The overlap of neural selectivity between faces and words: evidences from the N170 adaptation effect

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Abstract Faces and words both evoke an N170, a strong electrophysiological response that is often used as a marker for the early stages of expert pattern perception. We examine the relationship of neural selectivity between faces and words by using a novel application of cross-category adaptation to the N170. We report a strong asymmetry between N170 adaptation induced by faces and by words. This is the first electrophysiological result showing that neural selectivity to faces encompasses neural selectivity to words and suggests that the N170 response to faces constitutes a neural marker for versatile representations of familiar visual patterns.

Keywords N170 · Adaptation · Visual expertise · Neural selectivity

Introduction

The human brain has limited resources for representing the visual world (Dehaene and Cohen 2007). It makes sense that different categories of images share their visual representations to some degree. For example, many non-face expert stimuli recruit the face-selective parts of the visual system (Gauthier et al. 1999, 2000, 2003; Harel et al. 2010; Rossion et al. 2004). Two of the most familiar types of visual patterns are face and written language. Several ERP studies have found that the N170 amplitude elicited by faces is typically much stronger than for non-face objects, and its topography of N170 is more right-lateralized (Bentin et al. 1996; Eimer 2000; Itier and Taylor 2004; Rossion and Jacques 2008). In addition, fMRI studies have found selectivity for faces relative to objects in part of the right fusiform gyrus, a functional area known as the fusiform face area (FFA). The FFA has been proposed by some authors as the neural generator of the face-related N170 component (Grill-Spector et al. 2004; Kanwisher et al. 1997; Kanwisher and Yovel 2006; Rossion and Jacques 2008). By contrast, other work has found that the N170 component evoked by printed words/characters is also stronger than that elicited by other stimuli, such as consonant strings (Bentin et al. 1999; Maurer et al. 2005) or line drawings (Cao et al. 2011; Yum et al. 2011; Zhao et al. 2012), and it is more pronounced in the left hemisphere. The fMRI results also demonstrate that printed words activate a precise site in the left occipitotemporal sulcus, which is termed visual word form area (VWFA), and the VWFA is thought as the neural generator of the N170 to words (Cohen et al. 2000; Dehaene and Cohen 2011; Mei et al. 2010).

Despite their differences, current studies suggested that there may be a strong relationship between the visual representations for faces and words. For example, reading ability was associated with an increase in left fusiform activation for words and a reduced response to faces at this location (Dehaene et al. 2010). In a recent developmental study, the development of N170 for face processing was delayed by the reading experience of Chinese characters (Li et al. 2013).

In addition, deficits in word recognition in prosopagnosic individuals and in face recognition in pure-alexic individuals also suggest that each hemisphere may play a dual, albeit graded, role in both face and word recognitions. Gainotti and Marra (2011) reported that the face recognition impairment was more severe following bilateral than...
unilateral lesions (Gainotti and Marra 2011), and Coslett and Monsul (1994) also found that transcranial magnetic stimulation (TMS) of the right hemisphere impaired reading in patients with left-hemisphere lesions (Coslett and Monsul 1994). One recent study documented that a left occipital arteriovenous malformation resulted in both pure alexia and prosopagnosia (Liu et al. 2011).

Such neural evidence suggests that both faces and words evoke a representation that is shared to a certain degree. Behavioral studies also reveal important similarities between faces and words. Although the configural information critical for identity processing is different between faces and words, there are many similarities between the two categories. For example, extensive and long-term exposure, canonical upright orientation, high-level expertise, predominantly individual-identity level processing, and featural information critical for identity processing may all contribute to shape expert perception in both domains (McCleery et al. 2008). Moreover, Hsiao and Cottrell (2009) suggested that the visual expertise of faces and words may be decomposed into at least two components: a common component that involves an efficient coarse-coding and a stimulus-dependent component (Hsiao and Cottrell 2009).

Thus, these neural and behavioral studies suggest that the neural selectivity of early face processing overlaps, and perhaps encompasses, that of words. However, thus far, nothing is known about the nature of overlap between electrophysiological selectivity to faces and words.

The adaptation paradigm offers a sensitive method to investigate category-specific neural selectivity. Adaptation, reduced neural response following repeated presentation of a stimulus, is also a well-known electrophysiological phenomenon (Brown and Xiang 1998; Desimone 1996). Recently, many studies have used neural adaptation procedures to identify the mechanisms that are responsible for category-specific ERP components such as the N170 (Eimer et al. 2008). Moreover, Hsiao and Cottrell (2009) suggested that the visual expertise of faces and words may be decomposed into at least two components: a common component that involves an efficient coarse-coding and a stimulus-dependent component (Hsiao and Cottrell 2009).

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Procedure

The participants were asked to sit on a chair, with a distance of 90 cm away from the 17” CRT monitor (1,024 × 768 pixel resolution), on which all stimuli were presented against a dark gray background. E-Prime software was used for stimulus presentation and behavioral response collection (Psychology Software Tools, Pittsburgh, PA).

Subjects were tested in a dimly lit room. In each trial, an adaptor stimulus and a test stimulus were presented sequentially for 200 ms each with a 200-ms inter-stimulus interval and followed by a 1,500-ms intertrial interval, which was consistent with Eimer et al. (2010). Adaptor stimuli and test stimuli were always different. One of three possible adaptor stimuli—faces (F), Chinese characters (C), or houses (H)—was followed by one of two possible target stimuli (F or C). Therefore, there were six conditions: FF, CF, HF, CC, FC, and HC. Equal numbers of each category were presented in random order in each of the four experimental blocks. There were 108 trials in each block, 12 of which were target trials with a red outline shape aligned with the outer contours of the stimulus shape. These target trials were randomly intermixed with the experimental trials and presented with equal probability as adaptor stimuli or test stimuli. Participants were instructed to press a response button following the second picture presentation when they
detected a target. Response buttons were counterbalanced across subjects.

Electrophysiological recording and data analysis

Electroencephalography (EEG) was recorded using a 128-channel HydroCel Geodesic Sensor Net, with an electrode placed on the Vertex (Cz) serving as reference for the online recording. Electrode impedances were kept below 50 kΩ. Signals were digitized at a 500-Hz sampling rate and amplified with a 0.1–200-Hz elliptical band-pass filter. EEG data were offline digitally filtered with a 0.3–30-Hz band-pass filter and epoched from 200 ms before to 800 ms after stimuli onset with a 100-ms pre-stimulus baseline. Trials with artifacts exceeding ±100 μV were rejected. Any subject with more than 30% bad segments would be excluded from the group average. The remaining EEG data were re-referenced to the average of channels.

EEG data were analyzed for nontarget trials only. A group of channels over the left occipitotemporal regions (channels: 58, 64, 65) and right occipitotemporal regions (channels: 90, 95, 96) were analyzed, where the N170 components were maximal. EEG waveforms were averaged separately for each presentation condition of adaptor or test stimuli. Based on the visual inspection of the individual data, the N170 time window was defined as 130–210 ms for adaptor stimuli and 140–220 ms for test stimuli. Repeated-measures analyses of variance (ANOVA) were performed on the peak amplitudes and latencies of N170 component with stimuli category and recording hemisphere serving as within-subject factors.

Results

Adaptor stimuli data

The results of adaptor stimuli were shown in Fig. 1, Tables 1 and 2. A two-way repeated-measures ANOVA of N170 peak amplitudes and latencies was conducted for adaptor categories (faces, characters, houses) and hemispheres (left hemisphere and right hemisphere). A main effect of adaptor category on N170 amplitude \([F(2, 30) = 14.619, p < 0.001, \eta^2_p = 0.494]\) and an interaction between adaptor categories and hemispheres \([F(2, 30) = 8.227, p = 0.003, \eta^2_p = 0.354]\) were found. Post hoc tests revealed that the N170 amplitudes elicited by faces were much larger than Chinese characters \((p = 0.001)\) and houses \((p < 0.001)\). There was a main effect of adaptor category on N170 latency \([F(2, 30) = 10.990, p = 0.001, \eta^2_p = 0.423]\) and an interaction between adaptor and hemisphere \([F(2, 30) = 6.678, p = 0.005, \eta^2_p = 0.308]\). Paired comparisons showed that the N170 was earlier for characters relative to faces \((p = 0.003)\) and houses \((p = 0.001)\).

Test stimuli data

We analyzed the N170 amplitude elicited by the test stimuli in six combinations of adaptor and test category. One of three possible adaptor stimuli—faces (F), Chinese characters (C), or houses (H)—was followed by one of two possible target stimuli (F or C). Therefore, there were 6 conditions: FF, CF, HF, CC, FC, and HC. For example, CF refers to the N170 amplitude to faces in condition CF, after adapting to a character. The average wave shapes and the topographical map are shown in Fig. 2.

The results of the 6 conditions analysis were shown in Tables 3 and 4. The repeated-measures ANOVA of N170 peak amplitudes and latencies were conducted for the 6 conditions (CC, CF, FC, FF, HC, and HF) and hemispheres (left hemisphere and right hemisphere). For the N170 peak amplitude, a main effect of test category \([F(5, 75) = 12.910, p < 0.001, \eta^2_p = 0.463]\) and an interaction between conditions and hemisphere \([F(5, 75) = 6.877, p = 0.001, \eta^2_p = 0.314]\) were found. Post hoc tests are shown in Table 5. There was a main effect of 6 conditions on N170 latency \([F(5, 75) = 7.295, p < 0.001, \eta^2_p = 0.327]\).

To test the relationship between face N170 adaptation and word N170 adaptation, we focused the analyses as follows:

The adaptation effect of both face- and character-specific N170s is typically measured relative to a house-induced...
The adaptation effect: HF is significantly larger than FF in both the left \( p < 0.001 \) and right hemispheres \( p < 0.001 \). The results replicated the previous studies (Eimer et al. 2010, 2011). HC is significantly larger than CC in both the left \( p = 0.001 \) and right hemispheres \( p < 0.001 \).

The results of the cross-category adaptation effect between faces and Chinese characters were revealed by the following analysis:

We analyzed the face-specific N170 (FN) adaptation effect in the FF, CF, and HF conditions. The amplitude in the FF condition was significantly smaller than in the CF (left, \( p = 0.001 \); right, \( p < 0.001 \)) and HF (left, \( p < 0.001 \); right, \( p < 0.001 \)).

Table 1

|                         | Amplitudes (μV) | Latencies (ms) |
|-------------------------|-----------------|----------------|
|                         | LH              | RH             |
| Character               | –6.12 (3.15)    | –6.01 (3.71)   |
| Face                    | –7.07 (3.06)    | –8.35 (4.53)   |
| House                   | –5.40 (3.11)    | –6.27 (4.58)   |

Table 2

|                         | Amplitudes | Latencies |
|-------------------------|------------|-----------|
|                         | LH         | RH        |
| Character               | 156.52     | 151.94    |
| Face                    | 161.06     | 160.77    |
| House                   | 159.58     | 160.42    |

Fig. 2 Top row The averaged N170 waveforms elicited by test stimuli at the left and right hemispheres separately. Bottom row The N170 amplitudes elicited by the test stimuli in different-adaptation conditions.
right, \( p < 0.001 \) conditions. And the amplitude in the CF was similar to that in the HF condition. It suggested that Chinese characters and houses have the same effect to the rapid followed face stimuli, namely compare with face, both the Chinese characters and houses almost could not produce the adaptation effect to the faces. The results of the adaptation effect of the Chinese character N170 (CN) in the CC, FC, and HC conditions are as follows: The amplitude of CN in the HC condition was significantly larger than those in the FC (left, \( p = 0.012 \); right, \( p < 0.001 \)) and CC (left, \( p = 0.001 \); right, \( p < 0.001 \)) conditions. Most importantly, the amplitude of CN was similar in the FC and CC conditions (left, \( p = 0.443 \); right, \( p = 0.092 \)). The results suggested that both faces and Chinese characters produced the similar CN adaptation effect to the following Chinese characters.

In summary, the dramatic results show that faces produce an N170 adaptation effect on Chinese characters, but Chinese characters cannot elicit a similar adaptation effect on faces.

**Discussion**

The purpose of this study was to reveal the relationship of the neural selectivity between faces and words. In this experiment, our results show an asymmetric N170 adaptation effect between faces and Chinese characters, that is, faces produced full adaptation to Chinese characters, not vice versa. This surprising phenomenon provides many insights into the neural selectivity of the N170 component.

Together with the principle of adaptation (Frazier et al. 1967; He and MacLeod 2001), our results allow us to examine the nature of the overlap in neural selectivity to faces and Chinese characters. Just as shown in Fig. 3, the first three scenarios imply the symmetric adaptation, while the last two refer to the asymmetric one. The fourth scenario (Fig. 3d) shows that the neural selectivity of CN completely contains the neural selectivity of CN. But previous studies suggested that the N170 elicited by face stimuli was related to holistic/configural processing (Itier and Taylor 2004), which is a critical property of face perception but not of Chinese character (McCleery et al. 2008). Moreover, if this scenario is true, based on the principle of adaptation (Frazier et al. 1967; He and MacLeod 2001), the adaptation effect of Chinese characters on faces would be stronger than that of faces to Chinese characters. So this possibility cannot be supported. Therefore, the only possibility is that the neural selectivity of FN completely encompasses that of CN. But as shown in Fig. 3e, which can reasonably explain our main results and coincide with our hypothesis. This possibility also suggests that the complex component with bigger neural selectivity (e.g., FN) could produce complete adaptation of the smaller one (e.g., CN).

In the previous studies, there are two major views about the relation between faces and words of expertise processing (Plaut and Behrmann 2011). With the different characteristics of N170 component and neural area (FFA and VWFA) activated by faces and words, one view is that...
faces and words engage separate psychological and neural mechanisms and are essentially unrelated and independent (Kleinschmidt and Cohen 2006), as the option in Fig. 3b. Alternatively, other studies suggest an important relationship between the visual representations for faces and words (Plaut and Behrmann 2011), as the option in Fig. 3c. For example, both Dehaene et al. (2010) and Li et al. (2013) found that expert processing of words competes with that of faces. And many prosopagnosic/pure-alexic studies also provided strong evidence for the relationship between face and words processing (Coslett and Monsul 1994; Gainotti and Marra 2011; Liu et al. 2011). Our findings provide an opportunity for settling the dispute. Our results suggest that the N170 functions for face processing fully encompass the function for word processing. It supports the latter view that there is an important relationship between the visual representations for faces and words. Importantly, our results extend this view that the relationship of early expertise processing between faces and words is specific, that is, the face N170 function encompasses completely the N170 function for word processing.

The above analysis demonstrates that the face N170 reflects a broad range of functions that include those involved in Chinese character processing. The stimuli used in the present study were Chinese single characters, which elicited the similar N170 response with the Chinese words (Xue et al. 2008). But in alphabetic scripts, the results of how the length of words affects the N170 response are inconsistent (Hauk and Pulvermüller 2004; Wydell et al. 2003). Future studies may examine the adaptation effect between houses and line drawings (Cao et al. 2011). One reason may be that the non-face stimuli in the present study were all from the same category (house), while in the previous study the line drawings were from a variety of categories. Future studies may be designed to reveal the difference in N170 response between houses and line drawings.

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