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The time course of emotional picture processing: an event-related potential study using a rapid serial visual presentation paradigm

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The present study recorded event-related potentials using rapid serial visual presentation paradigm to explore the time course of emotionally charged pictures. Participants completed a dual-target task as quickly and accurately as possible, in which they were asked to judge the gender of the person depicted (task 1) and the valence (positive, neutral, or negative) of the given picture (task 2). The results showed that the amplitudes of the P2 component were larger for emotional pictures than they were for neutral pictures, and this finding represents brain processes that distinguish emotional stimuli from non-emotional stimuli. Furthermore, positive, neutral, and negative pictures elicited late positive potentials with different amplitudes, implying that the differences between emotions are recognized. Additionally, the time course for emotional picture processing was consistent with the latter two stages of a three-stage model derived from studies on emotional facial expression processing and emotional adjective processing. The results of the present study indicate that in the three-stage model of emotion processing, the middle and late stages are more universal and stable, and thus occur at similar time points when using different stimuli (faces, words, or scenes).

Keywords: emotional pictures, event-related potentials, rapid serial visual presentation, P2, late positive potential

Introduction

Rapid responses to emotional arousal stimuli, especially potentially biologically relevant stimuli, such as snakes, tigers, or pictures of accidents, particularly when attentional resources are limited, is believed to be evolutionarily significant to humans (Schupp et al., 2006; Vuilleumier and Pourtois, 2007). Understanding the temporal characteristics of rapid emotion processing can help improve emotion recognition, allowing us to make the proper response. In fact, many studies have explored the time course of emotion processing; in these studies, different stimuli, such as emotional words, facial expressions, and sounds, have been employed to induce different emotions. In addition, given its high temporal resolution, the event-related potential (ERP) technique has been widely adopted in studies of emotion processing.

Recently, researchers have begun to investigate the timing of emotional facial expressions processing. For example, the results of an ERP study by Utama et al. (2009), which used emotional facial images as stimuli and required the participants to distinguish the type of emotion and rate the emotional intensity of each image, revealed that the P1 component was significantly correlated with the correct recognition of facial images, while the N170 was significantly correlated with the intensity level rating of the images. Thus, the authors concluded that processing facial emotion is comprised of two different stages: (1) the rapid recognition of facial emotions, which occurs as early as 100 ms after image onset, and (2) detailed processing, such as the intensity assessment, which occurs around 170 ms post-stimulus.

Though the above mentioned two-stage model of emotional facial expression processing revealed the time course of emotional facial processing to some extent, it seems too rough to clarify the temporal characteristics 100 ms after image presentation. To solve this problem, based on the rapid serial visual presentation (RSVP) paradigm, Luo et al. (2010), who adopted emotional facial pictures (from the Chinese Facial Affective Picture System, CFAPS) as stimuli, proposed a three-stage model of facial expression processing? In this model, the brain distinguishes negative emotional facial expressions from positive and neutral facial expressions in the first stage, which explains why the posterior P1 and anterior N1 amplitudes elicited by fearful faces are larger than the amplitudes elicited by neutral and happy faces. In the second stage, the brain distinguishes emotional from non-emotional facial expressions, which explains why the N170 and vertex positive potential (VPP) amplitudes elicited by fearful and happy faces are larger than those elicited by neutral faces. In the third stage, the brain classifies different types of facial expressions, thus explaining why the P3 and N3 amplitudes elicited by fearful, happy, and neutral faces are different from one another. This three-stage model may help us to understand the time courses of emotional facial expression processing. Below, we introduce several representative ERP components that are involved in emotion processing.

When it comes to early emotional facial expressions processing, we cannot ignore two representative ERP components, namely P1 and N1. Both of these components are indicators of early processing (Brown et al., 2012) and represent comparatively automatic mechanisms of selective attention (Dennis et al., 2009). P1 is a positive-going potential that peaks around 80–130 ms after stimulus onset, and is presumed to indicate early visual processing (Jessen and Grossmann, 2014). Furthermore, it reaches its maximal amplitude over the occipital areas in emotional word and facial expression processing (Van Hooff et al., 2008; Cunningham et al., 2012). Moreover, P1 is related to the selective attention to emotional stimuli, i.e., the P1 amplitudes elicited by attended stimuli were higher than the P1 amplitudes to stimuli that were unattended (Dennis et al., 2009). Additionally, the P1 amplitudes elicited by negative emotional pictures and words were larger than the P1 amplitudes elicited by positive ones (Bernat et al., 2001; Smith et al., 2003; Delplanque et al., 2004). N1, a negative-going potential, appears shortly after P1, and is sensitive to the characteristics of facial expressions; for example, Eimer and Holmes (2002) found that fearful faces induced a shorter N1 latency than did neutral faces.

Another important component is P2. P2 is an attention-related component, with a typical peak latency of about 200–250 ms (Ferreira-Santos et al., 2012), which reflects the detection of visual features during the perceptual stage of processing (Luck and Hillyard, 1994; Carretié and Iglesias, 1995). Moreover, P2 is regarded as indexing some aspects of the stimulus categorization process (García-Larrea et al., 1992). Previous ERP studies on the relationship between the valence of stimuli and the P2 amplitude present conflicting results. On one hand, using both emotional pictures (Carretié et al., 2004) and emotional words (Herbert et al., 2006; Kanske and Kotz, 2007) as stimuli, researchers found that emotional stimuli elicited significantly larger P2 amplitudes than did neutral stimuli. However, Yuan et al. (2007) reported that the P2 amplitudes elicited by emotional and neutral stimuli were not significantly different. At the same time, some researchers found that the P2 amplitudes elicited by negative stimuli were significantly greater than those elicited by positive stimuli (Carretié et al., 2001; Delplanque et al., 2004; Huang and Luo, 2006; Wang and Bastiaansen, 2014), while others have reached the opposite conclusion (Schapkin et al., 1999). Thus, the exact role of the P2 component in emotion processing remains unclear.

The late positive potential (LPP, also known as LPC) is a positive, slow components elicited by both emotional (positive and negative) and neutral stimuli, and can be used as an indicator of continued attention to a motivationally striking stimulus (Jaworska et al., 2011; Weinberg and Hajcak, 2011; Leite et al., 2012; Gable and Adams, 2013; Novosel et al., 2014). Numerous studies (Dennis and Hajcak, 2009; Hajcak et al., 2009, 2013; Kessel et al., 2013; Smith et al., 2013; Yuan et al., 2014) showed that the amplitude of the LPP is sensitive to stimulus valence, i.e., emotional stimuli (positive and negative) elicited larger LPP amplitudes than did neutral stimuli. However, whether positive and negative stimuli differentially affect the LPP amplitude has not yet been agreed upon by researchers. By adopting emotional pictures from the International Affective Picture System (IAPS) as stimuli and controlling for the arousal dimension of the pictures, Schupp et al. (2004) and Codispoti et al. (2006) found that the LPP amplitudes elicited by positively and negatively valenced pictures were not significantly different in healthy subjects. In contrast, Huang and Luo (2009) and Weinberg and Hajcak (2010) demonstrated that unpleasant stimuli elicited larger LPP amplitudes than did pleasant stimuli. Hence, more research is necessary to resolve these inconsistencies.

Besides conveying emotional information through facial expressions, humans can convey emotional information through writing and speech, which inspired researchers to explore the time course of emotional word processing. Thus, with emotional words, the findings were quite similar to those obtained with faces, although some differences were also observed. However, our later studies indicate that, in general, the three-stage model still holds. For example, in one of our recent studies (Zhang et al., 2014), we adopted emotional Chinese adjective (selected from the Chinese Affective Word System, CAWS), and used the same paradigm (RSVP) as that in our previous study (Luo et al., 2010). In that study, we found that the processing of emotional adjective seemed to occur in the same three stages as did the processing of emotional facial expressions. Specifically, in the first stage, the brain distinguished negative adjectives from non-negative adjectives. Next, the brain discerned emotional adjectives from non-emotional adjectives. Lastly, negative, neutral, and positive adjective were separated. Soon after, in a separate study, we investigated the time course of emotional noun processing and found that the processing of emotional nouns (from the CAWS) also occurred in three different stages (Yi et al., 2015). Besides, we did not find the negativity bias for emotional noun processing that is usually found in the processing of emotional facial expressions and adjectives, i.e., the brain did not distinguish negative nouns from positive and neutral nouns in the first stage. The remaining two stages of emotional noun processing showed similar results to the results for emotional adjective processing, indicating that the brain distinguished emotional nouns from non-emotional nouns in the middle stage, and classified the three different types of nouns (negative, positive, and neutral) in the last stage. These major findings for the time courses of emotional facial expression and word processing are summarized in **Table 1**.

The existence of three temporal processing stages for emotional facial expression and word processing is easily demonstrated. However, there are also processing differences between the two stimulus types. Firstly, we found that negative expressions and adjectives elicited lager right (Luo et al., 2010) and left (Zhang et al., 2014) N1 amplitudes, respectively, than did positive and neutral expressions and adjectives; however, the N1 amplitudes elicited by negative, neutral, and positive nouns were not significantly different (Yi et al., 2015). Secondly, although the N170 effect has been found in all processes, the right hemisphere appears to be superior for processing emotional facial expressions, but the left hemisphere appears to be superior for word (both emotional adjective and noun) processing. These discrepancies may be explained by the different types of stimuli (facial expressions versus words) adopted in the two experiments. Indeed, the processing differences between these two common emotion inducing materials [words and pictures (facial expressions)] have been widely discussed in past years. Firstly, formally speaking, words transmit affective information on a symbolic level, while facial expressions convey emotion information through biological cues (Zhang et al., 2014). Comparatively, the latter is more direct, which is relevant to the processing difference between the two stimuli. Next, some researchers (Seifert, 1997; Azizian et al., 2006) discovered that processing superiority exists for pictures vs. words, i.e., pictures have quicker and simpler access to associations. Since words convey symbolic information, it is reasonable to suspect that the processing of words requires extra translation activity at a surface level before they access the semantic system. Additionally, different brain regions have been activated when processing pictures and words. A positron emission tomography (PET) experiment (Grady et al., 1998) has shown greater activity of the bilateral visual pathway and medial temporal cortices, during processing of pictures. In contrast, for processing of words, strong activation patterns was observed in prefrontal and temporoparietal regions.

As mentioned above, it has been showed that the processing of both emotional facial expressions and words occurs in three different stages; however, what about the time course of emotional pictures that are not of faces (e.g., scenes)? Considering the potential similarities between processing emotional facial expressions and pictures (for example, both types of stimuli could transmit emotion information more intuitively than words), we postulated that the processing of emotional pictures would also show different stages. The present study, adopting the RSVP paradigm and using both neutral faces and scenes as stimuli, aimed to explore the temporal characteristics of emotional picture processing under conditions of limited attentional resources. It is reasonable to speculate that the processing of emotional pictures will show similar temporal characteristics to those shown in facial expression processing.

The early ERP components are sensitive to the non-emotional perceptual features of the stimuli (De Cesarei and Codispoti, 2006; Olofsson et al., 2008). It has been found that in the earliest processing stages, the physical properties of a stimulus such as its color (Cano et al., 2009) and complexity (the latter producing a very early effect, i.e., 150 ms after stimulus onset; Olofsson et al., 2008) influence the affective waveforms. Considering these factors, it is reasonable to expect that the processing of emotional pictures in the early stage is not pure processing to isolate the emotion information conveyed by the pictures; therefore, it is not possible to distinguish whether the main effect was caused by

TABLE 1 | Summary of findings.

Stimuli/ERP/Time	First stage	Second stage	Third stage
Facial expression	P1, N1: R > L neg > neu, pos (ns)	N170: R > L VPP: M > R, L neg, pos (ns) > neu	N300: R > M, L P300: M, R > L neg > pos > neu
Emotional adjective	P1:L, R > M Left:neg > neu, pos (ns)	N170, EPN L: neg, pos (ns) > neu R:neg, pos vs. neu (ns)	LPC:M > R, Lvs. R, M (ns) pos > neg > neu
Emotional noun	PI pos, neu vs. neg (ns) pos vs. neu (ns)	N170: L > R L: pos, neg > neu R:pos, neg vs. neu (ns)	LPC:M > R, L vs. R, M (ns) neg > neu > pos

Comparisons of the time courses of emotional facial expression and word processing based on representative ERP components. neg, negative; neu, neutral; pos, positive; ns, no significant difference; R, L, and M = Right, left, and middle hemisphere.

physical attributes or emotions, even if there appeared to be a P1 main effect. Based on these considerations, the early processing of emotional pictures was not analyzed in the present study. We hypothesized that subjects would distinguish emotional pictures from non-emotional pictures in the middle stage of emotional picture processing and would distinguish the different valences of the pictures in the late stage.

Materials and Methods

Subjects

Eighteen (nine men) healthy undergraduates from Chongqing University of Arts and Sciences were tested. All participants reported normal or corrected to normal visual acuity and no history of mental illness and brain disease, and all of them were right-handed. Participants received a small amount of money for participation. All participants provided written informed consent, which was approved by the Ethics Committee of The Chongqing University of Arts and Sciences.

Stimuli

Materials consisted of four neutral face pictures, 18 emotional pictures, and 12 scrambled pictures (SPs), described in detail below. Four grayscale photographs of four different identities (two females) showing neutral expressions were selected from the CFAPS, while eighteen emotional pictures convey positive, neutral, or negative emotions (six neutral, six happy, and six fearful pictures) were selected from the Chinese Affective Picture System (CAPS). The emotional pictures were not face-related pictures, including landscapes, animals and events of life scenes. SPs made by randomly swapping small parts (18×18 pixels) of the same neutral pictures were used as distraction stimuli. The scrambled images had the same rectangular shape, size, luminance, and spatial frequency as the face pictures and emotional pictures, used as mask. The visual angle was $5.6 \times 4.2°$. To control the influence of arousal on the processing of emotional pictures, the arousals of all images having been measured on a 9-point scale before the formal experiment, the arousals of emotional pictures (M ± SD, positive: 5.61 ± 0.43, negative: 5.97 ± 0.59) were higher than neutral pictures (M ± SD, 3.76 ± 0.36), $F(2,15) = 8.40$, $p < 0.001$, $\eta^2 = 0.836$, and there was no difference between positive and negative pictures ($p = 0.607$), while the emotional pictures differed significantly in valence, $F(2,15) = 434.49$, $p < 0.001$, $\eta^2 = 0.983$; M ± SD, positive: 7.61 ± 0.15, neutral: 4.81 ± 0.23, negative: 2.53 ± 0.44.

Procedure

In order to restrict attention resources, the procedure of present ERP study was designed on the basis of the RSVP paradigm. The procedure includes four blocks, while each block comprised of 120 trials, a total of 480 trials. As showed in **Figure 1**, each trial structure consisted of fourteen pictures (two target stimulus), pictures were portrayed with a stimulus-onset asynchrony (SOA) of 116 ms and no blank inter stimulus interval (ISI). The T1 emerged randomly and equi-probably at the fifth, sixth, seventh position, nextly, two distracting stimulus, then the T2 (SOA = 348 ms), and the remaining distracting stimulus items were presented in turn succesively. All stimuli were presented in the center of the screen. The first target stimulus (T1, discriminate the gender showed in the picture, subjects were asked to press Key "1" when the stimuli was woman and Key "2" when if it was man) was one of the four gender pictures (two females) and the second target stimulus (T2, discriminate the valence showed in the picture, press Key "1" if T2 was negative, Key "2" when neutral, Key "3" when positive, Key "4" if T2 was blank) was one of the 18 emotion pictures. The question would disappear while participants pressed the index key, and this task without a specific time limit. All subjects were required to respond to the two questions with their right hand. Stimulus presentation was controlled by the E-Prime 1.1 software (Psychology Software Tools Inc., Pittsburgh, PA, USA).

This study was completed in a sound attenuated room, participants sat in front of a 17′′ computer screen (refresh rate 60 Hz) at a distance of 90 cm. In order to ensure them fully understand the experiment procedure, with 20 practice trials before the formal experiment. In front of each trial, a white fixation point present in the center of the screen for 500 ms. After the presentation of each trial, participants were asked to complete both task 1 and task 2 as accurately as possible. In terms of time sequence, they were told to complete task 2 as accurately as possible, based on the accurate response to task 1. The two tasks were appeared serially with fixed order at the end of each trial. Then, participants would be led into the following series after 500 ms during which the screen stayed black and blank. No feedback was provided for each trial. To avoid being overtired, all participants were forced to rest for 2 min after each block.

Data Recording and Analysis

Brain electrical activity was recorded from 64 scalp sites using tin electrodes mounted on an elastic cap (Brain Product, Munich, Germany) referentially against left mastoids. Horizontal electrooculographies (EOGs) were recorded from two electrodes sites at the outer canthi of each eye, while vertical EOGs were recorded from tin electrodes placed 1 cm above and below the right eye. All interelectrode impedances were kept below 5 kΩ. The EOG and electroencephalogram were collected with a bandpass of 0.01–100 Hz, sampled at a rate of 500 Hz, and re-reference offline to obtain a global average (Bentin et al., 1996). The EEG data were corrected for eye movements using the method proposed by Gratton et al. (1983), as implemented in the Brain Vision Analysis software (Version 2.0; Brain Product, Gilching, Germany). Horizontal EOGs and vertical EOGs were used to pick up eye movement artifacts. Trials with EOG artifacts (mean EOG voltage exceeding ±80 μV) and other artifacts (peak-to-peak deflection exceeding ±80 μV) were excluded from averaging. The averages were then digitally filtered (low-cut 30 HZ, 24 dB/octave).

The averaged epoch for ERP was 1200 ms including a 200 ms pre-stimulus baseline. Trials were accepted only if participants gave correct response to both T1 and T2. EEG images evoked by the positive, neutral, and negative emotions were overlaid and

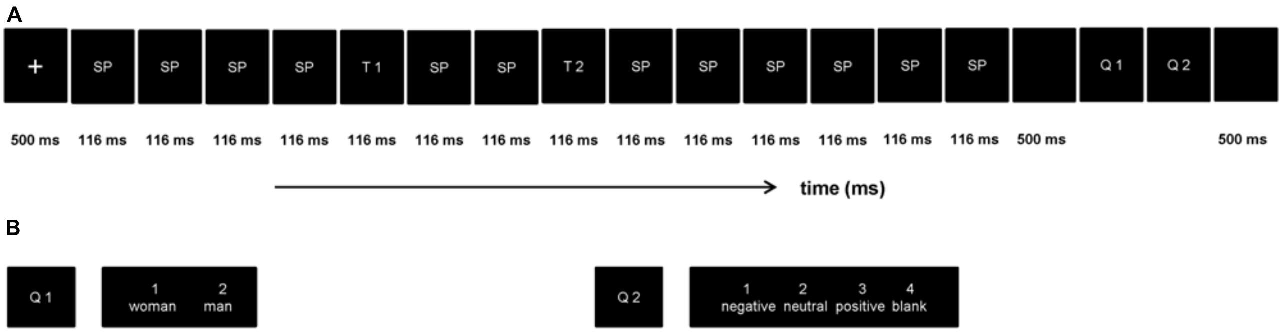

FIGURE 1 | The rapid serial visual presentation (RSVP) paradigm used in this experiment. (A) Each trial contained 10 scrambled pictures (SP), two target stimuli (T1 and T2), and two questions (Q1 and Q2). The T1 emerged randomly and equi-probably at the fifth, sixth, seventh position, T1 and T2 were presented within an interval of 232 ms. **(B)** Example for the two questions in each trail.

averaged. On the basis of the hypothesis and the topographical distribution of grand-averaged ERP activity, P2 and LPP were chosen for statistical analysis in the presented study. The P2 component (150–280 ms) were analyzed at the following nine electrode sites (Fz, F3, F4, FCz, FC3, FC4, Cz, C3, C4), we used local peak detection for each of the nine electrode sites (Fz, F3, F4, FCz, FC3, FC4, Cz, C3, C4) and applied a peak detection over the common (across three conditions) grand average (coming up with nine latencies), which was then commonly used even if a particular participant did not have a peak there, 21 sites (Fz, F3, F4, FCz, FC3, FC4, Cz, C3, C4, CPz, CP3, CP4, Pz, P3, P4, POz, PO3, PO4, Oz, O1, O2) were chosen for the analysis of LPP (400–500 ms). The baseline-to-peak amplitude was computed for P2 component while average amplitude was computed for LPP. Amplitudes and latency of each component were measured by a two-way repeated-measure analysis of variances (ANOVAs). Factors involved in the analysis were emotional types (three levels: positive, neutral and negative) and electrodes site, *p*-values were corrected by Greenhouse-Geisser correction.

Results

Behavior Results

The results of ANOVA for the accuracy revealed a significant main effect of emotional type, $F(2,34) = 5.40$, $p = 0.018$, $\eta^2 = 0.241$. The results of pairwise comparison showed that the accuracies of negative emotion pictures (97.06 ± 2.86%) were higher than positive emotion pictures (91.89 ± 7.05%) and neutral pictures (89.56 ± 11.55%), and there was no significant difference between positive and neutral pictures ($p > 0.05$).

ERP Data Analysis

P2

As showed in **Figure 2**, the P2 amplitudes revealed significant main effects of emotion type, $F(2,34) = 8.83$, $p = 0.003$, $\eta^2 = 0.525$, and electrode, $F(8,136) = 3.13$, $p = 0.026$, $\eta^2 = 0.155$, there was no significant interaction between emotional type and electrode. Positive pictures (3.29 μV, $p = 0.001$) and negative pictures (3.02 μV, $p = 0.001$) elicited greater amplitudes than neutral pictures (1.27 μV), and the amplitudes elicited by positive and negative pictures showed no significant difference ($p = 0.562$). Frontal electrode elicited lager P2 amplitudes than the other part. The P2 latency showed no significant difference both of main effect and interaction effect.

Late Positive Potential

In **Figure 3**, the LPP amplitudes revealed significant main effects of emotion type and electrode [$F(2,34) = 13.10$, $p < 0.001$, $\eta^2 = 0.435$; $F(20,340) = 4.93$, $p = 0.01$], there was no significant interaction between emotional type and electrode. Negative pictures elicited greater (7.69 μV) amplitudes than positive pictures (6.34 μV, $p = 0.015$) and neutral pictures (4.37 μV, $p < 0.001$), and the LPP amplitudes elicited by positive pictures was greater than neutral pictures ($p = 0.015$). Pz electrode elicited the largest LPP amplitudes (7.29 μV, see **Figure 4**).

Discussion

In this study, the behavioral data showed that the participants' accuracy on negative pictures was higher than their accuracies on positive and neutral pictures (showed no difference). This is in line with the notion that negative stimuli are prioritized in emotion processing given their strong biological significance. Furthermore, the ERP results showed that positive and negative pictures (no difference) elicited larger P2 amplitudes than did neutral pictures. Additionally, the LPP amplitudes elicited by negative pictures were larger than those elicited by non-negative pictures, while positive pictures elicited larger LPP amplitudes than did neutral ones.

In the RSVP paradigm, a series of stimuli, such as pictures, letters, words, or digits is presented in rapid succession at the same location. Usually, the stimuli are presented at the rate of 6–20 item per second, and the participants are instructed to only react to one or more stimuli (the target stimuli) that are different from the other stimuli in the series (distraction stimuli) in color, brightness or other features (Broadbent and Broadbent, 1987; Raymond et al., 1992; Isaak et al., 1999). Many studies (Broadbent and Broadbent, 1987; Weichselgartner

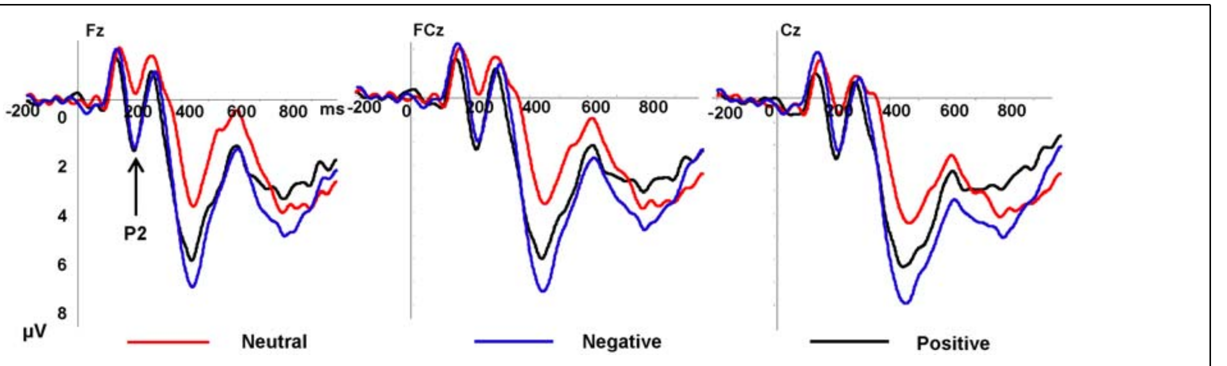

FIGURE 2 | Grand average event-related potentials (ERPs) of P2 components for negative (purple lines), neutral (red lines), and positive (black lines) conditions recorded at Fz, FCz, Cz.

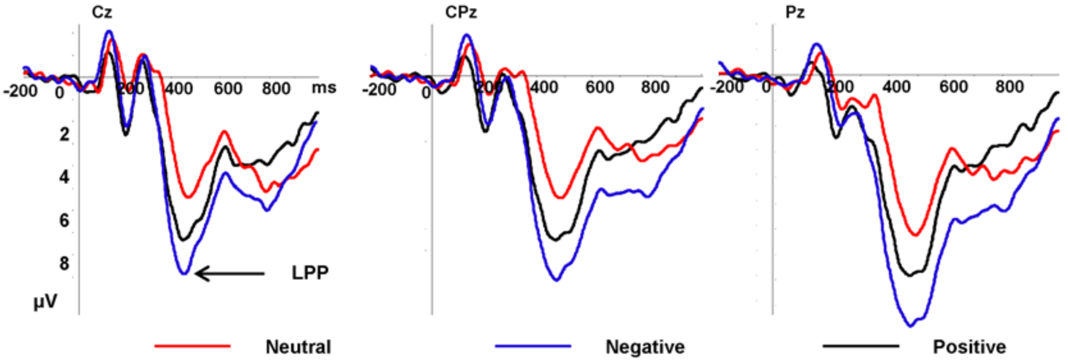

FIGURE 3 | Grand average ERPs of late positive potential (LPP) components for negative (purple lines), neutral (red lines), and positive (black lines) conditions recorded at Cz, CPz, Pz.

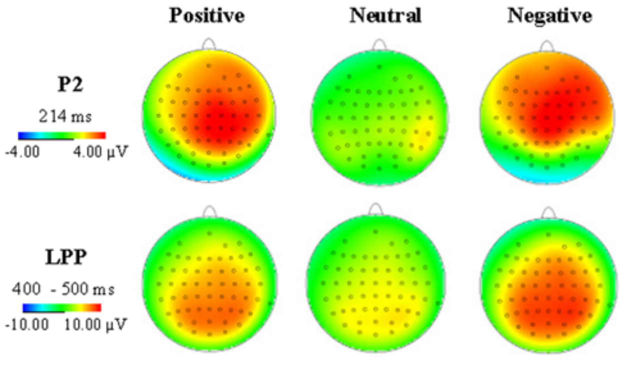

FIGURE 4 | Average ERP topographies of the P2 and LPP components across three emotional conditions.

and Sperling, 1987; Raymond et al., 1992; Isaak et al., 1999) have indicated that this special paradigm is useful for exploring the temporal characteristics of attentive processes. Additionally, previous studies (Chun, 1997; Kessler et al., 2005; Shapiro et al., 2006) revealed that the attentional resources and task difficulty were affected by two factors, the inter-stimulus interval (the attentional blink appeared when the inter-stimulus interval ranged from 200 to 500 ms) and the number of tasks (participants perform better on a single-task than on a dual-task, which is referred to as the attentional blink), especially in the middle and late stage of emotion processing (for details, please refer to our previous work). The three-stage model of emotional facial expressions and words processing proposed in our previous studies (Luo et al., 2010; Zhang et al., 2014; Yi et al., 2015), was based on the lack of attentional resources, i.e., a process is in accordance with the three-stage model only when the processing of emotional facial expressions and words is within the attentional blink time window. The present study aimed to test whether the processing of emotional pictures other than faces is also in line, or partly in line, with the three-stage model; therefore, the test needed to be conducted under conditions where the participants lacked attentional resources. Based on the above considerations, the present study adopted the dual-task experimental procedure based on the RSVP paradigm.

Utilizing this paradigm, we found that the P2 amplitude elicited by emotional pictures was higher over the frontal lobes compared to those elicited by neutral pictures. Since P2 is generally viewed as an index of certain stimulus attributes (García-Larrea et al., 1992), the P2 component mainly differentiated emotional stimuli from non-emotional stimuli.

Increased P2 amplitudes for emotional pictures compared to neutral pictures have also been found by other researchers (Peng et al., 2012; Wu et al., 2013). In addition, neither the main effect nor the interaction with the P2 latency was significant in the present study, which is supported by the results of Yuan et al. (2007). However, Carretié et al. (2001) stated that shorter P2 latencies were elicited in response to negative pictures than in response to positive pictures. However, there are several differences between their study and the present study. First, a different response method was used, i.e., oral report (Carretié et al., 2001) vs. keyboard press (present study). Second, different stimulus presentation times were used (longer in Carretié et al., 2001); the longer times in the study by Carretié et al. (2001) may have absorbed more attentional resources. The largest P2 amplitudes in the present study were identified at frontal sites at approximately the same position as the maximal VPP amplitudes in our previous work. Additionally, no significant differences were found regarding the interaction between the factors of electrode and emotion. In our previous study (Luo et al., 2010), we found that the brain ERPs were able to distinguish emotional expressions (fearful and happy) from neutral facial expressions, but could not distinguish fearful and happy expressions, during the second stage of emotional facial expression processing, as indicated by larger anterior VPP amplitudes in response to fearful and happy faces than in response to neutral faces. Since the VPP effect is largely specific for facial expression processing, we did not recognize a VPP effect in the present study, instead, we recognized P2 effect, but temporally speaking, the P2 effect corresponded to the VPP effect.

In our previous studies (Luo et al., 2010; Zhang et al., 2013a,b, 2014), we found that the brain could differentiate between three types of emotional stimuli during the third stage of emotion processing. In the present study, as expected, the main effect of emotion on the LPP amplitude was significant; specifically, the LPP amplitude was larger to negatively valenced pictures than it was to positively valenced and neutral pictures, and positively valenced pictures elicited larger LPP amplitudes than did neutral pictures, which was coherent with our previous results. Since both the P3 and LPP (or LPC) belong to the P3 family (González-Villar et al., 2014; Grzybowski et al., 2014), it is reasonable to compare these two components directly. Although researchers (Foti and Hajcak, 2008; Hajcak et al., 2010; Lang and Bradley, 2010; Yen et al., 2010; Zhang et al., 2012b) agree that emotional stimuli elicit larger LPP (P3) amplitudes than do neutral stimuli, they do not agree on the relationship between the LPP amplitudes and the valence of emotional stimuli. Some researchers (Ito et al., 1998; Huang and Luo, 2006; Frühholz et al., 2009) found that the LPP amplitudes elicited by negative stimuli were larger than the LPP amplitudes elicited by positive stimuli, which is in agreement with our results. However, in contrast to the present study, Solomon et al. (2012) found that girls displayed larger LPP amplitudes to neutral pictures than to positive pictures. This difference may be interpreted as the influence of developing cognitive and affective factors related to emotion processing, since Solomon enlisted children (between 5 and 6 years old) as participants, while all of the subjects in the present study were college students. Additionally, using emotional pictures as stimuli (selected from the IAPS), Brown et al. (2013) found that the LPP amplitudes elicited by low-arousal unpleasant, neutral, and low-arousal pleasant pictures were not significantly different from each other, which is in line with our results to some degree. However, the LPP amplitudes elicited by high-arousal unpleasant pictures were larger than those elicited by high-arousal pleasant and neutral pictures (the negativity bias). The differences can be interpreted in terms of different arousal levels, since the LPP is sensitive to the arousal levels of emotional stimuli (McConnell and Shore, 2011; Zhang et al., 2012a). The main effect of electrode was significant, with the LPP amplitude being the largest at the Pz electrode, which is supported by many previous studies (Amrhein et al., 2004; Schupp et al., 2004; Schutter et al., 2004; Smith et al., 2013).

As for the three-stage model, preliminary analysis of a threat during the early stage of processing can help individuals quickly escape from the threat, and therefore has strong adaptive significance (Vuilleumier, 2005; Corbetta et al., 2008; Bertini et al., 2013), but this analysis, although fast, is also very coarse. Emotion processing is a dynamic process; the first stage of the three-stage model of emotional facial processing identifies the negative stimuli, while the second stage distinguishes positive stimuli from neutral stimuli. Thus, if we link the first and second stages, it is easy to state that in the first two stages, the identification of these three emotions is basically completed. This raises the question of whether the third stage is necessary. Our previous experimental results (Luo et al., 2010; Zhang et al., 2014; Yi et al., 2015) suggested that fine processing of the three different emotions occurs; hence, the third stage is complementary to the first and second stages. Therefore, we believe the three-stage model of facial emotional expression processing is more appropriate than the two-stage model (Utama et al., 2009).

Since the arousal level affects the processing of visual stimuli (McConnell and Shore, 2011; Zhang et al., 2012a; Prehn et al., 2014), we originally intended to control for the arousal level when selecting the experimental stimuli. Unfortunately, we found that it was almost impossible to absolutely match the arousal level of neutral and emotional (positive and negative) pictures in our picture system. However, because the arousal level of neutral pictures was lower than the arousal level of positive and negative pictures, this seems to indicate higher ecological validity, since valence and arousal were plotted as horizontal and vertical coordinates, respectively, when establishing axes for evaluating the emotional pictures. The resulting scatter plot formed a slight U-shape. Therefore, the P2 amplitudes elicited by emotional pictures were larger than those elicited by neutral pictures in the present study, which might be due to valence or arousal difference between the stimuli, or to the interaction between valence and arousal; however, we were unable to determine the exact cause given the particularity of the emotional scene. Moreover, the interaction between valence and arousal is a very interesting question that we hope to investigate in future studies.

The present experiment only differs from our previous work Luo et al. (2010) in terms of the experimental stimuli, i.e., emotional scene pictures vs. emotional face pictures, respectively, while all other details remain the same (please refer to our previous work). The results of the present study suggest that, temporally speaking, different processing stages exist within the brain for emotional pictures. We found that the middle and late stages for emotional scene processing correspond to the middle and late stages of the three-stage model of facial expression processing. Because of the inherent limitation caused by the use of different types of stimuli, we could not compare emotion processing in the early phase between studies. The details and information in the emotional pictures varied, and these differences (i.e., physical complexity) could not be controlled for in the present study. Therefore, these factors might have affected the early processing stage. Collectively, the present study confirmed the latter two stages of the three-stage model of facial expression processing exist when processing images other than faces when attentional resources are limited, thus, we provide new evidence in supporting of the hypothesis of different temporal processing stages for emotional visual stimuli. Moreover, the results of the present study indicate that the time course of emotional processing is similar even when the emotions are conveyed by different types of stimuli.

Conclusion

In the present study, by adopting an RSVP paradigm that limited the participants' attentional resources, we explored the time course of emotional picture processing. The results demonstrated that emotional picture processing showed different stages (P2, LPP) similar to those observed during the processing of emotional faces. This suggests that in the late perceptual and cognitive processing stages, the time courses for processing the same emotions, regardless of whether they are conveyed by facial expressions, words, and pictures (scenes) are similar.

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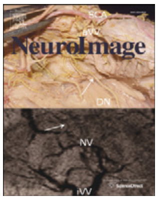

N170 changes reflect competition between faces and identifiable characters during early visual processing

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ABSTRACT

According to the neuronal recycling hypothesis, brain circuits can gain new functions through cultural learning, which are distinct from their evolutionarily established functions, creating competition between processes such as facial and identifiable character processing. In the present study, event-related potential (ERP) recording was used to examine electrophysiological correlates of identification levels of Chinese characters as well as the competition between facial and Chinese character processing after the characters were learnt. Twenty volunteers performed a lateralized face detection task, and N170 responses were recorded when the participants viewed only Chinese characters (identifiable or unidentifiable in *Xiaozhuan* font), or Chinese characters and faces concurrently. Viewing identifiable Chinese characters bilaterally elicited larger N170 amplitudes than viewing unidentifiable ones. N170 amplitudes in response to faces bilaterally declined when identifiable Chinese characters and faces were viewed concurrently as compared to viewing unidentifiable Chinese characters and faces concurrently. These results indicate that the N170 component is modulated by the observer's identification level of Chinese characters, and that identifiable Chinese characters compete with faces during early visual processing.

Introduction

The production of symbolic written language is an important milestone in the development of human civilization. It facilitates the exchange of ideas and has propelled human civilization forward. Since writing is thought to have emerged only 5400 years ago (Dehaene and Cohen, 2007), written language was not part of the human visual system's long-term historical milieu of stimulation. Thus, the emergence of written language raises questions about whether the human brain adapts by developing mechanisms that enable it to reallocate its limited resources for the processing of new kinds of information.

Brain resource reallocation mechanisms may be considered from the following theoretical perspective. The viewpoint is based on the "exaptation" notion of evolutionary theory (Gould and Vrba, 1982), which refers to the development of a new and completely different use for a pre-existing biological mechanism by reusing it in the process of evolution, and the neuronal recycling hypothesis of Dehaene and Cohen, which posits that an existing brain system can be repurposed for novel functions through plasticity in cultural learning (Dehaene and Cohen, 2007). This viewpoint wherein learning to read can invade and recycle cortical regions with older evolutionarily-driven functions is fitting with the evolutionarily recent emergence of written language in that it would not involve alterations of genetic mechanisms (Dehaene, 2005, 2009; Dehaene and Cohen, 2007). Therefore, when learning to read, pre-existing face processes may be recruited for the processing of symbolic written language by literate people, setting up a potentially competitive relationship between identifiable Chinese character and facial processing.

Such a potential competition may be reflected by the N170 component, a negative-going component with a waveform peaking at around 170 ms post-stimulus (Allison et al., 1994; Bötzel et al., 1995; Bentin et al., 1996; Schweinberger et al., 2002; Caharel et al., 2005; Luo et al., 2010). Previous ERP studies involving the relevant N170 effects have demonstrated a consistent pattern in which the ERP component is evoked by faces and Chinese characters, including a similar time range (Bötzel et al., 1995; Bentin et al., 1996; Campanella et al., 2000; Rossion et al., 2000; Liu et al., 2007; Jacques and Rossion, 2007; Maurer et al., 2008; Cao et al., 2011; Lin et al., 2011; Zhang et al., 2011; Fu et al., 2012; Zhao et al., 2012).

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Additionally, Rossion et al. (2004) and Rossion et al. (2007) found that subjects, who are highly knowledgeable about a topic after expertise training, exhibit larger-amplitude N170 components when they view objects related to that topic than novices (Rossion et al., 2004, 2007), indicating that the processing of visual stimuli for which one has expertise differs neurologically from the processing of lesser-known stimuli in an early visual processing stage. Similarly, Zhang et al. (2011) observed that Chinese characters elicited a larger N170 than pictographs and that the latter evoked a stronger N170 than objects, which may reflect specialization for linguistic versus nonlinguistic properties formed by reading experience. Moreover, Brem et al. (2006) and Maurer et al. (2006) found that N170 amplitude correlated positively with reading facility. However, whether the N170 effect induced by viewing Chinese characters may be modulated by the identification ability, which is formed by training to read, for those characters, has not been investigated yet. To address this issue, we recorded N170 amplitudes induced by Chinese characters, and we hypothesize that N170 amplitudes will be lower for unidentifiable Chinese characters than for identifiable ones following reading training.

The authors of several ERP studies that examined the competitive relationship between the processing of objects of expertise and faces concluded that, in an early stage of visual processing, nonface objects (e.g., Greebles and cars) of expertise competed with faces in the occipitotemporal cortex, as evidenced by a decrease in the N170 amplitude for faces when participants were experts rather than novices with the nonface objects (Rossion et al., 2004, 2007). Greebles may have a partial resemblance to human faces (e.g., a head with a nose) (Rossion et al., 2004), whereas Chinese characters are much more distinct from faces in appearance (Li et al., 2013). However, there are some similarities between faces and Chinese characters. As with faces, Chinese characters have a canonical upright orientation and are unique in their appearance and identity. Chinese characters are processed at an individual level, as are faces, and feature information plays an important role in processing both individual Chinese characters and individual faces. The squared visual configuration of Chinese characters is similar in terms of shape to the configuration of faces (Ge et al., 2006; Fu et al., 2012; Li et al., 2013). Some of these similarities that may not exist between faces and other objects (e.g., cars) may induce a competitive relationship between Chinese characters and faces in the neural development of processing (Li et al., 2013). Recently, Li et al. (2013) found that the left-lateralized N170 effect elicited by Chinese characters was related positively to vocabulary and that the face right-lateralization was influenced negatively by character left-lateralization and vocabulary. Such findings demonstrate that Chinese characters may compete with faces in the neural development of processing.

To expand on those findings involving object vs. face competitions and to investigate competition between facial and identifiable Chinese character processing directly, we conducted a study employing competition paradigms from previous studies (Rossion et al., 2004; Sadeh and Yovel, 2010). In our competition paradigm, a lateralized face stimulus and a central stimulus were presented concurrently to induce competition between visual processes, which is different from the paradigm presented by Li et al., in which the faces and Chinese characters appeared individually in different trials (Li et al., 2013). The time course of such a competition in a direct competition paradigm remains unclear. To determine this issue, we used ERP technology with high temporal resolution, to collect data induced by lateralized faces, with the notion that the corresponding ERP component should be present when the competition in processing occurs. We hypothesize that if the processing of identifiable Chinese characters recruits visual processes that are involved in processing faces, leading to a competition between the two, then the N170 component induced by faces should decrease in amplitude when faces are presented at the same time as identifiable Chinese characters as compared to when faces are presented at the same time as unidentifiable Chinese characters.

Methods

Participants

Twenty-four college students (12 males, 12 females; age = 18–26 years; mean age = 22.7 years) from Dalian, China participated in this study (two males and two females were excluded from the study because the number of bad channels exceeded 5% of the total, reducing the number of available trials to less than 40 after EEG and EOG artifacts were eliminated). All participants were right-handed, free of neurological and psychiatric disorders, and had normal or corrected-to-normal vision. They had never participated in similar experiments previously and provided informed consent. After completing the experiment, all participants were paid for their participation. The experimental protocol was approved by the local ethics committee.

Stimuli

Chinese characters (Fig. 1)

A total of 30 *Xiaozhuan* font characters were used (Fig. 1). Among the 30 characters, 20 characters used for training were completely distinct in terms of stroke type to avoid any migration effects (i.e., learning one of the 20 characters has no effect on learning the remaining 19 characters as they all were completely distinct in terms of stroke type), with 10 characters becoming identifiable after training and the other 10 characters being unidentifiable without training; the remaining 10 characters were used as distractors in the recognition task. The size of each character image was set to 7.5 cm wide (equal to 3.77° when viewed 114 cm from the monitor) and 8.5 cm long with MATLAB 2012 software. The characters were presented in white font color on a black background in an upright, inverted, or mirror form. The physical properties of all character pictures, including spatial frequency, contrast grade, and brightness (average grayscale value, 5.64×10^{-5}), were the same. Spatial frequency was normalized using the Gaussian filter in MATLAB 2012 software according to the prior study (Schyns et al., 2007). Contrast grade corresponds to the root mean square contrast over the whole image including background (Dering et al., 2011). Brightness of a picture was obtained by averaging the grayscale values of all pixels of a picture, which can be measured by MATLAB 2012 software.

Combinations of characters and faces

Six upright face pictures (three of women and three of men with neutral expressions) from the native Chinese Facial Affective Picture System (CFAPS) were selected. All faces were presented without hair, glasses, beards, or makeup. Each face image was cropped into the shape of an ellipse with Adobe Photoshop 8.0 software. All face pictures were edited with MATLAB 2012 software to be the same size as the character images. Their physical properties, including spatial frequency, contrast grade, and brightness (average grayscale value, 5.74×10^{-5}), were the same. Face and character pictures were combined in MATLAB 2012 software such that the characters would appear in the center of the computer screen, while the faces were located 1.5 cm to the left or right side of the characters. Hence, faces were presented 9 cm from the center of the screen (4.52°).

Procedure

During training, ten participants (5 males, 5 females) studied 10 characters, and the remaining ten participants (5 males, 5 females) studied a different set of 10 characters. Each participant had three training sessions; the durations of the training sessions were 1 h, 0.25 h, and 0.25 h, respectively, with a 0.5-h or 2-h break between sessions. Primarily, participants were required to know the pronunciations and meanings of the *Xiaozhuan* font characters according to the corresponding *Song* typeface characters. They were asked to perform a writing exercise and practice until they reached the familiarity criteria.

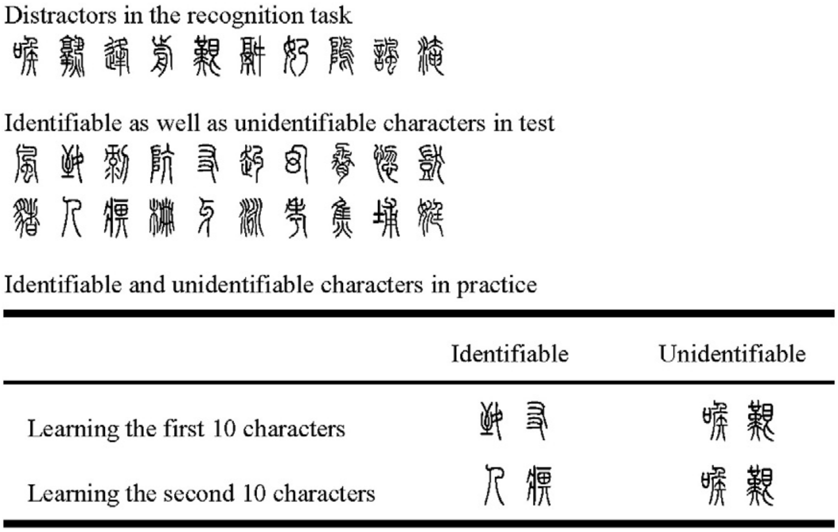

Fig. 1. *Xiaozhuan* font characters used in the present study.

The criteria involved two memory tasks and a recognition task. In the memory tasks, according to the *Xiaozhuan* (*Song*) font characters, participants had to be capable of writing the characters in one font (*Xiaozhuan* or *Song*) when shown the respective characters in the other font characters quickly, accurately, and consistently. For the recognition task, the participants were instructed to judge if they had studied the *Xiaozhuan* font characters that appeared in the center of the screen and were subjected to a 95% accuracy criterion (regardless of the three different forms of character presentation, one participant can make a mistake of one character at the most in the recognition task). In the recognition task, participants viewed 10 trained *Xiaozhuan* font characters and 10 distractors presented in an upright, inverted, or mirror form for 400 ms each, and after a black screen with a random interval of 1000–1500 ms, they were asked to judge if they have learned those characters in an interval of 2 s (participants can recognize upright identifiable characters as fast as inverted or mirror identifiable characters). After training, all the participants reached a high accuracy rate (95–100%) on every character in the recognition task. After training, the interaction between "identification level" (identifiable vs. unidentifiable) and "presentation form" (upright, inverted, vs. mirror) was not significant ($F_{2,38} = 1.61$, $p = .21$, $\eta2\ \mathrm{p} = 0.078$). For identifiable characters, the average response times were 288 ms for upright characters, 292 ms for inverted characters, and 293 ms for mirror characters. After reading training, participants who could accurately identify, read, and write their 10 training characters were deemed to know the characters.

In the formal experiment, participants were seated in a comfortable chair in a sound-isolated, dimly lit room 114 cm from a monitor controlled by a personal computer. Participants had to focus on the center of the screen throughout the experiment. The experimental procedure was programmed with E-Prime 1.2 (Psychology Software Tools, Inc., Pittsburgh, PA). The procedure consisted of four 60-trial blocks (inter-block-interval, 60–90 s). Our experimental procedure was similar to the paradigm — during each test trial, nonface objects were presented for 600 ms, and then faces appeared on the left or right side of objects for 400 ms with a lateralized detection task to accomplish later — used by Rossion et al. (2004) in their Greebles-face processing competition study. In our experiment, at the beginning of each trial, an identifiable or unknown *Xiaozhuan* font character was presented in the center of the screen for 800 ms, during which participants were asked to view it passively. This duration allowed the N170 waveforms to return to baseline before the faces appeared, preventing the N170 waveforms induced by faces from being contaminated by those evoked by characters. Then, faces were presented on the left or right side of characters for 400 ms, avoiding visual offset potentials influencing the N170 waveforms evoked by faces. Despite the possibility that lateralized pictures with a presentation duration of 400 ms may have given rise to eye movements, few lateral eye movements were observed during the experiment, and any trials showing lateral eye movement were excluded from analysis.

The two stimuli disappeared concurrently, leaving a black screen for 1000–1500 ms. Participants were then requested to press keys in response to the positions of faces as accurately and quickly as possible, pressing "1" or "2" on the number keypad when faces were presented on the left or right side of the characters, respectively. To avoid attentional bias caused by any type of character, we used a lateralized face detection task irrelevant to our hypothesis. Finally, a black screen appeared on the monitor for 600 ms, providing sufficient time for the baseline of the waveform to stabilize and thus not be affected by the act of pressing keys (Fig. 2). Once the experiment was finished, participants were asked if they could recognize the characters that had not been studied and none of them reported being able to identify any unstudied characters.

Of the 240 trials, 120 involved 10 recognizable *Xiaozhuan* font characters, and 120 involved 10 unrecognizable *Xiaozhuan* font characters. Faces were equivalently presented on the left or right side of the characters, resulting in 60 trials/side in each condition. The characters were presented in a random order so that the participants were unable to predict the next character, and faces were presented randomly on the left or right side so as not to produce an expectation effect.

Electroencephalogram (EEG) recording and data analysis

Data were collected from 64 scalp sites using tin electrodes mounted on an elastic cap (Brain Products) according to the extended International 10–20 System. EEG signals were recorded by Vision Recorder software (Brain Product) with the reference electrode situated at the Cz site. Vertical electrooculographies (EOGs) were measured via an electrode fixed on the infra-orbital ridge of the left eye. Horizontal eye movements were recorded via an electrode placed on the outer canthi of the right eye. All impedance levels between electrodes and the scalp were kept below 5 kΩ. After being amplified via a 0.01–100 Hz bandpass, EEG and EOG recordings were sampled at 500 Hz/channel and re-referenced offline to obtain a global average.

The EEG data were processed offline with Analyzer 2.0 software (Brain Products). We analyzed ERPs elicited by identifiable or unidentifiable characters and faces presented on the left or right side of the characters. The EEG data were filtered through a 0.1–30-Hz bandpass filter and segmented from 100 ms before to 500 ms after stimulus onset.

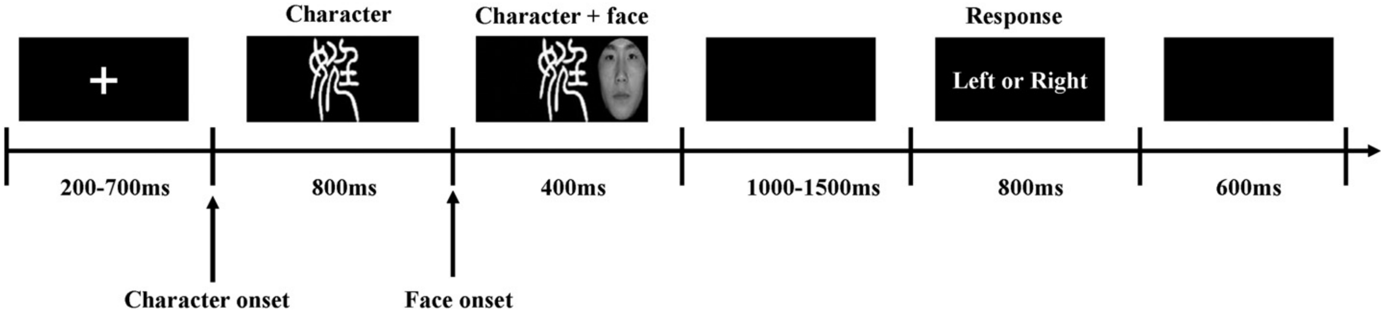

Fig. 2. Stimulus examples and the paradigm used in the experiment. At the beginning of each trial, an identifiable or unidentifiable *Xiaozhuan* font character was presented for 800 ms. Then, faces were presented on the left or right side of the characters for 400 ms. The two stimuli disappeared concurrently, leaving a black screen for 1000–1500 ms. Each trial ended with a lateralized detection task: pressing "1" or "2" on the number keypad when faces were presented on the left or right side of the characters, respectively.

After correction of baseline deviations during a 100-ms pre-stimulus period, EEG and EOG artifacts were eliminated when the amplitude of any electrode exceeded ±50 μV. Each correct segment was averaged for each condition separately. Based on the topographical distribution of grand-averaged ERP activity and previous studies (Rossion et al., 2004, 2007), we selected the four most representative electrode sites (PO7/PO8, P7/P8) located in the occipitotemporal cortex for N170 component analysis.

Based on visual inspection of the grand-averaged figures, depending on the criteria in the measurement of ERP waveforms and references (Picton et al., 2000), we acquired the respective mean amplitudes of the N170s elicited by characters, faces (contralateral processing) and faces (ipsilateral processing) that were presented along with characters from three 30-ms temporal windows near these mean latencies: 155–185 ms, 160–190 ms, and 190–220 ms.

We analyzed mean N170 amplitudes for stimuli with repeated measures analyses of variance (rmANOVAs) using SPSS 18.0 for Windows. When the N170 component elicited by characters was being analyzed, the identification level (two levels: identifiable or unidentifiable), hemisphere (two levels: left, right), and electrode site (two sites) were considered. The factor "visual field stimulated" (left, right) was added to the analyses of faces. The *p* values of all main effects and interactions were corrected by application of the Greenhouse–Geisser method.

Results

Behavioral performance

A two-way rmANOVA for accuracy and response time in the task in which participants determined the position of laterally presented faces was conducted with "identification level" (identifiable vs. unidentifiable) and "visual field stimulated" (left vs. right) as factors. In terms of accuracy, all participants were confirmed to have performed well, with a relatively high accuracy rate (92–100%) in all conditions (Table 1). There were no significant main effects of the above two factors ($F_{1,19} = 0.93$, $p = .35$, $\eta2\ \mathrm{p} = 0.047$; $F_{1,19} = 1.58$, $p = .23$, $\eta2\ \mathrm{p} = 0.077$). Accuracy was similar between the recognizable (mean ± standard error, 97.8 ± 0.5%) and unknown (97.4 ± 0.5%) character conditions and between the left (97.8 ± 0.4%) and right (97.3 ± 0.5%) visual field presentations. In addition, the interaction between the two factors was not significant ($F_{1,19} = 0.087$, $p = .77$, $\eta2\ \mathrm{p} = 0.005$).

In terms of response time, we did not observe main effects of the factors "identification level" ($F_{1,19} = 0.49$, $p = .49$, $\eta2\ \mathrm{p} = 0.025$) and "visual field stimulated" ($F_{1,19} = 2.68$, $p = .12$, $\eta2\ \mathrm{p} = 0.12$); nor a significant identification level × visual field stimulated interaction ($F_{1,19} = 0.046$, $p = .83$, $\eta2\ \mathrm{p} = 0.002$; Table 1). In other words, task response times did not differ significantly between the recognizable character (365.88 ± 16.78 ms) and unknown (368.32 ± 16.96 ms) character conditions or between the left (370.85 ± 17.55 ms) and right (363.35 ± 16.30 ms) visual fields. Overall, the behavioral results indicated that the participants were able to accomplish the lateralized face detection task accurately and quickly, regardless of whether they had studied the characters or whether the faces were presented on the left or right side of the characters.

Table 1
Behavioral results [mean (SD)].

	Accuracy (%)		Reaction time (ms)	
	Identifiable	Unidentifiable	Identifiable	Unidentifiable
Left visual field	97.92 (2.41)	97.67 (2.44)	369.35 (76.95)	372.35 (81.17)
Right visual field	97.58 (2.62)	97.08 (2.53)	362.42 (75.39)	364.29 (71.59)

ERP data analysis

We observed a significant main effect of character identification level on N170 amplitude ($F_{1,19} = 22.69$, $p = .000$, $\eta2\ \mathrm{p} = 0.54$). As shown in Fig. 3, the amplitudes of the N170 component elicited by identifiable characters (−7.60 μV) were larger than those elicited by unrecognizable ones (−6.59 μV; $p = .000$, *t*-test).

As shown in Fig. 4, the identification level of the characters influenced the amplitude of N170 components elicited by the faces ($F_{1,19} = 7.99$, $p = .011$, $\eta2\ \mathrm{p} = 0.30$), with N170 amplitudes preceded by identifiable characters being −5.54 μV on average and those preceded by unidentifiable ones being −6.01 μV on average ($p = .011$). There was a significant hemisphere × visual field stimulated interaction ($F_{1,19} = 27.12$, $p = .000$, $\eta2\ \mathrm{p} = 0.59$), with contralateral processing eliciting the larger N170 (Fig. 4). Simple-effects analyses indicated that faces presented in the right visual field (−5.97 μV) evoked larger N170 amplitudes in the left hemisphere than did faces presented in the left visual field (−4.21 μV; $p < .05$), and that faces presented in the left visual field (−7.94 μV) evoked larger N170 amplitudes in the right hemisphere than did faces presented in the right visual field (−4.99 μV; $p < .05$). Additionally, we observed a larger N170s over the right hemisphere (−6.46 μV) than over the left hemisphere (−5.09 μV) in response to faces ($F_{1,19} = 8.79$, $p = .008$, $\eta2\ \mathrm{p} = 0.32$).

In addition, the correlation between the increase in amplitude for identifiable vs. unidentifiable characters and the N170 competition effect, which was reflected by the reduction in amplitude for faces, was not significant ($r = 0.38$, $p = 0.10$).

Taken together, the present results show that the N170 elicited by *Xiaozhuan* font characters increased significantly after learning the characters, whereas the N170 elicited by faces decreased significantly when the faces were preceded by identifiable rather than unidentifiable characters.

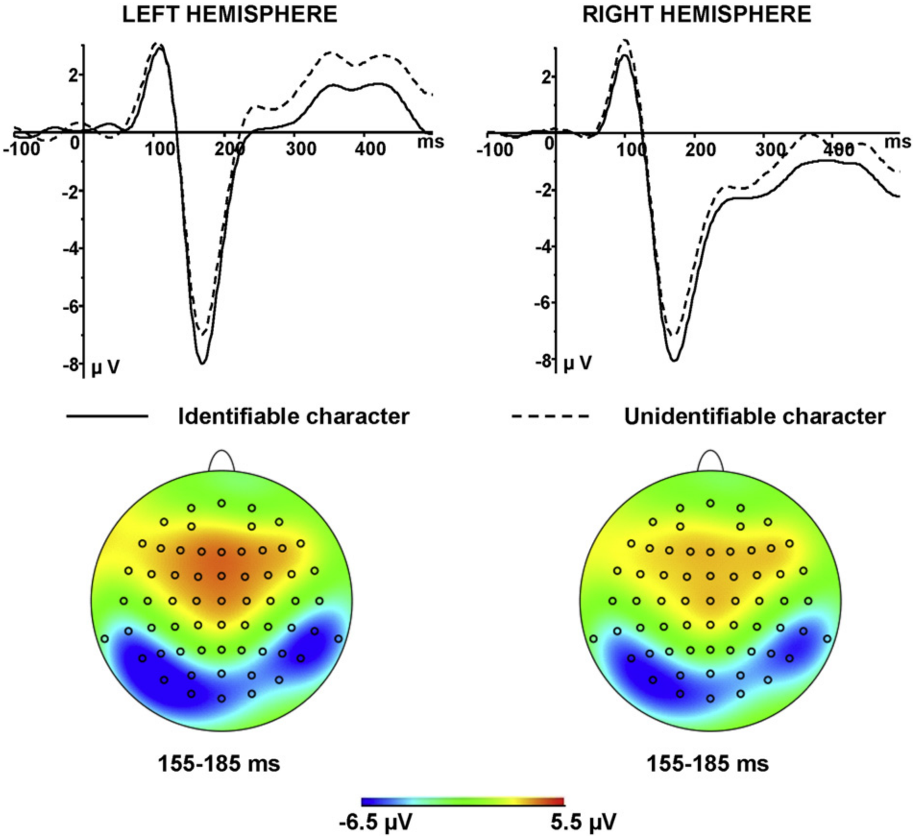

Fig. 3. Grand average ERP waveforms for identifiable character (solid lines) and unidentifiable character (dashed lines) conditions recorded at P7 and P8 electrode sites (top row). Topographic maps for identifiable characters (left) and unidentifiable characters (right) at 155–185 ms (bottom row).

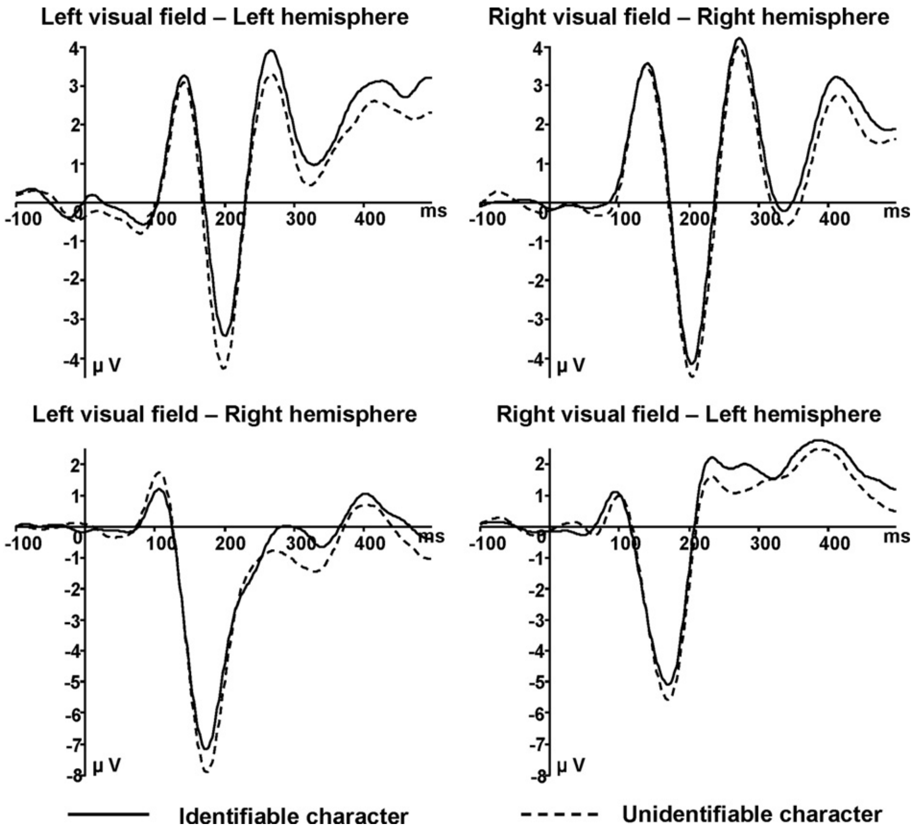

Fig. 4. Grand average ERP waveforms for faces preceded by identifiable character (solid lines) and unidentifiable character (dashed lines) conditions recorded at P7 and P8 electrode sites.

Discussion

In the current study, we used a direct competition paradigm and ERP technology to conduct a novel investigation of whether faces compete with identifiable Chinese characters during early visual processing. We probed the brain mechanisms mediating the processing of identifiable versus unknown characters, and examined the relationship between processing of Chinese characters from different identification levels and of faces, as reflected by elicited N170 component amplitudes. The participants were able to accomplish the lateralized face detection task accurately and quickly in all conditions. Identifiable Chinese characters bilaterally evoked larger N170 amplitudes than did unidentifiable characters, indicating that N170 was modulated by identification level in relation to training. Amplitudes of face-elicited N170 components were reduced bilaterally when identifiable characters and faces were viewed concurrently as compared to trials in which unidentifiable characters and faces were viewed concurrently, indicating that identifiable Chinese characters after learning competed with faces in an early stage of visual processing.

Modulation of N170 by identification level of Chinese characters

Regarding whether the different identification levels of participants for Chinese characters can be reflected by electrophysiological changes, we found larger N170 amplitudes for identifiable characters than for unidentifiable ones. These findings are expected since N170 amplitudes increased after a long-term “naturally developed” or trained expertise with objects or after an increase in reading ability for words (Tanaka and Curran, 2001; Rossion et al., 2002, 2004, 2007; Li et al., 2013).

Previous studies (Rossion et al., 2004, 2007; Li et al., 2013) observed an increase in N170 amplitudes by comparing object experts with object novices, or people with high reading ability and those with low reading ability in a between-subjects design. In the current study, reading training for certain *Xiaozhuan* font characters caused trained characters to become recognizable and untrained characters to remain unrecognizable. We used a within-subjects design, which indicated that the N170 amplitude is mediated by the identification level of the Chinese characters. Our interpretation is that, as a previous study (McDonald et al., 2010) found stronger responses to repeated words (presented 20 times) than to new ones (presented only once), in the present study, identifiable Chinese characters evoked larger N170 amplitudes than unidentifiable ones, perhaps due to prior high-frequency exposure to the former ones. Nevertheless, we observed an earlier response (150–200 ms vs. 200–240 ms), perhaps because both repeated and new words were identifiable in the prior study, whereas some of characters in our study were totally unidentifiable. Additionally, our finding supports Zhang et al.'s (2011) suggestion that the N170 effect reflects specialization for linguistic properties formed by reading experience in that only the recognizable characters contained linguistic information.

Interestingly, we found that the ERP effect was bilateral. In contrast, Brem et al. (2006), Maurer et al. (2006) and McDonald et al. (2010) found a lateralized left occipitotemporal response, perhaps because different effects are induced by different kinds of symbols. That is, English words, which were used in the prior study, elicited a left-lateralized effect (Rossion et al., 2003; Simon et al., 2007), whereas Chinese characters, which were used in the current study, elicited a bilateral effect. In addition, our results fit with a prior observation that character-resembling stimuli evoke a larger N170 bilaterally than stimuli that are less character-resembling (Zhang et al., 2011). In the current study, identifiable *Xiaozhuan* font characters become reminiscent of the corresponding common Chinese characters, which may make them more character-resembling than unidentifiable ones, and hence, lead to a bilateral N170 effect. Thus, these results showing a bilateral N170 effect provide electrophysiological evidence that N170 is modulated in both hemispheres by the identification level of Chinese characters.

Identifiable Chinese characters compete with faces during early visual processing

More importantly, our findings allowed us to investigate the relationship between the identification level of participants for characters and their responses to faces in a competition paradigm. Interestingly, we found that N170 amplitudes elicited by faces were larger when they were preceded by unidentifiable characters than when they were preceded by identifiable ones. Therefore, N170 amplitudes induced by faces could be modulated by the identification level of Chinese characters. Our findings support the hypothesis that visual processes involved in processing identifiable Chinese characters compete with those recruited for facial processing. When the experimenter delivered the instructions, s/he told participants that stimuli presented beside the characters were going to be faces. After training trials for the formal experiment and the formal experiment itself, when the experimenter asked participants if they perceived faces, their answer was consistently yes. In addition, according to the grand average ERP waveforms and analysis of the ERP data in relation to faces, we found larger N170 amplitudes in the right hemisphere than in the left hemisphere. This result is similar to the face N170 right-lateralization effect as described by Jacques and Rossion (2006) and Kovács et al. (2013).

In the current study, during the recognition of Chinese characters, visual processes engaged in processing the faces were recruited gradually for processing the characters, creating competition between the processing of faces and identifiable Chinese characters, when the two were presented simultaneously. Using fMRI technique, Dehaene et al. (2010) found that the activation of the visual word form area (VWFA), which processes words (Fiez and Petersen, 1998; McCandliss et al., 2003; Dien, 2009; Dehaene et al., 2010; Dehaene and Cohen, 2011; Thesen et al., 2012), in response to faces declined with increasing reading performance, which suggests that in the visual cortex, visual processes for the reading stimuli may compete with those for faces in literate people compared to illiterate people (Dehaene et al., 2010). Differently, we used the ERP technique and Chinese characters from different identification levels to obtain electrophysiological evidence for competition between facial and identifiable Chinese character processing in an early visual stage. Therefore, our study examined the time course of the relationship between different identification levels of Chinese characters and faces in a direct competition paradigm. Our interpretation is that our findings support the assumption based on the neuronal recycling hypothesis (Dehaene and Cohen, 2007), which suggests that after reading training, reading stimuli invade and reuse a pre-existing brain system used for processing faces. Visual processes for subsequent faces recruited at least part of certain processes that were still processing identifiable Chinese characters, which were formed by reading training. This led to a competition between facial and identifiable Chinese character processing at early visual stage, when faces and characters were presented concurrently. Thus, we observed a reduction of N170 induced by faces after reading training. As opposed to the prior results where the use of English words elicited a left-lateralized N170 effect (Rossion et al., 2003; Simon et al., 2007), Chinese characters elicited a bilateral N170 effect in the present study, which may lead to a bilateral N170 reduction for faces. In summary, our findings indicate that a short training session with Chinese characters can result in identifiable Chinese characters competing with faces in early visual processing, and such competition can be reflected by N170 changes.

Furthermore, consistent with the work of Rossion et al. (2004), we found that contralateral processing of faces induced shorter latency, larger amplitude N170 components than ipsilateral processing of faces. This may be due to stimuli first being processed in the contralateral hemisphere, before being transmitted for further processing to the ipsilateral hemisphere through the corpus callosum.

Our study had several limitations. Firstly, the relatively small number of *Xiaozhuan* characters used in the present study may have limited the scope of ERP differences observed. Thus, this phenomenon should be re-examined with larger arrays of stimuli in the future. Secondly, to probe the effect of character expertise on the N170 component effects, it would be interesting to compare the N170 components of expert calligraphers versus laymen. Finally, it may be pertinent to explore how particular physical properties of the characters might influence the competitive relationship between the processing of identifiable Chinese characters and faces.

Conclusion

In the current study, we documented electrophysiological correlates of different identification levels of Chinese characters and obtained evidence of competition between facial and identifiable Chinese character processing. Our findings support the hypothesis that the amplitude of a character-induced N170 component is modulated by the observer's identification level of Chinese characters. Concurrent presentation of identifiable Chinese characters with faces bilaterally reduced face-induced N170 amplitudes, providing evidence of early-stage processing competition between the two stimulus types. These results have theoretical implications for the co-processing of the various visual stimuli encountered in the environment.

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Self-reflection modulates the outcome evaluation process: Evidence from an ERP study

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ABSTRACT

Recent research demonstrated structural overlap between reward and self processing, but the functional relationship that explains how self processing influences reward processing remains unclear. The present study used an experimentally constrained reflection task to investigate whether individuals' outcome evaluations in a gambling task are modulated by task-unrelated self- and other-reflection processes. The self- and other-reflection task contained descriptions of the self or others, and brain event-related potentials (ERPs) were recorded while 16 normal adults performed a gambling task. The ERP analysis focused on the feedback-related negativity (FRN) component. We found that the difference wave of FRN increased in the self-reflection condition compared with the other-reflection condition. The present findings provide direct evidence that self processing can influence reward processing.

1. Introduction

The concepts of the self and reward are both important topics in the field of psychology. Great progress has been made recently in understanding how the self and reward are represented and processed in the human brain (Johnson et al., 2002; Schultz, 2006). The neural mechanisms of the self and reward have been investigated largely independently. However, neuroimaging studies have revealed neuronal networks that overlap in self and reward processing (for review, see Northoff and Bermpohl, 2004; Northoff and Hayes, 2011), mainly in cortical middle structures (CMSs), including the anterior cingulate cortex (ACC), posterior cingulate cortex (PCC), precuneus, and especially ventromedial prefrontal cortex (vmPFC). In addition to structural overlap, recent studies on the self and reward have demonstrated that self-specific stimuli induce changes in neural activity in regions that are recruited during reward (deGreck et al., 2008; Enzi et al., 2009; Ersner-Hershfield et al., 2009; Tamir and Mitchell, 2012), including the vmPFC, ventral striatum (VS), and ventral tegmental area (VTA). The aforementioned findings raise the possibility that vmPFC's processing of self-related content may reflect a valuation mechanism. Indeed, the vmPFC plays a broad role in affective and value-based processing (Phan et al., 2002; Roy et al., 2012). Some researchers have explicitly proposed that the vmPFC might signal the personal significance of self-related content. For example, Schmitz and Johnson (2007) proposed that the vmPFC subserves supramodal processes that contribute to monitoring the self-relevance of various types of stimuli. Northoff and Hayes (2011) proposed a reward-based view of the self and discussed three ways in which self-relevance and value-based processing are related. More relevant to the present study, D'Argembeau (2013) relied on the valuation hypothesis to explain the role of the vmPFC in self-processing. He proposed several lines of converging evidence to support this hypothesis. Increasing the psychological distance from self-representations leads to a decrease in vmPFC activation, and the magnitude of vmPFC activation linearly increases with the personal importance that is attributed to self-representations. However, the evidence reviewed by these authors mainly focused on either the self-relevance of external stimuli (e.g., pictures of emotional scenes or rewarding stimuli) or correlation between vmPFC activation and personal significance. Few studies have explored the ways in which self processing influences reward processing. To provide a better understanding of the interaction between self and reward, the present study employed the event-related potential (ERP) technique, combined the self-reflection task and a gambling task to investigate how self- and other-reflection influences the outcome evaluation process.

The self-and other-reflection task is an important approach that is used to assess the neural bases of self-related processes using functional neuroimaging methods (Christoff et al., 2011). This approach has addressed the relevance of trait adjectives with reference to oneself and compared brain activity to control conditions (e.g., the reference of trait adjectives that are related to close friends or others; van der Meer et al., 2010). The social neuroscience literature indicates that the evaluation of one's own personality and the personalities of others

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recruits shared neural networks, mainly in the CMS regions (Modinos et al., 2011; Murphy et al., 2010; Qin and Northoff, 2011; Schmitz et al., 2004). Nonetheless, some self-specific structures can differentiate processing of the self and others. For example, four important meta-analyses investigated cortical activation that is relevant to self-specific regions (Northoff et al., 2011; Qin and Northoff, 2011; van der Meer et al., 2010). Results indicated four particular regions that are sensitive to self-specificity: pACC (Qin and Northoff, 2011), dorsal anterior cingulate cortex (dACC; van der Meer et al., 2010), vmPFC, and anterior insula (AI; Northoff et al., 2011). These regions have also been implicated in diverse aspects of reward processing (Ruff and Fehr, 2014). The engagement of these areas during both self processing and reward processing may provide the basis for the possible interactions between them.

Reward processing can be divided into two sub-processes: anticipation of reward and outcome evaluation (Schultz, 2006). The present study focused on the latter. In ERP studies, two ERP components are particularly sensitive to the processing of outcome feedback. Feedback-related negativity (FRN) is a medial frontal negative deflection of the visually evoked ERP that peaks approximately 250 ms following feedback, indicating negative performance feedback compared with positive performance feedback and monetary loss or nonreward compared with monetary gain or reward (Gehring and Willoughby, 2002). Localization studies suggest that FRN is generated near the ACC (Nieuwenhuis et al., 2004), consistent with functional magnetic resonance imaging results that implicated the ACC and vmPFC in negative feedback processing (e.g., Nieuwenhuis et al., 2005). The most influential theories that have been proposed suggest that FRN reflects a reinforcement learning signal that is associated with prediction errors, especially when outcomes are worse than expected (Holroyd and Coles, 2002). However, recent accumulating evidence suggests the opposite viewpoint, in which the FRN amplitude is largely modulated by neural activity in gain trials. One proposal is that monetary gain feedback elicits a distinct positive-going deflection (Foti et al., 2014; Proudfit, 2015), and reward positivity directly reflects activity of the mesencephalic dopamine system (Foti et al., 2011), a neural network that is critically involved in reward processing (Schultz, 2006). The second component is the P3 or P300, which is a centro-parietal positivity that is often associated with allocation of cognitive resources, such that larger P3 amplitudes indicate more resources are allocated to the ongoing task (Polich, 2007; Molnár, 1999).

Self-reflection is not immune to the valence of the reflected content. According to the self positivity bias view, people have a need to view themselves positively (Mezulis et al., 2004). Cortical activity during self-reflection is also modulated by the valence of the content. For example, Moran et al. (2006) found that positive self-processing evoked larger vACC activity than negative self-processing. Given the anatomical proximity of the mPFC and vACC, a tempting speculation is that the self effect would be larger under positive reflection conditions than under negative reflection conditions.

Building on these aforementioned observations, in the present study, we used explicitly defined reflection task to determine whether self processing influences outcome evaluation. We predicted that the self-reflection task can influence the outcome evaluation process, and the modulatory effect will be manifested in FRN. Specially, the self-reflection evokes an enhanced vmPFC activity and it is generally thought that vmPFC is the source of the FRN, so we hypothesized that the FRN should be larger in the self-reflection condition than in the other-reflection condition. Further, we predicted the FRN should be larger in the positive reflection condition than in the negative reflection condition.

2. Methods

2.1. Participants

Sixteen college students (22.6 ± 0.8 years of age; range, 22–24 years; nine males) participated in the study. Informed consent was obtained prior to the experiment. All of the participants had normal or corrected-to-normal vision, and none of them had a history of neurological disease or brain injury. All of the participants were right-handed. The subjects were paid for their participation.

2.2. Self- and other-reflection task

Before the experimental task, each participant was asked to list eight positive and eight negative adjectives that best described themselves. Each word was used to form two sentences to describe a trait of the participant or a stranger (e.g., the word “brave” could be used to generate “I am brave” and “He/she is brave”). At the beginning of each trial, this sentence was presented on the screen for 3 s. When the sentence described the participants themselves, they were asked to reflect on the trait as mentioned in the sentence. If the subject of the sentence was a third person, then the participants were asked to reflect on someone who they did not know who possesses this trait.

Immediately after the reflection task, the subjects underwent the gamble task. The stimulus display and behavioral data acquisition were conducted using E-Prime 1.1 software (Psychology Software Tools). During the task, the participants sat comfortably in an electrically shielded room approximately 80 cm from a computer screen. Each trial began with the presentation of two white rectangles (2.5° × 2.5° of visual angle), in which two Arabic numerals (9 and 99) were individually presented to indicate two alternative options on the left and right sides of a fixation point. The positions of the two numbers were counterbalanced across trials. The participant was asked to make a selection by pressing the “F” or “J” key on the keyboard with the left or right index finger, respectively. The alternatives remained on the screen until the participant chose a rectangle, which was then highlighted by a thick red outline for 500 ms. Afterward, the outcome of the participant's choice was presented such that its valence and magnitude were sequentially displayed, with a 500 ms interval between presentations (Fig. 1). The task had four possible outcomes: $+9$, $+99$, -9, and -99. Each outcome indicated the number of points the participant won (when the valence of the outcome was positive [$+$]) or lost (when the valence of the outcome was negative [$-$]) in the current trial. The formal task consisted of four blocks with 64 trials each. Unbeknownst to the participant, the outcomes were provided according to a predetermined pseudorandom sequence, and each participant received exactly 64 of each kind of outcome.

Before the experiment, each participant was informed about the rules and meaning of the symbols in the task. The participants were also told that the gain or loss was unrelated to the reflection task. Additionally, the participants were encouraged to respond in a way that would maximize the total score. The participants were told that higher scores would result in more bonus money that they would receive at the end of the experiment. However, after the participant finished the task, he/she was briefed that there was no optimal strategy in the task. Each participant was paid 50 Chinese Yuan (approximately $8) for participation.

2.3. Electrophysiological recording and measurement

Electroencephalographic (EEG) activity was recorded from 63 scalp sites using tin electrodes that were mounted in an elastic cap (Brain Products) with online reference to the middle at Cz and Fz (FCz) and offline algebraic re-reference to the average of the left and right mastoids. Horizontal electrooculograms (HEOGs) were recorded from an electrode that was placed at the outer canthi of the right eye. Vertical electrooculograms (VEOGs) were recorded from an electrode that was placed above the left eye. All inter-electrode impedance was maintained at <10 kΩ. Electroencephalographic and EOG signals were amplified with a bandpass from 0.01 to 100 Hz and continuously sampled at 500 Hz/channel.

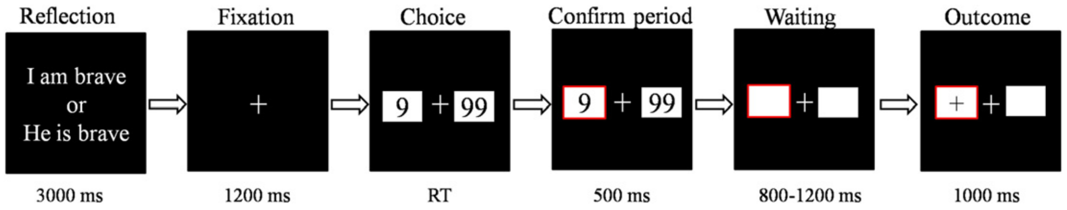

Fig. 1. The sequence of events within a single trial in the monetary gambling task. In each trial, the reflection information lasted for 3000 ms then the fixation point lasted for 1200 ms. The participant was then presented with a choice of two alternatives, and the participant responded using the left or right index finger. The alternatives remained until the participant made his/her choice. Afterward, his/her choice was highlighted for 500 ms. After a subsequent interval of 800–1200 ms, the participant received feedback, lasting 1000 ms, which indicated whether he/she gained or lost in that trial.

Offline analysis of the EEG was performed using Brain Vision Analyzer software (Brain Products, Gilching, Germany). The first step in data preprocessing was the correction of ocular artifacts using Independent Component Analysis of the continuous data using Brain Vision Analyzer software (Brain Products, Munich, Germany). The ocular-artifact-free EEG data were low-pass-filtered below 30 Hz (12 dB/oct) and high-pass-filtered above 0.5 Hz (12 dB/oct). Separate EEG epochs of 1000 ms (200 ms baseline) were extracted offline for the stimuli. Error trials were discarded from all of the analyses. All of the trials in which EEG voltages exceeded a threshold of ±75 μV during the recording epoch were excluded from the analysis.

According to previous studies, the FRN amplitude can be calculated in essentially two ways: using grand-averaged waveforms or creating a difference wave between error and correct trials (Holroyd et al., 2008). The main advantage of the difference wave approach is the minimization of overlap between FRN and other ERP components, including P3 (for detailed discussions, see Hajcak et al., 2007; Holroyd and Krigolson, 2007). Indeed, the application of the difference wave method generates clear FRN. To minimize the effects of overlap among FRNs with positive ERP components, we also created difference waves (dFRN) by subtracting the ERP responses in gain trials from the ERP responses in loss trials within the 220–320 ms window. The electrode at which the FRN reached a maximum was detected along the frontal midline (Fz and Cz). After examining the parietal-occipital regions, in which the P3 associated with outcome evaluation usually reaches its maximum, we determined that the P3 amplitude was largest at the CPz site. P3 was measured as the average amplitude in the 300–400 ms time window at CPz. For the dFRN amplitude analysis, we used the following within-subjects factors: electrode site (two sites: Fz and Cz), reflection valence (two levels: positive and negative) and reflection type (two levels: self-reflection and other-reflection). For the P3 amplitude, we used the following within-subjects factors: outcome valence (two levels: win and loss), emotional valence (two levels: positive and negative) and reflection type (two levels: self-reflection and other-reflection). For all of the analyses, p values were corrected for deviations according to Greenhouse and Geisser (1959).

3. Results

3.1. Behavioral results

We defined the choice of "9" as the risk-avoidant choice in our experiment, predicting that participants would make this choice to avoid the possibility of a large loss ("−99"). However, by making this choice, they also gave up the opportunity to receive the larger reward ("+99"). In contrast, the choice of "99" was defined as the risky choice (high-risk or high-return).

For the purpose of investigating the influence of reflection type and reflection valence on risk-avoid behavior, the average level of risk-avoidant choices that were made by each participant were entered into a 2 (reflection type: self and other) × 2 (reflection valence: positive and negative) ANOVA test. The main effects and interaction were not significant ($p > 0.05$, self positive: M = 31; self negative: M = 34, other positive: M = 31; other negative: M = 32).

3.2. ERP results

For the dFRN amplitudes, repeated-measures analyses of variance revealed no main effect was significant ($p > 0.05$). The interaction between emotional valence and reflection type was significant ($F_{1,15} = 6.32$, $p = 0.024$, $\eta^2 = 0.296$). Simple effect analysis revealed that self-reflection (M = −2.398 μV, SD = 1.50) evoked a larger dFRN than in the other-reflection (M = −1.418 μV, SD = 1.36) in the positive condition ($p = 0.019$) but not in the negative condition. All other interactions were not significant ($ps > 0.05$).

For the P3 amplitudes, repeated-measures analyses of variance revealed a main effect of emotional valence ($F_{1,15} = 7.52$, $p = 0.015$, $\eta^2 = 0.334$). P3 was larger in the positive reflection condition (M = 3.67 μV, SD = 2.66) than in the negative reflection condition (M = 3.14 μV, SD = 2.14). The main effect of outcome valence was also significant ($F_{1,15} = 12.30$, $p = 0.003$, $\eta^2 = 0.451$). P3 was larger in the win condition (M = 3.09 μV, SD = 2.37) than in the loss condition (M = 3.72 μV, SD = 2.33). The main effect of reflection type and all the interactions were not significant ($ps > 0.05$).

4. Discussion

The aim of the present study was to determine the effects of a self- and other-reflection task on the outcome evaluation process during a gambling task. After a decision was made that was unrelated to the reflection process, the participants received negative or positive feedback after they made a choice in a gambling task. Feedback-related negativity was larger in the self-reflection condition than in the other-reflection condition (Fig. 2A). These results indicate a significant influence of the self- and other-reflection task on the outcome evaluation process and provide additional support for a close link between the self and reward networks.

The present results appear to have important implications for the relationship between the self and reward networks. Northoff and Hayes (2011) proposed three relationship models to explain the relationship between self and reward: integration, segregation, and parallel processing. These relationship models mainly rely on overlapping structures between the self and reward networks. Few studies have explored the functional relationships between self processing and reward processing. The present FRN results support the view that the self and reward networks have a tight relationship and extend previous results by showing that the self process can functionally modulate reward processing. Schmitz and Johnson (2007) proposed that self-appraisal underlies the processing of fear, reward, emotion, pain, and others. The present FRN results provide direct evidence that the reflection process can modulate reward processing. The self process is involved in value assignment. The present results are consistent with these views, demonstrating that self-reflection can directly modulate the outcome evaluation process.

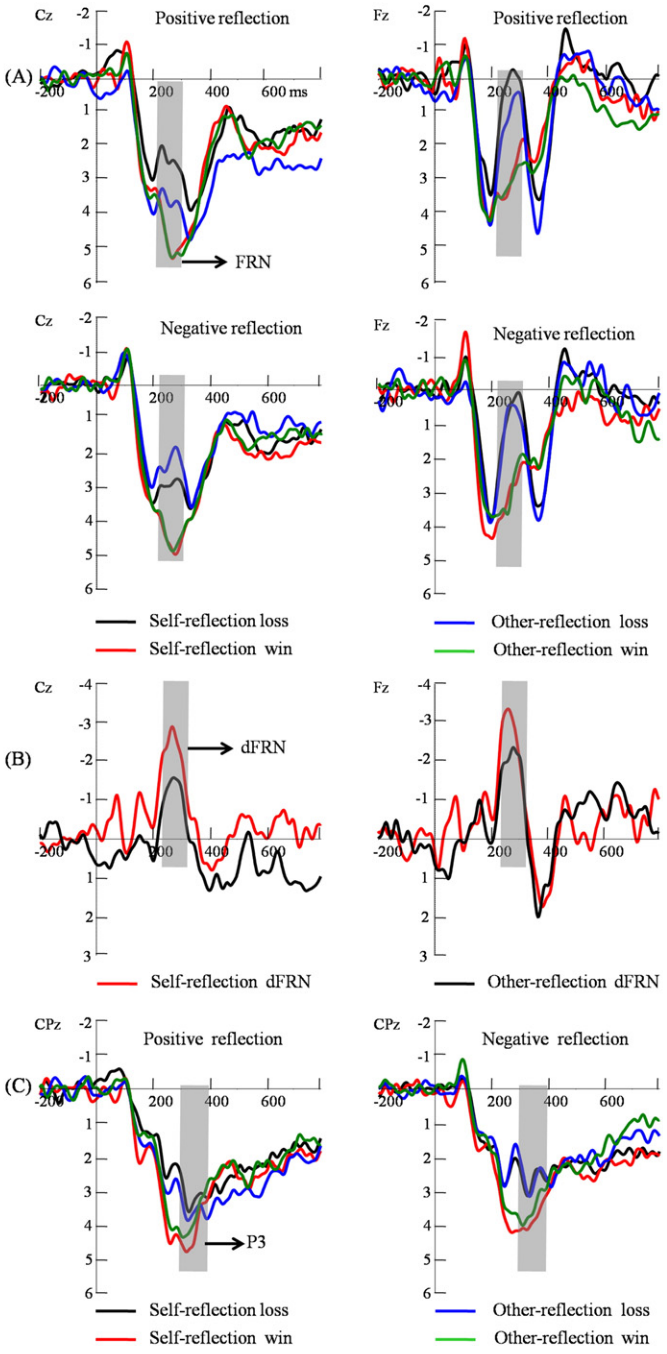

Fig. 2. (A) Grand average FRN waveforms in the positive and negative reflections and (B) dFRN waves collapsed over reward magnitudes at two electrodes post-onset of the feedback stimuli in the positive reflection condition. The gray shaded areas indicate the dFRN analysis window (220–320 ms) for average amplitudes. (C) Grand average P3 waveforms at CPz. The left is the P3 in the positive reflection condition and the right is the P3 in the negative reflection condition.

Self processing is proposed to reflect activation of the long-term value system, and outcome evaluation reflects activation of the short-term value system (Northoff and Hayes, 2011). The present results indicate that the activation of self-relevant information has an important impact on reward processing, supporting the view that activation of the long-term value system can modulate short-term reward processing. What mechanisms might account for the observed long-term value system's modulation of outcome evaluation? Given the nature of the self-reflection task that was used in the present study, a tentative explanation of our results may be based on some form of the modulation of activity in brain areas that are associated with self-reflection. In studies that evaluated self-reflection vs. other-reflection contrast (i.e., self > other), both the dACC (BA 32) and right vmPFC (BA 10) were more activated in the self-reflection condition than in the other-reflection condition. Importantly, source models of FRN often include vmPFC and ACC regions (Walsh and Anderson, 2012). Given the fact that the vmPFC is involved in both self referential and feedback processing, a reasonable speculation is that the vmPFC played an important role in the modulation of FRN in the present study. This possibility is supported by the hypothesis that the vmPFC is related to reinforcement expectancy, sensitive to biasing self-relevant characteristics of the stimulus (Murray et al., 2012). Self-reflection may cause greater activity in brain areas that are sensitive to reward, such as the vmPFC and ACC, whereas other-priming causes less activation in the same brain regions. The precise mechanisms that are involved in this baseline modulation cannot be determined from the present work.

In addition to the reinforcement-learning explanation of FRN, some researchers have also stressed the motivational/affective significance of FRN. Supporting the motivational/affective interpretation of FRN, much evidence has indicated that interpersonal relationships in reward processing (Leng and Zhou, 2010), responsibility (Li et al., 2010), and the extent to which others are included in the "self" concept (Kang et al., 2010) can modulate FRN. For example, a recent study manipulated the degree of responsibility by asking participants to execute a task themselves or to complete the task with two partners (Li et al., 2010). They found that FRN was enhanced when responsibility was high. The common feature of these factors is that they are all related to self involvement in the task. Previous studies showed that FRN amplitudes are correlated with the degree to which participants feel involved in the task (Yeung et al., 2005). The present results provide insights into how the self-involvement factor influences FRN. We propose that the common feature of these factors is that they all contain a certain level of self processing. Near social distance, a higher level of relevance, a higher proportion of responsibility, have all been shown to involve more in-depth processing than their respective control conditions. The in-depth processing of the self activates the reward network, leading to larger FRN in these conditions than in control conditions. Nonetheless, these are only speculations, and further research is needed to address the issue of such self-related modulation of FRN.

Self-reflection evoked a larger dFRN than other-reflection only in the positive condition and not in the negative condition (Fig. 2B). As mentioned in the Introduction above, self positivity bias makes people tend to view themselves positively (Mezulis et al., 2004). Therefore, participants were more likely involved in positive self-reflection than in negative self-reflection. Consistent with this possibility, a previous study reported a positive correlation between vmPFC activity and scores on a questionnaire that assessed one's interest in self-reflection (D'Argembeau et al., 2014).

Consistent with previous studies, the P3 could be differentiated between the loss and win conditions (Fig. 2C). Previous studies showed that positive feedback elicited a larger P3 amplitude than negative feedback (Hajcak et al., 2007; Wu and Zhou, 2009). P3 was larger in the positive condition than in the negative condition. Importantly, it was not modulated by the self-reflection type. P3 has been proposed to reflect a more elaborative evaluation, in which factors that affect the allocation of attentional resources are recruited in a top-down, controlled manner. The present results indicated that the participants devoted more attentional resources in the positive condition than in the negative condition. P3 was insensitive to self-reflection priming, indicating that the self-reflection priming effect occurred at an earlier semiautomatic outcome evaluation stage.

The experimental task in the present study consisted of a sentence that indicated the trial type, a period for mental reflection with no need for a response, and then a gambling task. To investigate the effects of self-reflection on outcome evaluation, the subjects were instructed to generate self-reflective cognition when presented with a sentence that contained a trait word that described themselves. The other-reflection condition involved reflection on an unknown person. When designing the experimental task, we purposely did not use a cognitive or behavioral task that would involve, for example, a finger response to avoid any interference with the self-reflection process, thus enabling us to focus on the mental component of the reflection task. The utilization of solely mental self-reflection was meant to ensure the absence of possibly interruptive motor responses. The lack of a behavioral response for task performance or a control for attentiveness during the task may be considered a limitation of the present study. There is the likelihood of non-engagement of the participants in the mental processes of interest. However, such an additional motor response would have directed the attention of the subjects toward performing this motor task and away from introspection. The reflection time was short, so attentiveness and cooperation may be presumed in the present study. To control for the participants' attentiveness and cooperation, the wakefulness of the participants was monitored to ensure that they were indeed engaged in the reflection task during the presentation of the sentences.

Another possible limitation of the present study is that we did not explore whether positive and negative trait reflection differentially influences outcome evaluation. A previous study found that the positive and negative self engages similar brain regions and also selectively recruits other regions (Fossati et al., 2003). For example, differences between the processing of positive and negative words were seen in regions outside the medial frontal cortex, with reductions in the insula, temporal and occipital regions, and inferior parietal regions associated with negative words. Further studies are needed to explore whether differential activation that is associated with the positive and negative self leads to the differential modulation of outcome evaluation.

In summary, the present findings support the notion that self-reflection can modulate the outcome evaluation process. Specifically, FRN is differentially modulated as a function of reflection on the self and others. Feedback-related negativity increased in the self-reflection condition compared with the other-reflection condition. The present results support the hypothesis that self-processing systems in the human brain modulate outcome evaluation. We provide direct evidence of a functional link between self-reflection and outcome evaluation.

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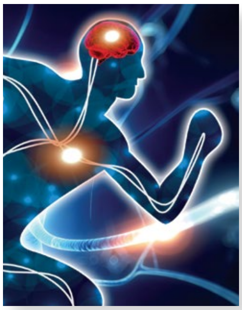

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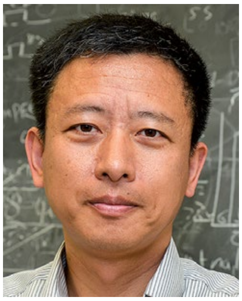

Computational psychophysiology

Working at the intersection of the mind and body, psychophysiology studies the effects of psychological states on physiological processes and vice-versa.

We are pleased to introduce this special supplement, *Advances in Computational Psychophysiology*, which encompasses contemporary research using computational methodologies to explore psychophysiological processes related to the interaction among the human brain, body, mind, and behavior. This special supplement also explores novel applications of computational psychophysiology, such as biomarker identification for mental illness.

The field of psychophysiology investigates the physiological basis of psychological processes. Working at the intersection of the mind and body, psychophysiology studies the effects of psychological states on physiological processes and vice-versa. In its nascent stages, psychophysiological research predominantly focused on relatively peripheral markers of autonomic nervous system activity by measuring fluctuations in a subject's electrodermal activity (EDA), electromyogram (EMG), electrogastrogram (EGG), electrocardiogram (ECG), heart rate, heart rate variability (HRV), respiration rate, electrooculogram (EOG), and pupillary dilation. In recent years, psychophysiology has begun to focus on the central nervous system, partially as a result of increasing accessibility and growth in measures of brain activity, such as event-related potentials (ERPs), magnetic encephalography (MEG), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI). These methodologies offer more proximal measurement of brain (and mind) activity than indicators of the autonomic nervous system, which require inferences from fluctuations in peripheral responses.

To study the human brain, mind, and behavior, autonomic and central psychophysiological indices must be analyzed in combination, a feat that requires advanced computational approaches. The implementation of these approaches in psychophysiology is the focus of this supplement. Computational psychophysiology is an interdisciplinary research field that employs methods from the disciplines of psychology, physiology, neuroscience, computer science, mathematics, physics, and others to model physiological activity in relation to the psychological components of human behavior. Computational modeling provides a framework for understanding the numerous physiological processes underlying complex human mental states and behavior. Computational models can be used to simulate and predict psychological outcomes based on different physiological states or experimental manipulations.

This new direction will broaden the field of psychophysiology by allowing for the identification and integration of multimodal signals to test specific models of mental states and psychological processes. Additionally, such approaches will allow for the extraction of multiple signals from large-scale multidimensional data, with a greater ability to differentiate signals embedded in background noise. Further, these approaches will allow for a better understanding of the complex psychophysiological processes underlying brain disorders such as autism spectrum disorder, depression, and anxiety. Given the widely acknowledged limitations of psychiatric nosology and the limited treatment options available, new computational models may provide the basis for a multidimensional diagnostic system and potentially new treatment approaches.

Applying computational data analysis and modeling to psychophysiological signals may thus help to identify new phenotypes for normal and abnormal psychological functions. The further development of computational strategies has the promise of providing large-scale models of the neural substrates of human behavior.

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Applying nontraditional approaches of electrophysiological data analysis to decision-making research

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Pengfei Xu[1], Wenbo Luo[3], Yue-jia Luo[1,4*]

Synchronous firing of populations of neurons, which is an important source of brain electrical activity, contributes significantly to the neurobiological basis of human cognitive processing (*1*). Electroencephalography (EEG) captures this mechanism by measuring voltage fluctuations that result from the summation of the simultaneous activity of millions of neurons (*2*). The EEG signals being recorded contain information arising from the activation of scattered brain regions, which may be located either near or far from the cerebral surface. EEG predominantly measures the activity of cortical pyramidal neurons, because the geometrically parallel organization of these cells ensures that their synchronous firing can be easily detected via electrodes placed on the subject's head (*3*). It has been suggested that scalp EEG amplitudes elicited by the onset (or offset) of a sensory or a cognitive event (i.e., event-related EEG) can be detected as distinct from spontaneous or background EEG signals (*4*). This methodology has proven to be a valuable tool for cognitive neuroscientists, including those interested in human decision making (Figure 1A). The process of decision making can be broken down into several steps, including situation perception, option evaluation, action selection, and learning from outcome (*5*). The temporal overlap between the different stages of decision making provides huge difficulties for investigating the separate neural mechanisms underlying each stage. The EEG can help address this problem because it enables high temporal resolution (*6*).

As pointed out by Makeig et al., traditional event-related EEG data processing consists of two approaches, namely, a time-domain approach using event-related potentials (ERPs) that focuses on temporal features of the data, and a frequency-domain approach using spectrum analysis that focuses on a spectrum of frequencies or energies of the data. Neither of these fully represents the neural dynamics of the brain, which have important implications for the underlying neurocognitive function (*1*). The drawbacks inherent in the classical methods have long been acknowledged (see below), and researchers have sought to explore novel techniques of data analysis in recent years. Below we discuss the pros and cons of these techniques and their applications in decision-making studies.

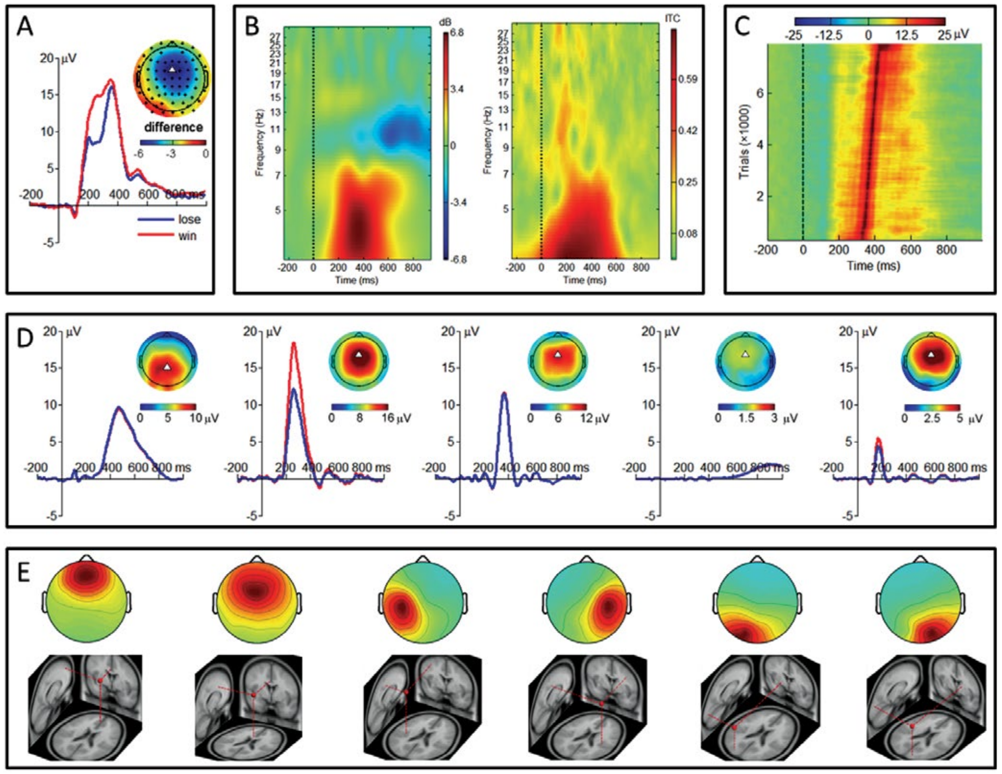

FIGURE 1. Examples of advanced electroencephalography (EEG) processing techniques. Participants took part in a monetary gambling game and the outcome feedback-elicited EEG data were analyzed. Refer to (*9*) and (*14*) for detailed experimental designs. **(A)** A traditional method for event-related EEGs, event-related potential (ERP) analysis. **(B)** A time–frequency analysis of EEG. Left panel: the event-related spectral perturbation (ERSP). Right panel: the inter-trial coherence (ITC). **(C)** The single-trial display of the P3-latency sorted ERPs. **(D)** Principle component analysis (PCA) of the data from (*9*). **(E)** Independent component analysis (ICA) of the data from (*14*).

Dynamics of neural synchronicity

Electrophysiological activity in the human brain is highly oscillatory, which means that the firing patterns of neighboring neurons tend to be synchronized because of the feedback connections between them (*3*). The theoretical significance of neural oscillation lies in the fact that it is the neuroelectric basis of distinct cognitive activities such as perception, memory, and consciousness (*7*). Data recorded from any given electrode contains power/phase dynamics that define the characteristics of neural oscillation (*3*). To decipher this information, a time–frequency analysis is necessary, which depicts the temporal synchrony of oscillatory activity over multiple frequency bands (Figure 1B). This approach helps unravel neural oscillation patterns in both the time and frequency domains simultaneously that cannot be reflected by traditional methods (for example, traditional cross-frequency coupling only results in a single index that reflects the intensity of synchronization between two oscillations over the whole time span) (*3*).

It is worth noting that a single EEG oscillation can be involved in different cognitive processes, because the combination of neurons that make up oscillations can belong to spatially overlapping or segregated functional networks (*8*). Therefore, it would be questionable to infer a one-to-one mapping relationship between a cognitive function and an oscillation response. Take medial frontal theta rhythms as an example. Numerous studies have reported that oscillations within the theta band (4–7 Hz) are critical for decision making under uncertainty, possibly reflecting neurophysiological processes underlying the way the brain learns from the environment (*9–11*). Nevertheless, frontal theta rhythms are also activated in a wide range of other cognitive tasks such as error processing and conflict detection, and thus likely represent a general operating mechanism involved in action monitoring, rather than a specific decision-making component (*11*).

Decomposing EEG data

The use of both principle component analysis (PCA) and independent component analysis (ICA) in EEG data processing is also becoming popular. The PCA approach treats the ERP waveform as a combined effect of temporally irrelevant voltages presenting simultaneously in the brain, and tries to provide a set of latent components that may index physiologically distinct processes (*1, 9*) (Figure 1D). By applying temporospatial PCA to ERP data, Foti et al. revealed that the feedback-

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related negativity (FRN)—represented as a negative wave elicited by the outcome feedback from decision-making tasks in conventional ERPs (*12*)—is actually a positive deflection localizing in the striatum (*13*). PCA components of ERP data are temporally or spatially orthogonal (or uncorrelated), because PCA specifically makes each successive component account for as much as possible of the remaining activity that has been unaccounted for by previously determined components. Unlike PCA, the ICA method seeks to maximize independent sources of activity and results in temporally independent components with unconstrained spatial distribution (*1*). By applying ICA to the EEG data recorded in a monetary gambling game, we found that the fronto-central theta component, the source of which is located in the anterior cingulate cortex, was closely associated with future risk-taking behavior (*14*) (Figure 1E).

PCA and ICA techniques enhance the precision of source localization of EEG data (*15*). However, we should keep in mind that as a data-driven method, neither PCA nor ICA is guaranteed to yield neurophysiologically meaningful results (*16*). Additional anatomical and empirical evidence is highly recommended (*17*).

Single-trial ERPs

Traditional analysis of event-related EEG data recognizes amplitude or energy changes time-locked to a given event by averaging epochs over a period of time, assuming that peaks at the same latencies are near-identical at the single-trial level (*18*). This oversimplified approach leaves a lot of the cognitively relevant information in the temporal dimension of EEG activity undiscovered (*3*). In contrast, single-trial analysis offers an opportunity to directly investigate systematic variations between trials (Figure 1C). This method does a better job of discovering potential links between cognitive processes and neural dynamics compared with conventional averaging (*3*). For instance, our recent study revealed that the P3 amplitudes in response to outcome feedback predict subsequent stay/switch decisions on a trial-by-trial basis (*14*). Importantly, single-trial analysis in the time–frequency domain could be used to determine whether averaged ERP features are shaped by stimulus-evoked power perturbations or phase synchronization/desynchronization of ongoing oscillatory activity (*19*). Delorme et al. showed that phase synchronization of the lower band of theta rhythm contributes significantly to the far-frontal positive component that indicates the speed of upcoming motor responses (*18*). This finding helps explain the neural mechanisms of motor decision preparation.

In summary, when appropriately used, newly developed methods of EEG processing can uncover novel aspects of decision-making dynamics that traditional analyses cannot. Still, researchers should be aware of the methodological shortcomings of these techniques to avoid producing results that are flashy but scientifically vague.

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Social Comparison Manifests in Event-related Potentials

Yi Luo[1], Chunliang Feng[1], Tingting Wu[2,3], Lucas S. Broster[4], Huajian Cai[5], Ruolei Gu[5] & Yue-jia Luo[2]

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Social comparison, a widespread phenomenon in human society, has been found to affect outcome evaluation. The need to belong to a social group may result in distinct neural responses to diverse social comparison outcomes. To extend previous studies by examining how social comparison with hierarchical characteristics is temporally processed, electroencephalography responses were recorded in the current study. Participants played a lottery game with two pseudo-players simultaneously and received both their own and the other two players' outcomes. Results of three event-related potential components, including the P2, the feedback-related negativity (FRN), and the late positive component (LPC), indicate that social comparison manifests in three stages. First, outcomes indicating a different performance from others elicited a larger P2 than evenness. Second, the FRN showed hierarchical sensitivity to social comparison outcomes. This effect manifested asymmetrically. Finally, large difference between the participant's outcome and the other two players' evoked a larger LPC than the medium difference and the even condition. We suggest that during social comparison, people detect if there is any difference between self and others, and then evaluate the information of this difference hierarchically, and finally interpret the situations in which oneself deviates from the group as most motivationally salient.

People choose and learn in social circumstances and their decisions are influenced by social contexts[1–5]. This kind of influence is based on social comparison between self and others[6]. That is, individuals evaluate their performances and earnings according to the comparison with those of others rather than the objective values per se. The sensitivity to social comparison facilitates the building of healthy group relations, which benefits individual and group development[7,8]. As a result, social comparison plays a crucial role in human survival and well-being.

With the rising of social neuroscience in recent years, an increasing number of studies have concentrated on neural underpinnings of social comparison[9–11]. For example, Fliessbach and colleagues found that the activation of the ventral striatum, a reward-related brain region, was affected by variations of social comparison contexts defined by the difference of payoffs between two players who performed the task simultaneously[6]. This finding was supported by following neuroimaging findings that relative reward in social comparison contexts elicits neural responses which show similar patterns with the absolute reward condition[12,13]. Social emotions like schadenfreude and gloating are found to be provoked by positive outcomes in social comparison, while negative outcomes in similar circumstances provoke emotions like envy and jealousy[11,14]. Electroencephalography (EEG) studies on social comparison have described temporal characteristics of outcome evaluation in social contexts, but their findings are heterogeneous. An event-related potential (ERP) study replicating the paradigm of Fliessbach *et al.*[6] showed larger negative waves elicited by inequitable outcomes than equitable ones in the time windows of 350–500 ms and

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500–750 ms[15]. ERP results of another study showed that the feedback-related negativity (FRN), which peaks around 200–300 ms post-stimulus and is larger following losses than gains[16], was significantly enhanced when another anonymous player won[17]. However, a recent study found that social comparison modulated not the FRN, but a later stage of outcome evaluation indicated by the late positive component (LPC)[18]. The conflicting results of these studies suggest that the temporal hallmarks of social comparison are not yet clear.

With EEG recording, the current study aims to investigate the temporal processing of outcome evaluation in a social comparison context. Based on prior findings[3,6,12,15,17], we hypothesized that ERP signals would be elicited during the process of outcome evaluation and that EEG responses to different kinds of social comparing outcomes would show distinct patterns. To extend previous studies, we have revised the social comparison paradigm designed by Boksem *et al.*[17], such that participants played the same task with two other players simultaneously. In this way, the comparison between self and others showed hierarchical characteristics; that is, a participant's performance feedback might be different from either of other players (similar with previous studies), or be different from both of others. It would be interesting to see if participants consider the latter condition as a larger violation of the good-group-member standard (i.e., being consistent with others in the same group), and whether such an effect would manifest in electrophysiological signals.

Three ERP components, the P2, the FRN, and the LPC, were selected as neural indexes. The P2 component is associated with stimulus evaluation[19,20] and attention capture modulation[21–23]. Information relevant to conflict with others was hypothesized to capture more attention, which would result in a larger P2 component. As mentioned above, the FRN is modulated by social contexts such that a larger interpersonal difference elicits an enhanced FRN[17]. Accordingly, we hypothesized that the FRN would increase as a function of levels of difference in social comparison. Moreover, the LPC is considered to represent levels of arousal in the late time window of approximately 500–800 ms[24,25]. It is larger for stimuli with high arousal levels[26,27]. Increased LPC amplitudes have been linked to enhanced attention[26], more intense evaluation[24,25], and better subsequent memory performance[28,29]. The hypothesis of this study was that the best and worst outcomes obtained in social comparison would elicit larger LPC than other conditions, since these two kinds of outcomes are more motivationally salient.

Methods

Participants. 20 healthy students (10 females; mean age 22.65 ± 1.90 years) from Beijing Normal University participated in the experiment. All participants had normal or corrected to normal vision and had no history of psychiatric, medical, or neurological illness. All were right-handed. During debriefing, no participants self-identified as red/green color blind. All participants provided written informed consent prior to the experiment. The experimental protocol was approved by the local Ethics Committee (Beijing Normal University) and was in compliance with the ethical guidelines of the American Psychological Association.

Procedure. To reinforce the social nature of the task, participants were told that they would play a lottery game with two other anonymous players simultaneously. In reality, there were no other people playing the game. Participants were instructed about the rules of the game and were informed that their payments depended on their choices in the task; the higher the scores participants earned the higher payment they would get at the end of the experiment. At the end of the experiment, each participant was inquired about the credibility of the cover story and none of them raised doubts.

During the game, each participant chose one of two cards on the left and right sides of a fixation point by pressing the F or J buttons on the keyboard with his/her left or right index finger. In any given trial, one card led to win whereas the other one led to loss (see Fig. 1a). Participants were instructed that there was no relationship between the location of cards and outcomes, and that the consequence of his/her decision would not affect the consequence of other players' choices or scores, and *vice versa*. After the participant finished his/her choice, the outcome of each trial was displayed as an equilateral triangle, with the colors of the three edges indicating the participant's own outcome and the other two players'. The color (green/red) of each edge of the triangle represented the valence (win/loss) of each player's outcome. The meanings of the locations and colors of each edge were counterbalanced across participants.

There were six types of feedback regarding the valence of the participant's outcome (win/loss) and the difference between this outcome and the other two players' (see Fig. 1c). Regarding the difference factor, there were three conditions in total: the large difference condition, in which the valence of participant's outcome was different from that of both other players (e.g., participant wins, the other two lose); the medium difference condition, in which the valence of the participant's outcome was the same with one of the other two players; and the even condition, in which the participant and the other two players all received the same outcome. Unbeknownst to participants, the game was preprogrammed such that different types of feedback were presented regardless of the participant's actual choice. For win conditions, the large difference outcome, the medium difference outcome, and the even outcome were labeled as *best win* (self-win, others-both lose, 60 trials), *better win* (self-win, others-one win and one lose, 120 trials), and *even win* (self-win, others-both win, 60 trials), respectively. Likewise, for loss conditions, the large difference outcome, the medium difference outcome, and the even outcome were labeled as *worst loss*

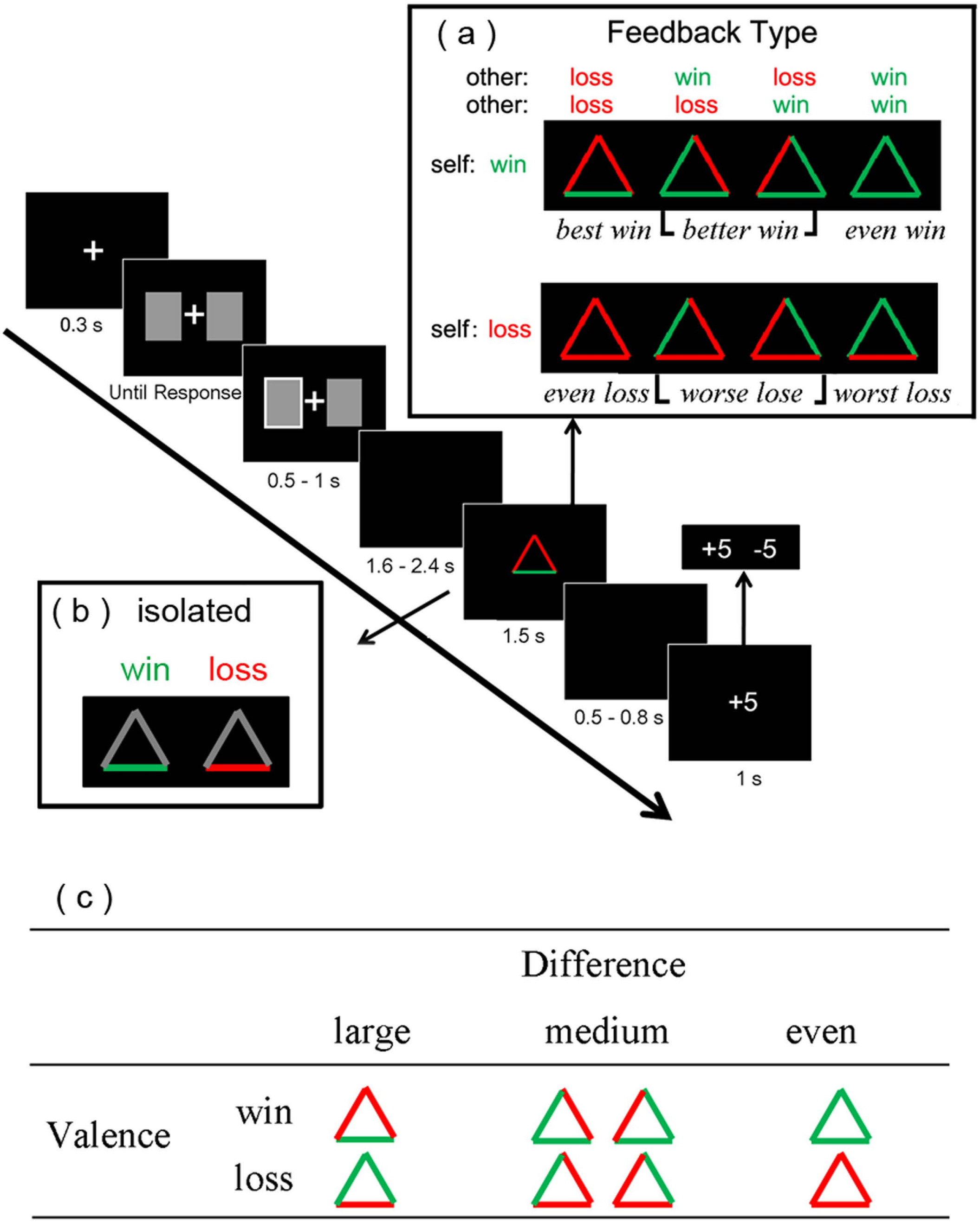

Figure 1. Schematic Illustration of a trial and feedback types. (**a**) Single-trial settings. A central fixation cross was presented for 0.3 s and then the participant chose between two cards. After a short delay (1.6–2.4 s), a feedback screen informed participants about all three players' outcomes (six types in total, see upper right). Following the brief display of a blank screen (0.5–0.8 s), relevant changes in the participant's score were displayed. (**b**) An example of outcome feedback presentation in the control block. (**c**) Six types of social feedback regarding the valence of the participant's outcome (win/loss) and the difference between his/her outcome and the other two players'. The color of the base of the triangle represents the participant's outcome while that of the other edges represents the other two players'. Green indicates a win whereas red indicates a loss in this example.

(self-lose, others-both win, 60 trials), *worse loss* (self-lose, others-one win and one lose, 120 trials), and *even loss* (self-lose, others-both lose, 60 trials), respectively.

In addition, participants also finished a control block, in which they played the same lottery game in a non-social context (i.e., isolated). This block contained two kinds of outcomes, that is, *isolated win* (60 trials) and *isolated loss* (60 trials), which were presented in a pre-determined pseudorandom order (see Fig. 1b). In this block, the outcome was also displayed as an equilateral triangle. However, only the edge that signified the participant's own outcome would change colors (green/red) across trials, while the other two edges remained in light grey, indicating that no other people were playing with the participant. The sequence of the task block and the control block was counterbalanced across participants.

Electrophysiological Recording and Analyses. The electroencephalogram (EEG) was recorded from 57 scalp sites using tin electrodes mounted in an elastic cap (Brain Products GmbH, Gilching, Germany) with an online reference to the left mastoid and offline algebraic rereference to the average of the left and right mastoids. Horizontal EOG was recorded from electrodes placed at the outer canthi of both eyes. Vertical EOG was recorded from electrodes placed above and below the right eye. All inter-electrode impedance was maintained at $< 5\,\text{k}\Omega$. EEG and EOG signals were amplified with a 0.01–100 Hz online band-pass filter and continuously sampled at 500 Hz/channel.

During the offline analysis, the EEG data were filtered with a 30 Hz low-pass filter (24 dB/oct) and were segmented into epochs time-locked to the onset of outcome presentation. Separate EEG epochs of 1200 ms were baseline-corrected by subtracting the average activity of that channel during the −200–0 ms baseline period from each sample. Any trial in which maximum EEG voltage exceeded a threshold of ± 100 μV during the recording epoch was excluded from further analysis. Epochs were then averaged separately for each participant and each condition.

P2 amplitudes were measured for each participant as the mean value within the 150–220 ms time window following outcome presentation. Visual detection into the averaged ERPs indicated that the P2 amplitudes were maximal at Fz along the midline electrodes. Accordingly, this electrode and five adjacent electrodes (F1, F2, FCz, FC1, and FC2) were chosen for further analysis. (The F* electrodes were the front-most row of electrodes on a 57-site cap, so there were only five electrodes around Fz.)

FRN amplitudes were measured as the mean value within the time window of 240–300 ms. Mean amplitudes of Cz, at which the mean amplitude was maximal along the midline electrodes (Fz, FCz, Cz, CPz, Pz, POz and Oz), and eight adjacent electrodes (FC1, FC2, FCz, C1, C2, CP1, CP2 and CPz) were obtained for further analysis.

LPC amplitudes were measured as the mean value within the time window of 500–800 ms. Mean amplitudes of CPz, where the LPC was maximal along the midline electrodes, and eight adjacent electrodes (C1, Cz, C2, CP1, CP2, P1, Pz and P2) were obtained for further analysis.

The P2, FRN, and LPC amplitudes were all analyzed using two-way repeated analysis of variance (ANOVA) of Valence (win vs. loss) × Difference (large difference vs. medium difference vs. even vs. isolated).

For all the analyses listed below, the significance level was set at .05. Greenhouse–Geisser corrections were used whenever appropriate. Post-hoc testing of significant main effects and interactions was conducted using the least significant difference (LSD) method. Partial eta-squared (η^2_{p}) values were provided to demonstrate effect size where appropriate, such that 0.05 represents a small effect, 0.10 represents a medium effect, and 0.20 represents a large effect[30].

Results

Behavioral Results. The average percentage of choosing the left card was 48.4 ± 3.4%, and the percentage of choosing the right card was 51.7 ± 3.4%. The average time for decision-making was 0.77 ± 0.27 s. Because there was no optimal strategy for the participants during the task, the behavioral data were not analyzed further.

ERP Results. *The P2 component*. The main effect of the difference factor was significant, $F(2,29) = 11.626$, $p = 0.001$, $\eta^2_{\text{p}} = 0.380$. Post-hoc analyses indicated that both the large difference (6.94 μV) and medium difference conditions (6.75 μV) elicited a larger P2 than the even condition (5.69 μV, p values < 0.001) and the isolated condition (4.98 μV, p values $= 0.001$). There was no significant difference between large difference and medium difference ($p = 0.290$), or between the even condition and the isolated condition ($p = 0.179$). The main effect of the valence factor was not significant, $F(1,19) = 1.043$, $p = 0.320$, $\eta^2_{\text{p}} = 0.052$. No significant interaction of Valence × Difference was found, $F(2,35) = 0.790$, $p = 0.504$, $\eta^2_{\text{p}} = 0.040$ (see Fig. 2).

The FRN component. The main effect of the valence factor was significant, $F(1,19) = 6.171$, $p = 0.022$, $\eta^2_{\text{p}} = 0.245$. Losses (6.98 μV) elicited a larger FRN than wins (8.1 μV). The main effect of the difference factor was also significant, $F(2,37) = 6.522$, $p = 0.004$, $\eta^2_{\text{p}} = 0.256$. Post-hoc analyses indicated that the large difference (6.62 μV), medium difference (7.03 μV), and isolated (7.43 μV) conditions all elicited larger FRN amplitudes than the even condition (9.09 μV), p values < 0.05. Furthermore, a significant interaction of Valence × Difference was revealed, $F(2,37) = 4.930$, $p = 0.014$, $\eta^2_{\text{p}} = 0.206$. Specifically, in response to wins, the FRN amplitude increased as a function of levels of difference in social context (*best win*: 6.45 μV; *better win*: 7.75 μV; *even win*: 10.06 μV, p values < 0.05). The FRN amplitude evoked by *isolated win* (8.13 μV) was smaller than *best win* and larger than *even win*, but it was not significantly different from that evoked by *better win*. Regarding losses, *even loss* (8.11 μV) elicited a smaller FRN than both *worst loss* (6.78 μV), $p = 0.028$, and *worse loss* (6.30 μV), $p = 0.001$, whereas no significant difference

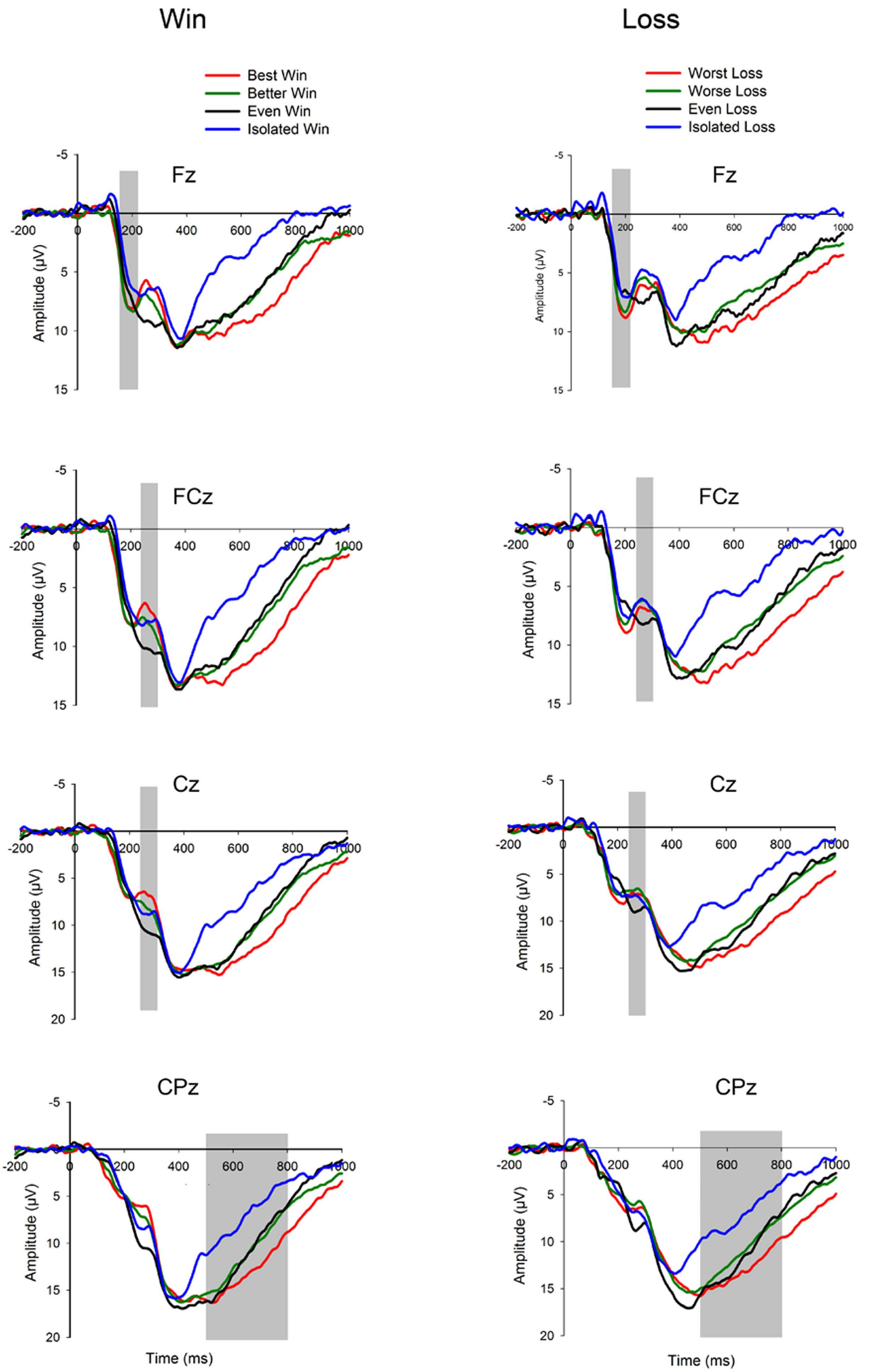

Figure 2. Grand-averaged ERPs at Fz, FCz, Cz and CPz for the eight types of feedback in the win and loss conditions separately. The time point 0 indicates the onset time of the outcome presentation (i.e., the equilateral triangle). Outcomes indicating differences from others elicited a larger P2 than even outcomes (upper panel). The FRN was sensitive to both value and differences from others (two middle panels). The larger difference condition evoked a larger LPC than other conditions (lower panel).

was found between *worst* and *worse loss*, $p = 0.183$ or between *isolated loss* (6.73 μV) and other loss conditions, p values > 0.05 (see Fig. 2).

The LPC component. The main effect of the difference factor was significant, $F(2,31) = 31.122$, $p < 0.001$, $\eta^2_p = 0.621$. Post-hoc analyses indicated that the LPC was larger in response to large difference (12.22 μV) than both medium difference (10.51 μV) and the even condition (10.66 μV), p values < 0.05. All of these conditions elicited a larger LPC than the isolated condition (6.64 μV, p values < 0.001). Neither the main effect of the valence factor, $F(1,19) = 0.115$, $p = 0.738$, $\eta^2_p = 0.006$, nor the interaction of Valence × Difference, $F(2,39) = 0.091$, $p = 0.965$, $\eta^2_p = 0.005$, was significant (see Fig. 2).

Discussion

The current study had participants playing a lottery game with two anonymous players, and participants received both their own outcomes and those of the other players after each trial. We aimed to investigate the ERP correlates of social comparison outcome evaluation, which may be divided into three stages according to the results. First, the conditions indicating differences from others were discriminated from the even condition. The detection of this difference, regardless of its level, elicited a larger P2. The second stage was labeled by the FRN, which was not only sensitive to the valence of participants' own outcomes, but also to their differences from others. Interestingly, the influence of outcome valence on the FRN showed an asymmetric pattern, with higher sensitivity to social comparison differences of wins than losses. Lastly, the large difference condition evoked a larger LPC than other conditions, suggesting an emphasis on the most salient stimuli in the third stage.

One might argue that, considering the variations of stimulus property between conditions, our ERP results may be explained in terms of perceptual difference rather than social comparison. We disagree with this viewpoint. Previous studies reveal that stimulus property (e.g., location and color) modulates early ERP components such as the C1, P1, and N1[31,32], none of which are included in our analysis. The P2, FRN, and LPC components are indeed sensitive to stimulus novelty[33,34], but this factor is not sufficient to explain the patterns of ERPs in the current study. Otherwise, the medium difference (240 trials in total) should elicit smaller ERPs than the larger difference and even outcome (120 trials each), which was not the case for any components in the analysis. Last but not least, the ERP patterns in the formal task significantly deviated from those when the participants played alone (i.e., the control block; see below for details). In brief, we suggest the current ERP findings are beyond perceptual difference, and should be attributed to the social context rather than perceptual processing. Below we propose our interpretation about the role of social comparison on our findings, which is divided into three stages.

The First Stage. In the first stage, the frontal-central P2 was larger when participants faced outcomes which were different from others'. This finding suggests an early and coarse identification of distinctions between one's own performance and others'. The P2 component may indicate the early detection of any deviation from the good-group-member standard (i.e., being consistent with others in the same group[35]), with large difference and medium difference drawing a greater amount of attention than even outcomes[23]. Additionally, the lack of sensitivity to the hierarchy of social comparison suggested that, at the early stage of outcome evaluation, social contexts which indicated people distinguishing from others might capture more attention, but detailed information was not yet processed until later stages. The P2 amplitude in the isolated condition was not significantly different from the even condition, which also suggest that at this stage, social comparison is rough and could not distinguish between the alone situation and the situation of having the same performance with others.

The Second Stage. In the second stage, the processing of outcomes in social comparison contexts, which was coarse during the time window of the P2, turned out to be more elaborated. Consistent with classical findings[16,36,37], monetary losses evoked a larger FRN than wins. Furthermore, the effect of social difference between the participant and other players was also significant, with a larger FRN for outcomes indicating nonconformity with others and a smaller FRN for even outcomes, regardless of outcome valence.

Disagreement with the opinions of others, nonconformity with the performance of others, and unequal incomes compared with others all induce social conflicts[2,3,15], which trigger neural responses analogous to "reward prediction error"[36–38]. People expect to be consistent with others in social contexts such that the good-group-member standard is satisfied[35]. Any deviation of this expectation might be detected as a "social reward prediction error"[3]. Our results revealed that both positive and negative social reward prediction error evoked a larger FRN than even outcomes, indicating that the FRN reflects the degree of expectation violation in social comparisons, regardless of actual outcome valence[39–41]. We suggest this is because in social contexts, receiving a better outcome than others may elicit negative emotions from others (such as envy) and lead to disadvantaged social consequences accordingly (e.g., being isolated). In this sense, "better" outcomes may violate personal expectation as "worse" outcomes do in social comparison. Notably, the FRN in the even condition was also smaller than the isolated condition, indicating that receiving the same outcome with other people is more rewarding than the single-player context.

Interestingly, an interaction of valence by difference was found, suggesting the FRN amplitude was hierarchically sensitive to social comparison in the win condition but not in the loss condition. This asymmetry is consistent with previous findings showing a larger weight on gains than losses in social outcome evaluation[14]. The reason of this asymmetric effect is not yet clear, but it might be associated with the positivity bias in self-relevant feedback processing. Previous studies proposed that human beings evaluate information in a positive direction to achieve and maintain a positive self-concept[42]. Positivity biases documented in social cognition research suggest that reward plays a more important role than punishment in social outcome evaluation[43,44], which may account for the stronger sensitivity to social comparison outcomes in response to wins than losses. When receiving monetary losses, in order to cope with potential threat to positive self-concept and the need to belong, people tend to withdraw from further attempts to evaluate detailed information and avoid upward comparisons, which could lead to a blunt social comparison evaluation[45,46]. Consistent with the above interpretation, the FRN following *isolated win* was significantly different from most conditions, but this is not the case for the FRN following *isolated loss.*

The Third Stage. In the third stage, the outcomes indicating the largest social comparison difference elicited a larger LPC, which might reflect the processing of stimuli with stronger motivational relevance[47] and higher levels of autonomic arousal[48,49]. In our task, both *best win* and *worst loss* indicate the participant went against the majority of the group, which might be the most rewarding/ harmful situations. In either case, timely and effective reactions would be necessary to reconcile the potential conflict between self and others in daily life. Thus, it is not surprising that these situations are evaluated as most motivational relevant, indicated by an enhanced LPC in this study. The isolated condition, irrespective of whether wins or losses, elicited the smallest LPC. This result supports our viewpoint and demonstrates that the LPC reflects an evaluation of social comparison which is insensitive to outcome valence[18]. In short, the LPC patterns indicate that participants focused on the outcomes with the most prominent social significance in the last stage of outcome evaluation, which is evolutionary adaptive and may improve the efficiency of social decision-making.

Conclusion

Taken together, the ERP findings in the current study reveal how social comparison is processed in three stages, which requires good understanding of context-dependent social norms and social structures among group members[8,35,50]. Specifically, people are conscious of social expectations of their behaviors and promptly detect any deviation from that expectation. Thereafter, an elaborative comparison between self and others appears to be executed hierarchically, which is crucial for recognizing different kinds of social relationships. Finally, strongest motivational salience is attributed to the difference between self and the group, so as to elicit behavioral adjustment in the current social context.

To sum up, using ERP signals as temporal hallmarks, the current study demonstrates that the human brain evaluates outcomes in a social context-dependent pattern[6,12,17]. The need to belong to a social group and the associated monitoring of violations from expectancy based on the good-group-member standard may be sources of distinct neural responses to diverse social outcomes. Our findings extend knowledge about the temporal processing of social outcome evaluation by providing a temporal description of social comparison.

Finally, a few issues need to be addressed for future research. First, it would be desirable to add intermediate experimental conditions into the task design. That is, if the number of other players increases to three or more, then researchers could examine whether the ERP amplitudes would gradually change as the deviation between the participant and the majority becomes larger, or they would show an all-or-none pattern. Second, regarding that all the participants were Chinese people, we suggest follow-up researchers to recruit their samples from Western culture, which is less social comparison seeking and less sensitive to the good-group-member standard due to its individualism characteristic[51]. Replicating the current study on Western participants would help to reveal whether social comparison is susceptible to cultural variation[52].

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Author Contributions

Conceived and designed the experiments: Y.L., C.F. and R.G. Performed the experiments: Y.L. and C.F. Analyzed the data: Y.L., T.W. and C.F. Wrote the manuscript: Y.L., C.F., L.S.B., H.C. and R.G. Contributed materials and analysis tools: Y.J.L. Provided lab equipment for running the study: Y.J.L.

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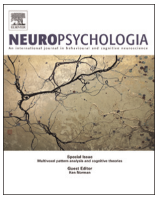

Attention modulations on the perception of social hierarchy at distinct temporal stages: An electrophysiological investigation

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ABSTRACT

Recent behavioral and neuroscientific studies have revealed the preferential processing of superior-hierarchy cues. However, it remains poorly understood whether top-down controlled mechanisms modulate temporal dynamics of neurocognitive substrates underlying the preferential processing of these biologically and socially relevant cues. This was investigated in the current study by recording event-related potentials from participants who were presented with superior or inferior social hierarchy. Participants performed a hierarchy-judgment task that required attention to hierarchy cues or a gender-judgment task that withdrew their attention from these cues. Superior-hierarchy cues evoked stronger neural responses than inferior-hierarchy cues at both early (N170/N200) and late (late positive potential, LPP) temporal stages. Notably, the modulations of top-down attention were identified on the LPP component, such that superior-hierarchy cues evoked larger LPP amplitudes than inferior-hierarchy cues only in the attended condition; whereas the modulations of the N170/N200 component by hierarchy cues were evident in both attended and unattended conditions. These findings suggest that the preferential perception of superior-hierarchy cues involves both relatively automatic attentional bias at the early temporal stage as well as flexible and voluntary cognitive evaluation at the late temporal stage. Finally, these hierarchy-related effects were absent when participants were shown the same stimuli which, however, were not associated with social-hierarchy information in a non-hierarchy task (Experiment 2), suggesting that effects of social hierarchy at early and late temporal stages could not be accounted for by differences in physical attributes between these social cues.

1. Introduction

Social hierarchy permeates organizations and societies of human and other species (Cummins, 2000). Social hierarchy not only is associated with disproportionate distribution of influence and resources (Fiske, 1992; Pusey et al., 1997), but also facilitates functional social interactions among people such that individuals adaptively adjust their behaviors according to the social status of others (Steckler and Tracy, 2014; Tiedens and Fragale, 2003). Therefore, the ability to readily detect and distinguish the social hierarchy of others provides adaptive values for individuals (Deaner et al., 2005; Maner et al., 2008). Unlike extensive investigations on the processing of other biologically and/or socially relevant stimuli (e.g., threatening scenes), however, much fewer studies have focused on the neurocognitive signatures underlying the perception of social hierarchy (Chiao et al., 2008, 2009; Kumaran et al., 2012; Pornpattananangkul et al., 2014; Zink et al., 2008).

Recently, a growing body of behavioral studies has demonstrated that superior-hierarchy targets are preferentially processed relative to inferior-hierarchy targets. For instance, attention systems of humans and nonhuman primates are more attuned to high-status than low-status targets in a gaze-cueing paradigm (Dalmaso et al., 2014, 2012; Shepherd et al., 2006), which probes automatic shifts of attention in response to others' gaze directions (Frischen et al., 2007). Further, previous eye-tracking studies have demonstrated that both humans and nonhuman primates prefer to take more time to view superior-hierarchy targets (DeWall, 2008; Foulsham et al., 2010; Haude et al.,1976; Maner et al., 2008), even at the expense of personal cost (Deaner et al., 2005). Finally, faces associated with high social status are more memorable than

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those associated with low social status, and perceivers process high-status faces in a more holistic way (Ratcliff et al., 2011). These intriguing findings indicate that superior-hierarchy targets are preferentially processed at multiple cognition stages.

The preferential processing of high-status targets at behavioral level has been supported by recent functional magnetic resonance imaging (fMRI) and event-related potential (ERP) studies. For instance, multiple neural networks are specially recruited in the perception of superior-hierarchy cues, including prefrontal cortex (e.g., ventrolateral and dorsolateral prefrontal cortex) and amygdala (Kumaran et al., 2012; Marsh et al., 2009; Zink et al., 2008). The former brain regions are thought to be associated with adjusting behavior in response to superior-hierarchy targets (Zink et al., 2008), whereas the latter has been associated with initializing rapid and coarse attentional bias to salient events (Öhman, 2005; Pessoa, 2005). Furthermore, although findings are currently not conclusive, preliminary evidence from ERP studies suggests that social hierarchy modulates both rapid attentional bias and sustained processing, which are manifested as more pronounced neural responses evoked by the high-status targets at the early (e.g., N170/N200) and the late (e.g., late positive potential [LPP]) temporal stages, respectively (Breton et al., 2014; Chiao et al., 2008; Pineda et al., 1994).

Although rapid attention bias towards and elaborative processing of superior-hierarchy targets provide essential information for functional social interactions, excessive processing of those high-status cues may also result in negative subjective feelings such as depression, shame and envy (Steckler and Tracy, 2014; Takahashi et al., 2009). For instance, inferior-hierarchy individuals tend to be more fearful than superior-hierarchy individuals (Plutchik and Landau, 1973). Furthermore, social hierarchy information can also preclude empathic feelings to superior-hierarchy targets, such that individuals reported stronger schadenfreude feelings in response to misfortune of those higher in the hierarchy (Takahashi et al., 2009). These findings suggest that hierarchy information does not only impair subjective wellbeing but also hampers prosocial connections among people in some contexts. In these regards, it is important to flexibly respond to superior-hierarchy cues according to specific contexts, such that individuals can voluntarily avoid the preferential processing of these social cues when it is not necessary or even detrimental. This viewpoint is well consistent with numerous studies in the domain of emotion regulation, which have indicated that top-down modulations (e.g., top-down attention, cognitive reappraisal processes) on the biased processing of other biologically salient stimuli (e.g., snakes) are crucial in maintaining psychological health (Gross, 1998; Ochsner et al., 2012). However, it remains unknown whether top-down cognitive processes such as top-down attention modulate the preferential processing of superior-hierarchy targets.

To address this gap, the current study was to investigate the modulations of top-down attention on the processing of superior-hierarchy cues by employing event-related potential (ERP) technique with the aim of elucidating whether top-down attention modulates temporal dynamics of neural responses to social hierarchy. We manipulated social hierarchy based on incidental skill in a game setting (Breton et al., 2014; Zink et al., 2008). Participants performed a simple task prior to ERP recording and were told that social hierarchy was based on their performance in the task. Covertly, participants' social hierarchy was always fixed (two-star players), and targets' hierarchy was either superior (three-star players) or inferior (one-star players) but not equal to participants' (see also Zink et al. (2008)). Notably, top-down attention to hierarchy cues was manipulated by asking participants either to judge hierarchy information or gender of presented targets. The hierarchy-judgment task required attention to hierarchy information whereas gender-judgment task withdrew attention from these social cues. Finally, we conducted Experiment 2 with the same stimuli sets to test whether hierarchy-related effects at multiple temporal stages could be accounted for by differences in physical attributes between the superior (i.e., faces presented together with three stars) and the inferior (i.e., faces presented together with one star) hierarchy. In Experiment 2, number of stars were not associated with social hierarchy but was just employed as classification symbols in a non-hierarchy judgment task. Specifically, participants of Experiment 2 were asked to judge how many stars in the presented stimuli (the attended condition) or gender of presented targets (the unattended condition).

To sum up, with fine-grain temporal resolution provided by the ERP technique, we aimed to distinguish modulations of top-down attention on the preferential processing of superior-hierarchy targets at distinct temporal stages. Both early (P1, N170/N200) and late (LPP) neural responses to social hierarchy were detected in the current study. We hypothesized that modulations of social status would be evident in early temporal stages such as the N170/N200 but not the P1 component (Chiao et al., 2008; Pineda et al., 1994). Importantly, we further hypothesized that modulations of social hierarchy on the N170/N200 would be evident in both attended and unattended conditions, given that salient stimuli evoke enhanced neural responses within such early temporal stages even when attention resources are limited (Carretié et al., 2004; Olofsson et al., 2008). Regarding the LPP component, we predicted that superior-hierarchy targets would evoke more pronounced LPP than inferior-hierarchy targets (Breton et al., 2014), and these effects on the LPP would be sensitive to the manipulations of top-down attention (Hajcak et al., 2009, 2013). Finally, we predicted that these hierarchy-related effects would be absent when the same stimuli were presented but not associated with social-hierarchy information in Experiment 2.

2. Experiment 1

Experiment 1 investigated the temporal dynamics of attention modulations on the perception of social hierarchy, which was conveyed by neutral faces presented together with one star (i.e., inferior hierarchy) or three stars (i.e., superior hierarchy).

3. Methods

3.1. Participants

Seventeen individuals (8 males) (mean age ± s.d.: 21.65 ± 2.71 years) participated in the current study for monetary compensation. All participants were right-handed, had normal or corrected-to-normal vision, and had no neurological or psychiatric history. This study was approved by the Institutional Review Board (IRB) at Beijing Normal University (BNU), Beijing, China. Written informed consents were collected from all participants.

3.2. Stimuli

A set of color photographs showing neutral faces from 60 college students (30 males) was employed in the current study. Each photograph was set to the same size of 346 × 290 pixels (width × height). Participants were instructed that those photographs were taken from subgroups of players who had performed a dot estimation task (see below).

3.3. Procedure

Prior to electroencephalographic (EEG) recording, all

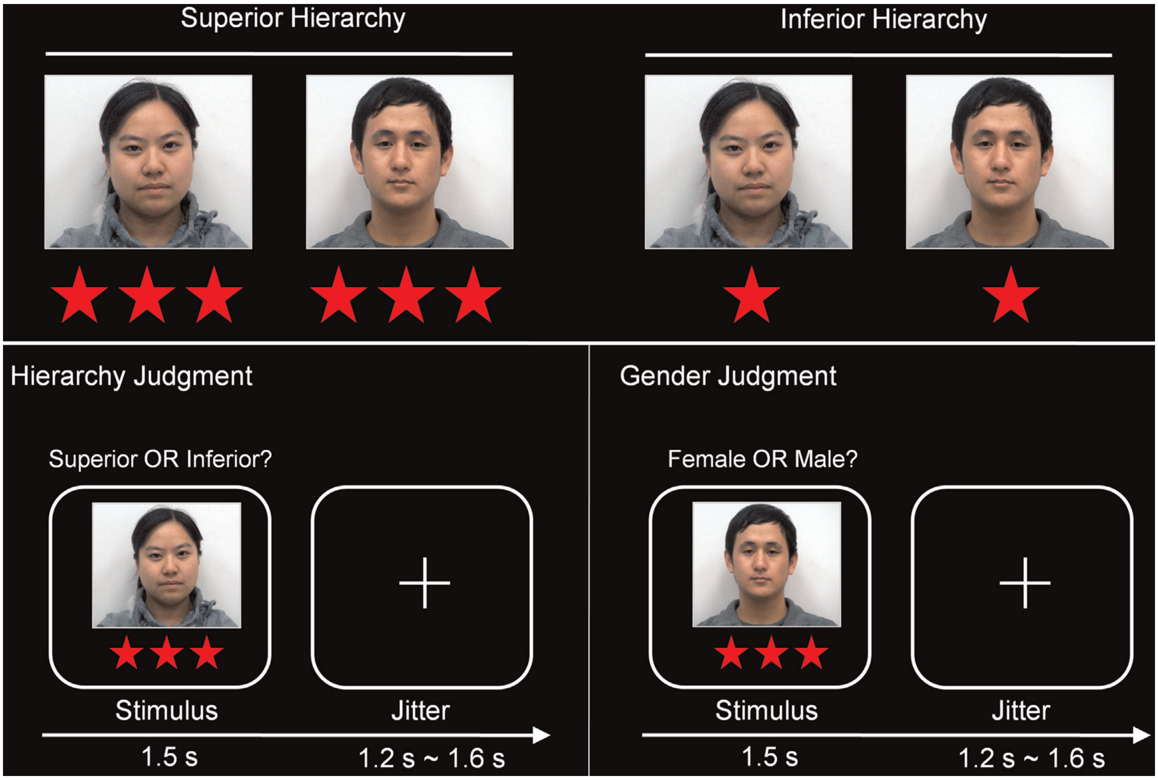

Fig. 1. Examples of stimuli and task structure for Experiment 1. Examples of the experimental stimuli set of 60 faces were illustrated in the top panel of the figure. There were 30 faces/targets associated with superior hierarchy and the other 30 faces with inferior hierarchy. Notably, these combinations between faces and social hierarchy were counterbalanced among participants. Task structure was illustrated in the bottom panel of the figure. In the current study, participants were asked to choose between “superior” and “inferior” for hierarchy judgment, and “female” and “male” for gender judgment.

participants were asked to perform a dot estimation task. In this task, participants needed to indicate whether there were more red dots scattering on the left or right side of a white blank with 100 red dots in total (for details, please see Feng et al. (2013)). Participants were instructed that their performance would be evaluated by both speed and accuracy in the task and would be compared with a sample of players who had performed the task. Covertly, outcomes of the task were always fixed, such that participants were told that their performance was medium (two-star players) according to their rank in a sample of players. The manipulation of social hierarchy was implemented by identifying other players' (i.e., 60 photographs/targets used in the current study) performance in the task (Breton et al., 2014; Zink et al., 2008). For the 60 targets employed in the current study, 30 of them (15 males) were identified as superior players (three-star players) and the other 30 (15 males) as inferior players (one-star players) relative to participants. The combinations of targets and hierarchy were counterbalanced across subjects to control for potential confounding factors such as physical attributes and attractiveness. Prior to EEG recording, participants were told that they would be presented with faces of superior (represented by three stars) and inferior (represented by one star) players.

On each trial (Fig. 1) of EEG recording, a photograph was presented together with one star or three stars to indicate social hierarchy (1.5 s). During the presentation of photograph, participants were asked to judge the social hierarchy of each presented target in two blocks and gender in the other two blocks by pressing instructed buttons. At the end of each trail, a fixation was presented to the center of the screen as a jitter (1.2–1.6 s). Each block consisted of 120 trials, with each target being presented twice. Within each block, photographs of targets were presented in random order with the following constraints: (1) the same condition was not presented successively more than twice and (2) face identities in two successive trials were always different. Finally, the order of hierarchy-judgment and gender-judgment blocks was counterbalanced across participants.

3.4. EEG recording

EEG was recorded from 64 scalp sites using Ag/AgCl electrodes mounted on a Quik-cap (Compumedics, Texas, USA), with the left mastoid (LM) being the physical reference. Vertical electro-oculographic (VEOG) activity was recorded from electrodes above and below the left eye, and horizontal EOG (HEOG) was recorded from electrodes placed at the outer canthi of both eyes. Impedance was maintained below 10 kΩ throughout the EEG recording session. The EEG and EOG were amplified using a 0.05–100 Hz band-pass and continuously sampled at 500 Hz.

3.5. Data analysis

Electrophysiological data were analyzed by using Neuroscan 4.3.1 software (Compumedics, Texas, USA). The EEG analyzing window was between −200 ms and 800 ms, with the 200 ms prestimulus EEG serving as baseline. EEG data were low-pass filtered below 30 Hz. EEGs were first re-referenced to the algebraic average of left mastoid and right mastoid and then were re-referenced to the average of all the electrodes. Artifact rejection was performed for all the EEG channels and the rejection criteria was ±80 μV. Trials with incorrect behavioral responses were also excluded before average.

Both early (P1 and N170/N200) and late (LPP) ERP components were chosen for analyses. For the P1 or N170/N200, a time window of 100–130 ms or 150–180 ms was respectively selected for mean amplitude measurement over PO7/PO8, PO3/PO4 and O1/O2 (Feng et al., 2012; Luo et al., 2010; Webb et al., 2012). The LPP component is typically maximal over centroparietal electrodes (Bradley et al., 2007; Cuthbert et al., 2000), and it was detected as mean amplitude between 400 and 550 ms over Pz according to previous studies (Hietanen and Astikainen, 2013; Yeung and Sanfey, 2004). A repeated measures analysis of variance (ANOVA) was used, with the within-subject factors of task (gender judgment vs. hierarchy judgment), hierarchy (inferior vs. superior), hemisphere (left vs. right), and electrode (PO7/PO8 vs. PO3/PO4 vs. O1/O2) for the P1 and N170/N200. The analysis of the LPP, reaction time (RT) and average accuracy (ACC) was implemented by an ANOVA with the within-subject factors of task and hierarchy. p Values were adjusted according to the Greenhouse–Geisser correction if necessary. Bonferroni correction was used for multiple comparisons.

4. Results

4.1. Behavioral data

RT and ACC: The ANOVA on the RT and the ACC did not yield any significant results ($p > 0.05$), and the ACC of participants' responses were higher than 97% in all conditions (Table 1).

4.2. ERP data

P1: The ANOVA on the P1 amplitudes yielded a significant hierarchy × electrode interaction ($F(2,32)=7.78$, $p=0.002$). Post-hoc comparisons revealed that the P1 amplitudes evoked by the high-status targets were larger over PO7/PO8 than PO3/PO4 (4.75 μV vs. 4.08 μV, $p=0.040$); whereas the P1 amplitudes evoked by the low-status targets were comparable among electrodes (Table 2, Fig. 2 and Supplementary Figs. 1–4).

N170/N200: The ANOVA on the N170/N200 amplitudes revealed a main effect of hierarchy ($F(1, 16)=11.27$, $p=0.004$), such that superior-hierarchy targets elicited larger N170/N200 responses than inferior-hierarchy targets (Table 2**,** Fig. 2 and Supplementary Figs. 1–4). This effect was stronger over left hemisphere than right hemisphere (.94 μV vs.54 μV) as revealed by a significant hierarchy × hemisphere interaction ($F(1,16)=6.89$, $p=.018$), although it reached significance in both hemispheres. Noteworthy, the task × hierarchy interaction was not significant ($F(1,16)=1.98$, $p=0.18$), and post-hoc comparisons revealed that superior-hierarchy targets evoked larger N170/N200 amplitudes than inferior-hierarchy targets when participants performed both hierarchy judgment (–86 μV vs. 0.05 μV, $p=0.002$) and gender judgment (0.05 μV vs. 0.62 μV, $p=0.044$).

LPP: The ANOVA on the LPP amplitudes yielded a significant task × hierarchy interaction ($F(1,16)=5.36$, $p=0.03$). Post-hoc comparisons revealed that superior-hierarchy targets evoked larger LPP amplitudes compared with inferior-hierarchy targets only when participants performed hierarchy judgment (2.96 μV vs. 2.33 μV, $p=0.03$) but not while performing gender judgment (2.81 μV vs. 2.70 μV, $p=0.61$) (Table 2 and Fig. 2).

Table 1
The average (with standard error) reaction times (RT, ms) and accuracy (ACC, %) in each condition of Experiment 1.

Hierarchies	Tasks	
	Hierarchy judgment	Gender judgment
RT		
Superior	633(24)	669(21)
Inferior	619(25)	661(19)
Superior–Inferior	14(10)	8(4)
ACC		
Superior	97.11(1.26)	97.35(0.58)
Inferior	97.11(0.80)	97.04(0.44)
Superior–Inferior	0.00(0.90)	0.31(0.43)

Table 2
The mean (with standard error) amplitudes (μV) of the P1, N170 and LPP components in each condition of Experiment 1.

Hierarchies	Tasks	
	Hierarchy judgment	Gender judgment
P1		
Superior	4.05(0.85)	4.60(.91)
Inferior	4.36(0.71)	5.00(0.74)
Superior–Inferior	−0.31(0.24)	−0.40(0.30)
N170/N200		
Superior	−0.86(1.25)	0.05(1.31)
Inferior	0.05(1.15)	0.61(1.24)
Superior–Inferior	−0.91(0.25)***	−0.56(0.26)*
LPP		
Superior	2.96(0.42)	2.81(0.47)
Inferior	2.33(0.38)	2.70(0.44)
Superior–Inferior	0.63(0.27)*	0.11(0.22)

Note: It is worth noting that the N170/N200 is a negative-going ERP component (please see Fig. 2). Therefore, smaller raw values of N170/N200 amplitudes (i.e., more negative-going) reflect stronger neural responses represented by the N170/N200 component.

*** $p < 0.005$.

* $p < 0.05$.

5. Experiment 2

Experiment 2 investigated whether hierarchy-related effects observed in Experiment 1 could be attributed to differences in physical attributes between inferior (i.e., one star) and superior (i.e., three stars) social hierarchy.

6. Methods

6.1. Participants

Sixteen individuals (8 males) (mean age ± s.d.: 21.00 ± 2.35 years) participated in the current study for monetary compensation. None of participants had taken part in Experiment 1. All participants were right-handed, had normal or corrected-to-normal vision, and had no neurological or psychiatric history. This study was approved by the Institutional Review Board (IRB) at Beijing Normal University (BNU), Beijing, China. Written informed consents were collected from all participants.

6.2. Stimuli

The facial stimuli were the same stimulus sets used previously in Experiment 1.

6.3. Procedure

The procedure used in Experiment 2 was similar to the procedure used in Experiment 1, with the main difference being that participants were not introduced to social hierarchy after the dot estimation task. Participants were told that faces of other players would be presented to them with either one or three star(s) under each face, and the number of stars represented classification symbols for a judgment task during EEG recording (see below).

On each trial (Supplementary Fig. 5) of EEG recording, a

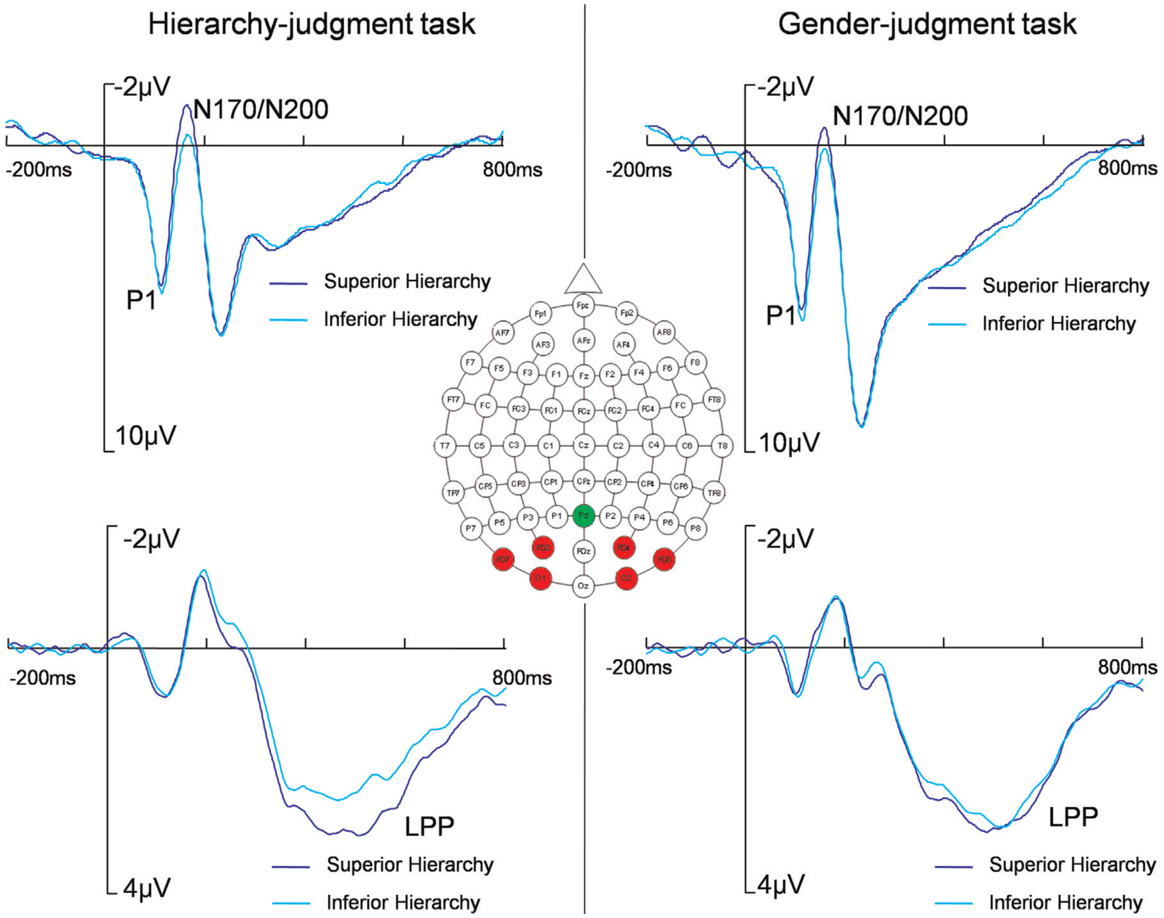

Fig. 2. The grand average ERPs evoked by superior and inferior hierarchies in hierarchy-judgment and gender-judgment tasks of Experiment 1. For P1 or N170/N200, a time window of 100–130 ms or 150–180 ms was respectively selected for mean amplitude measurement over electrodes of PO7/PO8, PO3/PO4 and O1/O2 (marked in red color), which were collapsed in the figure. LPP was detected as mean amplitude between 400 and 550 ms over Pz (marked in green color). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

photograph was presented together with one star or three stars (1.5 s). During the presentation of photograph, participants were asked to judge the number of stars (star judgment) in the presented stimuli in two blocks and gender of faces (gender judgment) in the other two blocks by pressing instructed buttons. At the end of each trail, a fixation was presented to the center of the screen as a jitter (1.2–1.6 s). Each block consisted of 120 trials, with each face photograph being presented twice. Within each block, photographs of targets were presented in random order with the following constraints: (1) the same condition was not presented successively more than twice and (2) face identities in two successive trials were always different. Finally, the order of star-judgment and gender-judgment blocks was counterbalanced across participants.

6.4. *EEG recording and data analysis*

The EEG data recording and pre-processing were the same as in Experiment 1. For the statistical analyses, a repeated measures analysis of variance (ANOVA) was used, with the within-subject factors of task (gender judgment vs. star judgment), number of stars (one vs. three), hemisphere (left vs. right), and electrode (PO7/PO8 vs. PO3/PO4 vs. O1/O2) for the P1 and N170/N200. The analysis of the LPP, reaction time (RT) and average accuracy (ACC) was implemented by an ANOVA with the within-subject factors of task and number of stars. *p* Values were adjusted according to the Greenhouse–Geisser correction if necessary. Bonferroni correction was used for multiple comparisons.

7. Results

7.1. *Behavioral data*

RT and ACC: The ANOVA on the ACC did not yield any significant results ($p > 0.05$), and the ACC of participants'responses were higher than 97% in all conditions (Table 3). The ANOVA on the RT only yielded a main effect of task ($F(1,15)=19.71$, $p=0.0005$), such that participants' responses were faster in the star task than the gender task (Table 3).

Table 3
The average (with standard error) reaction times (RT, ms) and accuracy (ACC, %) in each condition of Experiment 2.

Number of stars	Tasks	
	Star judgment	Gender judgment
RT		
Three	571(20)	642(23)
One	559(23)	646(22)
Three–One	12(8)	−4(5)
ACC		
Three	97.77(1.31)	97.71(0.50)
One	97.50(1.20)	98.45(0.37)
Three–One	0.22(0.35)	-0.74(0.41)

Table 4
The mean (with standard error) amplitudes (μV) of the P1, N170 and LPP components in each condition of Experiment 2.

Number of stars	Tasks	
	Star judgment	Gender judgment
P1		
Three	5.23(0.72)	5.67(0.66)
One	5.33(0.55)	5.49(0.64)
Three–One	−0.10(0.27)	0.18(0.16)
N170/N200		
Three	−1.10(1.13)	−0.47(1.16)
One	−0.74(1.05)	−0.40(1.08)
Three–One	−0.36(0.20)	−0.07(0.28)
LPP		
Three	2.97(0.58)	3.39(0.45)
One	2.66(0.52)	3.65(0.53)
Three–One	0.31(0.26)	−0.26(0.27)

7.2. ERP data

P1: The ANOVA on the P1 amplitudes did not yield any significant results ($p > 0.05$, Table 4, Fig. 3 and Supplementary Figs. 6–9).

N170/N200: The ANOVA on the N170/N200 amplitudes only yielded a significant task × hemisphere interaction ((F 1,15)=4.67, $p = 0.047$). Post-hoc comparisons revealed that stimuli-evoked N170/N200 amplitudes were more negative in the star-judgment task than the gender-judgment task over left hemisphere (−84 μV vs. –12 μV, $p = 0.04$) but not over right hemisphere (−1.00 μV vs. –0.75 μV, $p = 0.54$) (Table 4 and Fig. 3). Importantly, however, the ANOVA did not reveal the main effect of number of stars or any interactions related to it ($p > 0.05$, Table 4, Fig. 3 and Supplementary Figs. 6–9).

LPP: The ANOVA on the LPP amplitudes did not reveal any significant results ($p > 0.05$, Table 4 and Fig. 3).

8. Discussion

The current study employing ERP technique investigated the modulations of temporal dynamics of neural responses to hierarchy cues by top-down attention. Top-down attention to hierarchy cues was manipulated by asking participants either to judge hierarchy information or to judge gender of each presented face. The hierarchy-judgment task required attention to hierarchy cues whereas the gender-judgment task withdrew attention from these social cues. Furthermore, another group of participants viewed the same stimuli which were not associated with social hierarchy in Experiment 2.

At the behavioral level, there was no effect of social hierarchy on the RT or ACC. Participants' RTs of the hierarchy-judgment task in Experiment 1 (~625 ms) were generally slower than those of the star-judgment task in Experiment 2 (~565 ms), suggesting the influence of the informational context on the processing of the hierarchy cues. In particular, the star-judgment task might be based on relatively simple and direct associations between stimuli (one star vs. three stars) and responses (1 vs. 3); whereas the hierarchy-judgment task might require higher-level retrieval of the meanings (inferior vs. hierarchy) of the stimuli, which presumably delayed the response latency. These findings suggest that participants in the hierarchy-judgment task did not simply perceive presented cues as one or three star(s) but considered these stimuli as symbols of inferior or superior social hierarchy.

Regarding the ERP results, we identified the preferential

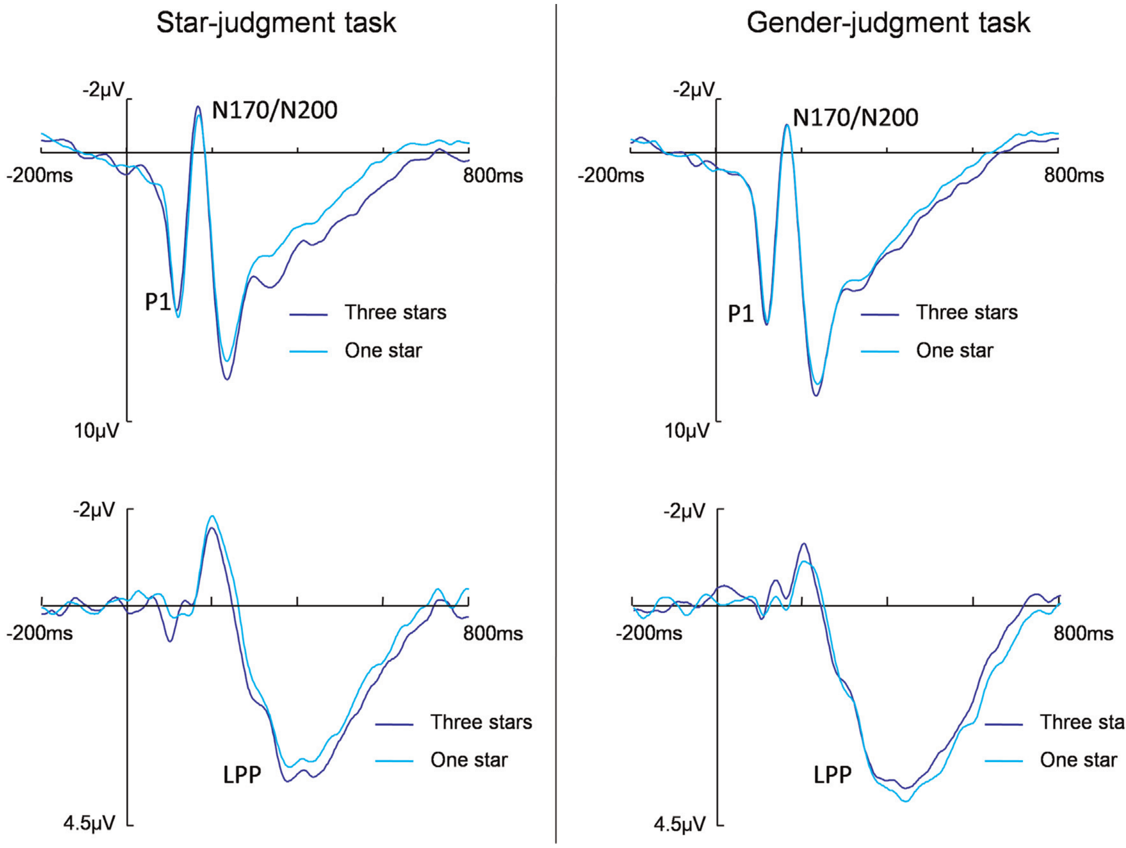

Fig. 3. The grand average ERPs evoked by stimuli associated with one and three stars in star-judgment and gender-judgment tasks of Experiment 2.

processing of high-status targets at both early (N170/N200) and late (LPP) temporal stages manifested as more pronounced neural activity evoked by superior-hierarchy targets than inferior-hierarchy targets. Importantly, The modulations of top-down attention on hierarchy effects were identified on the LPP component, such that the augmented LPP amplitudes evoked by superior-hierarchy targets were only observed in the attended condition but not in the unattended condition; whereas the modulations of the N170/N200 component by social hierarchy were evident in both attended and unattended conditions. These differential effects of top-down attention at early and late temporal stages may reflect flexible response to biologically and socially salient superior-hierarchy cues.

It remains controversial whether social hierarchy modulates neural responses at the early temporal stage. On the one hand, it has been demonstrated in both humans and non-human primates that superior-hierarchy targets elicit more pronounced neural responses than inferior-hierarchy targets within 150–200 ms (i.e., the N170/N200 component) (Chiao et al., 2008; Pineda et al., 1994). On the other hand, those early effects of social hierarchy were not replicated by a recent study employing neutral-expression conveyed social hierarchy (Breton et al., 2014), raising the possibility that differential facial features employed to manipulate high (e.g., directed gaze) and low (e.g., averted gaze) social status confound effects of social hierarchy on the N170/N200 component.

Here we demonstrate that modulations of social hierarchy on the N170/N200 component are evident after controlling for face postures. Importantly, these hierarchy-related effects on the N170/N200 component could not be attributed to other differences in physical characteristics between superior and inferior hierarchies (e.g., three stars vs. one star), given that they were not observed when participants were shown the same stimuli in a non-hierarchy task, i.e., the star-judgment task in Experiment 2. The current results, collaborating with Chiao et al.s (2008) findings, suggest that the enhanced neural responses evoked by high-status cues at early temporal stages are attributed to the social and biological relevance of these social cues which intrinsically induce rapid and relatively automatic attentional bias (Carretié, 2014). However, it is worth noting that the current study differed from Breton et al.s study (2014) in many other aspects, including the number of targets employed and the stability of participants' hierarchy. Therefore, results from these studies need to be compared with caution.

Notably, the preferential attention bias towards superior-hierarchy cues reflected by the N170 component was evident in both attended and unattended conditions. These findings are consistent with a tremendous of evidence that modulations of early neural responses by biological salient events (e.g., superior hierarchy) are evident in attention-limited environments (Carretié et al., 2004; El Zein et al., 2015; Olofsson et al., 2008). In accord with current findings, previous behavioral studies have demonstrated that high-status targets attract attentional bias in both attended and unattended contexts (Dalmaso et al., 2012; Foulsham et al., 2010). For instance, hierarchy cues presented in brief time (50 ms) are effective in modulating human social attention in the gaze-cuing task (Dalmaso et al., 2014). Another study have reported that high-status targets are preferentially attended to when individual's attention is limited (Maner et al., 2008). Taken together, these findings demonstrate the enhanced capability of superior-hierarchy cues to capture limited attention resources, presumably due to the biologically and socially relevance of these social cues. However, it should be noted that effects of the N170/N200 component may not be completely driven by automatic processes but also by higher-level cognitive mechanisms, such as the retrieval of the social meanings of hierarchy cues. In accord with this idea, the N170/N200 responses to hierarchy cues were generally stronger in the attended than the unattended condition, although the attention manipulation did not affect the effects of social hierarchy.

Superior-hierarchy targets are also associated with the elaborative processing at the late temporal stage, manifested as more pronounced LPP amplitudes evoked by high-status targets than low-status targets (Breton et al., 2014). The LPP component is thought to reflect sustained and elaborative processing for motivationally relevant stimuli (Bradley et al., 2007; Flaisch and Schupp, 2013). Therefore, the augmented LPP component evoked by superior-hierarchy targets in the hierarchy task may be attributed to the deeper processing of these socially salient stimuli (Foulsham et al., 2010; Ratcliff et al., 2011).

The LPP component does not only represent motivational responses implemented by subcortical brain areas (e.g., amygdala), but also reflects high-order cognitive processes mediated by prefrontal areas (Ferrari et al., 2008; Liu et al., 2012; Sabatinelli et al., 2007). For instance, recent studies employing simultaneous EEG-fMRI recording technique have demonstrated that the LPP amplitude is associated with blood-oxygen-level dependent (BOLD) activity in both subcortical brain regions such as amygdala and prefrontal brain areas such as ventrolateral prefrontal cortex (Liu et al., 2012). Furthermore, it has been demonstrated that stimulation of dorsolateral prefrontal cortex results in changes of LPP amplitudes in response to affective pictures (Hajcak et al., 2010). Finally, many studies have reported the top-down modulations on the LPP response to motivationally relevant stimuli, such that cognitive processes of reappraisal and top-down attention lead to alterations in LPP amplitudes (Hajcak et al., 2009; Hajcak and Nieuwenhuis, 2006; Krompinger et al., 2008). In accord with previous findings, here we demonstrate that modulations of superior-hierarchy targets on the LPP are sensitive to top-down attention, such that the advantage of superior-hierarchy targets in sustained processing was absent when hierarchy cues were unattended. These intriguing findings implicate flexible response to high-status cues, such that elaborative processing of those social cues could be voluntarily avoided when it is not relevant to current task demand. Given that excessive processing of superior-hierarchy cues can lead to negative subjective feelings and preclude prosocial feelings to others'misfortune in certain contexts (Steckler and Tracy, 2014; Takahashi et al., 2009), the ability to flexibly adjust sustained attentional resources to high-status cues in different contexts is adaptive for individuals.

The limitations of our study should be acknowledged. First, we did not find attentional bias to the superior hierarchy at behavioral level. In particular, one would expect that hierarchy-related attentional bias should have led to differences in reaction times and accuracy between superior and inferior social hierarchies. The null behavioral results might be attributed to the simple task employed in the current study, given that extremely high reaction accuracy (> 97%) implicates ceiling effects. However, the attention account on the N170/N200 and LPP components is consistent with previous behavioral studies reporting attentional bias to high-status targets with more sensitive paradigms (e.g., gaze-cueing paradigm) (Dalmaso et al., 2012; Shepherd et al., 2006), as well as numerous ERP studies reporting attention modulations on the N170 and LPP components by other socially and evolutionarily salient stimuli (Holmes et al., 2003; Krombholz et al., 2007; Luo et al., 2010; Olofsson et al., 2008; Wiens et al., 2012).

Second, like most previous studies (e.g., Chiao et al., 2008; Zink et al., 2008), the current study focused on the general effects of social hierarchy in males and females and ignored potential interactions between genders of participants and perceived targets. However, previous studies have indicated that high status males (but not females) capture perceiver's attention (DeWall, 2008), whereas attractive females (but not males) capture perceiver's attention (DeWall, 2008; Maner et al., 2007). Therefore, whether social hierarchy or other features of perceived targets are relevant to individuals is probably dependent on the genders of both perceivers and perceived targets, and future studies should investigate neural signatures of these processes in a more systematic way.

Third, it is conceivable that effects of social hierarchy on the ERP responses reflected the preferential processing of these social cues (superior vs. inferior) but not face targets associated with them. Although previous studies have demonstrated that social hierarchy alters holistic face processing (Ratcliff et al., 2011), the current findings may not be attributed to these effects: N170/N200 effects of social hierarchy were left-lateralized in the current study, whereas effects of holistic face processing within this temporal stage are usually right-lateralized (Rossion et al., 2003).

In summary, the current findings elucidated the modulations of top-down attention on the processing of social hierarchy at multiple temporal stages. Our study demonstrates that hierarchy cues influence the temporal dynamics of neural responses to neutral-expression targets at both early and late temporal stages, which are differentially modulated by top-down attention. The early attentional bias elicited by high-status targets is evident in both attended and unattended conditions, suggesting the enhanced capability of superior-hierarchy cues to capture limited attention resources. These neurocognitive processes may underlie the rapid detection of biologically and socially salient superior-hierarchy targets even when individuals are engaged by other task demands. The later and sustained evaluations of superior hierarchy are gated by top-down attention, suggesting a flexible and voluntary response to high-status targets at this temporal stage. These findings shed light on the temporal course of modulations of neural responses to superior-hierarchy targets by top-down attention, supporting and extending previous behavioral and fMRI results regarding on the preferential perception of superior hierarchy. Notably, the preferential processing of superior hierarchy observed in the current study could not be attributed to low-level physical characteristics associated with high status (e.g., three stars), since the same stimuli did not elicit these effects when these stimuli were not associated with hierarchy information in Experiment 2.

Conflict of interest

The authors declare no competing financial interests.

Acknowledgements

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Appendix A. Supplementary information

Supplementary data related to this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2015.02.013

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◆ **Human Brain Mapping 36:591–602 (2015)** ◆

Neural Signatures of Fairness-Related Normative Decision Making in the Ultimatum Game: A Coordinate-Based Meta-Analysis

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Abstract: The willingness to incur personal costs to enforce prosocial norms represents a hallmark of human civilization. Although recent neuroscience studies have used the ultimatum game to understand the neuropsychological mechanisms that underlie the enforcement of fairness norms; however, a precise characterization of the neural systems underlying fairness-related norm enforcement remains elusive. In this study, we used a coordinate-based meta-analysis on functional magnetic resonance imaging (fMRI) studies using the ultimatum game with the goal to provide an additional level of evidence for the refinement of the underlying neural architecture of this human puzzling behavior. Our results demonstrated a convergence of reported activation foci in brain networks associated with psychological components of fairness-related normative decision making, presumably reflecting a reflexive and intuitive system (System 1) and a reflective and deliberate system (System 2). System 1 (anterior insula, ventromedial prefrontal cortex [PFC]) may be associated with the reflexive and intuitive responses to norm violations, representing a motivation to punish norm violators. Those intuitive responses conflict with economic self-interest, encoded in the dorsal anterior cingulate cortex (ACC), which may engage cognitive control from a reflective and deliberate System 2 to resolve the conflict by either suppressing (ventrolateral PFC, dorsomedial PFC, left dorsolateral PFC, and rostral ACC) the intuitive responses or over-riding self-interest (right dorsolateral PFC). Taken together, we suggest that fairness-related norm enforcement recruits an intuitive system for rapid evaluation of norm violations and a deliberate system for integrating both social norms and self-interest to regulate the intuitive system in favor of more flexible decision making. *Hum Brain Mapp 36:591–602, 2015.* © **2014 Wiley Periodicals, Inc.**

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INTRODUCTION

Humans comply with social norms (e.g., equity and fairness pertaining to resource distribution) and they are willing to punish norm violators at the expense of personal costs [Fehr and Fischbacher, 2004; Fehr and Gächter, 2002]. This costly norm enforcement termed altruistic punishment is a hallmark of human culture and plays a key role in promoting widespread cooperation among genetically unrelated strangers in human societies [Fehr et al., 2002; Henrich et al., 2006]. Humans develop preferences for social norms as early as 7–8 year old [Fehr et al., 2008; Güroğlu et al., 2011; Steinmann et al., 2014] and maintain those prosocial preferences across lifespan [Harlé and Sanfey, 2012; Roalf, 2010].

A common, widely used research approach to probe human social norm enforcement is the employment of well-structured interactive economic games [Camerer, 2003; Fehr and Camerer, 2007; Sanfey, 2007]. For example, during the one-shot interaction in the ultimatum game (UG) [Güth et al., 1982], two players must assent to split of a sum of money or both get nothing. The first player (proposer) offers a way to divide the sum between the two players and the second player (responder) can either accept (both get paid accordingly) or reject (neither gets paid) the offer. Responders perceive fair offers (i.e., norm compliance) as rewards and simply accept those offers [Tabibnia and Lieberman, 2007; Tabibnia et al., 2008]. When responders are treated fairly, brain regions engaged in reward processing such as ventromedial prefrontal cortex (vmPFC) or striatum are involved [Baumgartner et al., 2011; Fliessbach et al., 2007; Guo et al., 2014; Tabibnia et al., 2008; Wu et al., in press].

In contrast, unfair offers (i.e., norm violation) induce motivational conflict between economic self-interest and norm enforcement: responders are tempted to accept those offers for monetary reward, whereas they are also motivated by prosocial preferences to reject those offers [Fehr and Camerer, 2007]. Researchers from various research disciplines are interested in studying the neuropsychological mechanisms underlying the reconciling of different motivations in response to norm violations. For example, previous studies have indicated that responders reject unfair offers at about 50% chance and punish proposers who violate fairness norms by offering less than 20%–30% of the sum [Camerer, 2003; Güth et al., 1982], demonstrating human willingness to incur personal cost to enforce social norms.

Early models addressing human social preferences in fairness-related norm enforcement have postulated the significant roles of inequality aversion [Fehr and Schmidt, 1999] and intention inference [Blount, 1995; Rabin, 1993]. In recent decades, those initial theoretical models have been extensively elaborated due to interdisciplinary studies in the fields of psychology, economics, and neuroscience [Rilling and Sanfey, 2011; Sanfey et al., 2006]. Recent evidence revealed that fairness-related norm enforcement in response to norm violations (as measured in UG) consists of multiple psychological components that are implemented by separable neural systems [Buckholtz and Marois, 2012; Sanfey and Chang, 2008], including a reflexive and intuitive system (System 1) and a reflective and deliberate system (System 2) [Lieberman, 2007; Sanfey et al., 2006].

In terms of UG, System 1 is thought to represent psychological components involved in the initial evaluations of norm violations, including brain areas such as the anterior insula (AI) signaling norm violations [Civai, 2013] or emotional processing via representations of (especially aversive) internal states [Chang and Sanfey, 2013; Corradi-Dell'Acqua et al., 2013; Guo et al., 2013; Sanfey et al., 2003], the amygdala signaling transient negative emotional response to norm violations [Gospic et al., 2011; Haruno and Frith, 2010; Haruno et al., 2014; Yu et al., 2014] and the vmPFC encoding subjective values of perceived offers [Baumgartner et al., 2011; Dawes et al., 2012; Xiang et al., 2013]. Those intuitive responses to norm violations contribute to altruistic punishments of transgressions [Gospic et al., 2011; Sanfey et al., 2003], supporting the notion that reflexive and emotional responses implemented by System 1 lie at the core of human prosocial preferences [Haidt, 2001; Roch et al., 2000; Sanfey and Chang, 2008; Scheele et al., 2012; Zaki and Mitchell, 2011, 2013].

System 2 presumably represents more deliberate psychological components responsible for reappraising and regulating System 1 in favor of either economic self-interest [Brüne et al., 2012; Sanfey and Chang, 2008] or enforcement of social norms (e.g., fairness) [Fehr and Camerer, 2007]. The unfairness-evoked aversive responses (norm enforcement) and self-interest (due to the possibility to gain the monetary reward) contradict each other and result into a motivational conflict that is monitored by the dorsal anterior cingulate cortex (dACC) [Fehr and Camerer, 2007; Sanfey et al., 2003]. This conflict can be resolved in two ways: on the one hand, the reflexive reactions of System 1 can be suppressed, probably implemented by brain regions associated with emotion regulation such as ventrolateral prefrontal cortex (vlPFC) and dorsomedial PFC (dmPFC), leading to an increased acceptance of unfair offers [Civai et al., 2012; Grecucci et al., 2013; Tabibnia et al., 2008]. On the other hand, the conflict can be also reconciled by over-riding economic self-interest, likely manifested as executive control in the right dorsolateral PFC (dlPFC) [Baumgartner et al., 2011;

TABLE I. Summary of studies included for the meta-analysis focusing on the responder in UG

Study	N	Task and contrast	No. of foci
Fair Offer			
Baumgartner et al. [2011]	32	Responders in UG, fair>unfair	4
Civai et al. [2012]	19	Responders in a modified UG/DG, equal>unequal	3
Harlé and Sanfey.[2012]	38	Responders in UG, fair>unfair	3
Roalf [2010]	27	Responders in UG, fair>unfair	2
Tabibnia et al. [2008]	12	Responders in UG, fair>unfair	1
Tomasino et al. [2013]	17	Responders in UG, fair>unfair	3
White et al. [2013]	20	Responders in UG, parametric analysis, negative correlation with unfairness level	1
White et al. [2014]	21	Responders in UG, parametric analysis, negative correlation with unfairness level	3
Wright et al. [2011]	30	Responders in UG, parametric analysis, negative correlation with inequity	10
Wu et al. [in press]	18	Responders in UG, parametric analysis, positive correlation with subjective utility	4
Zhou et al. [2014]	28	Responders in UG, fair>unfair	1
Unfair Offer			
Baumgartner et al. [2011]	32	Responders in UG, unfair>fair	17
Civai et al. [2012]	19	Responders in a modified UG/DG, unequal>equal	12
Haruno et al. [2014]	62	Responders in UG, parametric analysis, positive correlation with inequity.	4
Gospic et al. [2011]	17	Responders in UG, unfair>fair	4
Guo et al. [2014]	18	Responders in UG, unfair>fair	10
Guo et al. [2013]	21	Responders in UG, unfair>fair	13
Güroğlu et al. [2011]	68	Responders in UG, unfair>fair	9
Halko et al. [2009]	23	Responders in UG, unfair>fair	22
Harlé and Sanfey. [2012]	38	Responders in UG, unfair>fair	12
Kirk et al. [2011]	40	Responders in UG, unfair>fair	11
Roalf [2010]	27	Responders in UG, unfair>fair	8
Sanfey et al. [2003]	19	Responders in UG, unfair>fair	17
White et al. [2013]	20	Responders in UG, parametric analysis, positive correlation with unfairness level	8
White et al. [2014]	21	Responders in UG, parametric analysis, positive correlation with unfairness level	7
Wu et al. [in press]	18	Responders in UG, parametric analysis, negative correlation with subjective utility	7
Zheng et al. [in press]	25	Responders in UG, unfair>fair	15
Zhou et al. [2014]	28	Responders in UG, unfair>fair	4

N, number of subjects

Knoch et al., 2006, 2008]. Overall, System 2 may contribute to detect and reconcile the motivational conflict between norm enforcement and self-interest in favor of flexible decision making.

Recent neuroscientific studies have begun examining the neural signatures of isolated components of the fairness-related norm enforcement and a couple of descriptive reviews have explored the biological basis of human normative decision making from a larger perspective [Buckholtz and Marois, 2012; Rilling and Sanfey, 2011; Ruff and Fehr, 2014]. However, a precise characterization of the neural systems underlying fairness-related norm enforcement remains elusive. In this study, we used a coordinate-based meta-analysis on fMRI studies using the UG with the goal to provide an additional level of evidence for the refinement of the underlying neural architecture of fairness-related norm enforcement. We expect that enforcement of social norms in the UG recruits multiple brain regions, which have been previously separated into two interacting neural systems [Buckholtz and Marois, 2012; Sanfey and Chang, 2008]: (i) a reflexive and intuitive system (System 1: AI, amygdala, and vmPFC) for recognizing and evaluating norm violations and (ii) a deliberate system (System 2: dACC, dlPFC, vlPFC, and dmPFC) for reappraising and regulating System 1 in favor of either economic self-interest or norm enforcement.

TABLE II. ALE meta-analysis results for fair offers (fair > unfair contrast)

Brain regions	BA	MNI coordinates (mm) *x*	*y*	*z*	ALE ($\times 10^{-2}$)	Cluster size (mm^3)
vmPFC/vACC	32/10	6	46	−12	0.97	2736
R vACC	32	6	46	−12	0.97	
L vmPFC	10	−2	54	−12	0.97	
R vmPFC	10	6	52	−16	0.89	
L posterior insula/STG	13/22	−54	−12	6	0.92	1688
L STG	22	−54	−12	6	0.92	
L posterior insula	13	−40.5	−15	1.5	0.89	
L PCC	23	−8	−58	16	1.08	1192
L PCC	23	−8	−58	16	1.08	
R posterior insula	13	42	−24	24	0.92	952
R posterior insula	13	42	−24	24	0.92	
L precuneus	7	−8	−59	56	0.80	912
L precuneus	7	−8	−59	56	0.80	
R ITG	20	60	−48	−12	0.93	648
R ITG	20	60	−48	−12	0.93	

BA, Brodmann area; L, left; R, right; ALE, activation likelihood estimation; vmPFC, ventromedial prefrontal cortex; vACC, ventral anterior cingulate cortex; STG, superior temporal gyrus; PCC, posterior cingulate cortex: ITG, inferior temporal gyrus

MATERIAL AND METHODS

Literature Search and Selection

We performed a systematic online database search in July of 2014 on PubMed and ISI Web of Science by entering various combinations of relevant search items (e.g., [“normative decision making” OR “fair” OR “altruistic punishment” OR “ultimatum game”] AND [“fMRI” OR “magnetic resonance imaging” OR “neuroimaging”]) and conducted a follow-up search by examining the bibliography and citation indices of the preselected articles. The search resulted into 53 potential studies that were further assessed according to the following criteria: (i) subjects were recruited as responders in UG: (ii) fMRI was used as the imaging modality; (iii) whole-brain general-linear-model-based analyses (rather than region of

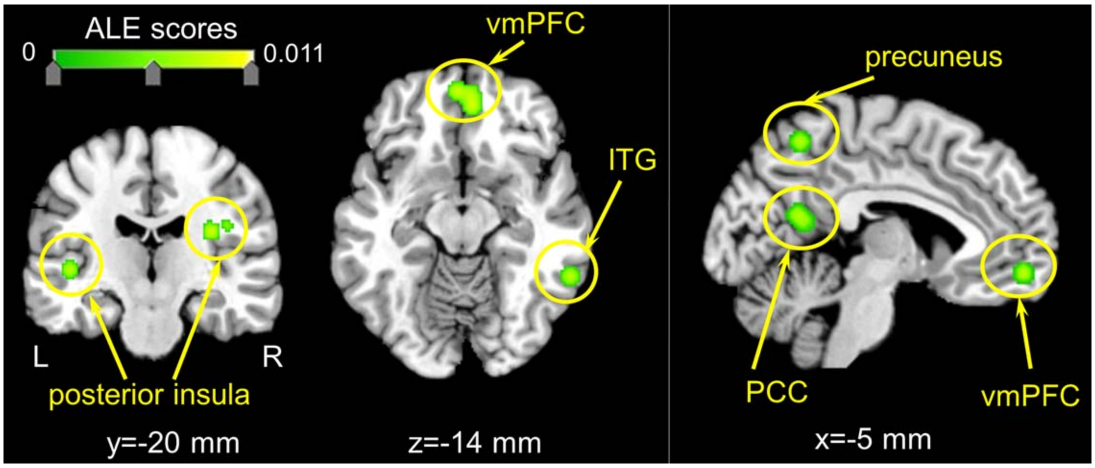

Figure 1.

Significant clusters from the coordinate-based activation likelihood estimation (ALE) meta-analysis (5,000 permutations, q(FDR) < 0.05, min. volume of 600 mm^3) for fair offers (fair > unfair contrast). Consistent maxima comparing fair with unfair offers in UG were found in posterior insula, ventromedial prefrontal cortex (vmPFC), inferior temporal gyrus (ITG), precuneus, and posterior cingulate cortex (PCC). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE III. ALE meta-analysis results of unfair offers (unfair > fair contrast)

Brain regions	BA	MNI coordinates (mm)			ALE ($\times 10^{-2}$)	Cluster size (mm^3)
		x	*y*	*z*		
dACC/pre-SMA	32/6	−4	16	48	2.59	14168
L dACC	32	−4	16	48	2.59	
R dACC	32	8	22	40	2.35	
L pre-SMA	6	−6	2	64	0.97	
R pre-SMA	6	10	24	58	1.46	
R AI/putamen/vlPFC	13/47	38	20	0	3.10	9456
R AI	13	38	20	0	3.10	
R putamen	/	22	12	2	0.96	
R vlPFC	47	34	21	−18	0.62	
L AI/vlPFC	13/47	−30	24	2	2.79	7376
L AI	13	−30	24	2	2.79	
L vlPFC	47	−44	24	−8	1.00	
R dlPFC: R middle frontal gyrus/SFG	9/8	40	36	26	1.95	3768
R middle frontal gyrus	9	40	36	26	1.95	
R SFG	8	38	22	48	0.82	
R dlPFC: R middle frontal gyrus/SFG	10	30	66	2	1.55	1272
R SFG	10	30	66	2	1.55	
R middle frontal gyrus	10	30	64	12	1.22	
R dlPFC: SFG/middle frontal gyrus	9/10	26	48	22	1.05	664
R SFG	9	26	48	22	1.05	
R middle frontal gyrus	10	34	48	18	0.87	
L dlPFC: L middle frontal gyrus	9/8	−30	38	30	1.03	1016
L middle frontal gyrus	9	−30	38	30	1.03	
L middle frontal gyrus	8	−36	40	38	0.88	
L dlFPC: SFG	9	−20	54	30	0.94	648
L SFG	9	−20	54	30	0.94	
R dmPFC	9	8	60	16	1.06	1024
R dmPFC	9	8	60	16	1.06	
R dmPFC	9	4	54	26	0.97	680
R dmPFC	9	4	54	26	0.97	
L rACC/medial PFC	10/32	−12	46	4	0.92	616
L medial PFC	10	−12	46	4	0.92	
L rACC	32	−7	47	4	0.31	
L IPL	40	−32	−46	42	0.93	1136
L IPL	40	−32	−46	42	0.93	
L IPL	40	−44	−46	52	1.24	816
L IPL	40	−44	−46	52	1.24	
L pSTG	22	−48	−40	4	0.91	632
L pSTG	22	−48	−40	4	0.91	
L STG/ATL	22	−52	−16	−8	1.03	664
L STG/ATL	22	−52	−16	−8	1.03	
R precuneus	7	14	−68	40	0.96	664
R precuneus	7	14	−68	40	0.96	
L fusiform gyrus	19	−44	−72	−8	1.07	672
L fusiform gyrus	19	−44	−72	−8	1.07	
R lingual gyrus	18	10	−80	0	0.98	672
R lingual gyrus	18	10	−80	0	0.98	

BA, Brodmann area; L, left; R, right; ALE, activation likelihood estimation; dACC, dorsal anterior cingulate cortex; pre-SMA, pre-supplementary motor area; AI, anterior insula; vlPFC, ventrolateral prefrontal cortex; SFG, superior frontal gyrus; dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; rACC, rostral anterior cingulate cortex; IPL, inferior parietal lobule; pSTG, posterior superior temporal gyrus; ATL, anterior temporal lobe.

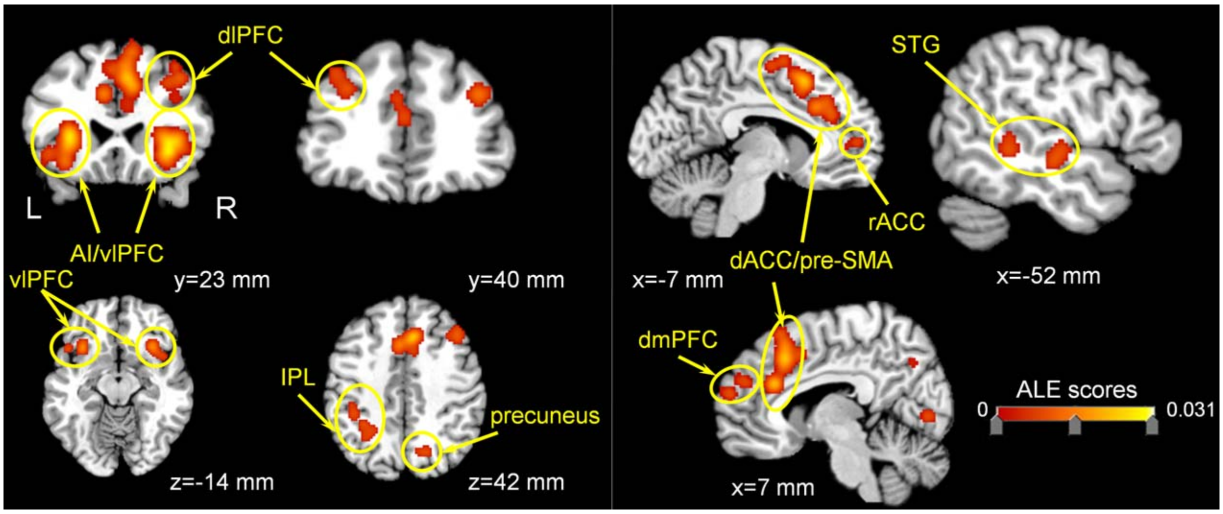

Figure 2.

Significant clusters from the coordinate-based activation likelihood estimation (ALE) meta-analysis (5,000 permutations, q(FDR) < 0.05, min. volume of 600 mm^3) for unfair offers (unfair > fair contrast). Consistent maxima comparing unfair with fair offers in UG were found in dorsolateral prefrontal cortex (dlPFC), anterior insula (AI), ventrolateral PFC (vlPFC), inferior parietal lobule (IPL), precuneus, dorsal anterior cingulate cortex/presupplementary motor area (dACC/pre-SMA), rostral ACC (rACC), dorsomedial PFC (dmPFC), and superior temporal gyrus (STG). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

interest [ROI] analyses) were applied; (iv) statistical models for fairness-related contrasts (i.e., fair > unfair or unfair > fair) or relevant parametric analyses were reported; and (v) activations were presented in a standardized stereotaxic space (Talairach or MNI). Note that for studies reporting Talairach coordinates a conversion to the MNI coordinates was implemented [Brett, 1999]. Filtering search results according to the inclusion/exclusion criteria yielded a total of 20 published fMRI articles with 17 "unfair > fair" contrasts (180 foci) and 11 "fair > unfair" contrasts (35 foci) reported in a standardized stereotaxic space (Table I).

Activation Likelihood Estimation *Approach*

A coordinate-based meta-analysis of reported fMRI experiments was conducted using the revised activation likelihood estimation (ALE) algorithm [Eickhoff et al., 2009] implemented in the GingerALE software (version 2.3, http://www.brainmap.org/ale/). Applying the ALE algorithm, the reported coordinates of brain areas associated with fairness-related norm enforcement were converged across different experiments. A random-effects analysis was performed to determine statistical significance using a permutation test of randomly generated foci with 5,000 permutations (full-width at half-maximum of 10 mm) [Eickhoff et al., 2012; Turkeltaub et al., 2012]. The resulting ALE maps were thresholded using the false discovery rate (FDR, $q(\text{FDR}) < 0.05$) correction for multiple comparisons [Genovese et al., 2002; Laird et al., 2005] and all clusters were set to a minimum volume of 600 mm^3 [Lamm et al., 2011]. The meta-analysis results were overlaid onto an anatomical template (Colin27_T1_seg_MNI.nii, www.brainmap.org/ale) and displayed using the Mango software (http://rii.uthscsa.edu/mango/).

RESULTS

Consistent maxima were found in the following brain regions comparing fair with unfair offers in UG: bilateral vmPFC and posterior insula, left posterior cingulate cortex (PCC) and precuneus, and right inferior temporal gyrus (ITG; Table II and Fig. 1). Comparing unfair with fair offers in UG, consistent maxima were found in the following brain regions: bilateral dACC/pre-supplementary motor area (pre-SMA), AI/vlPFC and dlPFC, left rostral ACC (rACC), posterior superior temporal gyrus (pSTG), STG/anterior temporal lobe (ATL), inferior parietal lobule (IPL) and fusiform gyrus, right dmPFC, precuneus, and lingual gyrus (Table III and Fig. 2). The AI clusters revealed in this contrast were primarily located in subregion of the dorso-AI, according to Kelly et al.'s (2012) templates of insular subregions (Fig. 3).

DISCUSSION

The willingness to incur personal costs to enforce prosocial norms represents a hallmark of human civilization. Recent neuroscience studies have used UG to understand

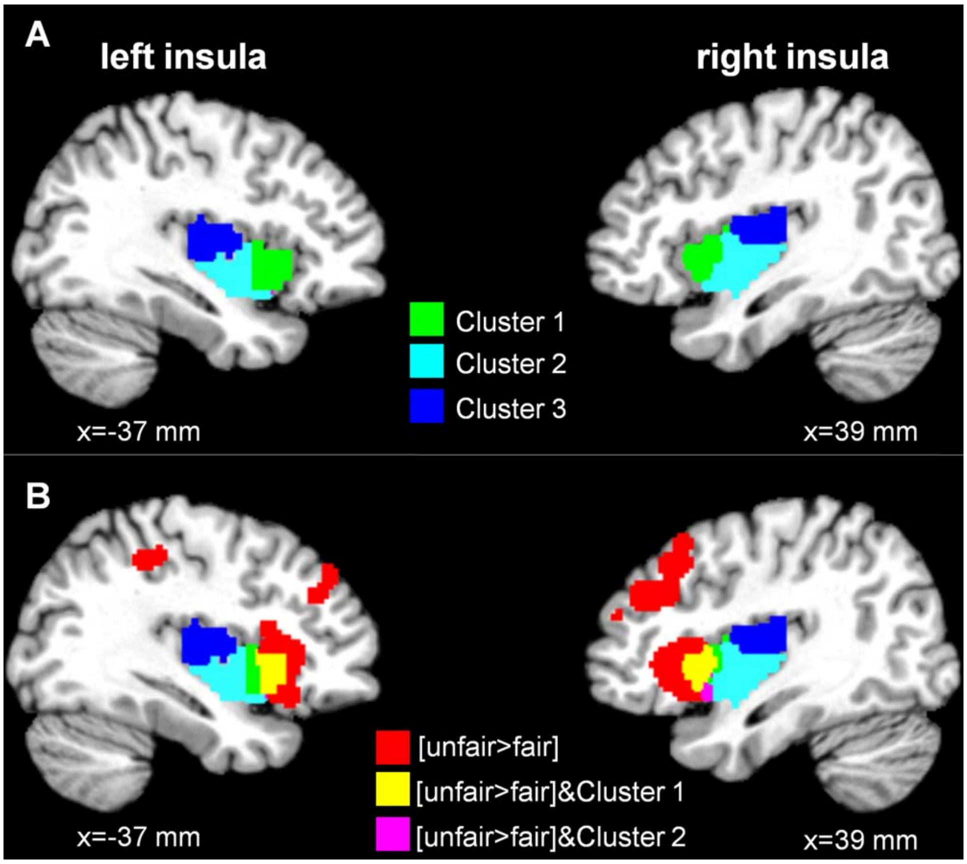

Figure 3.

Subregions of insular cortex. (**A**) Insular subregions (Cluster 1 [green]: dorsoanterior insula, Cluster 2 [cyan]: ventroanterior insula, Cluster 3 [blue]: posterior insula) according to Kelly et al.'s template ($K = 3$ solutions). (**B**) Significant clusters from the coordinate-based ALE (activation likelihood estimation) for unfair offers (red: unfair > fair contrast) and overlaps between those clusters and different insular subregions intersected by Kelly et al.'s template (yellow: intersection of clusters from ALE analysis for unfair offers and dorsoanterior insula; reddish yellow: intersection of clusters from ALE analysis for unfair offers and ventroanterior insula). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

the neuropsychological mechanisms that underlie enforcement of fairness-related norms [Fehr and Camerer, 2007; Sanfey, 2007]. The purpose of this coordinate-based meta-analysis study was to quantitatively synthesize the results of recent fMRI studies regarding fairness-related norm enforcement with the aim of identifying consistent activation patterns of the neural signatures underlying this human puzzling behavior. Our results demonstrated a convergence of reported activation foci in brain networks associated with normative decision making [Buckholtz and Marois, 2012; Krueger et al., 2008; Rilling and Sanfey, 2011; Sanfey and Chang, 2008], and these brain regions have been thought to represent two interacting neural systems [Buckholtz and Marois, 2012; Sanfey and Chang, 2008]: a reflexive and intuitive system (System 1) for recognizing and evaluating norm violations and a deliberate system (System 2) for integrating both social norms and economic self-interest to regulate System 1 in favor of flexible decision makings.

In UG, the responder has to decide whether to accept or to reject fair or unfair offers from proposers. Regarding fair offers, previous findings have indicated that those offers are considered as rewards [Harlé et al., 2012; Tabibnia and Lieberman, 2007; Tabibnia et al., 2008]. Accordingly, the vmPFC, a core region associated with reward processing showed consistent activation across fMRI studies in response to fair offers compared to unfair offers. Presumably, the vmPFC is associated with computing positive values of fairness, owning to its role in representing values of normatively valued goods [Aoki et al., 2014; Moretti et al., 2009; Tricomi et al., 2010]. In accord with this view, the activation of vmPFC to fair offers remains after controlling for momentary payoff [Tabibnia et al., 2008].

The meta-analysis also revealed the consistent involvement of the posterior insula in response to fair offers, which is consistent with its role in coding fairness or equality [Hsu et al., 2008; Wright et al., 2011]. Moreover, involvement of the PCC was identified, which role in reward processing has also been demonstrated in previous studies [Ballard and Knutson, 2009; Levy and Glimcher, 2011; McClure et al., 2007], but it remains unknown whether this region encodes the positive value of fairness or just the monetary payoff in UG. By contrast, the meta-analysis did not reveal consistent activation of the ventral striatum in response to fairness, since most of the previous studies reporting a ventral striatum response to fairness applied an ROI analysis approach [Tabibnia et al., 2008; Tricomi et al., 2010; Wu et al., in press].

Responders in UG react to unfair offers with negative emotional feelings, which are thought to play a pivotal role in costly punishment/norm enforcement [Koenigs and Tranel, 2007; Pillutla and Murnighan, 1996; Van't Wout et al., 2006; White et al., 2014; Xiao and Houser, 2005; Yamagishi et al., 2009]. Our meta-analysis revealed that brain regions of System 1 such as bilateral AI were consistently involved in those intuitive and reflexive responses [Sanfey and Chang, 2008; Sanfey et al., 2003]. The AI may be associated with the visceral experience of negative feelings by signaling aversive interoceptive states due to fairness-related norm violations [Critchley et al., 2004; Singer et al., 2009]. Previous studies using the UG have shown that emotion infusion [Harlé et al., 2012; Harlé and Sanfey, 2007] and emotion regulation [Grecucci et al., 2013] modulate the unfairness-evoked AI responses, which predict normative decision making at the behavioral level [Harlé et al., 2012; Kirk et al., 2011; Sanfey et al., 2003; Tabibnia et al., 2008]. However, recent studies have indicated that unfairness-evoked negative feelings cannot completely account for the activation of AI [Civai, 2013], because neural response to norm violations in the AI is also evident when participants play a role of indifferent third-party [Civai et al., 2012; Strobel et al., 2011] and when unfair offers are better than expectations [Xiang et al., 2013; Yu et al., 2014]. Furthermore, recent evidence has demonstrated a functional heterogeneity of different AI subregions related to norm violations in UG [Zhou et al., 2014]. In particular, a tripartite subdivision of the insula has been proposed with dorsoanterior, ventroanterior, and posterior portions contributing to cognitive, affective, and sensorimotor processing, respectively [Chang et al., 2013; Kelly et al., 2012]. Recent evidence suggests that the dorsal AI associated with cognition is consistently activated by norm violation in most of previous neuroimaging studies using UG [Zhou et al., 2014]. In lights of these recent findings, it is more likely that the consistent activation of primarily dorsal AI represents a cognitive heuristic to detect norm violations rather than emotional resentment [Civai, 2013; Civai et al., 2010, 2012, 2013].

The emotion processing in response to norm violations may be implemented by other brain regions, including vmPFC and amygdala, both of which are frequently associated with social decision making and affective processing [Buckholtz and Marois, 2012; Buckholtz et al., 2008; Gospic et al., in press]. As discussed above, numerous studies have revealed the role of vmPFC in tracking the positive and negative values/feelings of goods [Grabenhorst and Rolls, 2011; O'Doherty, 2004], including normatively valued goods such as equality [Baumgartner et al., 2011; Tricomi et al., 2010]. Therefore, the lower activation (and often deactivation) of vmPFC in response to unfair offers may reflect negative feelings to norm violations, a viewpoint supported by the correlation between subjective feelings of offers and vmPFC activation [Xiang et al., 2013].

The amygdala is thought to reflect the early and transient emotional response to norm violations, and the failure to detect a consistent activation of this region in the meta-analysis may be attributed to the coarse onset timing used in most studies [Gospic et al., 2011]. Nevertheless, recent studies have revealed the crucial role of this area in social preferences. For example, amygdala activation to unfair offers predicts individual differences in social preferences for equitable outcomes [Haruno and Frith, 2010; Haruno et al., 2014] and willingness to enforce social norms [Gospic et al., 2011; Yu et al., 2014]. Moreover, Gospic et al. [2011] demonstrated a causal role of amygdala in the norm enforcement by showing that pharmacological attenuation of amygdala response led to decreased costly punishment in UG.

Economic self-interest constitutes another essential motivation in UG and conflicts with the intuitive response mediated by System 1 [Sanfey and Chang, 2008; Sanfey et al., 2006]. The meta-analysis identified the dACC—a key region of System 2—in response to norm violations. Based on the role of the dACC in conflict monitoring [Botvinick et al., 2001, 2004], this region presumably monitors the conflict between economic self-interest and intuitive response to norm violations and signals the need to resolve it [Fehr and Camerer, 2007; Sanfey et al., 2003]. Previous evidence revealed that the neural response to norm violations in dACC is evident only when self-interest is involved in norm enforcement [Civai et al., 2012] and the response is stronger for those responders who are more prone to self-interest, and therefore, experience larger conflicts [Güroğlu et al., 2010, 2011; Xiang et al., 2013; Zhou et al., 2014]. However, other potential suggested functions of dACC in the context of UG, such as detection of norm violations [Chang and Sanfey, 2013; Güroğlu et al., 2010; White et al., 2013], emotion appraisal [Etkin et al., 2011; Harlé et al., 2012], and cognitive control [Grecucci et al., 2013; Kerns et al., 2004] have not been well dissociated and are worth elaborating in future studies.

On the one hand, the motivational conflict encoded in the dACC may be resolved by regulating/suppressing the reflexive response of System 1 [Rilling and Sanfey, 2011; Sanfey and Chang, 2008]. Our meta-analysis identified potential brain regions recruited in favor of the acceptance of unfair offers, including vlPFC [Halko et al., 2009;

Tabibnia et al., 2008], rACC [Yu et al., 2014], left dlPFC [Güroğlu et al., 2011; Harlé and Sanfey, 2012], and dmPFC [Grecucci et al., 2013], all of which are generally involved in emotion regulation or cognitive reappraisal [Buhle et al., in press; Etkin et al., 2006; Ochsner et al., 2012; Silvers et al., 2013]. Specifically, the vlPFC may exert top-down control in regulating AI activity [Tabibnia et al., 2008] by accessing conceptual knowledge represented in the lateral temporal areas as an intermediary to reinterpret the meaning of a situation, which then feeds forward the reinterpreted representation to dorsal AI as a target region of System 1 [Silvers et al., 2013]. The rACC is associated with resolving emotional conflict through top-down inhibition of amygdala activation [Etkin et al., 2006, 2011]. For example, Yu et al. [2014] observed that rACC suppresses amygdala-mediated negative emotional response to norm violations, and this coupling between rACC and amygdala predicts attenuated costly punishment. Furthermore, the modulations of left dlPFC on amygdala and vmPFC have been reported in the literature of reappraisal-relevant emotion regulation [Ochsner et al., 2012], and the left dlPFC may be recruited together with inferior parietal regions to direct attention to reappraisal-relevant events and maintain reappraisal goals [Ochsner et al., 2012; Silvers et al., 2013]. Finally, given the role of dmPFC in overtly thinking about the internal mental states of others (i.e., mentalizing) [Frith and Frith, 2003; Lieberman, 2007], this region probably supports selective attention to and elaboration of intentions of proposers in UG [Frith and Singer, 2008; Rilling et al., 2004].

On the other hand, the motivational conflict between self-interest and fairness norm enforcement could also be resolved by over-riding temptations of self-interest in favor of the rejection of unfair offers. The right dlPFC as identified in the meta-analysis has been previously associated with this cognitive mechanism of System 2 [Knoch and Fehr, 2007]. Previous evidence showed that activation of right dlPFC in UG is positively correlated with altruistic punishment behavior [Guo et al., 2014; Roalf, 2010; Zheng et al., in press]. Importantly, disruption of the right dlPFC due to transcranial magnetic stimulation or cathodal transcranial direct current stimulation diminishes the enforcement of fairness norms in UG, providing evidence for a causal role of the right dlPFC in enforcing social norms [Knoch et al., 2006, 2008; Van't Wout et al., 2005].

Besides the role of cognitive control implemented by the prefrontal and cingulate cortex (System 2), an alternative account proposes that these brain areas may contribute to integrating different sources of information (e.g., expectations) and optimizing response selection in specific social contexts [Buckholtz and Marois, 2012; Sanfey et al., 2014]. The "integration-and-selection" hypothesis is consistent with recent findings showing that functions served by System 2 are context-dependent [Grecucci et al., 2013; Ruff et al., 2013]. For instance, brain stimulation of right dlPFC caused opposite effects on norm compliance under different social contexts: it enhances the compliance of social norms in the context of potential sanctions but attenuates voluntary norm compliance [Ruff et al., 2013].

Taken together, normative decision making in the UG may engage two separable but interacting neural systems. System 1 (AI and vmPFC) may be associated with the reflexive and intuitive responses to norm violations, representing a motivation to punish the violators. Those intuitive responses conflict with economic self-interest, resulting into a conflict signal encoded by the dACC, which may activate cognitive control from a reflective and deliberate System 2 to resolve the conflict by either suppressing (vlPFC, rostral ACC, dmPFC, and left dlPFC) the intuitive responses of System 1 or over-riding self-interest (right dlPFC).

Several limitations should be noted as they relate to this meta-analysis. First, like most neuroimaging meta-analysis methods, the procedures of the ALE meta-analysis consider only the reported coordinates and number of subjects from each study, but not other potential mediator variables (e.g., fMRI-scanning and data-analysis parameters) that are different between studies and may influence final results. Second, the number of papers used in this meta-analysis was relatively small (especially for the [fair > unfair] contrast), but statistical power for interpretation of results will increase for future meta-analyses due to an accumulating number of neuroimaging studies on human normative decision making. In addition, because of the limited number of studies in this domain, it allowed us only to perform a basic contrast between unfair and fair but not moderator analyses (e.g., contextual factors and individual differences), which might have been helpful in differentiating the reflexive and reflective systems. Third, the potential functions of brain regions involved in fairness-related norm enforcement were evaluated in the context of evidence from neuroscientific studies in the past decades, but the specific functions of many brain areas remain to be clarified. For example, the potential functions of dACC in UG have been rarely dissociated in previous studies, although this brain region constitutes the most consistent reported cluster in this meta-analysis. Furthermore, to the best of our knowledge, no study has yet provided evidence for a causal role of AI in costly punishment, although many researchers have considered that psychological components mediated by this region play a pivotal role in norm enforcement. Finally, this study identified Systems 1 and 2 involved in the normative decision making; however, the interactions between these neural systems remain to be elucidated. Future functional and effective connectivity fMRI studies applying the UG are necessary to investigate the temporal and causal relationships among regions, which would provide a more comprehensive picture of human norm enforcement.

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When rapid adaptation paradigm is not too rapid: Evidence of face-sensitive N170 adaptation effects

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ABSTRACT

Recent findings have demonstrated that N170 adaptation effects evoked by face adaptors are general to face and non-face tests, implicating adaptor-locked interferences in the rapid adaptation paradigm. Here we examined the extent to which adaptor-locked interferences confound N170 adaptation effects in different experimental parameters by manipulating the stimulus onset asynchrony (SOA) duration and jitter between adaptors and tests. In the short SOA, those interferences were well visible for the grand-average ERP waveforms evoked by tests, and they are likely to render rapid adaptation paradigm with short SOA unreliable. The adaptor-locked interferences were attenuated by appropriately increasing SOA duration, such that face-sensitive adaptation effects were evident in the long SOA for both baseline-to-peak and peak-to-peak N170 measurements. These findings suggest that the rapid adaptation paradigm may work with a relative long SOA. Our findings provide useful information for future studies regarding the choosing of appropriate experimental parameters and measurements for the rapid adaptation paradigm. In addition, future studies are needed to investigate how to objectively subtract the overlaps of adaptors from tests and to validate the N170 adaptation effect with appropriate behavioral performance.

1. Introduction

Neural activity is reduced in response to repeated presentation of physically or categorically identical stimuli, a well-known phenomenon called adaptation (Grill-Spector, Henson, & Martin, 2006). This adaptation effect is compared with another one induced by successively presenting two stimuli which vary along a certain dimension (e.g., category), and differences between two effects are considered as evidence that neural activation is sensitive to that dimension (Grill-Spector & Malach, 2001). Therefore, the adaptation effect provides a promising index for the “sensitivity” of neural activity.Recent research has employed the adaptation paradigm to examine the category-sensitive processing reflected by the N170 or its MEG counterpart, the M170 (Eimer, Gosling, Nicholas, & Kiss, 2011; Eimer, Kiss, & Nicholas, 2010; Harris & Nakayama, 2008a, 2008b). In the rapid adaptation paradigm, the adaptor (S1) and test (S2) are presented successively with a short and un-jittered stimulus onset asynchrony (SOA) between them. The N170 adaptation effect is measured by comparing N170 amplitude evoked by the same S2 (e.g., face) preceded by different categories of S1 (e.g., face vs. house). Many studies have observed that N170 amplitude is smaller for face tests preceded by face adaptors than those by non-face adaptors (e.g., houses), suggesting a face-sensitive N170 adaptation effect at the adaptor level (Amihai, Deouell, & Bentin, 2011; Kovács, Zimmer, Volberg, Lavric, & Rossion, 2013; Nemrodov & Itier, 2011). The observation of face-sensitive N170 adaptation is important, not only because it demonstrates that face processing recruits a population of neurons not shared by the processing of non-face objects, but also it suggests that N170 adaptation effect could be applied as an index for the sensitivity of early visual perception in general. For this reason, accumulating studies have employed N170 adaptation effect to tag the sensitive processing of visual stimuli, such as inverted faces (Eimer et al., 2010; Nemrodov & Itier, 2011; Sadeh & Yovel, 2010), face identity (Caharel, d’Arripe, Ramon, Jacques, & Rossion, 2009; Jacques, d’Arripe, & Rossion, 2007; Kuehl, Brandt, Hahn, Dettling, & Neuhaus, 2013), visual words (Feng, Luo, & Fu, 2013; Maurer, Rossion, & McCandliss, 2008), and visual expertise with non-face objects (Rossion, Kung, & Tarr,

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2004). For instance, using N170 adaptation effect, Rossion et al. (2004) observed that face-sensitive N170 adaptation effect disappeared when participants obtained visual expertise with non-face objects, indicating that visual expertise with non-face objects might activate the same processes that are also engaged by face stimuli.

Against the back drop of these promising applications of N170 adaptation effect is recent evidence for adaptor-locked interferences in the rapid adaptation paradigm (Nemrodov & Itier, 2012). The authors argued that only one stimulus category (e.g., faces) was used as tests in most studies employing N170 adaptation effect, leaving the possibility that adaptation effect induced by an adaptor category is not specific to the following test category, but rather a general effect to other test categories. For instance, face adaptors, when compared with non-face adaptors, induced larger N170 adaptation effect for face tests, but it remains unknown whether such an adaptation advantage induced by face adaptors is specific to face tests or general to non-face tests. In the study of Nemrodov and Itier (2012), the authors observed the N170 adaptation advantage induced by face adaptors for both face and non-face tests, demonstrating a category-general N170 adaptation effect at test level. These findings led to the notion that the rapid categorical adaptation paradigm may not serve as a suitable tool to tag the sensitivity of neural activity.

The category-general N170 adaptation effect (at the test level) is presumably caused by adaptor-locked interferences such as late neural responses and offset effects evoked by S1 (Nemrodov & Itier, 2012), regarding that the SOA between S1 and S2 is short (400–500 ms) and un-jittered in most studies. Hence, there is an urgent need to systematically manipulate SOA parameters between S1 and S2 in order to reveal the extent to which adaptor-locked interferences confound N170 adaptation effect in different SOA parameters and to examine a suitable SOA parameter for future studies to use. To this end, the current study manipulated both the duration (short vs. long) and the jitter (constant vs. jittered) of the SOA between S1 and S2 in the N170 adaptation paradigm. The adaptor-locked interferences on the early neural response to tests could be easily avoided by increasing the duration of SOA; however, the N170 adaptation effect is attenuated or even eliminated in the long SOA (Harris & Nakayama, 2008b), indicating a balance between the two when choosing a long SOA. We chose 850 ms as a long SOA duration in the current study, given that N170 adaptation effect could be evident at this SOA duration (Amihai et al., 2011; Kuehl et al., 2013). More importantly, a previous study in our laboratory has demonstrated that the N170 adaptation effect induced by face adaptors at this SOA duration was specific to face tests in a blocked design (Feng et al., 2013). With regard to jitter, randomly jittering SOA around an average value is often used in ERP studies (Luck, 2005; Zhao, 2004), which is similar with a low-pass filtering operation and may partially cancel out adaptor-locked interferences on tests (Woldorff, 1993).

In light of previous findings, we expected that the face-sensitive N170 adaptation effect at the test level was most likely to be present in the long and/or jittered SOA. Specifically, we predicted that face adaptors, when compared with non-face adaptors (i.e., houses), would induce N170 adaptation effect for both face and house tests in the short SOA, demonstrating a category-general N170 adaptation effect. In contrast to those effects in the short SOA, we expected that face adaptors only induced N170 adaptation effect for face tests but not for house tests in the long SOA, demonstrating a category-sensitive N170 adaptation effect. With respect to the influence of SOA jitter, we predicted that the adaptor-locked inferences on the test would be smaller in the jittered SOA than in the constant SOA. Furthermore, we assessed the peak-to-peak N170 adaptation effect (i.e., N170–P1 effect) to supplement with baseline-to-peak N170 adaptation effect, given that substantial differences in preceding P1 component were observed between conditions in the rapid N170 adaptation paradigm (Bentin et al., 2007). Finally, the correlation of N170/N170-P1 adaptation effects (face adaptors vs. house adaptors) between face and house tests was also assessed. We expected a significant positive correlation in the short SOA, in which adaptor-locked inferences were substantial, but the correlation was not expected in the long SOA. We believe that the correlation provides another useful index to assess the adaptor-locked inferences on the tests.

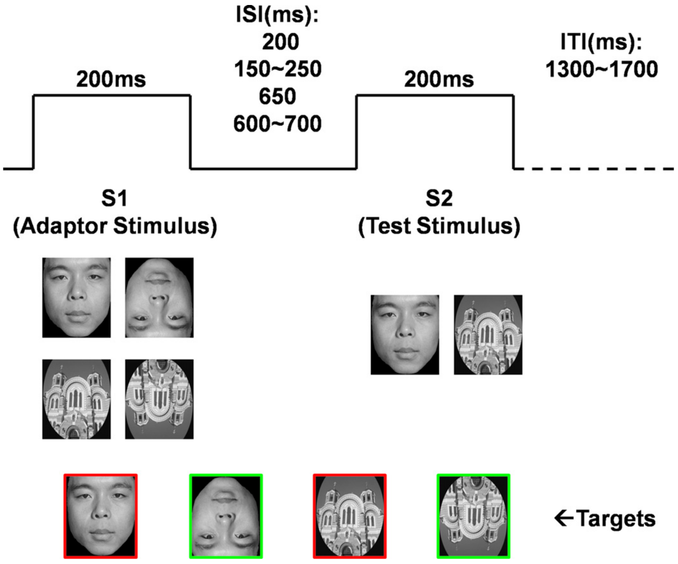

Fig. 1. Trial structure and examples of the stimuli employed in the experiment. On each trial, an adaptor stimulus (S1) was presented (200 ms) and followed after the interval (200, 150–250, 650, and 600–700 ms) by a test stimulus (S2, 200 ms duration). Participants were asked to detect infrequent target events (a red or green frame surrounding either adaptor or test stimuli) by pushing corresponding buttons. Test stimuli consisted of upright faces and houses, and adaptors included upright faces and houses as well as inverted faces and houses.

2. Methods

2.1. Participants

Twenty healthy students participated in the experiment as paid volunteers, and all of them signed informed consent. The experiment was approved by the Institutional Review Board at Beijing Normal University. All participants had normal or corrected-to-normal vision and had no neurological history. Three participants were excluded from data analysis due to the absence of the N170 component in response to faces (see also Eimer et al., 2010). The remaining 17 participants (nine males) were 18–26 years old (mean age 21.9 ± 2.6 years). All, except one, participants were right-handed.

2.2. Stimuli

Stimuli consisted of 44 neutral faces and 44 houses. The face pictures (22 male and 22 female faces) were chosen from the Chinese Facial Affective Picture System (CFAPS, National Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University). The house pictures were chosen from the Internet. The size of stimuli (faces or houses) was $4.53^\circ \times 3.55^\circ$. The luminance and contrast grade between faces and houses were matched to a pre-selected face picture. Inverted stimuli were created by rotating the face and house pictures by 180°. Target pictures were created by adding red or green frame (10 pixels in thickness) to the face and house pictures.

2.3. Procedure

Stimuli were presented to the center of the screen with black background (Fig. 1). On each trial, two images (S1: adaptor stimulus; S2: test stimulus) were presented successively for 200 ms each, separated by four types of SOA. Distinct types of SOA were present in separate blocks, resulting in 16 blocks in the current study: (a) four blocks of short constant SOA (400 ms); (b) four blocks of short jittered SOA (between 350 and 450 ms with an average of 400 ms); (c) four blocks of long constant SOA (850 ms); and (d) four blocks of long jittered SOA (between 800 and 900 ms with an average of 850 ms).

The sequence of 16 blocks was randomized for each participant to cancel out potential fatigue effects, with the constraint that the same SOA type was not present successively. Participants had a rest period of at least 20 s after each block. Within each block, upright faces, inverted faces, upright houses, and inverted houses were presented with equal probability as S1, whereas upright faces and houses were presented equally as S2. Therefore, each block consisted of eight combinations of the four S1 categories and the two S2 categories. Each combination (condition) was repeated 22 times, resulting in 176 trials in each block. On 16 trials (target trials, two trials in each combination), a red or green frame was presented together with S1 or S2, which asked for participants' responses. No response was required on the remaining 160 trials (non-target trials). The intertrial interval (ITI) was 1300–1700 ms with a fixation on the center of the screen. The task for participants was to fixate on the center of the screen and to respond to the targets during the ITI. Participants were instructed to respond to the color of the frame by pressing "J" with right index finger or "F" with left index finger. Response hands to red and green colors were counterbalanced across participants. No responses were required to the stimuli without a colored frame. In this way, trials of interest were uncontaminated by motor response (see also Eimer et al., 2010, 2011).

Participants were seated in a dimly lighted and sound-attenuated room, with their eyes 100 cm away from the screen. They were required to minimize eye blinks and eye movements. All combinations of S1 and S2 categories were presented in random order with three constraints: (1) the S1 and S2 pictures within a trial were always different in identity; (2) S1 on any given trial was as always different in identity from S2 on the preceding trial; and (3) identical combinations were not presented successively more than three times.

2.4. EEG recording

EEG was recorded from 64 scalp sites using Ag/AgCl electrodes mounted on a Quik-cap (Compumedics, Texas, USA), with the left mastoid (LM) being the physical reference. Vertical electro-oculographic (VEOG) activity was recorded from electrodes above and below the left eye, and horizontal EOG (HEOG) was recorded from electrodes placed at the outer canthi of both eyes. Impedance was maintained below 10 kΩ throughout the EEG recording session. The EEG and EOG were amplified using a 0.05–100 Hz bandpass and continuously sampled at 500 Hz.

2.5. Data analysis

Electrophysiological data were analyzed by using Neuroscan 4.3.1 software (Compumedics, Texas, USA). The EEG analyzing window was between −100 ms and 400 ms, with the 100 ms pre-stimulus EEG serving as baseline. EEG data were low-pass filtered below 30 Hz. EEGs were first re-referenced to the algebraic average of left mastoid (LM) and right mastoid (RM) and then were re-referenced to the average of all the electrodes. Artifact rejection was performed for all the EEG channels, and the rejection criterion was ±80 μV.

P1 and N170 amplitude of non-target trials was measured and analyzed. For both P1 and N170 components, the baseline-to-peak measurement was used in order to compare the current results with those of previous studies (e.g., Eimer et al., 2010; Nemrodov & Itier, 2012). Importantly, the baseline-to-peak measurement of N170 amplitude was supplemented with a peak-to-peak measurement (N170–P1 amplitude), in which baseline-to-peak P1 amplitude was subtracted from baseline-to-peak N170 amplitude (Goffaux, Gauthier, & Rossion, 2003; Itier & Taylor, 2002; Rossion, Joyce, Cottrell, & Tarr, 2003). Given that substantial differences in preceding P1 amplitude were observed between conditions (see Section 3), and the N170-P1 amplitude would help to avoid baseline differences between conditions (see also Bentin et al., 2007). The most positive amplitude between 90 and 200 ms was chosen as P1 peak, and the most negative amplitude between 130 and 240 ms was chosen as N170 peak. Two electrode pairs, one at the lower occipitotemporal areas (PO7/PO8) and the other at the temporal areas (P7/P8), were chosen for statistical analysis. These two sets of electrodes have been frequently used for N170 measurement, and the topographical distribution of N170 is maximal at these electrodes (Eimer et al., 2010; Latinus & Taylor, 2005; Rossion & Jacques, 2008). Data over all electrodes were collapsed during statistical analysis. This step was employed to reduce factors within the design, so that potential spurious results could be avoided and more robust measures of the actual underlying signal would be obtained. In addition, data for upright and inverted adaptors were also collapsed, because the current study focused on the category-sensitive N170 adaptation effects. It is worth noting that upright and inverted adaptors induced similar category-related N170 adaptation effects if data from those conditions were analyzed separately.

Repeated-measures analysis of variance (ANOVA) was used for statistical analysis. *P*-values were adjusted according to the Greenhouse–Geisser correction if necessary. Bonferroni correction was used for post hoc comparisons. Further, effect sizes and confidence interval (CI) were also calculated to better ascertain the weight of the results. For ERP amplitude evoked by tests, the factors in the contrast were SOA duration (short vs. long), jitter (constant vs. jittered), test category (faces vs. houses), and adaptor category (faces vs. houses). The face-sensitive N170 adaptation was assessed by comparing N170 amplitudes evoked by face tests preceded by face and house adaptors. Face-sensitive N170 adaptation effect was detected if (a) N170 amplitude was smaller for face tests preceded by face adaptors than by house adaptors, and (b) this N170 adaptation effect induced by face adaptors was not evident for house tests in the same condition, otherwise, category-general N170 adaptation effect was observed. Furthermore, N170 adaptation effects for face and house tests were also directly compared in order to examine whether face adaptors induced larger N170 adaptation effects for face tests than for house tests. Notably, the current study examined in which SOA parameters the face-sensitive N170 adaptation effect was evident.

Finally, correlations of adaptation effects between face and house tests were measured for short and long SOAs, collapsing over electrodes, hemispheres, adaptor-orientation and jitter conditions. A non-parametric method (Spearman's ρ) was used for correlation, regarding that Spearman's ρ tended to be more robust to outliers than Pearson's r (see also Rahnev, Lau, & de Lange, 2011; Rousselet & Pernet, 2012). However, it is worth noting that all significant correlations using Spearman's ρ were also significant when Pearson's r was employed.

3. Results

3.1. The influence of SOA duration and jitter on P1 adaptation effects

3.1.1. SOA duration

A SOA duration × test category × adaptor category interaction [$F(1, 16) = 9.12$, $p = 0.008$, $\eta_p^2 = 0.36$] revealed that P1 amplitude was larger for both face and house tests preceded by face adaptors than by house adaptors (Figs. 2 and 3 and Table 1), and such a category-general P1 adaptation effect was smaller for face tests than for house tests in the short SOA (95% CI for difference = −1.47 to −0.55 μV, $t(16) = -4.69$, $p = 0.0002$, Cohen's $d = 1.01$, Fig. 4a). In the long SOA, this category-general P1 adaptation effect was also evident for face and house tests, but was comparable between test categories (95% CI for difference = −0.47 to 0.14 μV, $t(16) = -1.16$, $p = 0.26$, Cohen's $d = 0.21$, Fig. 4a).

3.1.2. Jitter

A jitter × test category × adaptor category interaction [$F(1, 16) = 5.34$, $p = 0.04$, $\eta_p^2 = 0.25$] revealed that P1 amplitude was larger for both face and house tests preceded by faces than by houses in both constant and jittered SOA (Table 1). However, the magnitude of this category-general P1 adaptation effect differed between face and house tests, and such a difference was larger in the constant SOA than in the jittered SOA (P1 adaptation effect for house tests minus P1 adaptation effect for face tests: 95% CI for difference = −0.80 to −0.03 μV, $t(16) = 2.30$, $p = 0.04$, Cohen's $d = 0.68$).

3.1.3. SOA duration × jitter

No SOA duration × jitter interaction on P1 adaptation effect was observed.

To sum up, category-general P1 adaptation effect was evident for each SOA parameter, whereas duration and jitter only modulated relative magnitudes of the effect between face and house tests.

3.1.4. Correlations

P1 adaptation effects (face and house adaptors; Fig. 5a) of face and house tests were positively correlated in both short SOA (Spearman's $\rho = 0.64$, $p = 0.006$) and long SOA (Spearman's $\rho = 0.79$, $p = 0.0002$).

3.2. The influence of SOA duration and jitter on N170 adaptation effects

3.2.1. SOA duration

Baseline-to-peak N170 measurement (N170 amplitude): a significant SOA duration × test category × adaptor category interaction [$F(1, 16) = 10.20$, $p = 0.006$, $\eta_p^2 = 0.39$] was observed for the baseline-to-peak measurement of N170 amplitude (Figs. 2 and 3 and Table 1). In the short SOA, N170 amplitude was smaller for both face (95% CI for difference = 1.54–3.13 μV, $p = 0.0001$, Cohen's $d = 0.88$) and house (95% CI for difference = 1.59–3.29 μV,

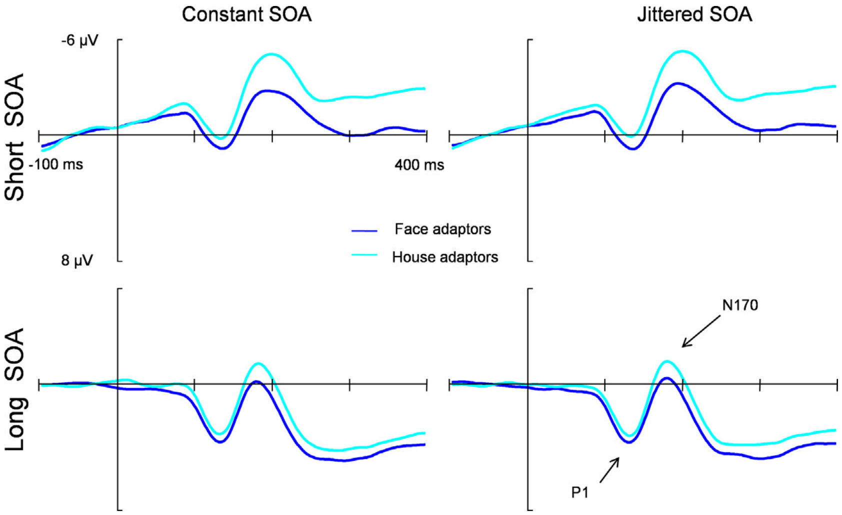

Fig. 2. Grand-averaged ERPs elicited by face tests (S2) in the function of adaptor category (face vs. house), SOA duration (short vs. long), and SOA jitter (constant vs. jittered). Data from all electrodes (the occipitotemporal: PO7/PO8 and temporal: P7/P8 sites) and adaptor orientations (upright and inverted) were collapsed.

$p = 0.0002$, Cohen's $d = 1.28$) tests preceded by face adaptors than by house adaptors, indicating a category-general N170 adaptation effect. Further, those effects were comparable between face and house tests in the short SOA (95% CI for difference = −0.50 to 0.30 μV, $t(16) = -0.55$, $p = 0.59$, Cohen's $d = 0.07$, Fig. 4b). In the long SOA, however, a face-sensitive N170 adaptation effect was observed, such that N170 amplitude was smaller for face tests (95% CI for difference = 0.58–1.65 μV, $p = 0.0004$, Cohen's $d = 0.34$) and marginally smaller for house tests (95% CI for difference = −0.02 to 0.88 μV, $p = 0.06$, Cohen's $d = 0.16$) preceded by face adaptors than by house adaptors. Importantly, the N170 adaptation effect in the long SOA was significantly larger for face tests than for house tests (95% CI for difference = 0.29–1.07 μV, $t(16) = 3.70$, $p = 0.002$, Cohen's $d = 0.71$, Fig. 4b). These results indicated that a category-general effect was observed in the short SOA, whereas a face-sensitive adaptation was evident in the long SOA.

Peak-to-peak N170 measurement (*N170–P1 amplitude*): no main effect of SOA duration on N170–P1 adaptation was observed.

3.2.2. Jitter

No main effect of jitter on baseline-to-peak N170 and N170–P1 adaptation was observed.

3.2.3. SOA duration × jitter

Baseline-to-peak N170 measurement (*N170 amplitude*): no SOA duration × jitter interaction on N170 adaptation effect was observed.

Peak-to-peak N170 measurement (*N170–P1 amplitude*): a significant SOA duration × jitter × test category × adaptor category interaction [$F(1, 16) = 6.40$, $p = 0.02$, $\eta_p^2 = 0.29$] on N170–P1 amplitude was observed (Figs. 2 and 3 and Table 1). In the short (both constant and jittered) SOA, N170–P1 amplitude was smaller for both face (95% CI for difference = 1.24–2.68 μV, $p = 0.00003$, Cohen's $d = 0.49$) and house (95% CI for difference = 0.21–1.25 μV, $p = 0.009$, Cohen's $d = 0.36$) tests preceded by face adaptors than by house adaptors, indicating a category-general adaptation effect. Notably, the N170–P1 adaptation effect in the short SOA was significantly larger for face tests than for house tests (95% CI for difference = 0.38–1.49 μV, $t(16) = 3.58$, $p = 0.002$, Cohen's $d = 0.85$, Fig. 4c). In the long SOA, jitter modulated N170–P1 adaptation effect: in the long jittered SOA, N170 amplitude was only smaller for face tests (95% CI for difference = 0.14–0.94 μV, $p = 0.01$, Cohen's $d = 0.13$) but not for house tests (95% CI for difference = −0.40 to 0.51 μV, $p = 0.80$, Cohen's $d = 0.02$) preceded by face adaptors than by house adaptors, a category-sensitive

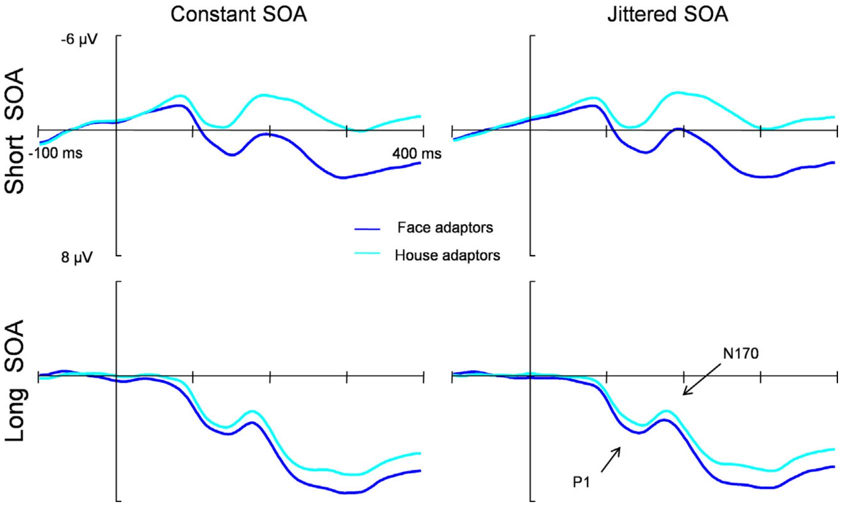

Fig. 3. Grand-averaged ERPs elicited by house tests (S2) in the function of adaptor category (face vs. house), SOA duration (short vs. long), and SOA jitter (constant vs. jittered). Data from all electrodes (the occipitotemporal: PO7/PO8 and temporal: P7/P8 sites) and adaptor orientations (upright and inverted) were collapsed.

Table 1
Average (standard error) amplitude (μV) of P1, N170, and N170–P1 for face and house tests in different experimental conditions.

Tests	Adaptors	Short SOA		Long SOA	
		Constant	Jittered	Constant	Jittered
P1					
Faces	Faces	1.53 (0.46)	1.66 (0.42)	4.99 (0.59)	4.75 (0.58)
	Houses	1.06 (0.41)	0.89 (0.38)	4.36 (0.52)	4.20 (0.51)
	Adaptation	0.47 (0.19)*	0.77 (0.17)***	0.63 (0.24)*	0.55 (0.21)*
Houses	Faces	2.37 (0.66)	2.34 (0.66)	5.08 (0.67)	4.95 (0.62)
	Houses	0.68 (0.48)	0.77 (0.47)	4.08 (0.59)	4.43 (0.60)
	Adaptation	1.69 (0.32)***	1.57 (0.30)***	1.00 (0.19)***	0.51 (0.24)*
N170					
Faces	Faces	−3.62 (0.46)	−3.99 (0.54)	−1.01 (0.78)	−1.15 (0.78)
	Houses	−6.04 (0.74)	−6.24 (0.79)	−2.15 (0.87)	−2.24 (0.78)
	Adaptation	2.42 (0.40)***	2.25 (0.37)***	1.14 (0.29)**	1.09 (0.25)***
Houses	Faces	−0.35 (0.56)	−0.57 (0.57)	2.49 (0.82)	2.16 (0.67)
	Houses	−2.82 (0.35)	−2.98 (0.35)	2.15 (0.57)	1.63 (0.63)
	Adaptation	2.47 (0.41)***	2.41 (0.41)***	0.34 (0.29)	0.53 (0.19)
N170–P1					
Faces	Faces	−5.14 (0.70)	−5.65 (0.80)	−6.00 (0.90)	−5.90 (1.00)
	Houses	−7.10 (0.93)	−7.13 (0.95)	−6.52 (1.02)	−6.44 (1.01)
	Adaptation	1.96 (0.34)***	1.48 (0.29)***	0.51 (0.25)	0.54 (0.19)*
Houses	Faces	−2.78 (0.52)	−2.92 (0.60)	−2.59 (0.54)	−2.80 (0.57)
	Houses	−3.50 (0.48)	−3.76 (0.51)	−2.83 (0.57)	−2.86 (0.55)
	Adaptation	0.72 (0.25)*	0.84 (0.27)*	0.24 (0.19)	0.06 (0.21)

* $p < 0.05$.
** $p < 0.005$.
*** $p < 0.0005$.

N170–P1 adaptation effect. Further, the N170–P1 adaptation effect in the long jittered SOA was marginally larger for face tests than for house tests (95% CI for difference = −0.06 to 1.03 μV, $t(16) = 1.89$, $p = 0.078$, Cohen's $d = 0.59$, Fig. 4c). In contrast to those results in the long jittered SOA, the N170–P1 adaptation effect was marginally significant for face (95% CI for difference = −0.03 to 1.04 μV, $p = 0.06$, Cohen's $d = 0.13$) but not significant for house tests (95% CI for difference = −0.16 to 0.66 μV, $p = 0.22$, Cohen's $d = 0.11$) in the long constant SOA. In addition, the N170–P1 adaptation effect in the long constant SOA was comparable for face tests than for house tests (95% CI for difference = −0.26 to 0.78 μV, $t(16) = 1.07$, $p = 0.30$, Cohen's $d = 0.28$, Fig. 4c).

3.2.4. Correlations

Baseline-to-peak N170 measurement (N170 amplitude): N170 adaptation effects (face adaptors–house adaptors; Fig. 5b) of face and house tests were positively correlated in both short SOA

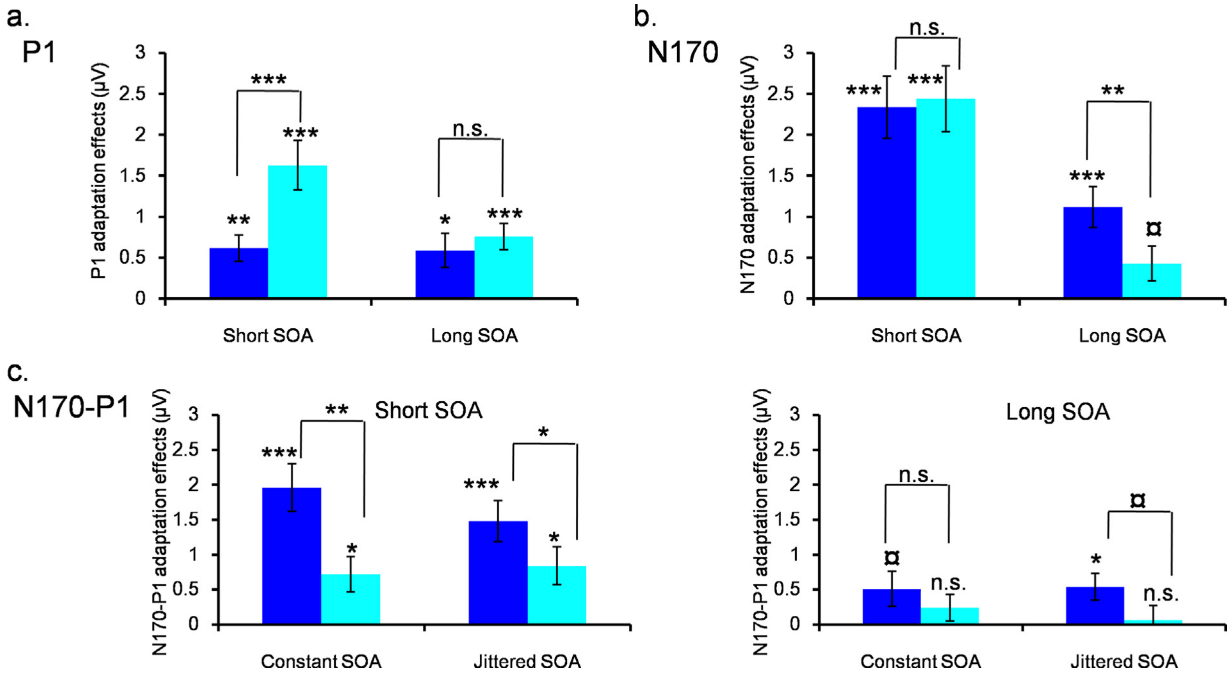

Fig. 4. Adaptation effects of face and house tests on the (a) P1, (b) baseline-to-peak N170, and (c) peak-to-peak N170 (N170–P1). Adaptation effects were defined as the differences in ERP amplitudes evoked by tests preceded by face and house adaptors. Data from all electrodes (the occipitotemporal: PO7/PO8 and temporal: P7/P8 sites) and adaptor orientations (upright and inverted) were collapsed. Error bars show 1 SE. ***$p < 0.0005$; **$p < 0.005$; *$p < 0.05$; ¤ $p < 0.08$; n.s., not significant.

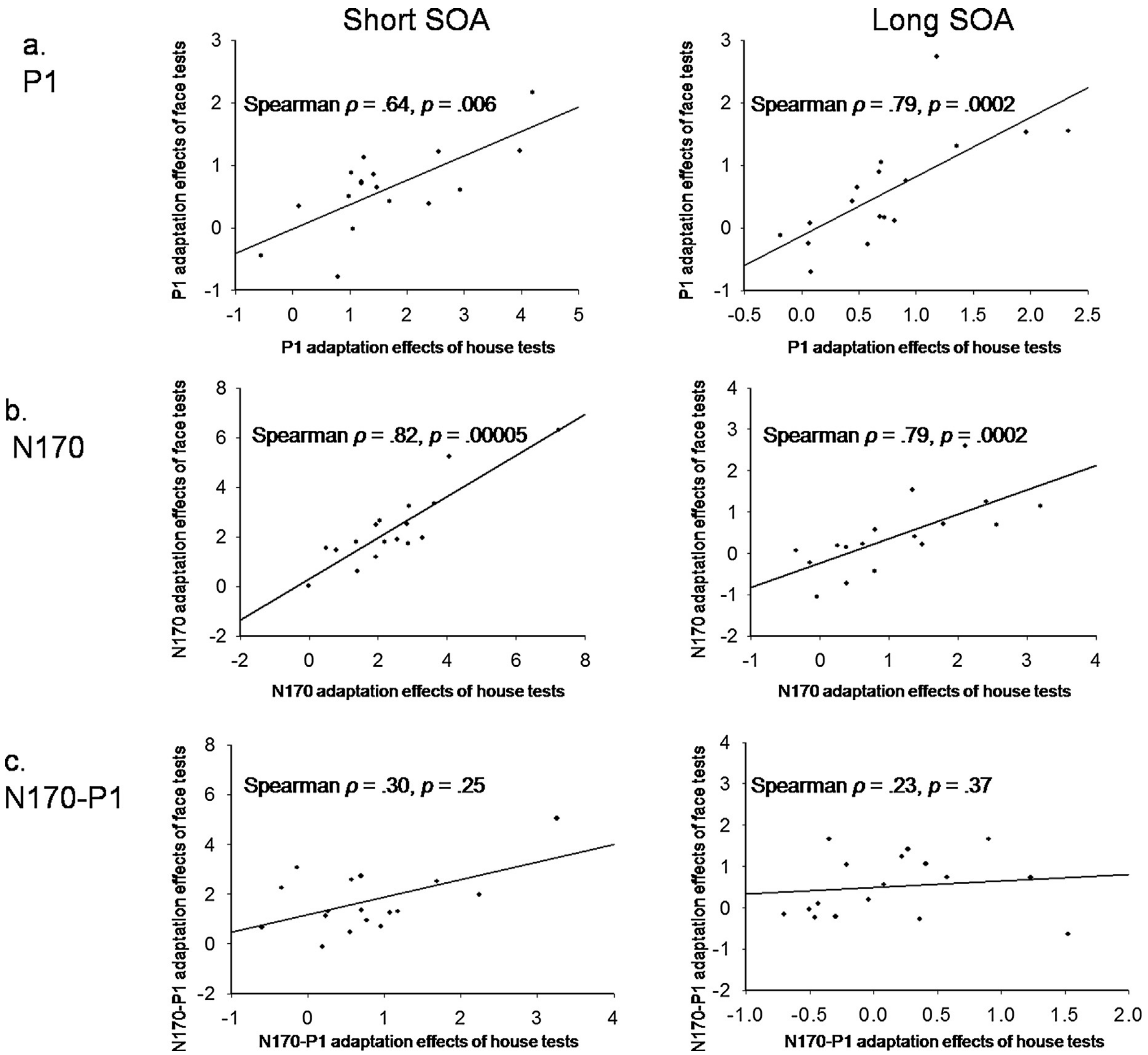

Fig. 5. Correlations of adaptation effects between face and house tests on the (a) P1, (b) baseline-to-peak N170, and (c) peak-to-peak N170 (N170–P1). Adaptation effects were defined as the differences in ERP amplitudes evoked by tests preceded by face and house adaptors. Data from all electrodes (the occipitotemporal: PO7/PO8 and temporal: P7/P8 sites), jitter (constant and jittered), and adaptor orientations (upright and inverted) were collapsed.

(Spearman $\rho = 0.82$, $p = 0.00005$) and long SOA (Spearman $\rho = 0.79$, $p = 0.0002$).

Peak-to-peak N170 measurement (*N170–P1 amplitude*): N170–P1 adaptation effects (face adaptors–house adaptors; Fig. 5c) of face and house tests did not correlate with each other in either short SOA (Spearman's $\rho = 0.30$, $p = 0.25$) or long SOA (Spearman's $\rho = 0.23$, $p = 0.37$).

In summary, SOA duration modulated both N170 and N170–P1 adaptation effects, such that category-general effects were evident in the short SOA, whereas category-sensitive effects were observed in the long SOA. For the N170–P1 adaptation effects, however, several category-sensitive characteristics were observed in the short SOA: (a) N170–P1 adaptation effect was larger for face tests than for house tests and (b) correlation of the N170–P1 adaptation effect between face and house tests was not evident, whereas the correlation was highly significant for N170 adaptation effect. The influence of jitter was only evident for N170–P1 adaptation effect in the long SOA, demonstrating that the category-sensitive N170–P1 adaptation effect was evident in the long jittered SOA but not in the long constant SOA.

4. Discussion

Our study explored the face-sensitive N170 adaptation effect by manipulating SOA duration and jitter in the rapid categorical adaptation paradigm. We demonstrated that category-general N170 adaptation effect was evident in the short SOA due to the adaptor-locked interferences. Those interferences were attenuated by employing a relative long SOA duration and using N170–P1 amplitude rather than the N170 amplitude. Given that rapid adaptation paradigm has been often employed to study the sensitivity of early visual processing (Jacques et al., 2007; Maurer et al., 2008) and properties of N170 itself (Schinkel, Ivanova, Kurths, & Sommer, 2014), the current results are important in indicating when this popular paradigm works for the category-sensitive adaptation.

We first replicated recent findings that face adaptors induced N170 adaptation effects for both face and house tests in the short SOA (Nemrodov & Itier, 2012). Those category-general effects are presumably attributed to the contamination of ERPs evoked by temporally adjacent adaptors and tests (Luck, 2005; Woldorff, 1993), implicating adaptor-locked interferences on early ERPs of tests (e.g., P1 and N170). Indeed, those interferences are well visible in the short SOA for the grand-average ERP waveforms evoked by tests, in which baselines are not aligned horizontally, suggesting systematic interferences from adaptors. Those potential confounding effects are likely to render rapid adaptation paradigm with short SOA unreliable and emphasize the need to examine the appropriate experimental and measuring parameters for N170 adaptation paradigm.

The adaptor-locked interferences at the test level were attenuated as expected in a long SOA, such that face adaptors induced face-sensitive N170 adaptation effect. Although these findings suggest that N170 adaptation paradigm might work with a relative long SOA, future studies still need to employ N170 adaptation effects with caution, given that a marginally significant category-general N170 adaptation effect and highly correlated N170 adaptation effects between face and house tests remained in the long SOA. In contrast to the function of SOA duration in reducing adaptor-locked interferences, the influences of SOA jitter were not evident for N170 adaptation effects. A possible reason for the absence of jitter influences is that the dominant interferences of adaptor ERPs on test ERPs are low-frequency (slow) waves, which can hardly be canceled out by limited SOA jitter range (100 ms) between adaptors and tests (Woldorff, 1993).

We next studied whether peak-to-peak N170 measurement (N170–P1) helped to attenuate the adaptor-locked interferences in the rapid N170 adaptation paradigm. N170–P1 measurement has been proposed as a solution to control for the baseline differences caused by differential preceding P1 amplitude between conditions (Bentin et al., 2007), and this method is recommended to report when differences in P1 amplitude are evident (Bentin et al., 2007; Rossion & Jacques, 2008). In general, results of N170–P1 measurement were congruent with (baseline-to-peak) N170 measurement, such that category-general N170–P1 adaptation was evident in the short SOA, whereas face-sensitive N170–P1 adaptation was observed in the long SOA. However, the N170–P1 measurement further reduced adaptor-locked interferences in the short SOA in sense of larger N170–P1 adaptation effects for face tests than house tests and the absence of correlation of N170–P1 adaptation effects between face and house tests.

Several limitations should be noted as they relate to the current study. First, similar to most studies focussed on N170 adaptation effects, the current study was not designed to capture adaptation-related behavioral performance, which is crucial in validating the theoretical interpretation of ERP findings (Picton et al., 2000). One of the behavioral measurements worth considering is adaptation-related aftereffect (e.g., Kovács et al., 2006; Walther, Schweinberger, Kaiser, & Kovács, 2013), although it remains to be elucidated whether the neural mechanisms underlying those behavioral aftereffects share a single adaptation process with N170 adaptation effects focused in current and most previous studies (see also Harris & Nakayama, 2008b). Recent studies also provide another promising way to validate the face-sensitive N170 adaptation effects by examining whether face-related processes (e.g., holistic processing vs. feature processing) modulate those adaptation effects (Eimer et al., 2011; Schinkel et al., 2014). Secondly, besides choosing appropriate experimental parameters, future studies are needed to investigate how to objectively subtract the overlaps of adaptors from tests (Luck, 2005; Woldorff, 1993), an intriguing and important topic beyond the scope of the current study.

In conclusion, the current study examined the extent to which adaptor-locked interferences confound N170 adaptation effects in different SOA parameters and whether peak-to-peak N170 measurement helps in attenuating those interferences. Our findings revealed category-general N170 and N170–P1 adaptation effects in a short SOA (450 ms) and face-sensitive N170 and N170–P1 adaptation effects in a relative long SOA (850 ms). These findings highlight the effect of (appropriately) increasing SOA duration on attenuating adaptor-locked interferences in the rapid categorical N170 adaptation paradigm. Furthermore, the N170–P1 measurement helped to further attenuate those interferences, reflected by the absence of correlation of N170–P1 adaptation effects between face and house tests. Our findings provide significant information for future studies, regarding the option of appropriate experimental parameters and measurements for the rapid adaptation paradigm and different ways of detecting adaptor-locked interferences.

Acknowledgments

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