Neural basis of hierarchical visual form processing of Japanese Kanji characters

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Abstract

Introduction: We investigated the neural processing of reading Japanese Kanji characters, which involves unique hierarchical visual processing, including the recognition of visual components specific to Kanji, such as “radicals.” Methods: We performed functional MRI to measure brain activity in response to hierarchical visual stimuli containing (1) real Kanji characters (complete structure with semantic information), (2) pseudo Kanji characters (subcomponents without complete character structure), (3) artificial characters (character fragments), and (4) checkerboard (simple photic stimuli). Results: As we expected, the peaks of the activation in response to different stimulus types were aligned within the left occipitotemporal visual region along the posterior–anterior axis in order of the structural complexity of the stimuli, from fragments (3) to complete characters (1). Moreover, only the real Kanji characters produced functional connectivity between the left inferotemporal area and the language area (left inferior frontal triangularis), while pseudo Kanji characters induced connectivity between the left inferotemporal area and the bilateral cerebellum and left putamen. Conclusions: Visual processing of Japanese Kanji takes place in the left occipitotemporal cortex, with a clear hierarchy within the region such that the neural activation differentiates the elements in Kanji characters’ fragments, subcomponents, and semantics, with different patterns of connectivity to remote regions among the elements.

Introduction

When we read words, we initially process the words in our brain as a form of visual information. Recent studies have focused on clarifying the neural basis specific to the visual processing of word forms, and neuropsychological and neuroimaging studies have demonstrated the involvement of the left occipitotemporal cortex in the ventral visual stream. For example, patients with pure alexia, which is linked with damage to the left occipitotemporal cortex, manifest letter-by-letter reading (Warrington and Shallice 1980; Arguin and Bub 1993). In addition, a number of neuroimaging studies have demonstrated activation of a patch of cortex to the fusiform gyrus in word and letter reading tasks but not in object recognition tasks (e.g., Dehaene et al. 2004; Szwed et al. 2011). Other researchers have shown that split brain patients show reading performance equivalent to that of healthy controls, with appropriate left fusiform gyrus activation, only when words are presented to their right visual field.

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Hierarchical Processing of Japanese Kanji

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The evidence suggests that the left (and not the right) fusiform gyrus specializes in word form processing, and Cohen and colleagues labeled this region the “visual word form area” (VWFA).

How is visual word form information processed within the occipitotemporal cortex? If we consider the visual information not restricted to words (e.g., general objects), numerous neuroimaging studies have been performed. According to the evidence, simpler visual features (e.g., dots) activate the more posterior part of the occipitotemporal cortex, whereas more complicated patterns (e.g., geometric figures) activate the anterior part of the inferior temporal regions (Grill-Spector et al. 1998; Lerner et al. 2001; Kamitani and Tong 2005; Dumoulin and Hess 2007). This suggests that visual information is processed through the occipitotemporal cortex from posterior to anterior, in a sequential manner according to its complexity. Visual word forms are supposed to be processed in the same manner in the ventral visual stream. Dehaene et al. (2005) proposed the “local combination detector” (LCD) model in which multiple levels of information of a word (e.g., fragments, features, single letters, bigrams, quadrigrams, and the whole word) are hierarchically encoded such that more anterior regions encode larger and more complex word components. The LCD model is supported by a functional magnetic resonance imaging (fMRI) study performed while subjects viewed alphabetic script; Vinckier et al. (2007) demonstrated that within the left occipitotemporal cortex, the posterior part is activated by false fonts, and the anterior part is activated by real words.

It remains unclear, however, whether this model would be applicable to the case of a nonalphabetical language, for instance, Japanese Kanji characters. Logographic Japanese Kanji characters have dramatically different visual forms than alphabetic letters: they generally have a square shape and consist of subcomponents such as ‘radicals’ that are combinations of “strokes,” which are also visual components constructing Kanji characters. From the perspective of hierarchical visual processing system, Kanji characters are likely processed based on different levels of structural complexity. To our knowledge, hierarchical visual processing of Japanese Kanji characters has not been assessed with neuroscientific methods, but some researchers have investigated Chinese character processing with neuroimaging. Both Chinese and Japanese Kanji employ logographic strategies. The visual processing hierarchy of Chinese characters was investigated using real and pseudo Chinese characters and Korean Hangul. Real Chinese characters activated the anterior part of the fusiform gyrus, while Korean Hangul activated the posterior fusiform gyrus (Chan et al. 2009). Because Korean Hangul has a simpler visual structure than real Chinese characters, the authors compared the two writing systems to assess the hierarchical visual processing of Chinese characters. However, because they compared different languages, the findings might be due to differential structural components between the two languages. Another problem is that participants were required to complete different tasks for three types of stimuli (semantic or character form matching tasks). Therefore, the hierarchy demonstrated by the results might be dependent on the different cognitive strategies, such that semantic processing is only recruited for real characters. Liu et al. (2008) examined left occipitotemporal activation pattern for Chinese character using real, pseudo, and artificial Chinese characters. Although the activation peak in response to real Chinese characters was located in the anterior part of the left occipitotemporal cortex relative to the peak for pseudo Chinese characters, the peaks for pseudo and artificial characters were located in the same region. The methodological issue is that radicals were confounding their artificial Chinese character stimuli, resulting in the absence of contrast between the pseudo and artificial tasks. Thus, it has not been clearly demonstrated whether different visual components (e.g., stroke, Kanji subcomponents, and whole character) of logographic characters like Kanji are processed in different brain regions in a hierarchical manner.

Here, we used fMRI to examine whether Kanji characters are processed hierarchically from posterior to anterior.

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**Figure 1.** Examples of Japanese Kanji characters, subcomponents, and strokes. A Japanese Kanji character consists of subcomponents, which are combination of strokes.
in the left occipitotemporal cortex. Based on a study by Liu et al. (2008), we used a size judgment task to minimize semantic and phonological processing of Kanji information and only focused on its visual processing. In the size judgments task, participants were required to judge the size of the stimuli. This size judgment task does not require any intentional efforts to ‘read’ the characters, so the experiment implicitly relies on the automaticity of the reading process, which would likely have implications of the language network that would be activated for the different character types. A previous study which used such a size judgment task (Liu et al. 2008) showed activation of language-related brain regions, including the left inferior frontal gyrus and fusiform gyrus. Therefore, these brain regions can be considered as the network regarding automaticity of reading process. We exposed participants to (1) real Kanji, (2) pseudo Kanji, (3) artificial characters, and (4) a checkerboard pattern in the MRI scanner. We created pseudo Kanji and artificial characters by mixing components included in real Kanji characters. Pseudo Kanji characters are made by exchanging the subcomponents between two Kanji characters. Therefore, the characters contain radicals but do not exist as real Kanji characters. We further decomposed the subcomponents to create artificial characters that morphologically have the same contrast as a real Kanji characters (consisting of fragmented lines “strokes”) but do not have any structural components (i.e., Kanji subcomponentss) that are necessary to construct Kanji. Checkerboards consist of straight lines and only contain photic/optical components. If our hypothesis is correct, real Kanji, pseudo Kanji, and artificial characters should activate different parts of the left occipitotemporal cortex, and the activation peaks should be aligned in a sequential manner from posterior to anterior according to the components’ complexity.

In addition, we investigated activations in different neuronal networks across the entire brain, centered on the left occipitotemporal cortex. For alphabetic script, real words produce functional connectivity among the VWFA, left superior temporal gyrus, and left inferior frontal gyrus (van der Mark et al. 2011). Another study used dynamic causal modeling (DCM) to show that Japanese real Kanji words induce effective connectivity across the left primary visual cortex, left ventral occipitotemporal cortex, and Broca’s area (Duncan et al. 2013). A pseudo Kanji character has subcomponents information but does not exist as a real character. An artificial character has strokes but not subcomponents. It is reasonable to assume that these stimuli are processed in different neural networks (connections) than real Kanji characters. To our knowledge, no study has investigated differential neural networks for real Kanji, pseudo Kanji, and artificial character. We employed functional connectivity analyses to investigate whether these three types of stimuli facilitate connections in different neural networks.

**Materials and Methods**

**Participants**

Twenty-eight right-handed healthy native Japanese speakers (age $M = 21.7$ years, $SD = 2.3$ years, age range: 18–28 years, 13 males) with normal or corrected vision and without language or speech impediments participated in the present study. Their handedness was affirmed with the Edinburgh handedness inventory (Oldfield 1971). We excluded 5 of the original 33 participants from the analyses because they failed to respond to the stimuli more than 5 times per session. All participants were undergraduate or graduate students who were already qualified by entrance exam to the universities, so that they are supposed to have sufficient sight word reading ability equally. This study was approved by Research and Ethical Committee of University of Tsukuba and National Center of Neurology and Psychiatry, and written informed consent was obtained from each participant prior to the study.

**Stimuli**

We created four types of stimulus: (1) real Kanji, (2) pseudo Kanji, (3) artificial character, and (4) a checkerboard pattern (Fig. 2A). Eighty Kanji characters with 8–12 strokes were chosen for the real Kanji character stimuli. In this study, a psycholinguistic database of lexical properties of Japanese (Amano and Kondo 1999, 2000) was used to examine the familiarity and frequency of these Kanji characters. This database includes subjective rating data for word familiarity, character familiarity, and visual complexity. For objective scale, this database contains word and character frequency in the newspaper. We collected highly familiar and frequent characters (>1 SD from the mean in the database) because these characters are used frequently in daily life. Additionally, all Kanji characters were chosen from 2136 commonly used Kanji which Japanese students commonly learn to read and write. This may attenuate startle effect of the stimuli. Both pseudo Kanji and artificial characters were created by recomposing subcomponents of real Kanji characters. Pseudo Kanji characters were made by replacing the subcomponents of a real Kanji character with a radical of another real Kanji, such that the pseudo Kanji stimuli include real subcomponents but are not fully structured as real Kanji characters. We prepared artificial characters by decomposing Kanji subcomponents as first and then randomly recomposing them. Hence, artificial characters were unpronounceable, meaningless, and never
included Kanji subcomponents. Thus, unlike the study by Liu et al. (2008), we decomposed artificial characters into a completely non-linguistic level, which enabled us to evaluate whether Kanji characters and subcomponents would activate different brain regions within the left occipitotemporal cortex. Half of the stimuli were 20% larger in terms of size than the other half, so we obtained even sets of “large” and “small” characters.

**Experimental design**

The participants were put in the scanner and then experienced four consecutive fMRI sessions, each of which consisted of the visual presentation of 20 real Kanji characters, 20 pseudo Kanji characters, 20 artificial characters, and 20 checkerboard stimuli. Each stimulus was presented for 600 ms, followed by the presentation of a fixation cross (Fig. 2B). The time periods of the presentation of fixation cross were randomized based on TR ranging from 2.5 to 12.5 s. The orders of the four types of stimuli were randomized across sessions. Participants were required to judge the size of the character (large or small) and press a response button with his/her right index or middle finger if the stimulus was large or small, respectively. During the fixation periods, participants maintained their gaze on the fixation point without any response. Sessions in which the participant did not respond over five times were excluded from later behavioral and fMRI data analyses. To confirm if cognitive efforts for this size-judgment task were equal between different character types and did not influence hierarchical Kanji processing, the reaction time and error rate were analyzed using two-way factorial analysis of variance (ANOVA) of character type (real, pseudo, anartificial, checkerboard) x size (large and small). Statistical threshold for behavioral data was set at $P < 0.01$. We used SPSS ver. 22 (IBM Corp., Armonk, NY, USA) for all statistical analyses.

**fMRI data acquisition and analysis**

**fMRI acquisition**

We obtained functional echo planar images (EPI) using a Siemens (Erlangen, Germany) 1.5-Tesla MRI system (TR = 2500 ms, TE = 40 ms, flip angle 90°, 4-mm-thick axial slices, in-plane resolution = 3.4 x 3.4 mm). The time-series of functional data of 190 whole-brain 3D EPI volumes were acquired in each session. After functional image acquisition, a T1-weighted high-resolution anatomical image was obtained (TR = 1900 ms, TE = 3.93 ms, flip angle 15°, voxel size = 1.4 x 1.0 x 1.3 mm).

**fMRI data analysis**

We analyzed the functional imaging data using SPM8 (Wellcome Department of Cognitive Neurology, London, UK, http://fil.ion.ucl.ac.uk/spm/). The first five images were excluded from further analyses to avoid T1 equilibration effects. To compensate the differential temporal offsets between slices, we applied slice-timing correction to the images. Then we spatially realigned the functional images to the first image for motion correction and coregistered the functional images to the individual structural image (high-resolution T1). The individual structural image was spatially normalized to the MNI T1 template image. By using the resulting normalization parameters, all functional images were spatially normalized. Finally, functional images were smoothed using a Gaussian filter (6-mm FWHM).

To model the hemodynamic time series in each condition, we convolved the stimulus presentation time...
(600 ms) with the canonical hemodynamic response function (HRF). Individual hemodynamic changes for each of four types of stimulus events (real Kanji, pseudo Kanji, and artificial characters and checkerboard) were assessed using a session-wise general linear model that included the linear combination of the regressors for the hypothetical hemodynamic responses to the four types of events, motion parameters, and high-pass filtering regressors (128 s). We estimated the parameters (beta-weights) for the four conditions, and the parameters were fed into the group analysis.

First we tried identifying the commonly activated regions across the three types of different stimulus events (real Kanji, pseudo Kanji, and artificial characters) relative to checkerboard. All beta-weight maps for the three conditions in comparison to checkerboard were fed into a conjunction analysis. The height threshold was set at \( P < 0.005 \) (uncorrected), and the cluster size threshold was \( P < 0.05 \) corrected with family wise error (FWE) (536 or more voxels). Finally, we investigated the differential loci of the peak activation for the three stimulus conditions to see if there was a topologically hierarchical peak distribution. The beta-weight maps for the three stimulus conditions were compared using one-way repeated measures ANOVA. For this analysis, the height statistical threshold was set at \( P < 0.001 \), uncorrected, and the cluster size threshold was set at \( P < 0.05 \) with FWE corrected (463 or more voxels).

**Region of interest analysis**

To differentiate spatial patterns of activation for real Kanji, pseudo Kanji, and artificial characters, five non-overlapping regions of interest (ROIs) were defined based on a previous study (Van der Mark et al. 2009). These ROIs cover the putative VWFA and the neighboring region. Each spherical ROI had a 3-mm radius, and all the ROIs were located along with the posterior–anterior axis (slightly declined toward the anterior direction). The center coordinates for the ROIs are as follows: (MNI coordinate [x, y, z] in mm) ROI1 (−45, −75, −12), ROI2 (−45, −67, −13), ROI3 (−45, −59, −14), ROI4 (−45, −51, −15), and ROI5 (−45, −43, −16). ROI3 was located on the proper VWFA region for Japanese Kanji characters that was described in a previous meta-analysis of culturally specific word regions (Bolger et al. 2005). Similarly, contralateral coordinate were defined as the center coordinate for ROIs of the right occipitotemporal cortex. The ROI definition and parameter estimates were conducted using the MarsBar toolbox (http://marsbar.sourceforge.net).

**Functional connectivity analysis**

To identify the neural networks engaged in different components of visual Kanji processing, we conducted functional connectivity analyses (i.e., the correlations of time courses in the seed ROIs with those in voxels across the entire brain). To compare functional connectivity between real Kanji, pseudo Kanji, and artificial characters, seed-based correlation analyses were performed using functional connectivity toolbox version 12 (http://web.mit.edu/swg/software.htm). Because real Kanji, pseudo Kanji, and artificial characters had been expected to induce peaks in different regions, we created seed regions for functional connectivity analyses after we obtained the peaks of event-related activations. The seed for real Kanji characters was defined as a 3-mm-diameter sphere centered on the peak coordinate shown in real Kanji character minus checkerboard contrast. The seeds for the pseudo Kanji and artificial characters were generated in the same manner, using pseudo Kanji character versus checkerboard and artificial character versus checkerboard contrast, respectively. After data preprocessing, the data were band-pass filtered between 0.008 and 0.2 Hz, which was the effective frequency range of task-related hemodynamic change as examined with a spectral analysis. Functional connectivity was estimated by a regression analysis co-varied with the main event-related task effect (i.e., the modeled hemodynamic response to the judgment events) and other nuisance variables (including white matter and cerebrospinal fluid signals and six head motion parameters). Thus, the resulting maps represent voxels within the brain in which the hemodynamic response during the fMRI sessions correlated with that of the seed regions. The height threshold was \( P < 0.0005 \) (uncorrected), and the extent threshold was \( P < 0.05 \) (corrected, \( k > 29 \)) based on the results of 5000 iterations of Monte Carlo simulation performed on ANFI’s AlphaSim (http://afni.nimh.nih.gov/pub/dist/doc/manual/AlphaSim.pdf), with single voxel \( P < 0.0005 \), FWFMC = 6 mm, cluster correction radius in 4 mm, and brain mask.

**Results**

**Behavioral data of the size judgment task**

Accuracy of all conditions was almost 100% (Table 1). Indeed, size judgment task accuracy did not differ significantly between different character sizes (large or small) or types (real, pseudo, artificial, or checkerboard), \( F(1, 27) = 1.34, P = 0.257 \) and \( F(1.4, 38.2) = 5.04, P = 0.020 \), respectively. We found interactive effect of size \( \times \) types, \( F(1.62, 27) = 8.94, P = 0.001 \), such that, although accuracy in response to large and small stimuli is mostly identical.
to each other on three types of characters, accuracy to large stimuli (98.3%) was a little lower than that to small stimuli (99.6%) on the checkerboard condition. We cannot put the plausible explanation for this lower accuracy judging larger checkerboard, but there were no interactive effect of size \(\times\) type at least within three character types on accuracy \([F(2,54) = 0.216, P = 0.806]\).

The reaction time did not differ between the character sizes (large or small) and types (real, pseudo, artificial, or checkerboard), \(F(1, 27) = 4.25, P = 0.049\) and \(F(3, 81) = 1.31, P = 0.278\), respectively. There was an interactive effect of size \(\times\) type on the reaction time, however, \(F(1.8, 49.6) = 7.11, P = 0.002\), such that participants responded faster to larger character stimuli than smaller characters although they responded slower to larger checkerboard stimuli than to smaller checkerboards (Table 1). As in the case with the interactive effect on accuracy, we could not find any interpretable reason for this interaction on reaction time. But there were no interactive effect of size \(\times\) type within three character types on reaction time \([F(2,54) = 0.417, P = 0.661]\).

Therefore, participants performed equally in terms of response accuracy and speed, at least for the three character types of stimuli that are focus of our study. Because size judgement is not a scope of this study, both big and small size conditions were fed into the same conditions in the fMRI analysis.

**fMRI data**

*Neural activations common to all types of Kanji characters*

To identify brain regions engaged in processing the three different types of Kanji characters, we contrasted three activation maps (for real Kanji, pseudo Kanji, and artificial characters) with the checkerboard map, and computed common activation areas across the three contrasts (Fig. 3 and Table 2). We were able to confirm that the task we created activated the bilateral occipital gyrus and fusiform gyrus.

| Region | x   | y   | z   | T     | Voxel | BA |
|--------|-----|-----|-----|-------|-------|----|
| R inferior temporal gyrus | 42  | -66 | -10 | 6.56** | 845   | 37 |
| R inferior occipital gyrus | 40  | -82 | -8  | 5.86** | 19    |    |
| R fusiform gyrus | 48  | -52 | -14 | 4.50*  |       | 37 |
| L inferior occipital gyrus | -40 | -78 | -6  | 4.72*  | 536   | 37 |
| L fusiform gyrus | -42 | -54 | -10 | 3.76*  | 37    |    |
| L sub-gyral | -42 | -44 | -12 | 3.70*  |       | 37 |

*Co-activated brain regions across real Kanji, pseudo Kanji, and artificial characters in comparison to checkerboard. Bilateral occipitotemporal cortices were commonly activated.** \(P < 0.005, k > 20, **P < 0.05 (FWE corrected).\)*

**Different spatial patterns of activation within the left occipitotemporal cortex for all Kanji character types**

For a more detailed illustration of the spatial distribution of activation for real Kanji, pseudo Kanji, and artificial characters in the bilateral occipitotemporal cortices, we mapped peaks of the brain activity for each stimulus relative to checkerboard (Fig. 4 and Table 3). The activation clusters for real Kanji, pseudo Kanji, and artificial characters were overlapped (Fig. 4A). However, once they were overlaid on an axial slice, the peak regions for the artificial, pseudo Kanji, and real Kanji characters appeared to be located in the left occipitotemporal cortex in a posterior to anterior order (Fig. 4B). Conversely, the peak locations for real and...
Figure 4. Activation clusters and the peaks for the real Kanji, pseudo Kanji, and artificial characters relative to the checkerboard. (A) The figures show the activated regions in response to the real Kanji, pseudo Kanji, and artificial characters contrasted with the checkerboard. Black dots indicate the peaks of the activated clusters. The height threshold was set at $P < 0.001$ (uncorrected), and the cluster size threshold was set at $P < 0.05$ (corrected with FWE, 463 or more voxels). Real, real Kanji character; Pseudo, pseudo Kanji character; Artificial, artificial character. (B) Overlay of the activation peaks for the real, pseudo, and artificial characters are colored in red, yellow, and green, respectively.

Table 3. Brain regions activated by each stimulus type.

| Region                  | MNI coordinates (mm) | T   | Voxels | BA |
|-------------------------|----------------------|-----|--------|----|
| Real > Checkerboard     |                      |     |        |    |
| R inferior temporal gyrus | 42 -66 -10           | 6.56* | 713    | 37 |
| R inferior occipital gyrus | 40 -82 -8            | 5.86* | 19     |    |
| R fusiform gyrus        | 48 -52 -14           | 4.50* | 37     |    |
| L fusiform gyrus        | -44 -58 -12          | 4.83* | 463    | 37 |
| L inferior occipital gyrus | -40 -78 -6          | 4.72* | 19     |    |
| L sub-gyreral           | -42 -40 -10          | 4.01* | 37     |    |
| Pseudo > Checkerboard   |                      |     |        |    |
| R inferior temporal gyrus | 44 -66 -10           | 9.70** | 1353  | 37 |
| R inferior occipital gyrus | 42 -78 -8            | 8.02** | 19     |    |
| R fusiform gyrus        | 46 -56 -12           | 7.68** | 37     |    |
| L inferior temporal gyrus | -48 -64 -10         | 8.89** | 1342  | 37 |
| L inferior occipital gyrus | -40 -80 -6          | 6.54** | 19     |    |
| L fusiform gyrus        | -36 -42 -22          | 4.48* | 20     |    |
| Artificial > Checkerboard |                  |     |        |    |
| R inferior occipital gyrus | 38 -82 -8            | 7.63* | 1033   | 19 |
| R middle temporal gyrus | 42 -64 -8            | 7.23* | 37     |    |
| R fusiform gyrus        | 46 -54 -12           | 5.10* | 37     |    |
| L inferior occipital gyrus | -40 -80 -6          | 6.55* | 522    | 19 |
| L fusiform gyrus        | -40 -44 -12          | 3.89* | 37     |    |
| L fusiform gyrus        | -42 -54 -10          | 3.76* | 37     |    |

*P < 0.001 (uncorrected), cluster size threshold of $P < 0.05$ (FWE corrected) **P < 0.05 (FWE corrected) for the height threshold.

pseudo Kanji characters in the right occipitotemporal cortex were adjacent to each other, suggesting that hierarchical localization of the activations was dominant in the left side of the occipitotemporal cortex. To statistically assess whether the three types of stimuli produced different spatial patterns of brain activity only in the left inferior occipital temporal cortex, we created consecutive ROIs within the region and compared the spatial patterns of activation across the three conditions (Fig. 5). The results clearly showed that the three types of characters produced significantly different spatial activation patterns. Two-way repeated ANOVA of the parameter estimate of activations revealed an interactive effect of ROI locations (1-5) x character types (real, pseudo, and artificial), $F(8,216) = 3.847$, $P = 0.009$. This interaction was explained by the differential spatial distributions (i.e., different locations for the most activated ROI) across the three types of characters (Fig. 5, left). For artificial characters, the most activated ROI was in the extreme posterior region (ROI1), and brain activities were decreased along the posterior-to-anterior axis. Pseudo Kanji characters evoked the strongest activity in the second ROI from the posterior region (ROI2). Conversely, real Kanji characters elicited the strongest activity in the middle ROI (ROI3), which corresponds to putative center of the VWFA for Japanese Kanji characters. In the right occipitotemporal cortex, however, we did not find interactive effect of ROI locations (1-5) x character types (real, pseudo, and artificial). As we expected, the result strongly supports the hypothesis that artificial, pseudo Kanji, and real Kanji characters are processed hierarchically from posterior to anterior in the left occipitotemporal cortex.
Functional connectivity analyses seeded in the left occipitotemporal cortex

To investigate which brain regions are remotely related to the hierarchical processes, we separately computed functional connectivity for real Kanji, pseudo Kanji, and artificial characters. The seed regions were set at the peak locations for the three character types in the left occipitotemporal cortex (Fig. 4B). First, we confirmed that the activities around each seed were strongly auto-correlated with the activities of the seed itself and the contralateral corresponding region within the bilateral occipital gyri, inferior temporal gyri, and fusiform gyri (Fig. 6A). We found that the three seeds were functionally connected to remote regions differently (Table 4): the seed for real Kanji characters was connected to the left inferior frontal gyrus (triangularis), which was not connected to the seeds for the pseudo characters or artificial Kanji characters (Fig. 6B). The seed for pseudo Kanji characters was functionally connected to multiple brain regions, including the bilateral cerebellum, bilateral inferior frontal gyri, left putamen, left superior temporal gyrus, and right middle frontal gyrus. The artificial character seed was only connected to the right superior temporal gyrus. As we predicted, the seeds for the real Kanji characters in the left inferior temporal region were connected to remote language-related brain regions, although pseudo Kanji characters induced different connections to remote regions, including the basal ganglia and cerebellum.

Discussion

The purpose of the present study was to examine whether the visual forms of Japanese Kanji are processed hierarchically. We found that, in the left occipitotemporal cortex, the peak regions for the artificial, pseudo Kanji, and real Kanji characters were localized in a posterior to anterior order, although this hierarchical organization was not found in the right occipitotemporal cortex. The ROI analysis of the left occipitotemporal cortex statistically confirmed our hypothesis such that the spatial activation...
patterns (i.e., the patterns of activations across five consecutive ROIs) were different between the stimulus types and the most activated ROIs for the three stimulus types lined up in order.

Some studies have shown hierarchical activation for visual word forms in the left occipitotemporal cortex for alphabetic script (Vinckier et al. 2007). For instance, Thesen et al. (2012) showed real words, pseudo words, and false fonts to participants in the scanner and observed hierarchical formation of the left fusiform gyrus. Pseudo words are meaningless but contain real letters. However, false fonts contain letter-like symbols, so the authors reasoned that letterforms would be indexed by the contrast of pseudo word versus false fonts, whereas word forms would be indexed by the contrast of real words versus pseudo words. They performed magnetoencephalography (MEG) and observed a letter-selective response occurring 60 ms earlier than the word-selective response, strongly suggesting temporally sequential processing of “letter” and “word” information in the left occipitotemporal cortex. Although we found interaction between ROIs and stimulus types, interpretation of this interaction remains only descriptive. Together with our peak analysis and previous studies, however, it is reasonable to think that results indicate hierarchical organization of Japanese Kanji character. Moreover, the peak for the real Kanji characters ($x = -44, y = -58, z = -12$) in our study was very close to the word form area reported by Thesen et al. ($x = -46, y = -52, z = -20$) (~10 mm apart). Similarly, the peak for the pseudo Kanji characters ($x = -48,$

![Figure 6](image)

**Figure 6.** Functional connectivity analyses seeded in the left occipitotemporal cortex. The colored blobs on the brain maps show the areas with significant functional connectivity to the seed regions in the left occipitotemporal cortex. The red blobs show the areas with differential functional connectivity between the real Kanji and the checkerboard. Yellow indicates areas with differential functional connectivity between pseudo Kanji and checkerboard, and the green indicates differential functional connectivity between artificial characters and checkerboard. The height threshold was $P < 0.0005$ (uncorrected) and the extent threshold was $P < 0.05$ (corrected; $k > 29$, AFNI AlphaSim). (A) Lateral view. The auto- and contralaterally correlated connections were found within the bilateral occipital gyri, inferior temporal gyri, and fusiform gyri. (B) Remote brain regions connected to the left temporal seeds. The auto- and contralaterally correlated brain regions were omitted for illustrative purposes. IFG (tri), inferior frontal gyrus (triangular); PCG, precentral gyrus.
The height threshold was $P < 0.0005$ (uncorrected) and the extent threshold was $P < 0.05$ (corrected; $k > 29$, AFNI AlphaSim). The auto- and contralaterally-correlated brain regions were omitted.

$y = -64, z = -10$ was not far from the letter form area ($x = -40, y = -78, z = -18$) with a distance of ~16 mm. Based on our findings, we suppose that, in terms of character form, an alphabetic word corresponds to an entire Kanji character in Japanese, and an alphabetic letter corresponds to Kanji subcomponents.

Because of the visual complexity of Japanese Kanji characters, one study suggested that they induce right lateralized activation (Nakamura et al. 2005). In the present study, however, we observed different peaks for different character types in the left occipitotemporal cortex, which was also confirmed by the ROI analysis. Evidence from brain lesion studies supports our hypothesis of left dominance for visual processing, even for Japanese Kanji; lesions in the left inferior temporal area cause alexia with agraphia for Japanese Kanji characters (Iwata 1984), and patients with damage to the left inferior temporal region exhibit poor lexical decision performance (Tani 2004). In addition, Korean cerebrovascular disease patients with damage to the left inferior temporal region show decreased performance when reading logographic Hanja (Korean Kanji) (Kwon et al. 2002). Collectively, the existing evidence indicates that visual forms of Japanese Kanji characters may be processed in the same manner in the left hemisphere as alphabetic scripts.

Another aspect to be concerned is the semantic and phonological information which each Japanese Kanji character has. Recent neuroimaging studies have shown that the fusiform gyrus is involved in phonological processing. The Japanese Kanji characters we used in our study can be read aloud, while pseudo Kanji and artificial characters do not contain phonological information at the whole character level. The different activation peak loci for the three types of Kanji character might be due to differences in phonological processing induced by the three types of characters. However, a neuroimaging study showed that brain activity in the left occipitotemporal cortex was elicited by a reading pseudoword but not reading words and silent reading (Dietz et al. 2005). Reading pseudowords requires grapheme to phoneme conversion, although reading real word can be achieved by using lexical knowledge. This implies that activation related to phonological processing in the fusiform gyrus is supposed to be task dependent. Similarly, semantic information might induce different activation peak loci, because real Kanji stimuli we used were highly familiar ones which perhaps easily activate semantic networks. In the present study, we exposed each stimulus for limited time period (600 ms) and we required the participants to judge the size of the stimulus in order to limit the participants’ time to read the stimulus with their “internal voice” or to recruit semantics of the stimuli. Nevertheless, stimulus presentation time may affect the cognitive process, that is, the different phonological and or semantic information between the character types could have affected activity in the left occipitotemporal cortex to some extent. More generally, however, existence of semantic and phonological information in each Japanese Kanji characters is a characteristic of this language system and we cannot completely distinguish between visual information of Kanji forms and semantics and/or phonological information.

Although we found different peak loci in the left occipitotemporal region, pseudo Kanji character produced stronger activation than real Kanji and artificial character. One of the conceivable possibilities of this strong activation is the visual novelty of the stimuli. Some researchers reported that object novelty activates the fusiform gyrus more than familiar objects (Zhang et al. 2013). Considering that pseudo characters created in this study do not exist in reality, these characters are supposed to be more novel than real Kanji characters. Thus, novelty of visual stimuli may induce larger brain activity for pseudo Kanji character. Moreover, because a pseudo Kanji character consists of multiple pronounceable subcomponents of real Kanji characters, we could speculate that it might activate

Table 4. Regions with functional connectivity to the inferior temporal region during observation of the three character types.

| Region                          | MNI coordinates (mm) | $T$  | Voxels | BA  |
|--------------------------------|----------------------|------|--------|-----|
| Real Kanji character           |                      |      |        |     |
| R cerebellum                   | 16 -66 -18           | 4.52 | 47     |     |
| L lingual gyrus (triangular)   | -16 -62 -4           | 5.17 | 41  19 |     |
| L inferior frontal gyrus       | -34 30 2             | 4.66 | 35 47  |     |
| Pseudo Kanji character         |                      |      |        |     |
| L cerebellum                   | -6 -72 -22           | 6.96 | 253    |     |
| R cerebellum                   | 30 -32 -28           | 4.59 | 61     |     |
| L amygdala                     | -26 0 -16            | 4.61 | 31     |     |
| R superior temporal gyrus      | 48 -6 -8             | 4.57 | 78 22  |     |
| L putamen                      | -28 12 -2            | 5.08 | 63     |     |
| R calcarine fissure            | 22 -62 10            | 5.94 | 179 30 |     |
| R inferior frontal gyrus       | 50 40 16             | 4.50 | 32 8   |     |
| (triangular)                   |                      |      |        |     |
| R precentral gyrus             | 48 10 32             | 7.15 | 226 9  |     |
| L precentral gyrus             | -50 4 26             | 5.14 | 79     |     |
| L superior occipital gyrus     | -18 -76 32           | 5.04 | 64 7   |     |
| L superior frontal gyrus       | -22 46 44            | 5.50 | 268 8  |     |
| R middle frontal gyrus         | 34 26 54             | 4.79 | 32 8   |     |
| Artificial character           |                      |      |        |     |
| R superior temporal gyrus      | 68 -26 8             | 4.53 | 41 42  |     |

The height threshold was $P < 0.0005$ (uncorrected) and the extent threshold was $P < 0.05$ (corrected; $k > 29$, AFNI AlphaSim). The auto- and contralaterally-correlated brain regions were omitted.
larger phonological process in occiptotemporal cortex. Further studies are needed to clarify such speculative ideas, such as the effect of stimulus novelty and subjects’ implicit attempts to pronounce pseudo Kanji character with multiple pronounceable subcomponents on visual word processing.

We found that activations in the left occiptotemporal cortex were differentially connected to remote brain regions, depending on the types of characters (real Kanji, pseudo Kanji, or artificial characters). We observed functional connectivity between the left inferior temporal region and left inferior frontal language area for the real Kanji characters (but not for the pseudo Kanji or artificial characters). This result is consistent with previous studies in which functional connectivity was observed between the left fusiform gyrus and left inferior frontal gyrus when the participants performed rhyme judgments and a lexical decision task (Booth et al. 2007; Duncan et al. 2013). A diffusion tensor imaging study showed anatomical connectivity between the primary visual cortex and inferior temporal gyrus via the middle and inferior temporal gyri (Yeatman et al. 2013), which is also consistent with our results. The left inferior frontal gyrus is thought to be involved in phonological processing (Tan et al. 2001; Gold and Buckner 2002; Turkeltaub et al. 2003; Matsuo et al. 2010). In our study, only the real Kanji characters possessed the complete set of visual components, including phonological information. Therefore, such information may automatically initiate functional connectivity with remote language areas, such as the left inferior frontal gyrus. We did not find any explicit local activity related to phonological or motor speech function (because phonological processes were suppressed in this study), but the brain might be, at least, “ready” to access and output the phonological and/or semantic information of the real Kanji characters by initiating connectivity between remote regions. Accordingly, phonological information in visual word recognition reaches a speech-related remote region (pars opercularis of the inferior frontal gyrus) very promptly (~100 ms), which has been shown by a MEG study (Wheat et al. 2010).

We found that the right cerebellum was functionally connected to the left inferior temporal seed region. Although the cerebellum has been regarded as being involved in motor control (Stein 1986), recent neuroimaging studies have revealed its involvement in nonmotor functions such as language, learning, and memory (Desmond and Fiez 1998; Frings et al. 2006). Bilateral cerebellar activation during a rhyme judgment task suggests that the cerebellum is engaged in phonological learning (Fulbright et al. 1999). In this regard, the cerebellum may work together with the inferior frontal regions for phonological processing. Anatomical investigations using transneuronally transported viruses in monkeys (Kelly and Strick 2003) and diffusion tensor imaging studies (Doron et al. 2010) have demonstrated a neuronal projection from the cerebellum to the anterior frontal lobe. A functional neuroimaging study also showed reciprocal connectivity between the cerebellum and left inferior frontal gyrus during a rhyme judgment task (Booth et al. 2007). Together with our results, the evidence indicates that left inferior temporal regions may cooperate with the inferior frontal gyrus and right cerebellum for the phonological processing of real Kanji characters.

In contrast, the pseudo Kanji characters produced functional connections with distinct brain regions, such as the bilateral cerebella, left putamen, bilateral precentral gyr, and bilateral middle frontal gyri. It is well-known that brain activity in visual regions is modulated by a task that invokes top-down control from the prefrontal cortex (Desimone and Duncan 1995; Morishima et al. 2009). We found a functional connectivity between the left inferior temporal seed and distributed frontal areas, including the right middle frontal gyrus corresponding to Brodmann areas 8 and 9. Gazzaley et al. (2007) found that functional connectivity between prefrontal and visual areas during encoding faces or scenes was stronger than connectivity that occurred while passively viewing the stimuli, suggesting that prefrontal-visual connectivity may be involved in learning visual stimuli. The pseudo Kanji characters we used were legitimate at the radial level, but they do not exist at the character level and would be novel visual stimuli. Therefore, the functional connectivity to Brodmann areas 8 and 9 might reflect the automatic processes that facilitate learning a novel visual stimulus as a new Kanji.

We also found that pseudo Kanji characters initiated functional connectivity from the left inferior temporal to the left putamen. The basal ganglia, including the putamen, constitutes a critical component of the cortico-basal ganglia-thalamus (CBT) loop (Haber and Calzavara 2009). Although this loop was originally considered to engage in motor control (DeLong et al. 1983), it is now believed to be involved in more advanced features such as planning, language learning, and reward (Rolls 2000; Tekin and Cummings 2002; Grace et al. 2007). The basal ganglia act as a “gating switch” to regulate even nonmotor functional connections between remote regions across cortices (Grace 2000), which was confirmed by a computational modeling study (O’Reilly and Frank 2006). van Schouwenburg et al. (2010) demonstrated that basal ganglia activity modulates top-down signals from prefrontal to visual areas. A novel stimulus like a pseudo Kanji, which might initiate some learning processes as discussed above, is supposed to engage the
functional connectivity to the putamen that might mediate and/or regulate top-down signals from the frontal lobe to the visual cortex.

Another functional connectivity we observed for pseudo Kanji characters was between the inferior temporal seed and the cerebellum. As mentioned before, the cerebellum is thought to be involved in phonological processing. Exposure to auditory novel pseudo words increased cerebellar activation, suggesting that the cerebellum is involved in phonological learning (Rauschecker et al. 2008). Another study also demonstrated fusiform-cerebellum connectivity during a rhyme judgment task (Booth et al. 2007). The cerebellum is reciprocally connected with the lateral inferior temporal region and the inferior frontal gyrus, so phonological information is likely to be processed in this cerebellar-inferior frontal loop. The cerebellar loop is involved in motor learning and other types of learning (Doya 2000). As discussed above, a pseudo Kanji character is visually similar to a real Kanji character, and the participants may recognize the pseudo character as a “new character.” This would implicitly introduce the visual information to the phonological learning process, which enhances functional connectivity from the inferior temporal lobe to the cerebellum. In sum, enhanced functional connectivity in response to pseudo Kanji characters is supposed to reflect the automatic phonological and visual learning processes. On the other hand, real Kanji characters do not initiate the learning process (because they are already known); rather, they connect the visual regions to the regions related to more advanced processes to output the information, such as language regions. These ideas here remain speculative and warrant further study in the future.

Conclusion

We found different peak locations for real Kanji, pseudo Kanji, and artificial characters spatially aligned in order of the structural organization of Kanji characters within the left occipitotemporal cortex, suggesting hierarchical visual processing of Japanese Kanji characters. Moreover, the three stimulus types facilitate different neuronal networks or functional connectivity. Future studies will be expected to examine the different components constructing Kanji, taking into account the effects of phonological, semantic, and learning processes and stimulus familiarity on left occipitotemporal cortex activities.

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Conflict of Interest

None declared.

References

Amano, S., and T. Kondo 1999. Nihongo-no Goi-tokusei [Lexical properties of Japanese]. Vols 1–6. Sanseido, Tokyo, CD-ROM version (in Japanese).
Amano, S., and T. Kondo. 2000. Nihongo-no Goi-tokusei [Lexical properties of Japanese]. Vol 7. Sanseido, Tokyo, CD-ROM version (in Japanese).
Arguin, M., and D. N. Bub. 1993. Single-character processing in a case of pure alexia. Neuropsychologia 31:435–458.
Bolger, D. J., C. A. Perfetti, and W. Schneider. 2005. Cross-cultural effect on the brain revisited: universal structures plus writing system variation. Hum. Brain Mapp. 25:92–104.
Booth, J. R., L. Wood, D. Lu, J. C. Houk, and T. Bitan. 2007. The role of the basal ganglia and cerebellum in language processing. Brain Res. 1133:136–144.
Chan, S., S. Tang, K. Tang, W. Lee, S. Lo, and K. K. Kwong. 2009. Hierarchical coding of characters in the ventral and dorsal visual streams of Chinese language processing. NeuroImage 48:423–435.
Cohen, L., S. Dehaene, L. Naccache, S. Lehericy, G. Dehaene-Lambertz, M. A. Henaff, et al. 2000. The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain 123:291–307.
Dehaene, S., A. Jobert, L. Naccache, P. Giuciu, J. B. Poline, D. Le Bihan, et al. 2004. Letter binding and invariant recognition of masked words: behavioral and neuroimaging evidence. Psychol. Sci. 15:307–313.
Dehaene, S., L. Cohen, M. Sigman, and F. Vinckier. 2005. The neural code for written words: a proposal. Trends Cogn. Sci. 9:335–341.
DeLong, M., A. Georgopoulos, and M. Crutcher. 1983. Cortico-basal ganglia relations and coding of motor performance. Exp. Brain Res. 7(Suppl.):30–40.
Desimone, R., and J. Duncan. 1995. Neural mechanisms of selective visual attention. Annu. Rev. Neurosci. 18:193–222.
Desmond, J. E., and J. A. Fiez. 1998. Neuroimaging studies of the cerebellum: language, learning and memory. Trends Cogn. Sci. 2:355–362.
Dietz, N. A., K. M. Jones, L. Gareau, T. A. Zeffiro, and G. F. Eden. 2005. Phonological decoding involves left posterior fusiform gyrus. Hum. Brain Mapp. 26:81–93.
Doron, K. W., C. M. Funk, and M. Glickstein. 2010. Fronto-cerebellar circuits and eye movement control: a diffusion imaging tractography study of human cortico-pontine projections. Brain Res. 1307:63–71.
Doya, K. 2000. Complementary roles of basal ganglia and cerebellum in learning and motor control. Curr. Opin. Neurobiol. 10:732–739.

Dumoulin, S. O., and R. F. Hess. 2007. Cortical specialization for concentric shape processing. Vision. Res. 47:1608–1613.

Duncan, K. J. K., T. Twomey, O. P. Jones, M. L. Seghier, T. Haji, K. Sakai, et al. 2013. Inter-and intrahemispheric connectivity differences when reading Japanese kanji and hiragana. Cereb. Cortex 24:1601–1608.

Frings, M., A. Dimitrova, C. F. Schorn, H.-G. Elles, C. Hein-Kropp, E. R. Gizewski, et al. 2006. Cerebellar involvement in verb generation: an fMRI study. Neurosci. Lett. 409:19–23.

Fulbright, R. K., A. R. Jenner, W. E. MencI, K. R. Pugh, B. A. Shaywitz, S. E. Shaywitz, et al. 1999. The cerebellum’s role in reading: a functional MR imaging study. Am. J. Neuroradiol. 20:1925–1930.

Gazzaley, A., J. Rissman, J. Cooney, A. Rutman, T. Seibert, W. Gold, B. T., and R. L. Buckner. 2002. Common prefrontal regions in verb generation: an fMRI study. Neurosci. Lett. 409:19–23.

Haber, S. N., and R. Calzavara. 2009. The cortico-basal ganglia integrative network: the role of the thalamus. Brain Res. Bull. 78:69–74.

Iwata, M. 1984. Kanji versus Kananeuropsychological correlates of the Japanese writing system. Trends Neurosci. 7:290–293.

Kamitani, Y., and F. Tong. 2005. Decoding the visual and subjective contents of the human brain. Nat. Neurosci. 8:679–685.

Kelly, R. M., and P. L. Strick. 2003. Cerebellar loops with motor cortex and prefrontal cortex of a nonhuman primate. J. Neurosci. 23:8432–8444.

Kwon, J. C., H. J. Lee, J. Chin, Y. M. Lee, H. Kim, and D. L. Na. 2002. Hanja alexia with agraphia after left posterior inferior temporal lobe infarction: a case study. J. Korean Med. Sci. 17:91–95.

Lerner, Y., T. Hendler, D. Ben-Bashat, M. Harel, and R. Malach. 2001. A hierarchical axis of object processing stages in the human visual cortex. Cereb. Cortex 11:287–297.

Liu, C., W. T. Zhang, Y. Y. Tang, X. Q. Mai, H. C. Chen, T. Tardif, et al. 2008. The visual word form area: evidence from an fMRI study of implicit processing of Chinese characters. NeuroImage 40:1350–1361.

van der Mark, S., P. Klaver, K. Bucher, U. Maurer, E. Schulz, S. Brem, et al. 2011. The left occipitotemporal system in reading: disruption of focal fMRI connectivity to left inferior frontal and inferior parietal language areas in children with dyslexia. NeuroImage 54:2426–2436.

Matsuoka, K., S.-H. A. Chen, C.-W. Hue, C.-Y. Wu, E. Bagarinao, W.-Y. I. Tseng, et al. 2010. Neural substrates of phonological selection for Japanese character Kanji based on fMRI investigations. NeuroImage 50:1280–1291.

Morishima, Y., R. Akaishi, Y. Yamada, J. Okuda, K. Toma, and K. Sakai. 2009. Task-specific signal transmission from prefrontal cortex in visual selective attention. Nat. Neurosci. 12:85–91.

Nakamura, K., T. Oga, T. Okada, N. Sadato, Y. Takayama, T. Wydell, et al. 2005. Hemispheric asymmetry emerges at distinct parts of the occipitotemporal cortex for objects, logograms and phonograms: a functional MRI study. NeuroImage 28:521–528.

Oldfield, R. C. 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113.

O’Reilly, R. C., and M. J. Frank. 2006. Making working memory work: a computational model of learning in the prefrontal cortex and basal ganglia. Neural Comput. 18:283–328.

Rauschecker, A. M., A. Pringle, and K. E. Watkins. 2008. Changes in neural activity associated with learning to articulate novel auditory pseudowords by covert repetition. Hum. Brain Mapp. 29:1231–1242.

Rolls, E. T. 2000. The orbitofrontal cortex and reward. Cereb. Cortex 10:284–294.

van Schouwenburg, M. R., H. E. den Ouden, and R. Cools. 2010. The human basal ganglia modulate frontal-posterior connectivity during attention shifting. J. Neurosci. 30:9910–9918.

Stein, J. 1986. Role of the cerebellum in the visual guidance of movement. Nature 323:217–221.

Szwed, M., S. Dehaene, A. Kleinschmidt, E. Eger, R. Valabregue, A. Amadon, et al. 2011. Specialization for written words over objects in the visual cortex. NeuroImage 56:330–344.

Tamaoka, K., and H. Yamada. 2000. The effects of stroke order and radicals on the knowledge of Japanese kanji orthography, phonology and semantics. Psychologia 43:199–210.

Tan, L. H., C.-M. Feng, P. T. Fox, and J.-H. Gao. 2001. An fMRI study with written Chinese. NeuroReport 12:83–88.

Tani, T. 2004. A case of alexia with agraphia of Kanji following left posterior inferior temporal lobe infarction (in Japanese). High. Brain Funct. Res. 24:343–352.
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Tekin, S., and J. L. Cummings. 2002. Frontal–subcortical neuronal circuits and clinical neuropsychiatry: an update. J. Psychosom. Res. 53:647–654.

Thesen, T., C. R. McDonald, C. Carlson, W. Doyle, S. Cash, J. Sherfey, et al. 2012. Sequential then interactive processing of letters and words in the left fusiform gyrus. Nat. Commun. 3:1284.

Turkeltaub, P. E., L. Gareau, D. L. Flowers, T. A. Zeffiro, and G. F. Eden. 2003. Development of neural mechanisms for reading. Nat. Neurosci. 6:767–773.

Van der Mark, S., K. Bucher, U. Maurer, E. Schulz, S. Brem, J. Buckelmüller, et al. 2009. Children with dyslexia lack multiple specializations along the visual word-form (VWF) system. NeuroImage 47:1940–1949.

Vinckier, F., S. Dehaene, A. Jobert, J. P. Dubus, M. Sigman, and L. Cohen. 2007. Hierarchical coding of letter strings in the ventral stream: dissecting the inner organization of the visual word-form system. Neuron 55:143–156.

Warrington, E. K., and T. Shallice. 1980. Word-form dyslexia. Brain 103:99.

Wheat, K. L., P. L. Cornelissen, S. J. Frost, and P. C. Hansen. 2010. During visual word recognition, phonology is accessed within 100 ms and may be mediated by a speech production code: evidence from magnetoencephalography. J. Neurosci. 30:5229–5233.

Yeatman, J. D., A. M. Rauschecker, and B. A. Wandell. 2013. Anatomy of the visual word form area: adjacent cortical circuits and long-range white matter connections. Brain Lang. 125:146–155.

Zhang, H., J. Liu, and Q. Zhang. 2013. Neural Correlates of the Perception for Novel Objects. PLoS One 8:e62979.

Supporting Information

Additional supporting information may be found in the online version of this article:

Figure S1. Functional connectivity analyses seeded commonly activated brain region in the left occipitotemporal cortex.

Table S1. Regions with functional connectivity from the inferior temporal region during observation of the three character types.