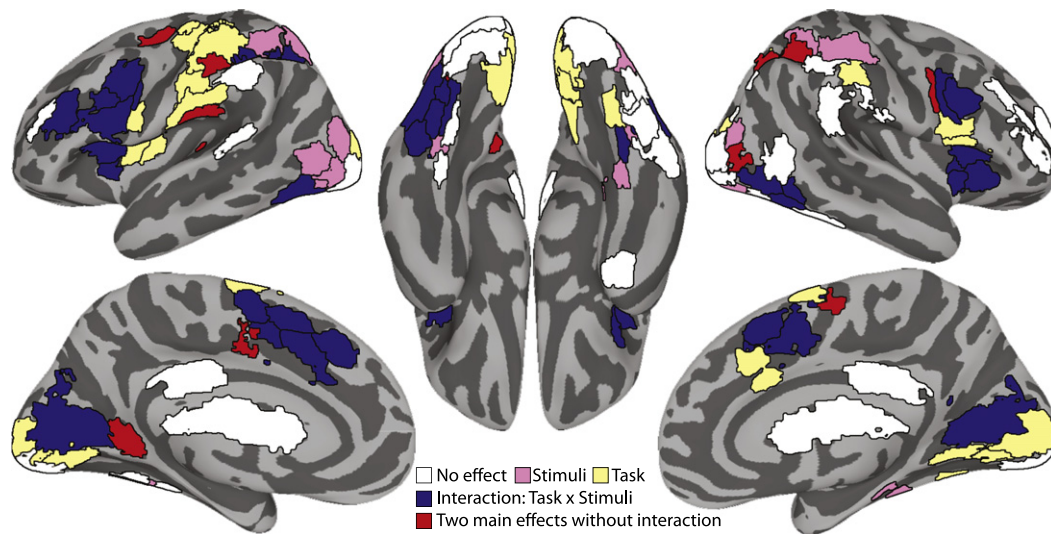
Fig. 2. Map showing all independent spatial components identified in the data set, color coded to indicate the results of Task × Stimulus ANOVAs conducted on percent signal change estimates from regions identified in this analysis.

Main effects of task

A map of regions showing Task main effect is shown in Fig. 4, along with bar graphs for percent signal change in representative ROIs (data for all ROIs are presented in supplementary materials),

and coordinates of the ROIs are given in Table 2. A main effect of task was found throughout a network of motor and somatosensory regions, driven by the greater motor demands of the LD task (in which a button press was required on every trial) relative to the SD task (in which button presses were relatively infrequent. In other
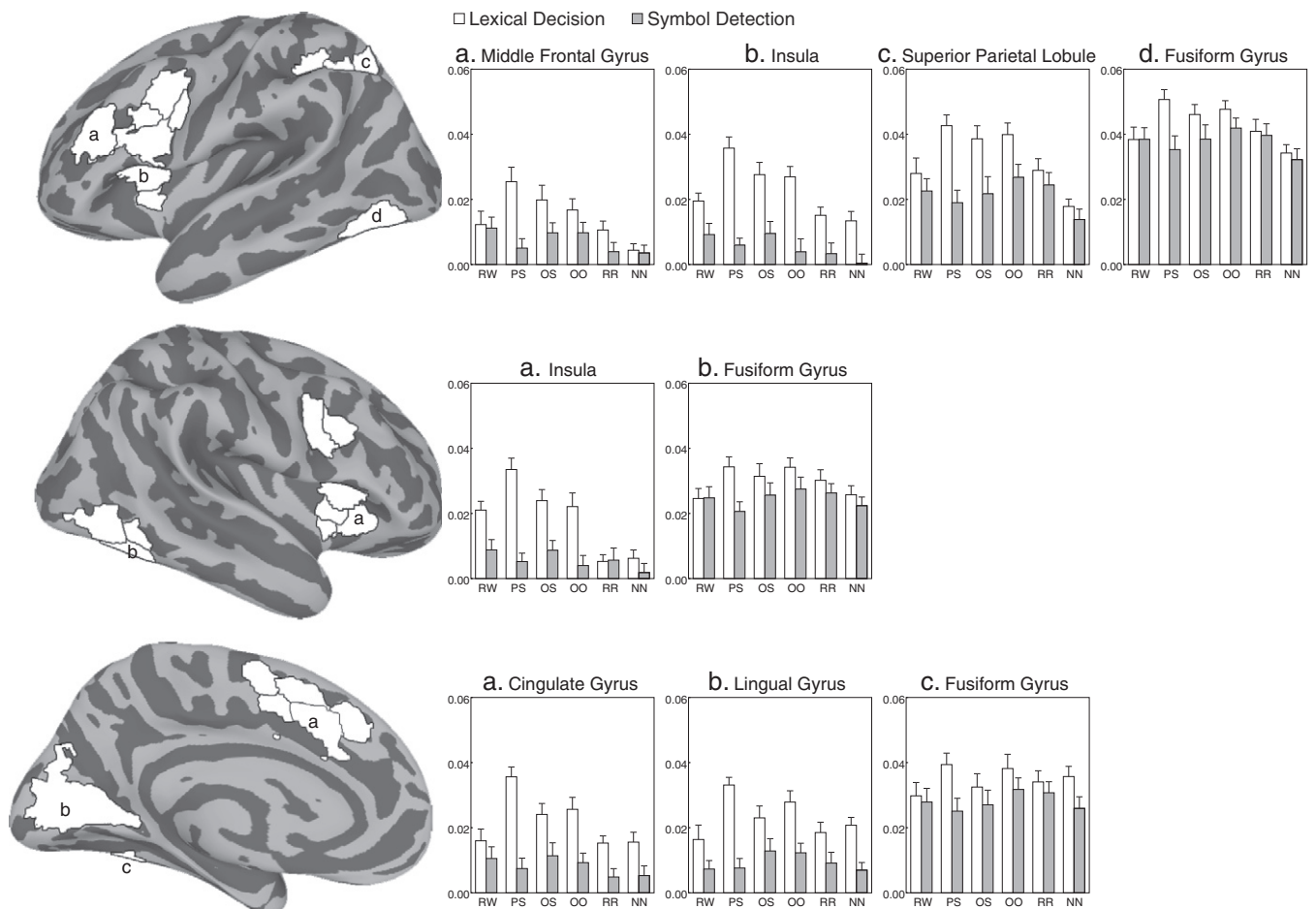

Fig. 3. Map of Task × Stimulus interactions, with bar graphs illustrating patterns of percent signal change for representative regions.

Table 1
Regions with a significant Task×Stimulus interaction.

Regions	Volume	Coordinates		
		x	y	z
Left hemisphere				
Med. frontal gyrus	255	−4	−5	56
	312	−2	25	41
Sup. frontal gyrus	233	−5	9	50
Mid. frontal gyrus	330	−40	33	25
	244	−36	10	30
Inf. frontal gyrus	588	−47	13	23
	184	−48	4	32
Precentral gyrus	325	−38	3	36
Insula	265	−33	18	13
	252	−36	18	6
Sup. parietal lobule	79	−43	−41	40
	351	−35	−48	41
	244	−32	−58	40
Precuneus	503	−26	−67	35
Fusiform gyrus	201	−40	−62	−16
	281	−32	−55	−16
	380	−43	−60	−9
	264	−44	−47	−13
	174	−41	−51	−18
Cingulate gyrus	204	−6	5	45
	212	−7	18	37
Right hemisphere				
Sup. frontal gyrus	223	5	16	49
Mid. frontal gyrus	223	36	11	29
Inf. frontal gyrus	181	38	19	−3
	319	41	5	29
Insula	215	32	27	1
	228	33	22	10
	243	37	19	5
Mid. occipital gyrus	266	44	−62	−6
Inf. temporal gyrus	206	53	−51	−12
Fusiform gyrus	230	49	−51	−16
Culmen	245	33	−39	−20
Cingulate gyrus	271	8	6	44
Lingual gyrus	2049	0	−68	9

Note: Sup., superior; Mid., middle; Med., medial; Inf., inferior; volume is given in number of voxels ($2 \times 2 \times 2$ mm³); x, y and z are coordinates of the centered voxel in each cluster given with reference to the Talairach atlas.

regions, including bilateral lingual, superior parietal, middle occipital, superior frontal and anterior cingulate gyri, as well as left insula, the overall pattern of results was more similar to the Task×Stimulus interaction observed in the reading network at large, although these interactions did not survive correction for multiple comparisons (see Supplementary Fig. 2 for graphs of signal change in all conditions for all regions identified as having a main effect of task by the ICA and ANOVA analysis).

Main effects of stimulus

The map of regions in which a main effect of Stimulus was observed is shown in Fig. 5, along with bar graphs for percent signal change in each ROI, and the coordinates of the ROIs are given in Table 3. Main effects of Stimulus were observed mainly in visual processing and spatial analysis regions at bilateral superior parietal lobule and fusiform gyrus, large regions of the left middle and inferior occipital gyri, as well as right middle occipital and parahippocampal gyri. Unlike the regions in which a significant interaction between Task and Stimulus was observed, the effect of Stimulus in these regions was not directly related to the behavioral results. Indeed, when considering just the pseudocharacters, there appears to be an inverse relationship between the presence of semantic or phonological information in the stimulus and activity in these (largely visual) regions. This is consistent with observations from Wang et al.

(2011) in a one-back task. It may be that these regions are engaged by novel but familiar orthographic patterns in a relatively task-independent way (see Supplementary Fig. 3 for graphs of signal change in all conditions for all regions identified as having a main effect of stimulus by the ICA and ANOVA analysis).

Main effects of task and stimulus

The map of regions in which main effects of both Task and Stimulus were observed, but without significant interactions is shown in Fig. 6, along with bar graphs for percent signal change in each ROI, and the coordinates of the ROIs are given in Table 4. Regions in which effects of both Task and Stimulus were observed include superior precentral gyrus, supramarginal gyrus, inferior parietal lobule, parahippocampal, middle cingulate cortex in the left hemisphere, and right dorsal visual stream regions from middle and superior occipital gyrus to superior parietal lobule, right medial frontal gyrus and inferior precentral gyrus. Throughout all regions, the effect of Task took the form of greater activity during LD than SD. Stimulus effects in these regions are more difficult to characterize in terms of a priori stimulus classifications, except that in most of these regions activity was greatest for the pseudocharacter (PS, OS, OO, see Supplementary Fig. 4 for graphs of signal change in all conditions for all regions identified as having main effects of task and stimulus by the ICA and ANOVA analysis).

Task×Stimulus interactions throughout the left fusiform

The stimulus selectivity of a portion of left fusiform gyrus (the visual word form area) is of particular interest as it has been the focus of much debate (Dehaene and Cohen, 2011; Price and Devlin, 2011). We therefore tested for Region×Task×Stimulus interactions throughout the left fusiform gyrus, in order to explore whether there was any evidence for a functionally distinct subregion that responds differentially to the wordlikeness manipulation. The only significant interaction with Region was Stimulus, $F (20, 300) = 2.18$, $p < .005$, reflecting very weak stimulus selectivity in the most medial portion of the FG (labeled C in Fig. 7).

Overall, the highly robust Stimulus×Task interaction, $F (5, 75) = 5.61$, $p < .001$ took a similar form throughout the gyrus, as shown in Fig. 7, mirroring the rest of the reading network. In the LD task, activity was again directly related to behavioral difficulty, resulting in greater activity for more word-like stimuli, but only when these were not real characters. In the SD task, the Stimulus effect was complex, and not particularly consistent with prior studies that have used a similar task (Vinckier et al., 2007). The greatest activity was observed to the OO pseudocharacters relative to the RR and NN conditions, potentially suggesting some selectivity for stimuli with regular orthographic structure, although other pseudocharacters, and of course real characters are also consistent with the regularities of the writing system and evoked relatively weak activity in these regions during the SD task.

To exclude the possibility that this pattern of activity was an artifact of response time (RT) or duty cycle, we generated new estimates of signal change for the stimulus conditions with RT as a covariate, by re-analyzing the data including z-scored RT as a regressor of no interest. We then extracted the values for all of the regions identified in the left fusiform gyrus (Fig. 7) and recalculated the ANOVAs for those regions. Strikingly, there is essentially no difference between the original analyses and the analyses using RT as a covariate (see Supplementary Fig. 5). Further, there is no significant effect of RT by itself on activity in these regions; when we convert the RT regressor to signal change, its effect (−0.0006) is obviously much weaker than the effect associated with any of the stimulus categories (ranging from 0.32 to 0.42). The lack of an RT effect in fusiform reflects the fact that the Stimulus by Task effects are not driven by duty cycle but are driven by stimulus-driven task difficulty.
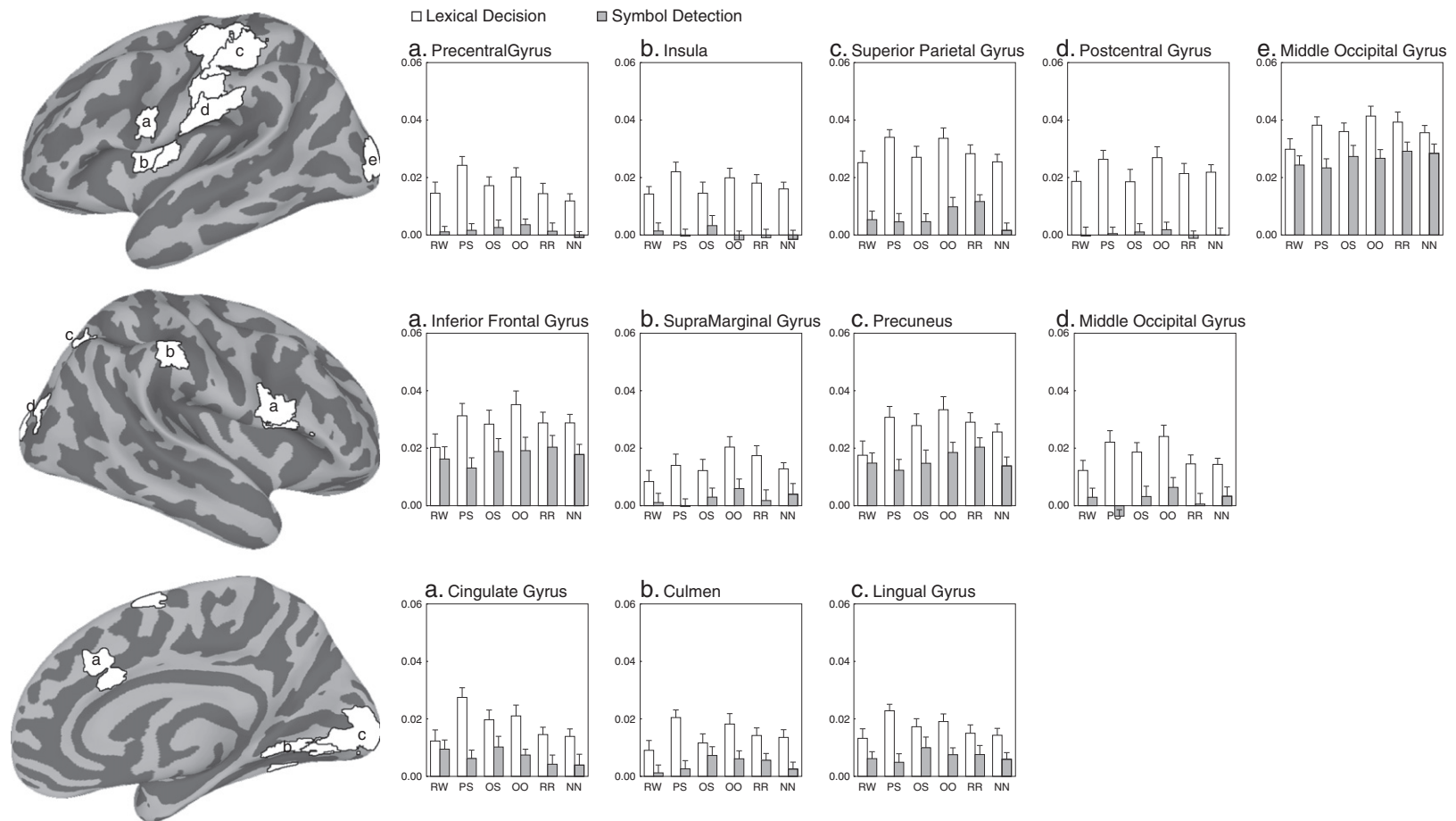
Fig. 4. Map of regions showing a main effect of Task, with bar graphs illustrating patterns of percent signal change for representative regions.

Table 2
Regions with a significant main effect of Task.

Regions	Volume	Coordinates		
		x	y	z
Left hemisphere				
Med. frontal gyrus	263	−10	−8	65
Inf. frontal gyrus	245	−55	4	23
Precentral gyrus	362	−34	−24	62
Insula	296	−36	6	12
	266	−39	−3	14
Postcentral gyrus	1054	−39	−26	54
	441	−58	−21	22
	254	−58	−19	34
Sup. parietal lobule	543	−45	−32	46
Mid. occipital gyrus	361	−26	−79	19
	392	−24	−89	3
Lingual gyrus	387	−9	−70	−5
Right hemisphere				
Frontal gyrus	207	7	−1	64
Inf. frontal gyrus	371	50	10	20
Supra marginal gyrus	284	59	−28	38
Precentral gyrus	254	52	15	9
Culmen	308	12	−52	−4
	215	30	−53	−14
Precuneus	60	22	−68	44
Mid. occipital gyrus	291	30	−81	15
Lingual gyrus	1674	2	−85	0
	272	10	−69	−3
Cingulate gyrus	312	6	21	32

Note: Sup., superior; Mid., middle; Med., medial; Inf., inferior; volume is given in number of voxels (2×2×2 mm³); x, y and z are coordinates of the centered voxel in each cluster given with reference to the Talairach atlas.

Table 3
Regions with a main effect of stimulus.

Regions	Volume	Coordinates		
		x	y	z
Left hemisphere				
Sup. parietal lobule	283	−35	−54	52
	225	−19	−71	52
Mid. occipital gyrus	372	−36	−80	9
	252	−43	−66	3
Inf. occipital gyrus	317	−39	−79	−3
	142	−43	−73	−4
Fusiform gyrus	252	−32	−42	−18
Right hemisphere				
Sup. parietal lobule	263	32	−55	51
	529	41	−35	44
Mid. occipital gyrus	262	36	−78	8
Inf. occipital gyrus	216	37	−76	−13
Fusiform gyrus	189	40	−45	−20
Parahippocampal	224	30	−26	−22

Note: Sup., superior; Mid., middle; Inf., inferior; volume is given in number of voxels (2×2×2 mm³); x, y and z are coordinates of the centered voxel in each cluster given with reference to the Talairach atlas.

Functional connectivity of left fusiform gyrus

In order to explore the relationship between activity in the left fusiform and other regions in the reading network, we characterized functional connectivity by correlating the mean time series of the activation in a functionally defined portion of left fusiform gyrus with
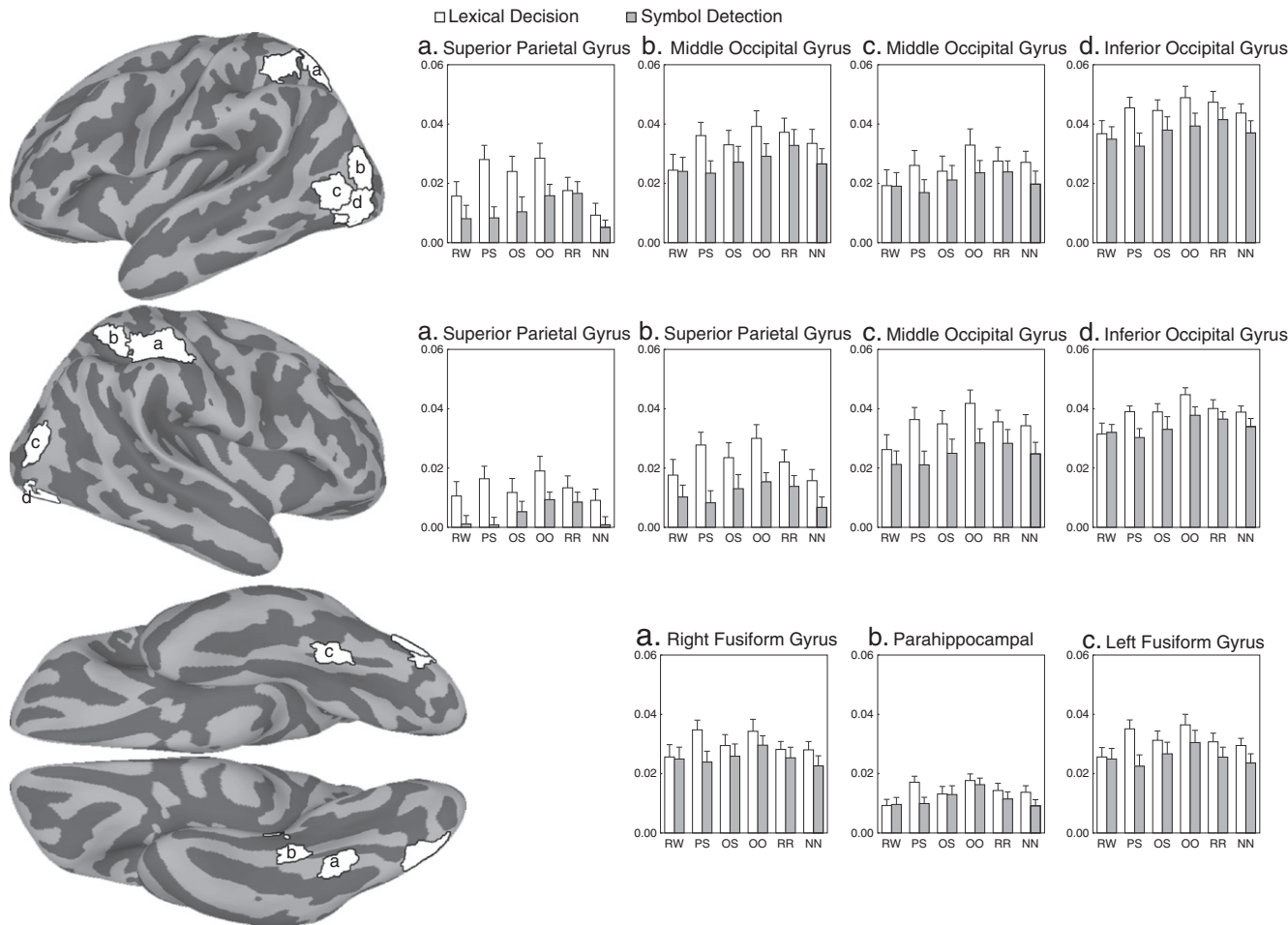

Fig. 5. Map of regions showing a significant main effect of Stimulus, with bar graphs illustrating patterns of percent signal change for representative regions.
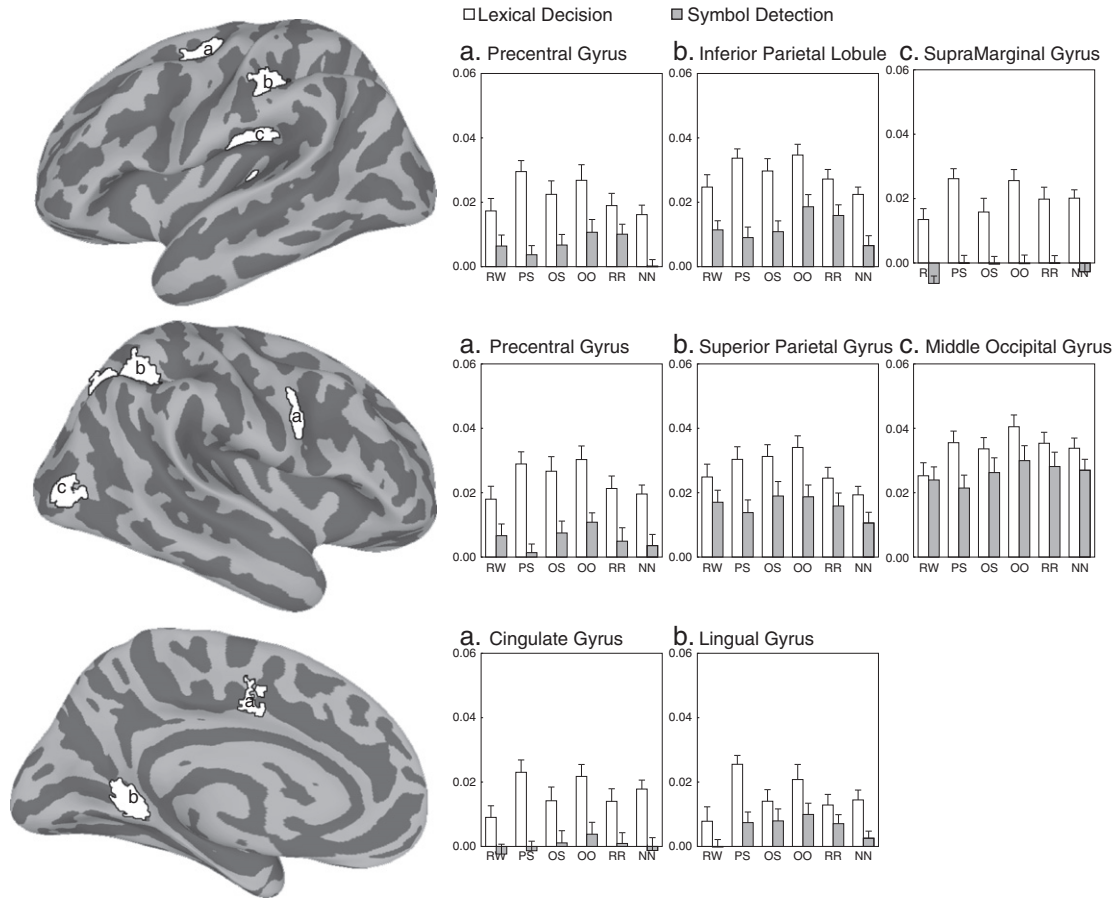
Fig. 6. Map of main effects of Stimulus and Task with no interaction, with bar graphs illustrating patterns of percent signal change for representative regions.

the time series of every other voxel in the data set for each task (see Fig. 8).

In both tasks, the strongest positive correlations with fusiform are in the visual system, bilaterally, and extend to include lower-level visual areas not thought to be specialized for word recognition. Other regions positively correlated with left fusiform include superior

Table 4
Regions with main effects of Stimulus and Task with no interaction.

Regions	Volume	Coordinates		
		x	y	z
Left hemisphere				
Precentral gyrus	278	−23	−9	50
Supramarginal gyrus	375	−48	−23	19
Inf. parietal lobule	215	−46	−33	38
Lingual gyrus	305	−17	−50	3
Cingulate gyrus	80	−8	−6	43
Fusiform gyrus	78	−38	−68	−17
Right hemisphere				
Med. frontal gyrus	67	7	−11	56
Precentral gyrus	215	51	6	32
Sup. parietal lobule	296	32	−56	43
Sup. occipital gyrus	377	26	−66	38
Mid. occipital gyrus	288	29	−71	25
	195	42	−77	4

Note: Sup., superior; Mid., middle; Med., medial; Inf., inferior; volume is given in number of voxels ($2 \times 2 \times 2$ mm³); x, y and z are coordinates of the centered voxel in each cluster given with reference to the Talairach atlas.

parietal regions implicated in spatial attention (Corbetta et al., 1995). These correlations with visual and spatial attention areas are perhaps surprising given the high demand on reading abilities (at least in the lexical decision task) but they are consistent with prior analyses of data from a one-back task (Wang et al., 2011) and with resting state data from English readers (Vogel et al., In Press).

Right precentral regions and bilateral insula were also positively correlated with fusiform, perhaps related to motor patterns for how characters are written. Negative correlations were observed for both tasks throughout the extent of superior temporal and angular gyri, two regions strongly implicated in phonological and semantic processing for text (Booth et al., 2006; Frost et al., 2005; Price, 2000).

Results of a direct contrast between the correlation in the LD and SD tasks are presented in Fig. 8C and Table 5. Positive correlations were stronger for the LD than the SD task, in regions associated with superior parietal lobule, typically associated with visuospatial and attentional processing (Colby and Goldberg, 1999; Nachev and Husain, 2006; Sack, 2009; Vandenberghe and Gillebert, 2009), and post-central regions likely driven by the higher response rate in the LD task (Carreiras et al., 2007). Positive correlations with left fusiform were also greater in the LD throughout the reading network (Bolger et al., 2005; Tan et al., 2005), including MFG, IFG/insula consistent with the greater reading-related task demands of lexical decision over symbol detection. In contrast, negative correlations were also stronger in AG and anterior STS during the lexical decision task, perhaps surprising given these regions' association with processing of semantic information (Booth et al., 2006; Frost et al., 2005; Price, 2000).
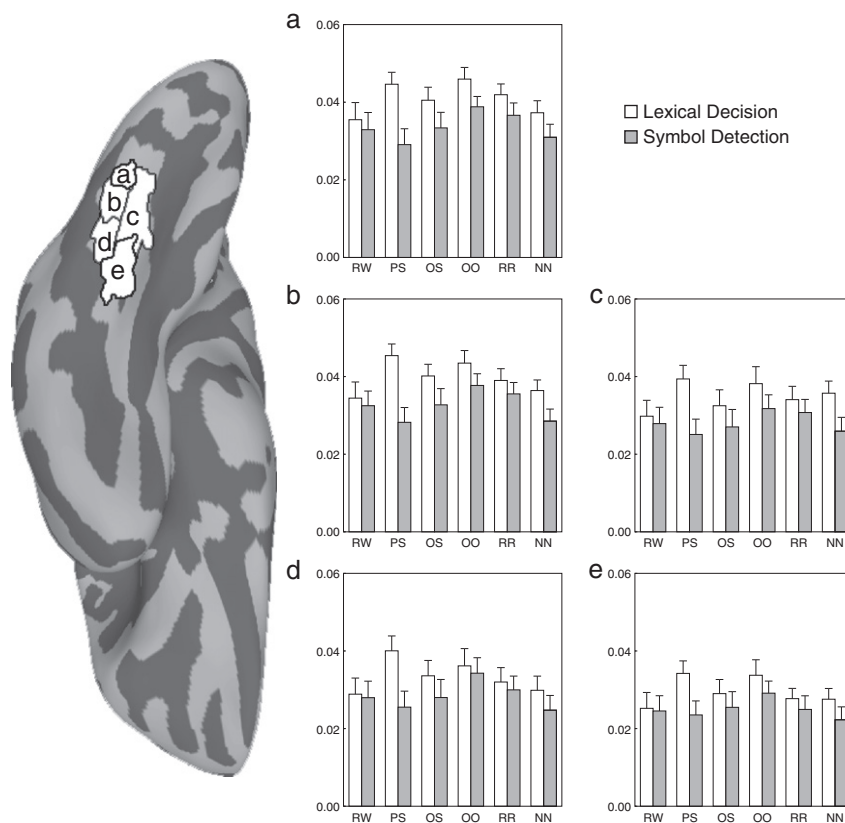
Fig. 7. Analysis of Task × Stimulus effects throughout the left fusiform gyrus.

Discussion

The overall network of regions engaged by reading across tasks broadly agrees with prior studies of Chinese reading, including a one-back experiment in which essentially the same critical stimuli were used (Yang et al., 2011). Specifically, the fusiform, middle and inferior frontal gyri were activated bilaterally, but more extensively in the left hemisphere. This points to a robust, distributed network of regions engaged by a wide variety of reading tasks. No task-related activity was observed in the middle temporal gyrus or superior temporal sulcus, possibly due to the low phonological task demands of the two tasks (Bolger et al., 2005). Although some prior studies have found activity in these regions for Chinese reading (Chen et al., 2002; Fu et al., 2002; Peng et al., 2003, 2004; Tan et al., 2001), many others have not (Siok et al., 2003; Tan et al., 2000, 2003; Xiang et al., 2000).

The analyses further revealed interactions between task and stimulus type throughout this network, suggesting that its function is not fixed, but can be reorganized in response to task demands (Song et al.,

2010; Starrfelt and Gerlach, 2007; Wang et al., 2011; Xue et al., 2010). The form of this interaction was remarkably similar throughout fusiform, middle and inferior frontal gyri, such that activity was overall quite low, and not influenced by stimulus class in the symbol detection task, but strongly affected by stimulus class in the lexical decision task.

Effects of stimulus type were observed in the lexical decision task that was directly related to stimulus difficulty, even when response time was statistically controlled. In this task, processing difficulty is determined non-linearly by word-likeness, such that the least word-like stimuli are easiest to process (i.e., reject as nonwords), with real words slightly more difficult to process (i.e., accept as real words), followed by pseudo-characters, which are the most difficult to reject. Thus, finding a pattern of activity consistent with these behavioral results in a particular brain region during this task is actually ambiguous as to whether the region is directly influenced by these stimulus/task features (as has been suggested for left middle frontal gyrus involved in Chinese phonological processing, Siok et al., 2004; Tan and Siok, 2006; Tan et al., 2003) or just the difficulty of the decision (as has been suggested for IFG, Blumstein et al., 2005;
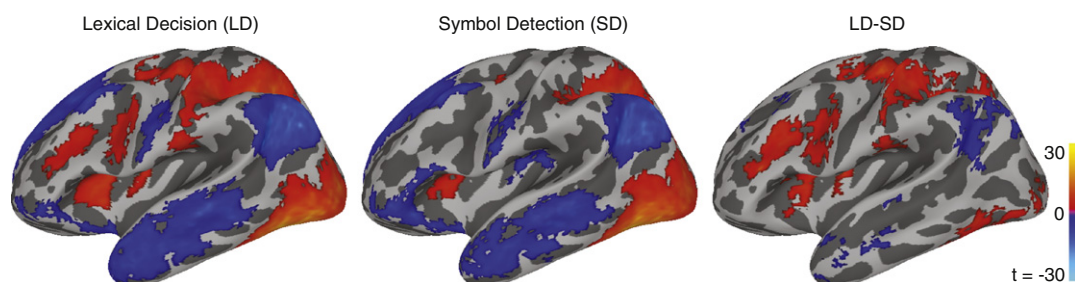

Fig. 8. Functional connectivity of left fusiform gyrus.

Table 5
Task contrast for functional connectivity (LD > SD).

	Volume	Z value	Coordinates		
			x	y	z
Positive correlation					
Left hemisphere					
Postcentral gyrus	2552	12.66	−39	−27	56
Med. frontal gyrus	915	9.30	−7	11	46
Mid. frontal gyrus	494	7.03	−47	1	38
	354	14.00	−41	31	16
Cuneus	296	6.91	−13	−73	12
	61	6.51	−17	−97	−2
Insula	244	8.79	−33	17	10
	153	8.87	−35	−1	14
Fusiform gyrus	234	7.33	−49	−55	−16
	122	6.67	−41	−65	−14
Mid. temporal gyrus	87	5.86	−37	−3	−24
Inf. occipital gyrus	125	7.64	−35	−85	−8
Inf. parietal lobule	41	5.00	−39	−51	54
Lingual gyrus	67	6.72	−21	−83	4
Right hemisphere					
Inf. frontal gyrus	189	7.64	27	27	0
Mid. frontal gyrus	42	4.87	43	29	24
Postcentral gyrus	66	5.87	49	−25	44
Cuneus	226	6.88	17	−69	12
Precuneus	488	9.14	23	−61	40
Inf. occipital gyrus	206	6.91	35	−81	−6
Fusiform gyrus	95	6.19	49	−57	−12
Lingual gyrus	91	6.56	15	−93	−8
Culmen	41	6.93	23	−41	−18
Negative correlation					
Left hemisphere					
Precuneus	1380	−8.23	−13	−49	40
Supramarginal gyrus	712	−7.97	−49	−53	24
Anterior cingulate	558	−8.94	−13	45	−2
Sup. frontal gyrus	216	−7.23	−7	51	22
	47	−6.34	−17	19	44
	42	−5.88	−9	51	38
Middle frontal gyrus	61	−6.66	−33	29	42
Sup. temporal gyrus	41	−6.20	−53	15	−16
Mid. temporal gyrus	65	−5.54	−55	−17	−8
	60	−6.89	−59	7	−16
	59	−6.91	−63	−15	−12
	53	−5.83	−43	11	−32
Right hemisphere					
Sup. frontal gyrus	161	−7.37	27	27	50
	89	−5.60	9	59	34
	50	−5.94	17	27	58
Sup. temporal gyrus	566	−8.01	53	−59	18
Mid. temporal gyrus	263	−8.68	55	−15	−10
Mid. temporal gyrus	156	−7.48	51	−39	2
Supramarginal gyrus	79	−5.46	57	−39	34

Note: Sup., superior; Mid., middle; Med., medial; Inf., inferior; volume is given in number of voxels ($2 \times 2 \times 2$ mm^3); Z = peak value of correlation Z; coordinates (x, y and z) for the most correlated voxel in each cluster are given with reference to the Talairach atlas.

Kostopoulos and Petrides, 2008; Lewandowska et al., 2010; Petrides, 2005), or, of course, both. For example, much of the anterior cingulate, which is thought to be engaged quite generally by response conflict (Botvinick et al., 2004; Ridderinkhof et al., 2004) had a similar task by stimulus interaction to the reading system at large.

Whatever the ambiguities that arise in interpreting Task × Stimulus interactions, they clearly raise questions about the generalizability of what is learned from studies of "best stimulus" responses in specific brain regions using passive or oblique tasks. For example, in contrast to prior work, our analyses designed to reveal differential specialization within subregions of fusiform gyrus did not reveal any such differentiation. Instead, the Task by Stimulus interaction throughout fusiform took essentially the same form as it did throughout the rest of the reading network. This pattern is inconsistent with the notion that a relatively circumscribed area within this gyrus is tuned to words or word-like properties of unfamiliar stimuli in a task-independent manner. In particular, the lack of stimulus-selectivity in the symbol detection task is in contrast to prior studies that have used this task. In a prior study with the same stimuli, Wang et al. (2011) observed a "reversed" pattern of selectivity throughout left fusiform during a one-back task. In explaining the difference between that study work by Vinckier et al. (2007), we speculated that the greater visual processing demands, and lower working memory demands of the symbol detection task were key for observing a pattern of activity that is positively related to word-likeness. Failure to find any such selectivity in the current symbol detection task suggests that the rate of presentation is also an important in determining the observed stimulus selectivity in this region.

In the current event-related design, stimuli were presented once every 6 s on average, whereas in the Vinckier et al. (2007) study, they were presented two per second. It may be that the shorter trials used in that and related studies prevented later, more elaborated processing of the stimuli, resulting in metabolic responses that are more similar in stimulus selectivity to early features of evoked, electrophysiological responses (Brem et al., 2010; Hsu et al., 2011; Lin et al., In press; Maurer et al., 2005a, 2005b, 2006, 2008; Xue et al., 2008). It is also possible that the function of this region differs between alphabetic writing systems and Chinese. Evidence from a wide range of studies in which putative VWFA activity is observed in similar tasks across languages (Liu et al., 2008; Nakamura et al., 2005; Thuy et al., 2004; Xue and Poldrack, 2007) seems to argue against this, but it may nonetheless be that the selectivity of this region for particular stimulus properties differs in subtle ways that are shaped by experience with one or the other type of writing system. That stimulus selectivity interacts with task so strongly throughout the fusiform, however, suggests that differences in task can have a dramatic impact on selectivity even for the same stimulus set.

Conclusions

Despite their importance to understanding basic phenomena in reading, task by stimulus interactions are rarely explored in neuroimaging studies. We used a novel analysis strategy to uncover such interactions throughout the reading system, and found that, for a wide range of stimulus classes, stimulus selectivity was driven by task parameters, and was closely related to behavioral difficulty. Taken together with prior work, in which yet another pattern of selectivity was observed for the same stimulus classes in a working memory task (Wang et al., 2011), these results raise doubts about whether regions involved in a complex cognitive task such as reading can be usefully described in terms of their responses to different stimulus types, without taking into account the specific tasks under which such responses were observed.

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