Electrophysiological correlates of processing facial attractiveness and its influence on cooperative behavior

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A R T I C L E   I N F O

Article history:
Received 23 November 2011
Received in revised form 14 February 2012
Accepted 24 February 2012

Keywords:
Facial attractiveness
Cooperative behavior
ERPs

A B S T R A C T

The present study investigated the temporal features of processing facial attractiveness, and its influence on the subsequent cooperative behavior. Event-related potentials (ERPs) were recorded for both face stimuli (attractive or unattractive faces) and feedback stimuli (loss or gain) while participants performed a modified trust game task, in which participants decided whether to cooperate with fictional partners (attractive or unattractive faces) for a chance to earn monetary rewards; feedback (loss or gain) were presented after their decisions. The behavioral results showed that participants were more likely to cooperate with the attractive partners than with the unattractive partners. The ERP analysis for face stimuli showed that a smaller P2 amplitude was elicited by attractive faces compared to unattractive faces. In addition, attractive faces elicited larger N2 and smaller late positive component (LPC) amplitudes than unattractive faces. More interestingly, a larger feedback related negativity (FRN) was elicited within the attractive face condition compared with the unattractive face condition. Therefore, our findings demonstrate that the discrimination of attractive and unattractive faces occurs at the early P2 stage, reflecting automatic processing of facial attractiveness. Moreover, the present study further demonstrates that facial attractiveness facilitates cooperative behavior, and that FRN elicited by outcome stimuli might be used as an index of how people judge and predict another’s behavior in a social game.

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1. Introduction

Physical attractiveness is an important characteristic in human social interactions. For example, it has been argued that facial attractiveness indicates good genetic quality and reproductive capacity [26]. Moreover, it has been widely reported that physical attractiveness may influence human social behavior [16,30]. Mulford et al. found that people were more likely to cooperate with attractive partners in the Prisoner’s Dilemma games [16]. Attractive partners were also considered to be more trustworthy than unattractive partners [30]. Interestingly, several studies revealed that attractive people were more likely to be hired and promoted [15], and earn more money than unattractive people [2].

As described above, behavioral studies have shown that physical attractiveness plays an important role in human social interactions. Recently, some neuroimaging studies have found that the reward-related brain area, the orbitofrontal cortex (OFC), is involved in attractiveness perception, with enhanced OFC activation for attractive faces compared to unattractive faces [1,31]. Additionally, Johnston and collaborators found that a larger late positive component (LPC) was elicited by attractive faces compared to unattractive faces when subjects were performing an attractiveness rating task [11,17]. Werheid et al. used an attractiveness category task and found that the facial attractiveness effect occurred not only in the early processing stage, as indexed by a posterior negative component, but also occurred in the late LPC processing stage [29]. Furthermore, Schacht et al. [21] found that larger P2 and LPC amplitudes were elicited for attractive and unattractive faces than for faces of intermediate attractiveness when using an attractiveness rating task, and no event-related potential (ERP) differences were observed between attractive and unattractive faces. More interestingly, the attractiveness effects were absent when using an attractiveness-irrelevant gender classification task in the Schacht et al. study, suggesting that the attractiveness effects could be modulated by task requirements, and that the appraisal of facial beauty is rapid but not automatic [21]. However, some behavioral and neuroimaging studies indicate that facial attractiveness can be detected in a single brief glance or in a task unrelated to the explicit task of judging facial attractiveness, suggesting the automatic processing of facial attractiveness [1,14,18,25,31].

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0304-3940/$ – see front matter © 2012 Elsevier Ireland Ltd. All rights reserved.
doi:10.1016/j.neulet.2012.02.082
Given the variation in the reported findings relating to how facial attractiveness is processed, it would be interesting to test whether facial attractiveness can be detected automatically in a social context. Therefore, the first aim of the present study is to explore the temporal features of processing attractive and unattractive faces by using the high temporal resolution of ERPs while participants perform a modified trust game task, in which participants are instructed to play with fictional partners, and decide whether they want to cooperate with the partners for a chance to earn a monetary reward. Based on the automatic and effortless processing of attractiveness reported by previous behavioral studies [1,14,18,25,31], we predict that the dissociative neural processing of attractive and unattractive faces will occur in the early bottom-up processing stage, even when participants perform a trust game unrelated to the explicit task of judging facial attractiveness.

The second aim of the present study is to further explore the influence of attractiveness on cooperative behavior in the trust game task, a task typically used to explore cooperative behavior [6,12]. Given the reports which suggest that attractive people are more likely to be hired and promoted, and be judged more trustworthy compared to unattractive people [16,30], it is predicted that participants will be more likely to cooperate with the attractive partners. In other words, the level of reward expectations will be stronger in the attractive relative to the unattractive partner condition.

The FRN component is a negative-going deflection that peaks approximately 250–300 ms after the onset of external feedback. The magnitude of the FRN difference wave (negative minus positive feedback) is modulated by reward expectation, with a larger FRN difference wave in the strong than in the weak expectation condition [7,8]. Therefore, consistent with previous studies, we further predict that the FRN difference wave will be larger in the attractive partner condition than in the unattractive partner condition.

2. Materials and methods

2.1. Subjects

Fourteen undergraduate students (7 females), aged 19–23 years (\(M = 21.9\)), were paid to participate in the experiment. All subjects were healthy, right-handed, with normal or corrected-to-normal vision, and reported no history of affective disorders. Furthermore, all subjects gave written informed consent.

2.2. Stimulus materials

All face images were obtained from the Internet, and were unfamiliar to the participants, with no movie stars, musicians, or other celebrities. All faces were characterized by neutral expression, frontal view and forward eye-gaze, and edited to equal luminance and uniform size (11 by 8.5 cm; 450 by 350 pixels).

Prior to the ERP experiment, 420 Chinese faces were rated by 32 college students (16 females, aged 18–23 years, \(M = 20.8\)). These faces were rated for attractiveness (from 1 = ‘not attractive at all’ to 7 = ‘extremely attractive’) and emotional expression (from 1 = ‘extremely angry’ to 7 = ‘extremely happy’). On a 7-point scale [21,29]. Finally, a total of 120 faces were selected for the ERP experiment: 60 attractive faces (30 female faces) and 60 unattractive faces (30 female faces). The ratings of the two categories of faces were compared by paired \(t\)-test, whereas the attractiveness was significantly different \(M_{\text{attractive}} = 4.68 (SD = 0.65), M_{\text{unattractive}} = 2.55 (SD = 0.83); t(31) = 12.78, p < 0.01\), but the emotional expression was similar \(M_{\text{attractive}} = 4.08 (SD = 0.51), M_{\text{unattractive}} = 3.94 (SD = 0.54); t(31) = 0.72, p = 0.35\). There were no significant differences between male and female faces in the attractive \(M_{\text{male}} = 4.57 (SD = 0.83), M_{\text{female}} = 4.8 (SD = 0.88); t(31) = -1.18, p = 0.25\) and unattractive \(M_{\text{male}} = 2.43 (SD = 0.97), M_{\text{female}} = 2.67 (SD = 0.93); t(31) = -1.62, p = 0.12\) face categories.

2.3. Task and procedures

Prior to the experiment, participants were informed they would take part in a game in which they should make a decision of whether or not to cooperate with fictional partners, represented by attractive or unattractive face pictures (Fig. 1). Participants were given 2000 cents (about US$3.15) at the start of the game, and they could either keep 50 cents on a given trial or invest it, in which case the partner would receive 200 cents. Then the partner could either keep the entire 200 cents or give half of it back to participants. The amount of money accumulated could be increased by such investment behavior. Participants were offered remuneration equal to the amount accumulated at the end of the game.
Participants were seated in a quiet room approximately 150 cm from a computer screen with the horizontal and vertical visual angles below 5°. In order to familiarize participants with the task, the experiment started with 12 practice trials. Each trial was initiated by a small black cross presented for 1000 ms duration on a gray screen (Fig. 1); then, a partner’s face (attractive or unattractive face) appeared in the center of the screen for 1000 ms. Subsequently, two boxes showing “invest 50” and “keep 50” were presented below the partner’s face, and participants were required to choose one of the two boxes by pressing the “F” or “J” key on the keyboard. Half of the participants were instructed to press the “F” key if they wanted to invest 50 cents, or to press the “J” key if they wanted to keep the money. For the remaining participants, the response pattern was reversed. Once their decision had been made, the chosen box would be highlighted to emphasize the choice made. If the participants invested 50 cents, after a 600–1000 ms gray screen, a feedback stimulus of either “1” (the partner returned 100 cents to the participant), or “0” (the partner kept the entire 200 cents), was presented in the center of the screen for 1000 ms. If the participant kept 50 cents, they would retain the current amount of money. Each feedback stimulus was followed by 1500 ms of gray screen, and then another trial started. The gain/loss outcomes were determined in pseudorandom sequence, with half of the trials gaining and the other half of the trials losing. However, participants were not told about these manipulations. Each face was repeated four times, and each of the faces was equally often associated with wins as with losses. The task consisted of eight blocks, with 60 trials each. E-prime 1.0 was used for stimulus presentation, sending markers, and response recording.

In order to test whether face attractiveness modulates participants’ reward expectations, 40 additional participants (20 females, aged 18–23 years, M = 21.4) were selected to judge the extent to which the partners would return monetary rewards using 7-point scales (from 1 = ‘not likely at all’ to 7 = ‘very likely’). The procedure and stimuli were the same as those used in the main ERP experiment except that participants were instructed to rate the degree of reward expectation and were not asked to decide whether to cooperate with the partners.

2.4. Behavioral data analysis

The number of invest and keep choices for both attractive and unattractive face conditions were calculated. The bias of cooperation was obtained by comparing the number of invest choices for the attractive and unattractive face conditions. The paired t-test was conducted for this difference comparison.

2.5. ERP recording and analysis

Electroencephalography (EEG) was recorded from 64 scalp sites using tin electrodes mounted in an elastic cap (Brain Products), with references on the left and right mastoids and a ground electrode on the medial frontal aspect. The vertical electrooculogram (EOG) was recorded with electrodes placed above and below the left eye. Horizontal EOG was recorded as the left vs. right orbital rim. All electrode impedance was maintained below 5 kΩ. EEG and EOG activity was amplified with a DC ~ 100 Hz bandpass and continuously sampled at 500 Hz/channel. ERP averages were computed offline. The EEG data was time-locked to the onset of face stimuli and feedback stimuli, and epoched from −200 ms to 1000 ms. ERP trials with EOG artifacts, amplifier clipping artifacts, or peak-to-peak deflections exceeding ±80 V were excluded from averaging. Artifact-free ERP trials were averaged separately for each stimulus condition within “investment” trials. After artifact rejection there were: 75.14 trials in the attractive-win condition, 74.29 trials in the attractive-loss condition, 51.15 trials in the unattractive-win condition, and 49.43 trials in the unattractive-loss condition.

In order to examine the causality and laterality effects associated with facial attractiveness processing, the following 15 electrode sites were selected for statistical analysis: F3, FC3, C3, CP3, P3 (5 left sites); Fz, FCz, Cz, CPz, Pz (5 midline sites); F4, FC4, C4, CP4, P4 (5 right sites). The peak amplitudes and latencies of P2 (130–170 ms) and N2 (180–230 ms) components were measured, as well as the average amplitude of the LPC component (450–650 ms). A three-way repeated measures analysis of variance (ANOVA) was conducted for each component. ANOVA factors were: face type (attractive and unattractive faces), causality (front, fronto-central, central, central-parietal and parietal sites), and laterality (left, midline and right sites).

To assess the ERP waves elicited by feedback stimuli, we measured the average amplitude of FRN (240–290 ms) from the following six sites: FPz, Fz, FCz, Cz, CPz, and Pz. These electrodes were chosen based on previous research which found FRN to be maximized at the fronto-central midline [7,8], while the time window was chosen based on the difference waves. Following the methods of Holroyd and Krigolson [8], we calculated the FRN by subtracting the gain-ERP from the loss-ERP. Specifically, we subtracted the gain ERP from the loss ERP in the attractive partner condition to obtain the attractiveness-related difference wave, and subtracted the gain ERP from the loss ERP in the unattractive partner condition to obtain the unattractiveness-related difference wave. We then compared the amplitudes of the FRN difference waves for the attractive partner and unattractive partner conditions. A two-way ANOVA was conducted on the FRN component. ANOVA factors were face type (attractive and unattractive faces) and electrode site (FPz, Fz, FCz, Cz, CPz, and Pz). The ERP data were analyzed using Brain Products Analyzer software, and the statistical analysis was conducted with SPSS 16.0. The degrees of freedom of the F-ratio were corrected according to the Greenhouse-Geisser method.

3. Results

3.1. Behavioral performance

The paired t-test showed that participants made more cooperation choices in the attractive partner condition than in the unattractive partner condition [M_{attractive} = 157 (SD = 31.84), M_{unattractive} = 104.15 (SD = 32.79), t(13) = 3.56, p < 0.01]. Furthermore, the behavioral rating for reward expectation showed that the level of reward expectation was higher in the attractive partner condition than in the unattractive partner condition [M_{attractive} = 4.68 (SD = 0.5), M_{unattractive} = 3.7 (SD = 0.88), t(39) = 7.13, p < 0.01].

3.2. ERP analysis

3.2.1. Face attractiveness effects

As shown in Fig. 2, obvious P2, N2, and LPC components were elicited by both attractive and unattractive faces. A three-way repeated measures ANOVA on P2 amplitude demonstrated a significant face type by causality interaction effect [F(4,52) = 3.41, p = 0.05]. The simple effect analysis showed that a smaller P2 amplitude was elicited by attractive faces than by unattractive faces at frontal [M_{attractive} = 8.37 μV (S.E. = 1.28), M_{unattractive} = 9.05 μV (S.E. = 1.41), F(1,13) = 7.39, p = 0.02] and fronto-central sites [M_{attractive} = 7.56 μV (S.E. = 1.23), M_{unattractive} = 8.17 μV (S.E. = 1.4), F(1,13) = 5.09, p = 0.04], but there were no significant differences at central, central-parietal and parietal sites [all p > 0.05]. In addition, there were no significant face type by laterality [F(2,26) = 1.82, p = 0.18] or face type by laterality by causality interaction effects.
[F(8,104) = 2.18, p = 0.12] observed for P2 amplitude. As for P2 latency, there were no significant main effects for face type [F(1,13) = 1.02, p = 0.33] or any other interaction effects [all p > 0.1].

For the N2 component, the ANOVAs demonstrated a significant face type by laterality interaction effect [F(2,26) = 4.11, p = 0.03], in addition to a main face type effect [F(1,13) = 12.36, p < 0.01]. The attractive faces elicited a more negative N2 deflection than unattractive faces at the left sites [M attractive = 0.49 μV (S.E. = 0.7), M unattractive = 1.44 μV (S.E. = 0.78), F(1,13) = 11.59, p < 0.01]. Midline sites [M attractive = 0.62 μV (S.E. = 0.98), M unattractive = 1.76 μV (S.E. = 1.11), F(1,13) = 13.68, p < 0.01] and right sites [M attractive = 0.55 μV (S.E. = 0.75), M unattractive = 1.4 μV (S.E. = 0.92), F(1,13) = 10.3, p < 0.01], and the attractiveness effect had a midline maximum. However, there were no significant face type by caudality or face type by laterality by caudality interaction effects (all p > 0.3). As for N2 latency, there were no significant main effects for face type [F(1,13) = 0.05, p = 0.83] or any other interaction effects (all p > 0.1).

The ANOVAs on LPC (450–650 ms) amplitude demonstrated a significant main face type effect, with a larger LPC amplitude elicited by unattractive faces than by attractive faces [M attractive = 6.93 μV (S.E. = 0.63), M unattractive = 7.87 μV (S.E. = 0.71), F(1,13) = 14.98, p < 0.01]. However, there were no face type by caudality, face type by laterality or face type by caudality by laterality interaction effects (all p > 0.3).

3.2.2. Feedback valence effect

The ANOVA performed on the difference waves of FRN amplitude showed that the main effect of face type was significant, with a larger FRN in the attractive face condition than in the unattractive face condition [M attractive = −4.17 μV (S.E. = 1.06), M unattractive = −3.33 μV (S.E. = 1.03), F(1,13) = 4.64, p < 0.05; Fig. 3a]. In addition, the main effect of electrode was also significant [F(5,65) = 13.33, p < 0.01], with more negative FRNs at the frontal than at the posterior sites (Fig. 3b). The frontal and fronto-central distribution of the FRN difference waves was consistent with most previous research.

4. Discussion

The ERP results show that the early P2 component was smaller in the attractive face condition than in the unattractive face condition. It has been suggested that frontal P2 activation is an index of rapid detection of typical stimulus features [27]. Specifically, a smaller P2 amplitude is elicited by negative emotional pictures compared with positive or neutral emotional pictures, reflecting the automatic and
rapid detection of negative emotional stimuli [3,4]. Thus, the P2 effect observed in the present study suggests that attractive faces were differentiated from unattractive faces rapidly and automatically in the brain. Extending on previous studies [14,18,20,25], we have provided the ERP evidence to support the automatic processing of facial attractiveness.

During the 180–230 ms interval, a greater negative N2 deflection was elicited by attractive faces than by unattractive faces. The N2 has been implicated in attentional orienting to emotional stimuli [5]. Some studies have demonstrated that threat faces elicit a larger N2 amplitude compared to neutral faces [13,24], which can be explained from an evolutionary perspective, suggesting that it is adaptive to pay rapid and sustained attention to stimuli that pose a threat to survival [19]. It has also been suggested that attractiveness possesses evolutionary importance [26]. Hooff et al. further suggest that, in addition to threat-related stimuli, other evolutionary relevant information such as attractive faces are also prioritized by our attention systems [28,29]. Therefore, the N2 effect observed in the present study may be interpreted as reflecting the enhanced attention towards attractive faces due to its biological significance.

As shown by the neural activity during the 450–650 ms interval, unattractive faces elicited a larger LPC than attractive faces. It is suggested that the LPC is related to motivated attention [22,23]. Specifically, larger LPC amplitudes are elicited by negative stimuli than by positive and neutral stimuli [9,10]. In the present study, it is possible that the unattractive faces induced negative emotion, and the attractive faces induced positive emotion. So, the current finding of an increased LPC for unattractive faces compared to attractive faces might be explained as an emotional effect. However, this result is inconsistent with previous studies wherein a larger LPC was observed for attractive faces than for unattractive faces [11,17,21,29]. A possible explanation for the discrepancy between the present and previous findings might be the different experimental paradigms used in these studies. Whereas the previous studies used an explicit facial attractiveness rating or categorization task, the present study used an implicit decision-making task.

The findings of the present study also revealed that facial attractiveness influenced the participants’ cooperative behavior such that participants were more likely to cooperate with the attractive partners than with the unattractive partners. Furthermore, the analysis of feedback valence demonstrated that the FRN (loss minus gain feedback) was larger in the attractive face condition than in the unattractive face condition. In the present study, participants revealed a stronger cooperation bias toward attractive partners, indicating that participants expected attractive partners to be more likely to return the monetary rewards relative to unattractive partners. The additional (degree of reward expectation) behavioral test further supports this interpretation by showing that the level of reward expectation was higher in the attractive partner condition.

![Fig. 3. (a) Grand average ERPs at Fz, FCz, Cz and CPz for each condition of feedback valence effect. (b) Left: loss minus gain difference wave in attractive face and unattractive face condition at FCz; right: scalp topography maps of voltage amplitudes for loss minus gain difference wave in attractive face and unattractive face conditions from 240 to 290 ms.](image-url)
than in the unattractive partner condition. Therefore, it is reasonable to suggest that the different expectations modulated the FRN amplitude. The current study extends on previous behavioral studies by providing original ERP evidence to support the positive influence of facial attractiveness on cooperative behavior. Moreover, the present study also provides an example of how the elicited FRN component associated with the outcome stimuli might be used as an index of how people judge and predict another’s behavior in a social game.

5. Conclusion

Taken together, the present study provides further insight into the electrocortical activity associated with the processing of facial attractiveness. Specifically, the discrimination of attractive and unattractive faces occurs at the early P2 processing stage, reflecting the automatic processing of facial attractiveness. Moreover, the present study demonstrates that facial attractiveness can facilitate cooperative behavior, and the reward expectation further modulates the strength of the FRN effect, with larger FRN effects observed in an attractive partner condition than in an unattractive partner condition.

Acknowledgments

This research was funded by the Special Public-welfare Project of the Ministry of Health (201002003).

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