

Title	Phonetic processing of letters in lateral occipital cortex
Sub Title	
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Publisher	Centre for Advanced Research on Logic and Sensibility The Global Centers of Excellence Program, Keio University
Publication year	2009
Jtitle	CARLS series of advanced study of logic and sensibility Vol.2, (2008.) ,p.103- 113
JaLC DOI	
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Notes	Part 1: Brain and Evolution
Genre	Research Paper
URL	https://koara.lib.keio.ac.jp/xoonips/modules/xoonips/detail.php?koara_id=KO12002001-20090331-0103

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Phonetic Processing of Letters in Lateral Occipital Cortex

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Abstract

Letters/syllables contain information only about their shape and sound in contrast to visual words which carry semantic, phonological, and orthographic information. The features—shape, sound, or both—by which the letter-sensitive areas of the brain discriminate letters are not known. To study the process of letter recognition, we used refractory suppression phenomenon in functional MRI and Japanese kana letters each of which represents a syllable. Kana consists of two groups of letters, hiragana and katakana; they differ in shape but each letter in one group has a same-sound counter part in the other. We found that phonetic information is an important form of information used in distinguishing letters.

INTRODUCTION

It is widely accepted that visual words are processed along the visual ventral pathway from the extra striate cortex to the visual word form area (VWFA) located in the anterior of the left occipitotemporal cortex. Through this pathway, features of letters are analyzed and letters and words

are represented in the VWFA (Cohen, 2004; Coren, 1994; McClelland, 1981; Vinckier, 2007). It is known that the VWFA is sensitive to real words and pseudo words and that a portion of the occipitotemporal cortex posterior to the VWFA is sensitive to letters and letter-strings (Pammer, 2004). The posterior region also responds more significantly to letters than to digits (Polk, 2002). However, no area has generally been accepted as letter-specific in the way that the VWFA is specific for visual words. Visual words contain semantic, phonological, and orthographic information, and these attributes can be used in discriminating a word from others. However, letters and letter-strings contain information only on shape and sound. There are previous studies on letter recognition suggesting that letters are processed to an abstract graphemic level of representation before being identified (Ellis, in press) and that orthographic effects occur earlier than phonological effects (Grainger, 2006). However, what kinds of information—shape, sound, or both—letter-sensitive areas use to discriminate letters are not known.

To study the strategy the brain uses for letter recognition (i.e., for the discrimination of letters), we used Japanese kana letters. Japanese kana uses a syllabic system and each letter has its own sound. Kana consists of two groups of letters, hiragana and katakana.

Hiragana and katakana are different in shape but each letter in hiragana has a counterpart in katakana with the same sound; that is, each kana phoneme has two graphemes. The letter recognition system for kana should therefore discriminate letters using information on the shape and sound of letter. The system needs to translate shapes into sounds in order to establish whether a hiragana letter and its katakana counterpart are phonologically the same.

We used the refractory suppression phenomenon in functional MRI (fMRI) response to investigate the strategy used for letter recognition. This is a similar phenomenon as reduction of the activity of a neuron when a stimulus is given repeatedly (Budd, 1998). The refractory suppression has been observed in the primary visual area by a pair of stimulus inputs with an inter stimulus interval (ISI) of about 200 ms (Ogawa, 2000). The extent of suppression depends on the ISI and the similarity of the input into the area where processing occurs. When the sequential inputs are identical, suppression is strong and recovery from refractoriness is slow. Such

refractory suppression phenomena have been observed not only in primary sensory areas but also in some higher order functional areas (Sung 2006, 2007). They depend on the features of inputs that match the processing specificity of the input-receiving areas. Therefore, it may be expected that, when two phonetically identical but graphemically different kana letters are presented as a pair, a reduction in neural response should appear at some stage of the visual recognition process in spite of the difference in shape of the letters, if the stage is involved in processing of the phonological information.

We found suppression in the lateral occipital area (LO) of the left hemisphere when graphemically different but phonetically identical letters were presented (hiragana–katakana pairs), but not when we used letters that differed in both shape and sound (a pair of different hiragana letters). This indicates that, even at the letter recognition level, phonetic information is the dominant form of information used for the discrimination of letters. In addition, the results suggest that the neuronal circuits used for processing two phonetically different letters given in short succession do not show much interaction with each other.

Materials and methods

To evaluate the suppression of neural response we prepared single letter stimulation and paired letter stimulation. As for the single stimulation two sets of single letters of hiragana (H0) and katakana (K0) were used and H0 was used as a reference response for evaluation of the suppression in the paired stimulation. Each element of H0 had its phonetically same counterpart in K0. As for the paired letter stimulation three sets of pairs of phonetically and graphically same letters (pSgS: pair of same hiragana letters), phonetically and graphically different letters (pDgD: pair of different hiragana letters) and phonetically same and graphically different (pSgD: pair of a hiragana and a katakana with the same sound). We performed those stimulation sets in two separate experiments to improve the signal-to-noise ratio because our event-related-like experiment gives low signal-to-noise ratio, H0, pSgS and pDgD in the experiment 1, and the H0, K0 and pSgD in the experiment 2. fMRI responses to those stimulation sets were compared after normalized by H0 in each experiment.

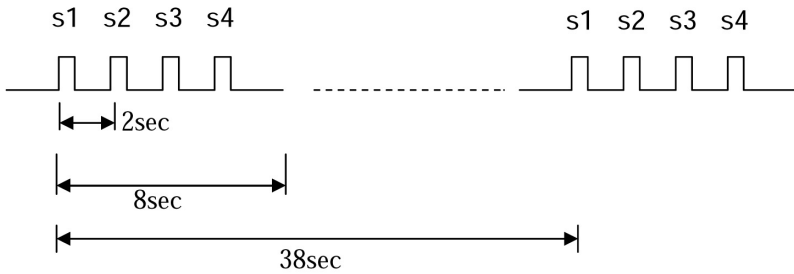


Fig. 1

Stimulation procedure

The experimental run of 106s comprised an initial resting state of 30s, two 8-s trials with an inter-trial interval of 30s, and a post-stimulus resting state of 30s.

During the resting state, the inter-trial interval, and the post-stimulus state, only the fixation point was presented. In each trial, the stimuli were four different single letters or four pairs of letters and stimuli in each trial were given at intervals of 2 s (Fig. 1). Two trials in an experimental run consisted of one of the three stimulation sets in experiment 1 and 2 respectively. Four runs were performed for a stimulation set per subject. Subjects attended to the fixation point passively through every run. The visibility of the subjects was monitored by checking which one of the stimulation sets they looked through the interphone mounted to the MR system after each run.

Experiment 1

The stimuli in each run consisted of single hiragana letters (H0), paired stimuli consisting of two phonologically similar hiragana letters with an ISI of 200ms (pSgS), or paired stimuli consisting of phonetically and graphically different hiragana and hiragana letters with an ISI of 200ms (pDgD). The order of runs was arranged randomly with respect to H0, pSgS, and pDgD for each subject.

Experiment 2

The stimuli in each run consisted of single hiragana letters (H0', the same as H0), single katakana (K0), or paired stimuli consisting of phonetically identical but graphemically different hiragana and katakana letters with an ISI of 200ms (pSgD). The order of runs was arranged randomly with respect to H0, K0, and pSgD for each subject.

Subjects

Subjects were healthy volunteers with a mean age of 23.1 \pm 3.2 (SD) years. Eighteen subjects took part in the first experiment and another seventeen in the second experiment. All participants had normal vision or vision corrected to an acuity of 20/20. They were all right-handed. They had neither a history of neurological disease nor any medical condition contraindicating MRI, such as pregnancy, presence of a cardiac pacemaker, or claustrophobia. After the subjects had been given a complete description of the study, written informed consent was obtained from each of them in accordance with the Declaration of Helsinki. This study was approved by the Institutional Review Board of Hamano Life Science Research Foundation.

Measurements

All MRI experiments were performed using a 3-tesla Allegra scanner (Siemens, Erlangen, Germany) with a standard head coil. After initial localizer images had been acquired, T1-weighted anatomical images were obtained with an inversion-recovery-prepared and magnetization-prepared rapid acquisition with gradient echo sequence with a matrix size of 256 \times 256 over a field of view of 256 mm, and a slice thickness of 1 mm. For functional imaging, we used single-shot gradient-echo echo planar imaging with a repetition time of 1000 ms, echo time of 20 ms, flip angle of 75°, field of view of 200–230 mm, matrix size of 64 \times 64, and slice thickness of 5 mm with a 0.8 mm gap. For each volume, 21 slices parallel to the anterior commissure–posterior commissure plane were acquired.

Visual stimulation

Stimuli were projected on an overhead screen (LP-FX31; Sanyo Co, Japan; spatial resolution 1024 × 768, refresh rate 60 Hz) outside the scanner room. Letters were used as visual stimuli. They occupied 0.5° × 0.5 degrees of the subject's visual field around the fovea. A gray cross-point of 0.34 × 0.34 degrees on a black background (2 cd/m²) was presented throughout the experiment. The "on" duration of all pictures was 33 ms throughout the experiments. The letters were presented in grayscale with an average contrast of 20cd/m².

Image data analysis

The fMRI image data were processed using the software Brain Voyager QX (Brain Innovation B.V., Postbus, Netherlands). All image data acquired during the functional session were motion-corrected by the 3-D motion correction function and preprocessed (linear trend removal, correction for slice scan time, and high-pass filtering with cut-off frequency 0.005 Hz) using Brain Voyager QX. In each functional run, the first 20 volumes were discarded to ensure that a steady state was reached. Two-dimensional data in the functional session were incorporated into 3-D data by trilinear interpolation and transformed into Talairach space using Brain Voyager QX. For multi-subject analysis, 3-D Gaussian spatial smoothing (full width at half-maximum 5.8mm) was applied to the data sets. A multi-subject random effect analysis of the data was conducted. Statistical analysis was performed with a procedure based on the general linear model using Brain Voyager QX. Each experimental condition (except for the control) was defined as a separate predictor. The analysis was performed independently for the time course of each individual voxel, for each subject. For this purpose, the time series of images for all subjects were converted into Talairach space and z-normalized. Then, for each subject, the relative contributions of the predictors for each contrast were estimated separately, and from the set of values obtained (one mean value and variance for each subject), the significance at the multi-subject level (random effect) was calculated. The multi-subject functional maps for each statistical test were superimposed on a Talairach normalized brain of one subject. Functional

areas showing greater responses to phonologically and graphemically different paired stimuli (H0) than other areas were identified by conjunction analysis of pDgD contrasted with pSgS; and pDgD contrasted with H0. The time-courses of the fMRI responses to stimuli in Experiments 1 and 2 were derived from the regions of interest.

RESULTS

Functional activation maps of responses to stimuli in Experiments 1 and 2 showed that the left hemisphere was predominant for stimulation with kana letters in the visual ventral stream. The activated region of the visual ventral stream included the VWFA and the lateral occipital areas (Fig. 2a, b). The response to stimulation with phonetically and graphemically different hiragana–hiragana pairs (pDgD) was greater than those to stimulation with phonetically and graphemically identical hiragana–hiragana (pSgS) pairs and to single hiragana stimulation (H0) only in the LO around $(-41, -68, -6)$ in the left hemisphere (Fig. 2c). Area BA19 $(35, -74, -16)$ in the right hemisphere was the only area which showed a greater response to pDgD than to pSgS and H0 (Fig. 2d).

The time-courses recorded in Experiments 1 and 2 in the LO in the left hemisphere and BA19 in the right hemisphere led to the following

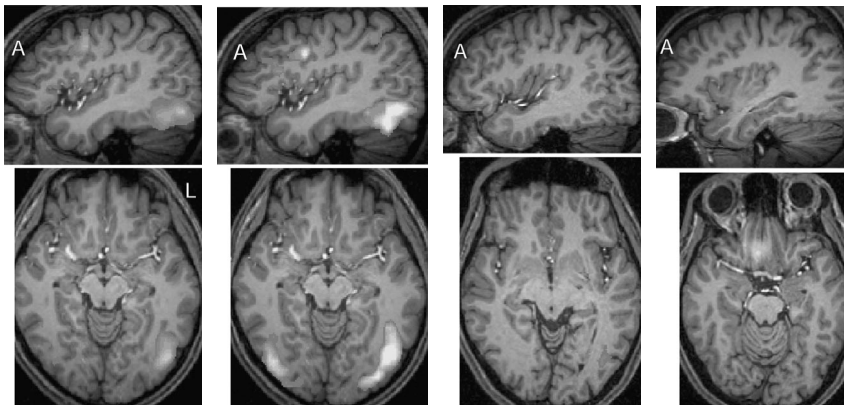


Fig. 2a

Fig. 2b

Fig. 2c

Fig. 2d

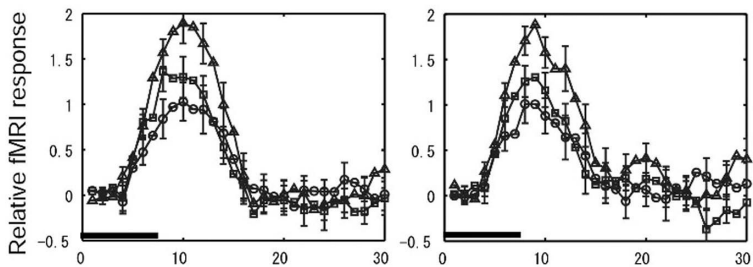


Fig. 3a

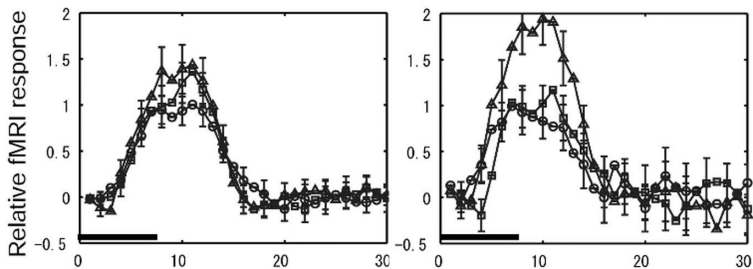


Fig. 3b

observations. The response to paired pDgD stimulation was greater than the responses to H0 and pSgS (Fig. 3a). Whereas, there was no significant difference between H0 and pSgS. The response to phonetically identical but graphemically different hiragana–katakana pairs (pSgD) was not significantly greater than the response to single hiragana letters (H0') and single katakana letters (K0) in the LO of the left hemisphere, but the response to pSgD in BA19 in the right hemisphere was greater than those to H0' and K0 (Fig. 3b). A comparison of responses between pDgD and pSgD showed that pDgD was greater than pSgD in the left LO but not significantly different in the right BA19.

DISSCUSSION

The functional maps show that the left hemisphere dominated responses to kana letters. This laterality is consistent with the language dominance of the

left hemisphere. The response to pSgS shows that there was suppression in the LO and BA19 for phonetically and graphemically identical letters. The response to pDgD shows that there was no significant suppression in the LO and BA19 between the letters different in their shapes and sounds each other. Since refractory suppression occurs when a neuronal circuit is shared by two stimuli presented successively (Ogawa, 2000; Sung, 2007a), our results indicate that, in the LO and BA19, the two letters of each pair in pDgD stimulation were processed almost non-interactively by different neuronal circuits and that the two letters of each pair in pSgS stimulation were processed highly interactively by essentially identical neuronal circuits. Therefore it can be inferred that the LO and the BA19 processed the two letters of pDgD as different ones and the two letters of pSgS as identical ones. This can be easily conceived when one considers that the two letters used in pDgD trials were different phonetically as well as graphemically whereas the two letters used in pSgS trials were identical phonetically and graphemically.

The response to pSgD shows that suppression occurred in the LO but not in the BA19. This indicates that two letters were processed by the same circuit. The suppression is likely resulted from the same phonetical identity of the letters because they were graphically different. This is reasonable when one considers that visual words are processed with in 200 ms during reading after the presentation of stimulus (Huang, 2004, Shirahama, 2004). A similar suppression with respect to a particular attribute of paired inputs was observed in the right occipitotemporal cortex in a study in which paired rectangular frames of different sizes were used. Strong suppression was observed at an ISI of 240 ms in anterior, but not posterior areas of the occipitotemporal cortex (Sung, 2007b), suggesting that the anterior area processed the shape information common to the two inputs regardless of size. The responses to pDgD and pSgD in the present study, therefore, demonstrate that the LO processes kana letters using phonetic information rather than graphemical information and that two different phonetic information are processed in different neuronal circuits from each other (Usui, 2005). This is consistent with are port that phonological information plays an important role in visual word recognition (Conrad, 2007). The non-suppressive response to pSgD in the BA19, on the other hand, indicates that the two letters were processed in this area by different

neuronal circuits in spite of their phonetic identity. This observation and the response to pDgD suggest that the BA19 processes kana letters by grapheme rather than phonetic information if the area deals with linguistic processing. There is, however, a strong possibility that The BA19 processes kana just for shape information regardless of linguistic contents because the left-dominant response to linguistic input is present in the LO and the right LO near to the BA19 is known to be involved in processing shapes of visual objects (Kourtzi, 2000; Lerner, 2001). These results, taken together, provide evidence that the left LO is involved in processing the phonetic content of kana letters and indicate that even at the level of letter recognition, phonetic information is the dominant factor indistinguishing kana letters in Japanese speakers. In addition, the results suggest that separate neuronal circuits are present in the LO for distinguishing phonetic letters, as seen in the response to phonetically nonidentical pairs of letters.

Acknowledgments

The work was supported in part by a subcontract under National Institutes of Health Grant 5R01-EB 00329-02.

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