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Research report

The inversion effect in visual word form processing

Chien-Hui Kao^a, Der-Yow Chen^{a,b} and Chien-Chung Chen^{a,*}^aDepartment of Psychology, National Taiwan University, Taipei, Taiwan^bDepartment of Electrical Engineering, National Taiwan University, Taipei, Taiwan

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ABSTRACT

Reading is one of the best well-practiced visual tasks for modern people. We investigated how the visual cortex analyzes spatial configuration in written words by studying the inversion effect in Chinese character processing. We measured the psychometric functions and brain activations for upright real-characters and non-characters and their inverted (upside down) versions. In the psychophysical experiment, the real-characters showed an inversion effect at both 1° and 4° eccentricities, while the non-characters showed no inversion effect for all eccentricities tested. In the functional magnetic resonance image (fMRI) experiment, the left fusiform gyrus and a small area in the bilateral lateral occipital regions showed a significant differential activation between upright and inverted real-characters. The bilateral fusiform gyri also show differential activation between upright real- and non-characters. The dorsal lateral occipital regions showed character-selective activation when compared with scrambled lines. The result suggested that the occipito-parietal regions may analyze the local features of an object regardless of its familiarity. Therefore, the lateral occipital regions may play an intermediate role in integrating the local information in an object. Finally, the fusiform gyrus plays a critical role in analyzing global configurations of a visual word form. This is consistent with the notion that the human visual cortex analyzes an object in a hierarchical way.

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1. Introduction

Reading may be one of the most well-practiced visual tasks for a person living in a modern society. It is very likely that a reader may have read hundreds of millions of words in his or her lifetime. For instance, skilled Chinese readers can, on average, read about 600 characters per minute (Sun et al., 1985). Assume that a 20-year-old college student, since the fourth grade, has spent only two hours per day reading at half of his or her top reading speed. This student would have read $300 \text{ char/min} \times 120 \text{ min/day} \times 3650 \text{ days} = 1.3 \times 10^8$ characters in just 10 years. With this amount of practice, our visual

system may have developed an efficient way to process word information.

It is suggested that, to perform a well-practiced visual task, such as recognizing a face, the visual system tends to analyze the configuration, or spatial relationship among image elements, rather than the image elements themselves (Tanaka and Farah, 1993). At the behavioral level, such configurational processing is best manifested in the inversion effect (Diamond and Carey, 1986; Ying, 1969). In the inversion effect, an observer has more difficulty recognizing an object in a picture when the image is placed upside down than when the image is in the upright position. Since the image elements

* Corresponding author. Department of Psychology, National Taiwan University, 1, Sec. 4, Roosevelt Rd., Taipei 106, Taiwan.

E-mail address: c3chen@ntu.edu.tw (C.-C. Chen).

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in the upright and the inverted images are the same and only the spatial relationship among image elements is changed by the inversion, such impairment of performance implies a mechanism for analyzing spatial configurations whose function is disrupted by the image inversion. Such an inversion effect has been found in recognizing human faces in normal populations (Carey and Diamond, 1977; Leder and Bruce, 2000; Rhodes et al., 1993; Ying, 1969), recognizing dogs by dog training experts (Diamond and Carey, 1986) and recognizing novel objects by observers trained to identify those objects (Gauthier and Tarr, 1997).

In this study, we investigated the spatial configuration processing of orthographic objects using Hanzi, also called “Chinese characters” in some literature. Hanzi, pronounced as Kanji in Japanese, is a set of characters used in several East Asian written languages. There is behavioral evidence of spatial configuration processing in Hanzi. It showed that skilled readers of Hanzi (e.g., Taiwanese or Japanese college students) tended to sort Hanzi with similarities in global spatial relationships among character components, while non-readers (e.g., American college students) tended to sort Hanzi with similarities in character components (Yeh and Li, 2002; Yeh et al., 2003).

There may be two ways to analyze spatial configurations in a Hanzi character. First, the visual system may analyze the spatial configurations in a hierarchical way. A character is composed of several character components and each of these components is composed of several strokes. Hence, the analysis of spatial configurations may occur on both levels: one is concerned with the spatial relationship among strokes in a character component, while the other is concerned with the spatial relationship among components in a character. For the purpose of this discussion, we will refer to the former as the local configuration and the latter as the global configuration. Second, the visual system may directly analyze the spatial relationship of the strokes relative to the whole characters. Hence, character components are just a set of strokes and play only a small role in spatial configuration processing.

To make distinctions among possible types of configuration processing, in this study we use only characters that are semantic–phonetic composites. About 90% of frequently used characters are of this type (DeFrancis, 1984). These characters are composed of two components, arranged in a left–right global configuration (see Fig. 1a for an example). The spatial configurations of a character were manipulated in the following ways: first, we swapped the position of the left and right components of a character as shown in Fig. 1b. This manipulation altered the global configuration but left the local configuration intact. For semantic–phonetic composites, this left–right swapping is the same as the construct of “non-characters” referred to in some literature (Hue and Tzeng, 2000). Thus, to be consistent with previous studies, we will identify the original characters as real-characters and the left–right swapped characters as “non-characters”. We then inverted both real-characters and non-characters to disrupt both local and global configurations (Fig. 1c and d).

There are studies using mirror reversed words (Dong et al., 2000; Poldrack et al., 1998; Proverbio et al., 2007; Ryan and Schnyer, 2007). At first glance, such manipulation is similar to ours. However, those studies focused on skill learning and did

Fig. 1 – Examples of the stimulus types used. (a) An upright real-character; (b) an upright non-character; (c) an inverted real-character; (d) an inverted non-character.

not address the issue of the visuospatial analysis of the stimuli. As a result, while they showed extensive occipito-temporal activation in the mirror reading tasks, these studies failed to analyze or separate the functions of different loci of activation in the occipitotemporal cortex during word processing.

While the inversion effect has been demonstrated in several categories of objects, to the best of our knowledge, it has not been reported for Chinese words or characters. Therefore, we first demonstrated an effect with a psychophysical experiment by showing an impairment of the discrimination performance for inverted real-characters, compared with that for upright real-characters. In addition, it is reported that the inversion effect may have different properties for foveal and peripheral presented stimuli (McKone, 2004; McKone et al., 2007). We, therefore, also tested the inversion effect at the parafoveal and the peripheral eccentricities. We then investigated the cortical activation for spatial configurations in Hanzi. The cortical areas that are sensitive to all spatial configurations should show an inversion effect for real-characters. Furthermore, the areas that are sensitive to the global configurations should show the differential activation between real- and non-characters. The areas that are sensitive to the local configurations should show an inversion effect for non-characters.

2. Methods

2.1. Psychophysics

2.1.1. Participants

Twelve right-handed observers (6 males, 6 females) between 20 and 24 years old were participated in this study. All participants were undergraduate or graduate students at the National Taiwan University. They are all fluent in reading

Chinese. They were naïve as to the purpose of the experiment and were compensated financially for the hours in the experiment. All of them provided written consent for participation in the experiment. Data from one participant was discarded due to a performance near the chance level in all conditions. As a result, there were eleven participants in the final data set.

2.1.2. Apparatus

The stimuli were presented on an HP P1130 (Trinitron 21" CRT) monitor controlled by a RADEON 9800 XT video card on a PC. The monitor resolution was 1280 (H) × 1024 (V). The monitor input-output intensity function was measured with a light mouse photometer (Tyler and McBride, 1997). This information allowed us to compute linear lookup table settings to linearize the output. The mean luminance of the monitor was 30 cd/m². At a viewing distance of 54 cm, each pixel on the monitor had a size of .03° in visual angle.

2.1.3. Stimuli

Fig. 1 shows examples of stimuli used in this study. All the characters were semantic-phonetic composites with two components arranged in a left-right configuration, with a phonological component on the right and a semantic component on the left side (Fig. 1a). It is estimated that 90% of the characters used by a typical college student are such compounds (Hue, 2003). The 40 real-characters we used were selected from the 1500 most frequently used characters in the *Academia Sinica Balanced Corpus* (1998). A non-character (Fig. 1b) was constructed by interchanging the positions of the phonetic and semantic components of a real-character. Thus, a non-character kept the components, and in turn local configurations, of a character, whereas the spatial relationship between components was altered. The 40 non-characters were selected from the norms prepared by Hue and Tzeng (2000). The inverted real- and non-characters (Fig. 1c and d respectively) were simply the upside-down versions of their upright counterparts.

The stimuli were presented at either 1° (parafoveal condition) or 4° (peripheral condition) away from the central fixation along the horizontal meridian. The stimuli size was 1.6° in the parafoveal condition and 3.2° in peripheral condition. The contrast level of the stimuli ranged from –26 to –2 dB in 4 dB step. The unit dB is 20 times the log base 10 of the linear contrast.

2.1.4. Procedure

We used a two-alternative forced-choice (2AFC) paradigm to measure the proportion of correct responses in a matching task. The experiment was composed of four blocks (upright, inverted real-characters, upright and inverted non-characters). In each block, each trial had a stimulus presented in either central or peripheral vision and the contrast threshold of a stimulus was varied with 7 levels. In each trial, two characters of the same type and orientation were presented. One was on the left and the other was on the right of the fixation point. The two stimuli were presented simultaneously for a 100 msec duration. The participants were asked to press one of two buttons to indicate whether these two characters were the same or not. Feedback was provided via

an auditory cue for both correct and incorrect trials. During the experiment, the participants were asked to fixate on the center fixation point. The presentation order within a block was randomized and the order between blocks was counter-balanced across participants. Each block consisted of 560 trials. Thus, each participant was presented with 2240 trials in the psychophysical experiment (4 types of stimuli × 2 eccentricities × 7 contrast thresholds × 40 trials).

2.2. Functional magnetic resonance image (fMRI)

2.2.1. Participants

Thirteen healthy volunteers (6 males, 7 females) between 22 and 36 years old participated in this study. All the participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All the participants were native speakers of Chinese and none of them had participated in the psychophysical experiment. They were naïve as to the purpose of the experiment and were compensated financially for the hours of the experiment. Informed consents of the participants were obtained before scanning. The experiment was approved by the IRB of the National Taiwan University Hospital.

2.2.2. Stimuli

The stimuli were the same as those used in the psychophysical experiment except for the addition of the scrambled versions of the test characters as control stimuli. The stimuli, which had approximately 80% Michaelson contrast (–2 dB), were presented at the fovea. They were constructed first by dividing the image of a character into squares in 4 by 4 grids. Then, the positions of the 16 squares were scrambled.

2.2.3. Procedure

We used a block design to measure the differential cortical activations between different types of stimuli. Each of the four experimental runs had an 18-sec epoch of the presentation of one stimulus type alternating with an 18-sec epoch of the other types. The stimuli were presented randomly within each 18-sec epoch. There were six cycles of 36 sec periods in each run. Each epoch consisted of 18 presentations of the stimulus for 500 msec followed by a 500 msec blank period. Two of the four runs had the real-characters alternating with their scrambled or inverted versions respectively, while the other two runs had the non-characters alternating with their scrambled or inverted versions respectively. To keep the participants' attention, the participants were instructed to perform a 1-back matching task in which they had to press a key when the stimulus presented in the current trial matched that presented in the previous trial. In each run, the proportion of matches between stimuli in trial *N* and trial *N* – 1 was .25.

2.2.4. Data acquisition and analysis

All images were acquired with a 3 T Bruker MRI scanner located at the Interdisciplinary MRI Laboratory at the National Taiwan University. A high-resolution anatomical (T1-weighted) MRI volume scan of the entire head was conducted once on each participant (voxel size = 1 × 1 × 1 mm). Within each scanning session, both functional [T2*-weighted,

blood oxygenation level dependent (BOLD)] responses and anatomical images were acquired in identical planes. The images were collected in 20 transverse planes parallel to the anterior commissure–posterior commissure (AC–PC) line. An echo-planar imaging sequence (Stehling et al., 1991) was used to acquire the functional data [repetition time (TR) = 3000 msec, echo time (TE) = 33 msec, flip angle = 90°, voxel resolution = $2.34 \times 2.34 \times 4$ mm]. The main experiment lasted 225 sec (75 images). The first 9 sec (3 images) were excluded from further analyses to avoid the start-up transient. Thus, the data analyzed for each scan spanned 216 sec (72 images). To correct head-motion artifacts, we used SPM2 (Wellcome Department of Imaging Neuroscience, University College London; <http://www.fil.ion.ucl.ac.uk/spm/>) to realign the acquired echo-planar imaging (EPI) images. The realigned images, as well as the anatomic images, were then normalized to a standard template using SPM. The normalized images were fed into the mrVista analysis package (Wandell et al., 2000) for coregistration, data analysis, and 3D visualization. Statistical analysis of the BOLD activation was based on the spectral correlation between the BOLD activation time series and the experimental sequence (Engel et al., 1997).

For each participant in each run, the Fourier transform was applied for each BOLD time series. The spectral correlation or coherence for each voxel was computed as the amplitude of the stimulus frequency divided by the summation of amplitude of all frequencies up to the Nyquist limit. The differential activation of a voxel was considered significant if its coherence was greater than .475. This criterion was equivalent to an α -level about 10^{-6} for each individual voxel and Bonferroni corrected α -level, based on the number of gray matter voxels in a flatmap (see Figs. 4 and 5), less than .001. The coherence value and phase of each voxel were also used to calculate fitted response amplitude of the time series (i.e., “ β ” in the general linear model) for the group analysis.

The group, or second level, analysis was basically a linear regression of the fitted response amplitude across participants (Penny et al., 2003). The second level analysis only considered voxels that were significant at the first level for all participants. The voxels with significant activation reported in Results had an α -level of .05 for the second level t-test group analysis. For our data, considering cortical voxels, the α -level .05 corresponded to the false discovery rate .07, this is below the “reasonable range” of .1–.2 recommend by Genovese et al. (2002) and .1 level suggested by Mosig et al. (2001). This criterion was to ensure the activation level surpassed that of the inter-participant variability. To test differential contrasts across different runs, we followed the procedure proposed by Joseph et al. (2002). We first identified regions of interest (ROIs) defined by a specific parametric contrast for individual runs. The signal amplitude of the average waveform over the voxels in these (ROIs) from each subject was then analyzed with a repeated measure analysis of variance (ANOVA) that assessed the effect of conditions for the specified contrast. In addition, to acquire detailed information of the differential contrasts in specific ROIs defined by the localizers, we followed up significant main effects in the ANOVA with pairwise comparison t-tests of differences in activation between conditions in the specified ROIs.

3. Results

3.1. Psychophysics

Fig. 2 shows the proportion of correct responses as a function of contrast levels for the real-characters (top row, panels a and b) and the non-characters (bottom row, panels c and d) at 1° (left column, panels a and c) and 4° (right column, panels b and d) eccentricity. For all conditions, the proportional correct responses increased with contrast until they reached an asymptotic level. Such data was fit into the function

$$p(x) = \gamma + (1 - \gamma) \times \rho \times \Phi(x, \mu, \sigma) \quad (1)$$

where $p(x)$ was the proportional correct response at contrast level x ; γ was the guessing factor for 2AFC and was fixed at .5; ρ determined the asymptotic level of the psychometric function, $\Phi(\mu, \sigma)$ is the Gaussian cumulative distribution function with the location parameter (“mean”) μ and the scale parameter (“standard deviation”) σ . The smoothing curves in Fig. 2 were fits of this function. The root of the mean squared error (RMSE) of the model fit was about .02 which is close to the mean of the standard error of measurement .04. The values of parameters are shown in Table 1.

At high contrasts, the proportional correct responses for matching two upright real-characters were significantly better than those for matching two inverted real-characters at α -level .05 (denoted by the symbol “*” in Fig. 2a and b). In the parafovea viewing conditions, the psychometric function for upright real-characters was asymptotic to the percentage correct level of 82%, while the function for inverted characters was 67%. In the peripheral viewing conditions, the psychometric function for upright real-characters was asymptotic to the percentage correct level of 80% while the function for inverted characters was 64%. That is, in both parafoveal and peripheral viewing conditions, at high contrasts, turning the real-characters upside down reduced the percentage correct level by about 15%.

Fig. 2 (Panel c and d) shows the psychometric functions for matching non-characters. There was no difference between the proportional correct responses for matching upright and matching inverted non-characters in either the parafovea or in the periphery. The psychometric function was asymptotic to the level 77% and 70% for upright and inverted characters respectively in the parafovea, and was asymptotic to 68% and 64% for upright and inverted characters respectively in the periphery. The decline in performance was about 6% and showed no statistical significance. Thus, there is no inversion effect for non-characters in either the parafovea or the periphery.

Fig. 3 replots the data for upright characters, to compare the matching performances for real- and non-characters. With the exception of the lowest test contrast where the performance is always at the chance level, the matching performance for real-characters was better than that for non-characters at all contrasts and the magnitude of the difference is statistically significant (α -level = .05) at high contrasts. The difference is even more pronounced in the peripheral viewing condition.

Fig. 2 – The Gaussian accumulative distribution functions as a fitting model for the data. Proportional correct responses of upright real-characters, inverted real-characters, upright non-characters, and inverted non-characters at different contrast thresholds. (a) Real-character stimuli were presented at 1° eccentricity, (b) real-characters were presented at 4° eccentricity, (c) non-characters were presented at 1° eccentricity, (d) non-characters were presented at 4° eccentricity. In each panel, the circle and square symbols denote the proportion of correct responses averaged across eleven observers. * $p < .05$ and ** $p < .01$. Error bars are ± 1 standard error of the mean, SEM.

The parameter μ in Eq. (1) was the location parameter of the Gaussian cumulative distribution function. Thus, it controlled the position where the psychometric function was at its half height and in turn determined the dynamic range of the psychometric function. The μ of four conditions are from -16.648 to -19.126 dB contrast level. There was essentially no difference in the dynamic range for all the psychometric functions.

Table 1 – The resulting model fits to combined data set of eleven observers. The parameter μ is the mean of the contrast, σ and ρ are the scale parameters, and RMSE indicates the goodness-of-fit.

	μ	σ	ρ	RMSE
Parafovea				
Upright real-character	-17.5887	4.5907	32.0973	.0189
Inverted real-character	-19.1264	1.7208	16.7225	.0221
Upright non-character	-16.6484	3.6514	27.0651	.0095
Inverted non-character	-17.0390	3.5190	20.2507	.0099
Periphery				
Upright real-character	-17.5505	3.4870	30.2563	.0248
Inverted real-character	-18.5808	4.5234	13.8820	.0049
Upright non-character	-18.0782	.4955	18.1800	.0126
Inverted non-character	-17.9132	.7077	15.6250	.0185

3.2. Behavioral performances in the fMRI experiment

The 1-back matching task was used here to keep participants' attention as it was also used in some fMRI studies on face inversion effects (e.g., Chen et al., 2007; Yovel and Kanwisher, 2005). Nevertheless, we did record the performance of 11 (out of 13) participants. While the purpose of this task was simply attention control and the number of trials collected during scanning was small, we did find behavioral inversion effects in the 1-back task. The proportional correct response for upright real-characters was higher than that for inverted real-characters [96% vs 93%, pairwise $t(10) = 3.187$, $p < .05$]. However, there was no difference in performance for upright and inverted non-characters [95% vs 94%, pairwise $t(10) = 1.44$, $p > .05$]. This result was consistent with the main psychophysical experiment reported above. Note that, since the averaged proportional correct responses were all greater than 93%, we did not separate the cortical activation for correct and incorrect trials in our fMRI data analysis.

3.3. Cortical activation to upright characters

Fig. 4a shows the differential activation for contrasting real-characters with their own scrambled versions in axial slices from a group analysis. The pseudo-colored patches in the figures denote voxels showing a significant activation change

Fig. 3 – Proportional correct responses of upright real- and non-characters at different contrast thresholds. (a) Real-characters and non-characters were presented at a 1° eccentricity, (b) real-characters and non-characters were presented at a 4° eccentricity. * $p < .05$ and ** $p < .01$.

between real-characters and their scrambled versions at α -level .05. The majority of activated voxels were located in the occipitotemporal regions, including the fusiform gyrus, the middle and the superior occipital gyri (MOG and SOG, respectively) in both hemispheres and the inferior occipital gyrus (IOG) in the left hemisphere. The activated areas on the lateral surface overlapped with the lateral occipital complex (LOC) reported in the literature (Kourtzi and Kanwisher, 2001). Small patches of activation were also observed in the inferior frontal gyrus (IFG), the left middle temporal gyrus (MTG) and the right postcentral gyrus. Table 2 lists the Talairach coordinates (Talairach and Tournoux, 1988) of the major activated areas. The left fusiform showed a more extensive activation than the right fusiform [$\chi^2(1) = 428.96$, $p < .05$]. This is consistent with what was reported in the literature regarding the visual word forms in English (Cohen et al., 2000, 2002). On the other hand, the right dorsal occipital cortex showed more extensive activations than the left [$\chi^2(1) = 1153.42$, $p < .05$]. This is consistent with the studies which used logograph words as stimuli (Tan

et al., 2001a, 2001b). For a better understanding of the spatial relationships between the activated areas, we replotted the activation pattern on a flatmap (in Fig. 4b). The flatmaps in this paper were 100 mm radius disks centered at a point near the occipital poles on inflated cortical surfaces. The gray shading denotes the gyral (light) and sulcal (dark) layouts. The criteria for choosing ROIs will be discussed below.

Fig. 4c shows the group-averaged activation map for contrasting non-characters with scrambled versions of characters in axial slices. The pseudo-colored patches denote voxels showing significant activation change differences between non-characters and their scrambled versions at α -level .05. The majority of activated voxels were also located in the occipitotemporal regions, including the left fusiform gyrus, the bilateral MOG, SOG and the right cuneus. Small patches of activation were also observed in the IFG and right postcentral gyrus. The activation pattern of non-characters is also shown in Fig. 4d. Talairach coordinates of the major activated areas are also given in Table 2.

For the convenience of discussion, we defined three ROIs in each hemisphere from the activation maps for the real- and non-characters conditions. The colored contours in Fig. 4 show the boundary of these ROIs: the fusiform character area (FCA, blue contours), the lateral occipital character area (LOCA, cyan contours) and the occipitoparietal character area (OPCA, magenta contours). A voxel is a part of an ROI if it shows significant differential activation either in the real- or in the non-character conditions. The FCAs were on a cluster of activation in the middle fusiform gyrus. The character-selective activations in the dorsal occipital cortex were separated into two areas of interest: the lateral character area (LOCA) and the OPCA, due to their proximity to the LOC and kinetic occipital respectively. In the left hemisphere, these two ROIs were separated clusters of activations while in the right hemisphere, where there was no clear boundary, these two ROIs were separated by the intra-occipital sulcus.

3.4. Differential activations between real- and non-characters

We then applied a conjunction analysis (Joseph et al., 2002) to study the brain areas showing differential activation to real- and non-characters (see Methods). Fig. 4e shows the areas with significant differential activation between real- and non-characters on flatmaps with ROIs. The FCA of both hemispheres showed a significant activation difference between the real-characters and non-characters ($F_{12,24} = 6.16$, $p = .03 < .05$ for the left and $F_{12,24} = 4.72$, $p = .05$ for the right). The percentage of amplitude change dropped from .62% for real-characters to .41% for non-characters in the right FCA [$t(12) = 2.36$, $p = .018 < .05$] and from .86% for non-characters to .66% for real-characters in the left FCA [$t(12) = -3.074$, $p = .0096 < .05$]. This result was consistent with the study of the visual word form areas (VWFAs) in the fusiform gyrus for reading Chinese (Liu et al., 2008).

3.5. Inversion effect

We then compared the brain activation for upright and inverted characters. As shown in Fig. 5a, contrasted with their

Fig. 4 – (a) Activation maps are shown in the standardized brain slices for the real-characters versus their scrambled versions. Orange color denotes the average activation pattern. **(b)** The real-characters activation depicted in flatmaps centered on the occipital poles. **(c)** Activation maps are shown in the standardized brain slices for the non-characters versus their scrambled versions. **(d)** The non-characters activation depicted in flatmaps centered on the occipital poles. **(e)** Differential activation between real-characters and non-characters in flatmaps. The blue border denotes the extent of the activated areas in the FCA. The cyan border denotes the extent of the activated areas in the LOCA. The magenta border denotes the extent of the activated areas in the OPCA. Gyral (light) and sulcal (dark) denoted by shading. Yellow-orange coloration codes the negative log base 10 of the significance value of a 2-side t-test (threshold at $p < .05$). L: left hemisphere; R: right hemisphere.

inverted versions, the upright real-characters showed robust differential activation in the left FCA and the LOCA defined above. Table 3 lists the Talairach coordinates of the activated areas. Fig. 5b shows that contrasted with their inverted version, non-characters showed no differential activations greater than the noise level in any voxels.

The amplitudes of the inversion effect in different areas are shown in Fig. 6. With the conjunction analysis, we found that the inversion effect for the real-characters in the left FCA was significantly greater than that for the non-characters ($F_{12,24} = 18.17$, $p = .001 < .05$). The percentage of amplitude change dropped from .83% for real-characters to .34% for non-characters [$t(12) = 4.49$, $p = .00037 < .05$]. The bilateral LOCA also showed an inversion effect for the real-characters greater than that for the non-characters ($F_{12,24} = 5.48$, $p = .037 < .05$ for the left hemisphere; $F_{12,24} = 5.50$, $p = .037 < .05$ for the right hemisphere). The percentage of amplitude change dropped from .96% to .54% [$t(12) = 2.57$, $p = .012 < .05$] in the left LOCA, and from .83% to .47% [$t(12) = 2.50$, $p = .014 < .05$] in the right LOCA.

Note that we found no activation in the precuneus, which was considered to be an area associated with mental rotation (Bonda et al., 1995; Cohen et al., 1996; Jordan et al., 2001). Thus, we did not find evidence of our participants engaging in mental rotation when processing inverted characters.

4. Discussion

In the psychophysical experiment, we showed that the proportional correct responses for matching upright real-characters were significantly better than those for matching inverted real-characters. Such an inversion effect was not observed in non-characters. The matching performance for upright real-characters was better than that for upright non-characters. In addition, the psychometric functions showed the same dynamic range in luminance contrast for all character types. With the fMRI experiment, we found that part of the left fusiform gyrus and a small area in the bilateral lateral occipital regions had a significant differential activation between upright and inverted real-characters. The fusiform gyri in both hemispheres also showed differential activation between upright real- and non-characters. The occipitoparietal regions showed the character-selective activation when characters were compared with scrambled lines, but was indifferent to any manipulations of characters used in this study.

4.1. Behavioral evidence for inversion effects

The proportional correct responses for matching real-characters reduced significantly when the characters were turned

Fig. 4 – continued

upside down. This inversion effect was reported only with well-practiced visual objects, such as faces (Carey and Diamond, 1977; Leder and Bruce, 2000; Rhodes et al., 1993; Ying, 1969). The inversion effect, as suggested by Carey and Diamond (1977), reveals the spatial configuration processing in the visual analysis of those objects. After all, the relative spatial relations among image elements are turned upside down in the inverted images. Hence, the response of a mechanism that is specialized for the spatial configurations of image elements would be reduced by the inversion. Thus, our result may suggest that a spatial configuration process is also involved in character processing.

We also showed that the matching performances for real-characters were significantly better than those for the

non-characters. In addition, the proportional correct responses for upright non-characters were similar to those for the inverted real- and non-characters. As discussed above, a non-character was constructed by swapping the left and right parts of a real-character. Hence, the non-characters disrupted the global configuration while keeping local configuration intact. Thus, our result suggests that the function of the character processors in the visual system is to analyze the global configuration among character components and not local information.

The psychometric functions showed the same dynamic range in luminance contrast for all character types. The location parameters of all the fitted psychometric functions were almost identical. This result may suggest that the early

Table 2 – The brain areas showing differential between characters and scrambles.

Brain regions	Hemisphere	Talairach coordinate			Volume (mm ³)
		X	Y	Z	
Real-characters					
Fusiform gyrus	Left	−41	−58	−16	1816
	Right	36	−64	−9	764
MOG and IOG	Left	−31	−90	20	1015
		−39	−84	0	1435
	Right	38	−86	−5	5473
SOG	Left	−34	−88	24	2292
	Right	32	−76	28	1346
Non-characters					
Fusiform gyrus	Left	−43	−58	−16	1597
MOG	Left	−37	−85	−8	3232
	Right	38	−87	−4	4768
SOG	Left	−29	−88	20	351
	Right	34	−88	24	2292

visual mechanisms were not decisive factors in our character matching tasks. The early visual mechanisms are sensitive to the local orientations and contrast in an image (Campbell and Robson, 1964; Hubel and Wiesel, 1962, 1969). The local orientations of different types of characters varied substantially in our stimuli. And yet, there is no contrast effect across character types. Therefore, the mechanisms underlying character matching tasks must be able to take the whole character, rather than local features, into account.

Strong inversion effects for real-characters were found both in the parafovea and in the periphery. This result was consistent with the face inversion effect which was also found both in the fovea and in the periphery (McKone et al., 2007). However, it was reported that, after a few hours of training, the inversion effect for trained objects can emerge in the fovea but not in the periphery (McKone et al., 2003). Such eccentricity difference in the inversion effect has been used as an argument for the uniqueness of face processing (McKone et al., 2003). Our result suggests that the eccentricity invariant inversion effect is not unique to faces. After all, visual word forms, similar to faces, are well-practiced visual stimuli. Perhaps the mechanisms for visual word form processing shared more common properties with those for face processing than those for object processing.

Fig. 5 – (a) Differential activation between upright and inverted real-characters and (b) differential activation between upright and inverted non-characters depicted in flatmaps centered on the occipital poles. Blue borders: FCA; cyan borders: LOCA; magenta borders: OPCA. Activation colors as in Fig. 4.

Table 3 – The brain areas showing inversion effects of real-characters.

Brain regions	Hemisphere	Talairach coordinate			Volume (mm ³)
		X	Y	Z	
Fusiform gyrus	Left	–44	–62	–15	641
IOG	Left	–34	–89	–3	582
	Right	41	–87	–4	269

4.2. The role of the fusiform gyrus in character processing

It has been reported that part of the left fusiform gyrus specifically responds better to words than nonsense letter strings (non-words) and was named the VWFA by some authors (e.g., Cohen et al., 2000, 2002). On the other hand, it is also suggested that the area designated as VWFA may also respond to other categories of visual objects (e.g., Price and Devlin, 2003). Similarly, another part of the fusiform gyrus was reported to be specific for face processing, termed the fusiform face area or FFA (Kanwisher et al., 1997). Again, there is an argument that the FFA is also responsible for other types of visual objects (Gauthier et al., 1999; Haxby et al., 2001). In particular, it was suggested, the FFA may be responsible for expertise in perceiving objects (Gauthier and Tarr, 1997; Gauthier et al., 1999, 2000). Since both word and face recognitions are well-practiced visual tasks, it is difficult to separate category dependent and familiarity dependent responses from faces and words in the FFA.

In this study, we found that the fusiform gyrus showed greater activation for the upright real-characters than the inverted ones. Previous studies also reported that the fusiform gyrus responded better to upright faces than inverted faces (Chen et al., 2007; Yovel and Kanwisher, 2004, 2005). The inversion effect we found in the study is consistent with that reported in previous studies on face inversion effect in the FFA. One possible interpretation is that the neurons in the fusiform are insensitive to inverted stimuli.

At the behavioral level, the inversion effect to an object category seems to relate to the experience of an observer to

Fig. 6 – Percentage change of activation between the upright and inverted real- and the non-characters in FCA and LOCA. The error bars denote the standard error calculated across participants.

that object category. If the function of the fusiform is for category-specific processing, we would expect the character inversion effect to be limited to character-selective areas. On the other hand, if the fusiform gyrus is related to expertise and is not category specific, we should expect the area showing an inversion effect to be widely spread.

While both words and faces can increase activation in the fusiform, the peak activations occur in different parts of the left fusiform gyrus. The green and red symbols in Fig. 7 denote the locations of peak activation for words (Cohen and Dehaene, 2004; Cohen et al., 2000, 2002; Reinholz and Pollmann, 2005; Vigneau et al., 2005) and for faces (Chen et al., 2007; Kanwisher et al., 1997; Rossion et al., 2003) respectively. The peak locations were computed from the reported Talairach coordinates in those papers. The word activations tend to be located in regions that are lateral to the regions for face activations. The black contour in Fig. 7 indicates the region showing significant differential activation between the real- and the non-characters as shown in Fig. 4e. That is, this region is an equivalent of VWFA, which was defined as the brain region showing differential activations between words and non-words, for Chinese characters. This region is similar to the VWFA reported in the literature. This suggests a similarity in the visual processing of characters in Asian languages and word processing in alphabetic languages. The colored patch denotes the area showing the inversion effect as in Fig. 5. The area showing the inversion effect overlapped with the VWFA but not with face-selective regions. This result implies that (1) the function of VWFA is to analyze global spatial configurations among character components (Starrfelt and Gerlach, 2007) and (2) the character inversion effect is character-specific processing. The former may be consistent with the report that English-speaking pure alexia patients may have an impairment reading words, but have normal letter identification performances (Farah and Wallace, 1991; Sekuler and Behrmann, 1996). It suggests that expertise alone cannot explain the function of the fusiform gyrus. Instead, the function of the left fusiform gyrus shows a certain degree of categorical specification. Note that we do not suggest that expertise plays no role in the function of the fusiform gyrus. After all, the fusiform gyrus showed strong differential activation between the familiar and the novel after training (Baker et al., 2007; Gauthier et al., 1999, 2000). In addition, written languages, being words or characters, were only invented less than ten thousand years ago. It is unlikely for human beings to have evolved a brain area specifically for reading characters. Instead, at least in characters, the categorical specification may be acquired through extensive practice.

The right fusiform gyrus showed a difference in activation only between real- and non-characters. However, the inversion effect is absent in this region. This may imply that the right fusiform gyrus is not sensitive to the orientation of character components.

4.3. The dorsal activation

A small portion of the LOCA showed an inversion effect while the OPCA did not. None of these areas showed a significant difference between the activations to real- and non-characters. The lateral occipital regions are known to be responsive

Fig. 7 – Activation maps for the upright versus inverted real-characters on the occipital-poles flatmaps. The Talairach coordinates of each study were presented. The black border denotes the differential activated region between real- and non-characters. Cyan borders: LOCA; magenta borders: OPCA. Colored symbols indicated mean locations of activations in other studies (see key). Activation colors as in Fig. 4.

to visual objects (Kanwisher et al., 1996; Kourtzi and Kanwisher, 2000, 2001). Hence, it is surprising that these areas responded differently to characters and scrambled line segments. The LOCA responded differently to upright and inverted characters, which were different in both global and local configurations. However, this region was indifferent to real- and non-characters, which were different only in global configurations and it showed no differential activation between upright and inverted non-characters, which were different in local configurations. Neither carried any familiar global configuration. That is, the differential activation in the LOCA requires a difference in both the local and global configurations. This may be consistent with the notion of the involvement of the lateral occipital in integrating local fragments of an object for the global analysis in the brain areas further downstream (Chen and Han, 2005; Hayworth and Biederman, 2006; Ostwald et al., 2008).

The OPCA was indifferent to all character manipulations. Hence, it may be that the OPCA responds only to local features, such as corners and junctions that were changed when we scrambled the characters. Previously, studies on character recognition showed that the occipitoparietal region was involved in the processing of the spatial arrangement of strokes or character components (Fu et al., 2002; Kuo et al., 2001; Tan et al., 2001a, 2001b).

The real-characters produced an extensive activation in the right dorsal occipitoparietal region. Such activation was not often reported in the brain imaging studies of words in alphabetic languages (for a review, see Fiez and Petersen, 1998). Instead, the occipitoparietal activation to visual word forms in alphabetic languages seemed to be confined to the left hemisphere. On the other hand, the extensive right occipitoparietal activations, as we report here, were often reported in studies with words in logograph languages (Tan et al., 2001a, 2001b). Such right hemisphere activation was often

attributed to the requirement of more intensive spatial analysis of the written words in logograph languages (Tan et al., 2001a, 2001b).

4.4. Hierarchical processing in the occipitotemporal cortex

From the above discussion of our fMRI results, we conclude that from dorsal to ventral, the visual system may analyze characters in a hierarchical way. The occipitoparietal regions may analyze the local features of an object regardless of its familiarity. Then, the lateral occipital regions may play an intermediate role in integrating the local information in an object. Finally, the fusiform gyrus plays a critical role in analyzing global configurations in a character. This is consistent with the notion that the human visual cortex analyzes the image of an object in a hierarchical way. That is, while the local features in an image are analyzed in the early visual cortex, the information processing is becoming more global and more complicated as the information flows to brain areas further downstream.

Such hierarchical processing was also found in studies with other visual stimuli. Ostwald et al. (2008) showed that the activations in the early visual areas were influenced by the local features, such as dipole orientation, of a Glass pattern (Glass, 1969), which those in the lateral occipitotemporal regions were determined by the global forms (Chen and Han, 2005). Similarly, Kourtzi and Huberle (2005) also found the early visual areas were sensitive to the local orientations of contour elements, whereas the LOC was sensitive to the global form of the contours.

For a more complicate visual stimulus, Chen et al. (2007) showed that the activations in the FFA were influenced by the global configuration of a face, such as symmetry, while the activations in the dorsal occipital cortex were only influenced by

local features. Yovel and Kanwisher (2005) showed that the face inversion effect was mainly observed in the FFA and the effect is not very robust in the occipital cortex. Taylor et al. (2007) showed that the activation in the occipital cortex is selective to parts of a body whereas the activation in the fusiform is selective to the configuration of body parts. These studies drew similar conclusions to ours with regard to visual word form.

However, studies with Navon figures (Navon, 1977) showed a different picture. A Navon figure is a large letter with strokes composed of smaller letters. Han et al. (2002) showed that the medial occipital was activated when participants gave responses based on the larger letter (global feature) and the parieto-occipital sulcus, when based on the smaller letter (local feature). With a similar task, Han et al. (2004) showed that the temporal cortex was activated when the participants were asked to attend to the larger letter, and the superior parietal cortex, when they were asked to attend to the smaller letter. Despite the inconsistency in the Navon's figure literature itself, there is one major difference between Navon's figure studies and ours. Similar to the Glass pattern contour integration, face and body part studies discussed above, our study focused on the visual analysis of local features and global configurations while the Navon's figure studies focused on the local and global attention strategy. Hence, these two types of studies may tag into completely different neural mechanisms. This notion is consistent with the finding of Davidoff et al. (2008) who found that people from a remote culture had global representations only for faces but not for Navon's figures.

5. Conclusions

Taken together, we used psychophysical and functional MRI methods to investigate the character processing. The behavioral evidence showed that performance for matching upright real-characters was significantly better than that for matching inverted real-characters. Such an inversion effect was absent for non-characters. We also found that the matching performance for upright real-characters was better than that for upright non-characters. In addition, the psychometric functions showed the same dynamic range in luminance contrast for all character types. These results suggested that the recognition of real-characters involved spatial configuration processing. In the fMRI evidence, the left fusiform gyrus and a small area in the bilateral lateral occipital regions showed a significant differential activation between upright and inverted real-characters. The bilateral fusiform gyri also show differential activations between upright real- and non-characters. The occipitoparietal regions showed character-selective activation when compared with scrambled lines. It suggests that the visual system may analyze the spatial configurations of a visual word form in a hierarchical processing.

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