Dissociation of category versus item priming in face processing: an event-related potential study

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Abstract The underlying specificity of visual object categorization and discrimination can be elucidated by studying different types of repetition priming. Here we focused on this issue in face processing. We investigated *category priming* (i.e. the prime and target stimuli represent different exemplars of the same object category) and *item priming* (i.e. the prime and target stimuli are exactly the same image), using an immediate repetition paradigm. Twenty-three subjects were asked to respond as fast and accurately as possible to categorize whether the target stimulus was a face or a building image, but to ignore the prime stimulus. We recorded event-related potentials (ERPs) and reaction times (RTs) simultaneously. The RT data showed significant effects of *category priming* in both face trials and building trials, as well as a significant effect of *item priming* in face trials. With respect to the ERPs, in face trials, no priming effect was observed at the P100 stage, whereas a *category priming* effect emerged at the N170 stage, and an *item priming* effect at the P200 stage. In contrast, in building trials, priming effects occurred already at the P100 stage. Our results indicated that distinct

neural mechanisms underlie separable kinds of immediate repetition priming in face processing.

Keywords Category priming · Item priming · P100 · N170 · P200

Introduction

Previous studies have made great progress in elucidating two generally distinct but mutually complementary processes involved in visual object encoding: object categorization—to allocate visual inputs to distinct object categories according to categorical perceptual boundaries (e.g. Harnad 1987; Koutstaal et al. 2001; Kovács et al. 2006); and object discrimination—to differentiate among objects with similar structural features or names (e.g. Jacques and Rossion 2006; Koutstaal et al. 2001; Schweinberger et al. 2002a). Nonetheless, it remains controversial when and where these two processes take place in the human visual system.

Using appropriate task paradigms, the investigation of repetition priming can provide important information about the mechanisms underlying particular perceptual or cognitive processes: at the time point (or brain area) when (or where) repetition priming occurs, the specific perceptual or conceptual processing takes place in the brain (Henson 2003). However, very few studies have investigated category versus item priming in parallel. As far as we know, only one fMRI study (Koutstaal et al. 2001) has probed these two kinds of repetition priming simultaneously, but due to the restriction of their measuring method, the researchers employed long-lag repetition paradigm and focused on the spatial characteristics of the neural data.

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Focusing on either one of the two types of repetition priming, a substantial portion of event-related potentials (ERP) studies have investigated face processing, and various groups have reported distinct modulations, especially for ERP components such as the N170 and N250r (e.g. Caharel et al. 2009; Eimer et al. 2010; Engst et al. 2006; Guillaume et al. 2009; Henson et al. 2004; Itier and Taylor 2002, 2004a; Jacques and Rossion 2006; Jacques et al. 2007; Kloth et al. 2010; Kovács et al. 2006; Martens et al. 2006; Schweinberger et al. 1995, 2002a, 2004; Trenner et al. 2004; Werheid et al. 2005).

The N170 is a face-sensitive negative ERP component peaking at ~130–190 ms after stimulus onset over the occipito-temporal electrodes sites (e.g. Bentin et al. 1996). Given that it displays increased magnitude and right-hemisphere dominance in response to face images relative to other object categories, the N170 was generally accepted as an indicator of structural encoding of faces at a categorical rather than individual recognition level (e.g. Bentin and Deouell 2000; Caharel et al. 2002; Eimer 2000; Itier and Taylor 2004b, c; Rossion et al. 1999, 2000; Rousselet et al. 2004; Schweinberger et al. 2002a, 2004; Tanaka et al. 2006), and was proposed to be correlated with perceptual processes tuned to discriminating faces from non-face objects (e.g. Bentin et al. 1996; Bentin and Deouell 2000; Eimer 2000; Haxby et al. 2000; Rossion and Jacques 2008; Schweinberger et al. 2002a). In addition, ERP studies have also reported that individual face discrimination (face recognition) takes place at about 250 ms following stimulus onset, much later than face detection (e.g. Bentin and Deouell 2000; Eimer 2000; Schweinberger et al. 2002a). The above-mentioned ERP results are largely in line with classic face and object recognition models (Bruce and Young 1986; Ellis and Young 1996), which suggest that faces or objects are initially reduced to specific object categories according to their global visual features, and then the products of initial pictorial and structural encoding are matched with the structural representations of known faces or objects stored in the face recognition units (FRUs) or object recognition units (ORUs), allowing the recognition of a specific face or object.

However, using a continuous stimulation paradigm, in which one stimulus shifted to another without any blank period, a recent ERP study showed that individual face discrimination might be achieved in humans at around 150 ms after stimulus onset, approximately in parallel with face detection (Jacques and Rossion 2006).

To elucidate this issue, the present study used two kinds of immediate repetition: category and item repetition. We focused on ERP modulations reflective of *category* and *item priming* at early visual information processing stages. Importantly, *category priming* was addressed by comparing the ERPs elicited by the target stimulus in within-

category conditions (e.g. a face prime followed by a face target) versus between-category conditions (e.g. a building prime followed by a face target). In contrast, *item priming* was addressed by comparing the ERPs elicited by the target stimulus in identical-exemplar conditions (e.g. a face prime followed by the same face as a target) versus different-exemplar (but same object category) conditions (e.g. a face prime followed by a different face as a target).

The investigation of *category* versus *item priming* may shed light on the neural processes that support relatively abstract category discrimination as opposed to highly image-specific perceptual matching of visual objects. Furthermore, by using different categories of objects as target stimulus (face versus building images), we were able to investigate whether *category* and *item priming* in face processing represent general properties of visual object processing, and whether the temporal characteristics of the involved neural processes are similar across different object categories.

Methods

Subjects

A total of 23 Kyushu university students (10 female, all right-handed) participated in the data collection of this study. The mean age of the subjects was 24.9 ± 2.2 years (range: 22–29). All subjects reported normal or corrected-to-normal visual acuity and none had a history of neurological disease. Two further subjects were excluded because of high error rates in task performance (>50%), and another was excluded because of technical problems during data recording. The experiments were conducted with the understanding and the written consent of each subject, as according to the requirements set by the Declaration of Helsinki. The experimental protocol was formally approved by the ethical committee of Kyushu University.

Stimuli

Photographs of 300 Japanese people's faces from a face database (Softopia Japan) and 300 Japanese style houses were used as the visual stimuli in the present experiment. The photographs were all software-edited using Photoshop 7.0: each photograph was converted to grayscale, and framed within an area of 230 pixels wide $\times$ 325 pixels high (8×10 cm), forming a visual angle of $5.7^\circ \times 7.2^\circ$. An attempt was made to homogenize the stimuli with respect to average luminance and contrast. The stimuli were presented to the subjects using a CRT monitor (Flex ScanT561).

Procedure

After the EEG electrodes were applied and prior to the experiment, participants received written and verbal task instructions. During the experiment, the subjects were comfortably seated in a dimly lighted shielded room. A fixed chinrest was used to maintain a constant viewing distance of 80 cm. A total of 40 practice trials preceded the critical trials; the faces and buildings used in these practice trials were different from those used in the critical trials. In the entire experimental procedure, each face or building image was used only once.

Experiments were designed and performed with STIM2 (NeuroScan). At the very beginning of each experimental block, a message “Are you ready” was presented until the subjects were well prepared to press the mouse to start. Each trial consisted of the presentation of a prime stimulus and a target stimulus successively: at the center of the screen (the background was dark gray throughout the experiment), first, a white fixation crosshair appeared for 300–500 ms and was then replaced by a prime stimulus (a blank, a face or a building image) presented for 33 ms, followed by a stimulus onset asynchrony (SOA) of 600 ms and finally the target stimulus (a face or a building image) presented for 33 ms. The inter-trial interval was randomly set to 2,200–2,700 ms (Fig. 1a). During the stimulus presentation of a pair, the subjects were asked to avoid blinks and ocular movement as much as possible.

There were 8 conditions of stimulus pairs. Listed as *prime-target*, the conditions were: (1) blank_face, (2) build_face, (3) face_face(d), (4) face_face(s), (5) blank_build, (6) face_build, (7) build_build(d), and (8) build_build(s). Note that “blank” refers to a gray neutral (entirely empty) image, “(d)” stands for a target stimulus that was different from the prime, and “(s)” denotes a target stimulus that was the same as the prime. For the face_face(d) condition, the prime and the target faces were always of the same gender and age. Examples for each condition are shown in Fig. 1b.

The conditions 1–4 represented face trials; 5–8 were building trials. *Category priming* could be investigated for face processing by comparing conditions 1 and 2 with 3 and 4, and for building processing by comparing conditions 5 and 6 with 7 and 8. *Item priming* could be investigated for face processing by comparing condition 3 versus 4, and for building processing by comparing condition 7 versus 8. The conditions with blank primes (1 and 5) were included as controls without priming, but with visual transients of the same timing parameters as the visual transients in the other conditions. Thus, interference effects from different category primes could be investigated for face processing by comparing condition 1 versus 2, and for building processing by comparing condition 5 versus 6.

It should be noted that, in the present paradigm, there was an equal likelihood of face and building trials. However, to maximize the opportunity to observe repetition priming, we opted to include an equal number of all types of trials. This implied that, given a face prime, there was an equal likelihood of three types of trial: face_build, face_face(d) and face_face(s). In other words, given a face prime, there was a chance of 1/3 that there would follow a building and a chance of 2/3 that there would follow a face (vice versa in case of a building prime). Importantly, in our study we did not aim to disentangle explicit (attentional) versus implicit (automatic) mechanisms of repetition priming. (There is no “perfect” constant probability to disentangle implicit versus explicit mechanisms of repetition priming; also with a constant chance of 1/2 for a face to follow a face, one would not be able to make any claims about automatic versus attentional processes in repetition priming.) Obviously, any research that wishes to disentangle these mechanisms should systematically *vary* the probabilities of prime-target combinations, rather than keeping the probabilities constant as we did, and as is usually done.

Participants were asked to decide by speeded two-choice mouse clicks whether the target stimulus in each trial was a face or a building image, but to ignore the prime stimulus. Speed and accuracy were emphasized. The arrangement of left and right mouse click was counterbalanced across subjects. Incorrect or missing responses were indicated by a feedback tone of (500 Hz, 3,000 ms) and a red-colored cue indicating “ERROR” (2,000 ms).

The experiment consisted of 8 blocks; 50 trials were presented in each block, with self-paced breaks between blocks. All 400 trials were shown in randomized order. Thus, each condition consisted of 50 critical trials.

Performance recording

Responses were scored as correct if the appropriate mouse click was pressed within a time window of 100–2,000 ms after stimulus onset. Mean reaction times (RTs) were calculated for correct responses only.

EEG acquisition

The EEG was recorded with 64 sintered Ag/AgCl electrodes in an electrode cap (Easy-cap) at scalp positions in accordance with the extended international 10–20 system. Impedances of all electrodes were generally kept below 5 K Ω . EEG was measured relative to the system reference (C3, C4), and an electrode placed at the nasion served as the ground. Amplified analog signals (with a band-pass ranging from 0.16 to 120 Hz) were digitized at 1,000 Hz (Neurofax1000, Nihon Kohden, Japan). Offline, EEG data were digitally low-pass filtered at 30 Hz. Trials with

Fig. 1 **a** Time sequence of the experiment. **b** Examples of the 8 types of priming. *Left side* the target stimulus is a face image; *Right side* the target stimulus is a building image. For ease of description, we use “build” instead of “building”, “(s)” instead of “(same)” and “(d)” instead of “(different)”

eye-blinks and other artifacts ($>100 \mu\text{V}$) were initially rejected automatically (using software BESA 5.2) and further scrutinized manually. Incorrect trials and trials containing artifacts were excluded. Then, for the target stimulus of each pair, in all the conditions for all subjects, the averaging epochs began 100 ms prior to target stimulus onset (-100 to 0 ms serving as the baseline) and continued

until 1,000 ms after target stimulus onset. The averaged data were re-referenced to the average-reference.

Data analysis

ERP analyses were performed with BESA5.2. For statistical analyses, repeated measurement ANOVAs were

conducted with three within-subject factors: (1) prime content (PRIME), (2) target material (MATERIAL), and (3) hemisphere (LATERALITY).

For the factor PRIME there were four levels: (1) blank (*blank*), (2) different-category (*diff_cat*), (3) same-category-different-item (*diff_item*), and (4) same-category-same-item (*same_item*). For the factors MATERIAL and LATERALITY, there were two levels each: faces versus buildings, and left versus right, respectively.

In the analysis of RTs, only the first 2 factors were included. When necessary, Huynh–Feldt adjustment was applied in case of sphericity violations. Uncorrected degrees of freedoms, but corrected P values were used in the results description. Significant interactions, if any, were clarified by breaking them into simple effects. For post hoc pair-wise comparisons, Tukey's HSD test was used. When the sphericity assumption was not met, Huynh–Feldt corrected mean square error and degrees of freedom were used in calculating the HSD critical value.

Results

For ease of description, the eight priming conditions were abbreviated in italics below: *blank_face*, *build_face*, *face_face(d)*, *face_face(s)*, *blank_build*, *face_build*, *build_build(d)* and *build_build(s)*. For results description, values of Mean $\pm$ SD (standard deviation) were used.

Behavioral performance

Means and SDs of RTs and error rates (ERs) for both face and building trials are shown in Table 1. No omission of response was observed. RTs in correct trials and ERs were submitted to ANOVAs with repeated measures on PRIME and MATERIAL.

With respect to ERs, there was a main effect of MATERIAL [$F(1,22) = 6.20$, $P = 0.021$], disclosing a higher error rate in building trials ($1.48 \pm 1.31\%$) than in face trials ($0.96 \pm 0.89\%$). Neither the factor of PRIME [$F(3,66) = 1.90$, $\epsilon = 0.834$, $P = 0.149$] nor the interaction of MATERIAL $\times$ PRIME [$F(3,66) = 1.23$, $P = 0.307$] produced a significant effect.

As expected, the ANOVAs on RTs revealed a significant main effect of PRIME [$F(3,66) = 58.35$, $P < 0.001$], with mean values of 533.25, 539.76, 495.10 and 481.55 ms for *blank*, *diff_cat*, *diff_item* and *same_item* trials, respectively. Since the MATERIAL $\times$ PRIME interaction also reached significance [$F(3,66) = 3.27$, $P = 0.026$], one-way ANOVAs (with factor PRIME) were performed on face trials and building trials, respectively. The results showed that main effect of PRIME reached significance in both face trials [$F(3,66) = 62.04$, $P < 0.001$] and building trials [$F(3,66) = 31.92$, $P < 0.001$]. Therefore, post hoc pair-wise comparisons were performed on face trials and building trials, separately. In building trials, RT in *blank_build* trials was slower than both *build_build(d)* trials ($q = 7.20$, $P < 0.001$) and *build_build(s)* trials ($q = 9.18$, $P < 0.001$); and RT in *face_build* trials was also slower than both *build_build(d)* trials ($q = 9.84$, $P < 0.001$) and *build_build(s)* trials ($q = 11.81$, $P < 0.001$). Similarly, in face trials, RT in *blank_face* trials was slower than both *face_face(d)* trials ($q = 10.87$, $P < 0.001$) and *face_face(s)* trials ($q = 15.41$, $P < 0.001$); and RT in *build_face* trials was slower than both *face_face(d)* trials ($q = 11.10$, $P < 0.001$) and *face_face(s)* trials ($q = 15.65$, $P < 0.001$). Moreover, there was also a significant difference between *face_face(d)* trials and *face_face(s)* trials ($q = 4.54$, $P = 0.011$). It took a shorter time to categorize a face stimulus as a face when it was primed by an identical face rather than another face exemplar. Significant pair-wise differences in RTs were denoted for face and building trials separately as shown in Fig. 2. There was no significant main effect of MATERIAL [$F(1,22) = 2.24$, $P = 0.149$].

ERPs analyses

ERP repetition priming effects were investigated on three early ERP components: P100, N170 and P200. For each subject, the ERPs elicited by the target stimulus of each pair of stimuli were analyzed. Mean amplitudes of these ERP components were measured in their respective time windows and pooled scalp region of interest (ROI), when and where these components were most prominent: 90–130 ms at electrodes O1/2, PO3/4, PO5/6 and PO7/8 for P100; 140–180 ms at electrodes P5/6, P7/8, PO5/6 and

Table 1 Means and standard deviations (SD) of reaction times (RT) and error rates (ER)

Conditions	RT($\pm$ SD) ms	ER($\pm$ SD) %	Conditions	RT($\pm$ SD) ms	ER($\pm$ SD) %
Blank_face	534.68 $\pm$ 126.48	0.67 $\pm$ 0.81	Blank_build	531.81 $\pm$ 133.69	1.40 $\pm$ 1.93
Build_face	535.60 $\pm$ 114.00	1.64 $\pm$ 1.98	Face_build	543.93 $\pm$ 122.40	1.59 $\pm$ 1.87
Face_face(d)	491.59 $\pm$ 121.05	0.68 $\pm$ 0.95	Build_build(d)	498.62 $\pm$ 123.26	1.58 $\pm$ 2.04
Face_face(s)	473.57 $\pm$ 116.17	0.86 $\pm$ 1.38	Build_build(s)	489.53 $\pm$ 140.05	1.36 $\pm$ 1.07
Face mean	508.86 $\pm$ 118.41	0.96 $\pm$ 0.89	Building mean	515.98 $\pm$ 128.62	1.48 $\pm$ 1.31

Fig. 2 Reaction times (+SE), separately for each condition. *Left side* face trials; *Right side* building trials. (* $P < 0.05$, *** $P < 0.001$)

PO7/8 for N170; and 200–250 ms at electrodes CP5/CP6, TP7/TP8, P5/P6 and P7/P8 for P200. The time segments were chosen to cover the peak latencies of each component in each condition for each subject. The electrode positions were selected on the basis of face-preferred effects in the previous literature (e.g. Eimer 2000; Itier and Taylor 2004a; Rossion et al. 2000; Schweinberger et al. 2002a) and our examination of both the grand averages and individual data. The mean amplitudes of each component were then submitted to three-way repeated measurement ANOVAs, with PRIME, MATERIAL and LATERALITY as within-subjects factors.

P100 component

This component was most pronounced at occipital sites. As shown in Fig. 3, for face trials, the magnitude of the target-elicited P100 was hardly affected by the content of the prime stimulus. In contrast, for building trials, the content

of the prime stimulus greatly influenced the amplitude of the target-elicited P100. When the prime and target stimuli were the same building image [*build_build(s)*], the P100 was the smallest; when the target building stimulus was primed by a face stimulus (*face_build*), the P100 was the largest.

Three-way ANOVAs on P100 mean amplitudes confirmed main effects of LATERALITY [$F(1,22) = 4.48$, $P = 0.046$] and PRIME [$F(3,66) = 9.56$, $\epsilon = 0.686$, $P < 0.001$], and an interaction of MATERIAL $\times$ PRIME [$F(3,66) = 11.45$, $P < 0.001$]. None of the other main effects and interactions reached significance: MATERIAL [$F(1,22) = 1.38$, $P = 0.253$]; MATERIAL $\times$ LATERALITY [$F(1,22) = 2.47$, $P = 0.130$]; LATERALITY $\times$ PRIME [$F(3,66) = 1.38$, $\epsilon = 0.594$, $P = 0.263$]; MATERIAL $\times$ LATERALITY $\times$ PRIME [$F(3,66) = 0.53$, $\epsilon = 0.754$, $P = 0.616$].

With respect to the significant main effect of LATERALITY, the mean amplitude of the target-elicited P100 was

Fig. 3 Grand averaged P100 component elicited by the target stimulus of each pair of stimuli. The waveforms were obtained by pooling over electrodes O1/O2, PO3/PO4, PO5/PO6 and PO7/PO8, as shown in gray in the scalp model. *Left side* face trials; *Right side* building trials. It can be observed that in face trials, there were almost

no differences for the P100 components in the 4 conditions; however, in building trials, there emerged apparent differences already at this stage: the amplitude of the target-elicited P100 was smallest in *build_build(s)* and largest in *face_build*

slightly larger in the right pooled electrodes ($4.39 \pm 2.48 \mu\text{V}$) than in the left pooled electrodes ($3.78 \pm 2.10 \mu\text{V}$). The MATERIAL $\times$ PRIME interaction was further evaluated by performing separate one-way ANOVAs (with factor PRIME) on face trials and building trials. A main effect of PRIME was observed in building trials [$F(3,66) = 16.60$, $\varepsilon = 0.906$, $P < 0.001$], but not in face trials [$F(3,66) = 0.92$, $\varepsilon = 0.831$, $P = 0.422$]. Post hoc analyses on building trials revealed that significant differences were found in five pair-wised comparisons (Fig. 4). Specifically, the target building stimulus in *face_build* ($4.89 \pm 2.55 \mu\text{V}$) elicited a larger P100 than in *blank_build* ($3.90 \pm 2.03 \mu\text{V}$) ($q = 5.14$, $P = 0.003$), *build_build(d)* ($3.97 \pm 2.00 \mu\text{V}$) ($q = 4.75$, $P = 0.007$) and *build_build(s)* ($3.06 \pm 2.23 \mu\text{V}$) ($q = 9.49$, $P < 0.001$). The target building stimulus in *build_build(s)* elicited a smaller P100 than in *face_build* ($q = 9.49$, $P < 0.001$), *blank_build* ($q = 4.35$, $P = 0.016$) and *build_build(d)* ($q = 4.74$, $P = 0.007$).

In view of the fact that divergence already emerged at the P100 stage in building trials, it is difficult to exclude the possibility that any later ERP modulations in building trials were influenced by the differences at the P100 level. For this reason, further analyses focused on face trials only.

N170 component

Consistent with previous literature, the N170 component appeared to be most prominent in the occipito-temporal sites. For face trials only, priming induced N170 modulation is shown in Fig. 5. It can be observed from the waveforms that, the target-elicited N170 amplitude in *blank_face* and *build_face* were moderately larger than

those in *face_face(d)* and *face_face(s)*, but there was virtually no difference between *face_face(d)* and *face_face(s)*.

Two-way ANOVAs (within-subject factors: PRIME and LATERALITY) were performed on the mean amplitudes of the target-elicited N170 in face trials. The results revealed a main effect of PRIME [$F(3,66) = 6.79$, $\varepsilon = 0.720$, $P = 0.002$] and an interaction of LATERALITY $\times$ PRIME [$F(3,66) = 3.51$, $\varepsilon = 0.748$, $P = 0.033$], but no main effect of LATERALITY [$F(1,22) = 2.02$, $P = 0.169$]. To elucidate the LATERALITY $\times$ PRIME interaction, one-way ANOVAs (with factor PRIME) were performed on the pooled electrodes in the left and right hemisphere, respectively. A significant main effect of PRIME was found in both the left [$F(3,66) = 5.37$, $\varepsilon = 0.636$, $P = 0.002$] and the right [$F(3,66) = 7.25$, $\varepsilon = 0.826$, $P < 0.001$] hemisphere. Post hoc analyses as shown in Fig. 6 disclosed that in the left hemisphere, the amplitude of the target-elicited N170 in *build_face* ($-1.56 \pm 2.42 \mu\text{V}$) was significantly larger than in *face_face(d)* ($-0.33 \pm 2.29 \mu\text{V}$), ($q = 4.37$, $P = 0.018$); in the right hemisphere, *build_face* ($-1.19 \pm 2.71 \mu\text{V}$) was not only larger than in *face_face(d)* ($0.34 \pm 3.12 \mu\text{V}$) ($q = 5.06$, $P = 0.004$), but also larger than in *face_face(s)* ($0.29 \pm 3.30 \mu\text{V}$) ($q = 5.25$, $P = 0.003$).

P200 component

The grand averaged P200 (200–250 ms) elicited by the target stimuli in face trials is shown in Fig. 7. Since the *blank_face* and *build_face* trials had already diverged from the *face_face(d)* and *face_face(s)* trials at the N170 stage, we concentrated the analyses of the P200 component on the latter

Fig. 4 Bar graphs showing the pooled mean amplitudes of the P100 component elicited by the target stimulus of each pair of stimuli. *Left side* face trials; *Right side* building trials. Time window: 90–130 ms after stimulus onset. Pooled electrodes: O1/O2, PO3/PO4, PO5/PO6 and PO7/PO8. The asterisks indicate reliable differences between conditions. It can be observed that there were significant P100

magnitude differences in building trials only. Specifically, the amplitude of the target-elicited P100 was larger in *face_build* than in *build_build(s)*, *build_build(d)* and *blank_build*, and was smaller in *build_build(s)* than in *blank_build* and *build_build(d)*. (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

Fig. 5 Grand averaged N170 component elicited by the target stimulus of each pair of stimuli in face trials. *Left side* waveforms pooled over electrodes in the left hemisphere (P5/P7/PO5/PO7); *Right side* waveforms pooled over electrodes in the right hemisphere (P6/

P8/PO6/PO8). It can be observed that the amplitudes of the target-elicited N170 in *face_face(s)* and *face_face(d)* were smaller than in *blank_face* and *build_face*, especially in the right hemisphere

Fig. 6 Bar graphs showing the *left and right* pooled mean amplitudes of the N170 component elicited by the target stimulus of each pair of stimuli in face trials. *Left side* left hemisphere (pooled over P5/P7/PO5/PO7); *Right side* right hemisphere (pooled over P6/P8/PO6/PO8). Time window: 140–180 ms after stimulus onset. The asterisks

indicate reliable differences between conditions. It can be observed that the amplitude of the target-elicited N170 in *build_face* was significantly larger than in *face_face(d)* in both hemispheres, and also larger than in *face_face(s)* in the right hemisphere (* $P < 0.05$, ** $P < 0.01$)

two types of trials. From the waveforms, it can be observed that comparing with *face_face(d)*, the amplitude of the target-elicited P200 in *face_face(s)* shrank to a great degree.

A two-way ANOVA was performed on the mean amplitudes of the target-elicited P200 in face trials, with repeated measurements of PRIME [*face_face(d)* and *face_face(s)*] and LATERALITY. The results revealed main effects of LATERALITY [$F(1,22) = 13.74$, $P = 0.0012$] and PRIME [$F(1,22) = 24.73$, $P < 0.001$], but no significant interaction of PRIME $\times$ LATERALITY [$F(1,22) = 1.47$, $P = 0.238$]. With respect to LATERALITY, the magnitude of the target-elicited P200 was larger in the right hemisphere ($2.96 \pm 2.24 \mu V$) than in the left hemisphere ($1.42 \pm 1.34 \mu V$). As shown in Fig. 8, with regard to PRIME, the amplitude of the target-elicited P200 decreased significantly in *face_face(s)* ($1.56 \pm 1.32 \mu V$) relative to *face_face(d)* ($2.82 \pm 1.97 \mu V$).

Discussion

It has been reported that if two sensory stimuli are presented consecutively with a short inter-stimulus interval (several hundreds of milliseconds), the stimulus-sensitive brain activity will be reduced for the second stimulus (Ogawa et al. 2000). Taking the present SOA of 600 ms into consideration, any decrement in ERP amplitudes in response to the target stimulus might be indicative of inhibited neuronal activity as a consequence of successive stimulation.

Some researchers surmised that such suppressed neuronal activity might possibly be due to neuronal interactions that occur when the neural circuits are partially shared for encoding some common features of the sensory inputs, or when they are spatially close enough to influence each other; the more the neuronal interaction, the stronger the suppression (e.g. Sung et al. 2007). Moreover, theoretical

Fig. 7 Grand averaged P200 component elicited by the target stimulus of each pair of stimuli in the *face_face(d)* and *face_face(s)* conditions. The waveforms were obtained by pooling over electrodes CP5/CP6, TP7/TP8, P5/P6 and P7/P8, as shown in gray in the scalp model. It can be observed that the amplitude of the target-elicited P200 in *face_face(s)* was much smaller than in *face_face(d)*

Fig. 8 Bar graph showing the pooled mean amplitudes of the P200 component elicited by the target stimulus of each pair of stimuli in the *face_face(d)* and *face_face(s)* conditions. Time window: 200–250 ms after stimulus onset. Pooled electrodes: CP5/CP6, TP7/TP8, P5/P6 and P7/P8. The asterisks indicate reliable differences between conditions. It can be observed that the amplitude of the target-elicited P200 in *face_face(d)* was significantly larger than in *face_face(s)* (***) ($P < 0.001$)

and computational studies routinely presume that the spatiotemporal dynamics in neural circuits are crucial in determining the strength of the representation of object features, and therefore also the priming effect observable in

behavior (e.g. Singer 2009; Ursino et al. 2011). The present study has made an effort to empirically test these assumptions in both behavioral and electrophysiological responses of humans by manipulating different types of priming with faces versus buildings as visual stimuli.

The results showed clear effects of immediate repetition priming measured with both RTs and ERPs. The RT data revealed significant effects of *category priming* in both face trials and building trials, as well as a significant effect of *item priming* in face trials. With respect to the ERPs, in face trials, no priming effect was observed at the P100 stage, whereas decreased neural activity was observed for repeated category at the N170 stage and for repeated item at the P200 stage. In comparison, in building trials, priming effects arose already at the P100 stage. The obtained neural data are further discussed below for each ERP component.

P100 component

The P100 is a positive-going shift typically recorded over the occipital electrodes with a peak latency of 80–130 ms after stimulus onset (e.g. Mangun 1995). It is generally accepted to reflect early visual processing in the extra-striate cortex and to be sensitive to basic visual properties of the stimulus, such as contrast, luminance and size, etc. (e.g. Schendan et al. 1998).

Since the low-level visual attributes (contrast, luminance, size) of both the face and building stimuli were controlled to be roughly constant throughout the present experiment, we expected that the target-elicited P100 would remain approximately invariable among the 4 conditions in both face trials and building trials. However, the data turned out differently. No priming induced P100 modulation was observed in face trials, being largely in line with most previous immediate repetition studies (e.g. Caharel et al. 2009; Engst et al. 2006; Jacques and Rossion 2006; Schweinberger et al. 2002a, 2004). In contrast, in building trials, depending on the physical similarity between the prime and target stimulus, distinct levels of facilitation or inhibition in visual processing were reflected in the amplitude of the target-elicited P100. These results revealed that, as compared to a face, the covert structural representation of a building stimulus might be more susceptible to the influence of an immediate prime. Several possibilities might account for this difference between face and building trials.

Firstly, it was recently suggested that the P100 may reflect not solely the low-level visual processing, seeing as it showed some sensitivity to face inversion (e.g. Itier and Taylor 2004c) and visual adaptation (e.g. Hoffmann et al. 2001; Kovács et al. 2006). Relevant to the present study, perceptual processing of face and building images may occur differently in terms of structural analysis—possibly in a more configural manner for face encoding than for

building encoding (e.g. Gauthier et al. 2000). Such different structural encoding might be indexed by the P100 amplitude (e.g. Itier and Taylor 2002, 2004a).

Secondly, according to a number of ERP studies (e.g. Clarck and Hillyard 1996; Luck et al. 1994), early visual processing indexed by P100 can be modulated by attention. Given the social importance of faces, as well as our intrinsic expertise in face processing, it is possible that faces attract attention more easily than buildings do. Importantly, both of these two possibilities reinforce the viewpoint that face processing involves specific neural circuits (e.g. Kanwisher 2000; Sung et al. 2007; Yovel and Kanwisher 2004). In the context of the present study, the implication is that a target face stimulus would immediately attract full attention, regardless of previous stimulation. This would explain why the P100 was immune to effects of priming in face trials. On the other hand, a target building stimulus might not have captured attention as imperatively as a target face stimulus, leaving the possibility open for previous stimulation to have a strong impact on the P100, as was observed in building trials.

It should be noted that the global visual features (i.e., the relevant unique diagnostic features) of both face stimuli and building stimuli were controlled for similarity as much as possible in our study. Nevertheless, we cannot exclude the possibility that the physical variability among building stimuli was relatively larger than among face stimuli, particularly with respect to the arrangement of geometric ions (geons): by definition, this arrangement is relatively homogeneous among faces but diverse among buildings. Indeed, this basic difference between faces and buildings in terms of structural variability may be the principal reason why configural processing would be more relevant for faces (as suggested above).

N170 component

The obtained data showed that when the target face stimulus was primed by either another face exemplar [*face_face(d)*] or exactly the same face [*face_face(s)*], a small but significant reduction in N170 amplitude was observed relative to *build_face*, in the occipito-temporal cortex. Several former studies provided analogous evidence (Eimer et al. 2010; Kloth et al. 2010; Kovács et al. 2006). For example, using a visual adaptation paradigm, Kovács et al. 2006 investigated ERP correlates of shape-selective adaptation to human faces and body parts. They found that the N170 amplitude decreases when the adaptor and test stimulus belong to the same object category, but not when they belong to different object categories. They suggested that the lack of cross-category N170 adaptation supports the “domain specific” theory advocated by Kanwisher (2000) and Yovel and Kanwisher (2004), which postulates

that visual processing of faces and non-face objects involve separate and specialized networks in the ventro-lateral temporal cortex. Such “domain specific” theory is also consistent with the present results.

Although not precise, by source analysis, previous ERP studies indicate that the main neural generator of the N170 component lies in the lateral occipito-temporal cortex (e.g. Itier and Taylor 2004b; Rossion et al. 2003). Moreover, neuroimaging studies have identified both a face-specific area (FFA: fusiform face area) and a place-specific area (PPA: parahippocampus place area) in this region (Aguirre et al. 1998; Epstein and Kanwisher 1998; Ishai et al. 1999; Kanwisher et al. 1997). Thus, it is plausible that the N170 elicited by faces and buildings might both originate from the lateral occipito-temporal cortex, but from different neuron population networks located in the FFA and PPA. As demonstrated in a neural adaptation study, neuronal activity is reduced when two successive stimuli activate the same subpopulation, but not when they stimulate different ones (e.g. Krekelberg et al. 2006). With respect to the present study, in *face_face(d)* and *face_face(s)*, both the prime and target stimuli belong to the face category. Thus, one may postulate that they should activate the face-selective neuronal populations in the FFA to a similar degree. In contrast, in *build_face*, the prime and target stimuli might elicit the activity of at least partially distinct neuron populations, in the FFA and PPA. Put differently, the increased perceptual distance between the prime and target stimulus in *build_face* (between-category) could be physiologically reflected by a lesser overlap of neural activity as compared to *face_face(d)* or *face_face(s)* (within-category). The lesser overlap in turn causes more variation in neural responses and leads to a larger brain potential.

Yet, several previous studies did not find repetition effects over the N170 (e.g. Engst et al. 2006; Schweinberger et al. 1995, 2002a, 2004; Trenner et al. 2004), whereas others observed N170 modulation using various paradigms (e.g. Caharel et al. 2009; Campanella et al. 2002; Eimer et al. 2010; Guillaume et al. 2009; Jacques and Rossion 2006; Jacques et al. 2007; Kloth et al. 2010; Kovács et al. 2006; Werheid et al. 2005). This incongruity across studies should be attributed to discrepancies between stimuli (e.g. familiar versus unfamiliar), task demands (e.g. semantic decision versus perceptual classification) and experimental design (e.g. visual adaptation versus repetition priming; immediate repetition versus delayed repetition). Here, we found clear *category priming*, but not *item priming*, for faces in the N170, with immediate repetition in a visual categorization task.

P200 component

In the present study, with respect to *item priming*, we found a distinct ERP modulation in the occipito-temporal regions

~200 ms after target onset—the P200 component, which is a positive deflection that peaks around 200–250 ms after stimulus onset. We observed that the target-elicited P200 in *face_face(s)* was significantly reduced in magnitude as compared to *face_face(d)*.

Research on the visual P200 is still at an early stage, partially owing to the fact that it is modulated by a broad range of cognitive tasks, including visual feature analysis (Itier and Taylor 2002; Luck and Hillyard 1994) and retention of words (Evans and Federmeier 2007), and by a wide variety of factors such as pre-experimental stimulus familiarity (Caharel et al. 2002; Webb et al. 2010), stimulus repetition (Evans and Federmeier 2007; Webb et al. 2010), and attention (Luck et al. 1994). The precise neural origin and function of P200 are not yet understood. In visual search and visual priming studies, however, several researchers propose that the P200 reflects high-order perceptual matching processes that occur when sensory inputs are compared with relevant prior information such as internal representations or mnemonic expectancy (Freunberger et al. 2007; Luck and Hillyard 1994). Accordingly, in the present study, relative to *face_face(d)*, the observed decrement of P200 amplitude in *face_face(s)* might reflect facilitated perceptual processing of the target face by using the transiently stored representation that was newly deposited by the face prime.

Former priming studies also repeatedly mentioned the “face representation” in relation to the N250r, but most of these studies investigated familiar face processing (e.g. Engst et al. 2006; Guillaume et al. 2009; Jemel et al. 2003; Martens et al. 2006; Schweinberger et al. 2002a, 2004; Trenner et al. 2004). This might lead one to wonder whether only a glance at an unfamiliar face, as in the present experiment, can produce a “face representation” in the semantic sense implied by the previous studies on familiar face processing. Schacter (1990) suggested that a single exposure to a specific stimulus can indeed, in principle, leave some residual trace, establishing a pre-semantic structural representation of this specific stimulus. Similarly, we suggest that the stored memory trace of an unfamiliar face in the present study more likely refers to a highly image-specific and short-lived new structural representation, rather than an image-independent and relatively long-term “face representation” stored for individual recognition.

Beyond the P200, the previous literature has provided relatively consistent data on the short-lived N250r, a bilateral or right inferior temporal negativity peaks at ~230–300 ms, caused by immediate repetitions of familiar faces, reflecting retrieval of facial identity (e.g. Begleiter et al. 1995; Pfützte et al. 2002; Schweinberger et al. 1995, 2002a, 2004). The N250r is commonly most robust when identical familiar faces are immediately repeated, but

largely reduced when different pictures of familiar faces are employed (e.g. Pfützte et al. 2002). It has been suggested to be more clear-cut for familiar faces than for unfamiliar faces (e.g. Begleiter et al. 1995; Schweinberger et al. 1995, 2002b). In the present data, we found a very weak N250r-like component only in left-side electrodes (e.g. P5 and P7) in *face_face(s)*. Our null results for the N250r, therefore, appear to confirm the role of familiarity in face processing indexed by this component.

Summary

All in all, two kinds of priming-induced perceptual facilitation were observed. At the behavioral level, RT facilitation due to *category priming* was observed both in face trials and in building trials. In face trials, there was also a significant RT facilitation due to *item priming*. At the physiological level, we observed perceptual facilitation as decrements in ERP amplitude. In face trials, *category priming* emerged at the N170 stage and *item priming* at the P200 stage. In contrast, in building trials, priming effects occurred already at the P100 stage, suggesting vulnerability of early stage processing in building encoding.

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