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The wandering mind of men: ERP evidence for gender differences in attention bias towards attractive opposite sex faces

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To examine the time course and automaticity of our attention bias towards attractive opposite sex faces, event-related potentials (ERPs) were recorded from 20 males and 20 females while they carried out a covert orienting task. Faces that were high, low or average in attractiveness, were presented in focus of attention, but were unrelated to task goals. Across the entire sample larger P2 amplitudes were found in response to both attractive and unattractive opposite sex faces, presumably reflecting early implicit selective attention to distinctive faces. In male but not female participants this was followed by an increased late slow wave for the attractive faces, signifying heightened processing linked to motivated attention. This latter finding is consistent with sexual strategy theory, which suggests that men and women have evolved to pursue different mating strategies with men being more attentive to cues such as facial beauty. In general, our ERP results suggest that, in addition to threat-related stimuli, other evolutionary-relevant information is also prioritized by our attention systems.

Keywords: attention bias; attractiveness; gender difference; event-related potentials; evolutionary psychology

INTRODUCTION

Many of us would probably be distracted if we see a highly attractive individual of the opposite sex walking by on the street. This attention capturing power of attractive individuals seems to be a fast and automatic process over which we have little or no control, yet its function and underlying mechanisms are unclear. In this study, event-related brain potentials (ERPs) were recorded during a covert orienting paradigm to examine the time course and automaticity of this attention grabbing effect. In addition, gender differences were investigated to verify whether, consistent with sexual strategy theory (Buss and Schmitt, 1993), the anticipated attention biases would be more pronounced in men relative to women.

Attention biases in early visual processing have been investigated predominantly in the context of emotionally negative stimuli. For example, cognitive psychologists have reported that pictures of unpleasant or threatening stimuli, such as snakes or angry faces, capture our attention faster (e.g. Fox *et al.*, 2000; Öhman *et al.*, 2001) and hold it for longer (e.g. Fox *et al.*, 2001; Koster *et al.*, 2004). Similarly, PET and fMRI studies have shown that such pictures generate larger brain responses than neutral ones, presumably to prioritize and facilitate access (Vuilleumier, 2005). Most of these results have been explained from an evolutionary perspective, asserting that it is adaptive to pay rapid and sustained attention to stimuli that pose a threat to survival (Pratto and John, 1991; Öhman *et al.*, 2001). This raises the question that inspired our research: do similar attention biases also operate in the pursuit of other evolutionary-relevant goals, such as mating and parenting, and could this perhaps explain the attention-grabbing power of attractive opposite sex individuals?

As preliminary evidence for this idea, Maner and colleagues used a dot-probe task to examine early attention allocation to attractive sexual mates and rivals and found that on attention-shift trials target objects were categorized relatively slower when they followed a picture of a highly attractive female face (Maner *et al.*, 2007a and b). This response delay was interpreted as reflecting increased attention 'adhesion' to attractive female faces. From an evolutionary viewpoint, this would make sense, since attractive females may signal a potential mating opportunity for men and a potential threat to one's own reproductive success for women (Maner *et al.*, 2007a and b). What cannot be deduced from these results, however, is the onset of this attention effect and whether, for example, attractive faces also 'capture' our attention, in the sense that perceptual processing of these faces is facilitated through selective allocation of attention resources. Information about the temporal dynamics of attention biases can be obtained from scalp-recorded ERPs, which enable monitoring of the various processing stages between stimulus onset and response production. This brings us to the

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first aim of our study: to investigate the time course of a possible early attention bias towards attractive opposite sex faces, through ERP recording.

Similar to cognitive and brain imaging research, the vast majority of ERP attention studies have focused on the enhanced processing of threatening or harmful stimuli in comparison to neutral ones (for review see, Olofsson *et al.*, 2008). Cortical responses to such negative stimuli are typically found to be larger, reflecting selective employment of attention resources at perceptual—as well as subsequent evaluation stages. The ERP effects most consistently reported in response to 'positive', high-arousing stimuli, like erotic scenes or adventure/sports pictures, concern increased amplitudes of late positive potentials, invariably referred to as positive slow wave (PSW) or late positive complex (LPC) (e.g. Cuthbert *et al.*, 2000; Schupp *et al.*, 2004). These enhanced positive amplitudes, observed within the 300–800 ms post-stimulus time window, are typically taken to reflect 'heightened processing' linked to increased 'motivated attention', as they have been found to be largest for stimuli that (i) are motivationally relevant, (ii) receive the highest reports of affective experience, (iii) activate the appetitive system in the brain and (iv) prompt the largest levels of autonomic arousal (Schupp *et al.*, 2004; Briggs and Martin, 2009).

Pictures of attractive individuals or faces may fall in this category of pleasant stimuli, although they are not necessarily highly arousing. Consistent with this view, larger LPCs have been found in response to attractive faces as compared to unattractive faces (Johnston and Oliver-Rodriguez, 1997; Werheid *et al.*, 2007) as well as to faces of beloved ones relative to those of friends (Langeslag *et al.*, 2007). More specifically, Johnston and Oliver-Rodriguez (1997) found that the amplitude of the LPC correlated positively with post-experimental beauty ratings of female but not male faces, in an all-male sample. Werheid *et al.* (2007), using a mixed-gender sample, not only observed larger LPCs for attractive than unattractive faces (in their study no distinction was made between male and female faces) but also a more pronounced early posterior negativity (EPN) in a time-window preceding that of the LPC. This early ERP effect has been suggested to signal 'emotional significance', directing attention to the processing of high-priority stimuli (see also Schupp *et al.*, 2007b). A similar function has been assigned to the P2 component, which in several studies has been found to be larger for pleasant as well as unpleasant pictures (Amrhein *et al.*, 2004; Carretié *et al.*, 2004). The P2 occurs in the same time window as the EPN (150–250 ms), but is recorded with the more typical linked-ears reference method (as opposed to the average-reference method used by Schupp *et al.*, 2007b and Werheid *et al.*, 2007). Together, these results suggest that attention and emotion likely interact at more than one information processing stage, thereby demonstrating the importance of studying the temporal course of attention bias effects. In the present study, we therefore looked for ERP evidence for differential attention allocation as a function of attractiveness level in both LPC and P2/EPN time windows.

Because participants in the study by Werheid *et al.* (2007) were asked to categorize the presented faces as attractive or unattractive, it is unclear to what extent their observed ERP effects reflect automatic, stimulus-driven processes. Moreover, because in most ERP affective processing studies participants are asked to either passively watch the presented stimuli or rate them on a certain valence/arousal dimension (Olofsson *et al.*, 2008), the spontaneous nature of the much-reported late positive effects can likewise be questioned. This leads to the second aim of our study: to investigate whether attention biases towards attractive opposite sex faces occur automatically. To achieve this aim, ERPs were recorded during a covert orienting paradigm, comparable to that of the dot-probe task. In this paradigm (modelled after Fox *et al.*, 2001, Experiment 5), participants are required to identify small targets that are briefly presented at peripheral locations (top, bottom, left, right) relative to a centrally presented image/cue. The rationale of this paradigm is that if a particular cue holds the observers' attention (or makes it difficult to 'disengage' attention from) than the object identification time will be longer. In our study, the main focus was on the ERPs recorded in response to these cues, which were opposite sex faces with varying levels of attractiveness. These face cues were thus 'in focus' of attention but, unlike many earlier ERP studies in this field, 'unrelated' to the goal of the task. Consequently, if enhanced ERP components are found in response to attractive face cues, then the processes responsible for these amplitude increases can be considered to have occurred spontaneously.

Finally, the third aim of our study relates to a possible evolutionary explanation of the anticipated attention biases. More specifically, from an evolutionary perspective it is important to establish whether there are functionally relevant gender differences in accord with the different mating goals that men and women pursue. That is, sexual strategy theory posits that, as a function of differences in parental investment, men and women pursue somewhat different mating strategies, leading men to value youth and good looks more (as signs of high fertility) and women to value ambition and status more (Buss, 1989; Buss and Schmitt, 1993; Li *et al.*, 2002). Accordingly, if humans are indeed naturally biased to pay attention to attractive faces of the opposite sex, then this should be more pronounced in men than in women. The third aim of our study therefore is: to test the hypothesis that men would show a greater attention bias towards attractive opposite sex faces than women. Maner and colleagues (2007a and b) already provided some behavioural evidence for this suggestion, but gender differences have not yet been systematically investigated in ERP attractiveness studies. Given its link to motivated attention (described above), the late positive wave/complex is the most likely ERP component to show such predicted gender difference. In the present study, we therefore expected to observe larger late positive amplitudes for attractive opposite sex faces 'first and foremost' in our male participants.

In summary, the main aims of the current study were: (i) to investigate the temporal dynamics of our attention bias towards attractive opposite sex faces by means of ERP recording, (ii) to examine whether such attention bias occurs automatically by using a covert orienting paradigm in which the stimuli of interest are not related to task goals and (iii) to test the evolutionary-inspired hypothesis that an attention bias towards attractive opposite sex faces should be more evident in men than in women.

METHOD

Participants

Students participated (20 male and 20 female) in return of £5 per hour. All participants were hetero-sexual and Caucasian with no prior history of neurological or psychiatric illness. Ages for male (mean 22.6 years, s.d. 3.4) and female (mean 22.4 years, s.d. 3.0) participants did not significantly differ from each other [$t(38) = 0.15$, $P = 0.88$). The experiment followed APA ethical guidelines and received approval from the local Psychology Research Ethics committee. All participants signed a consent form before the start of the experiment.

Stimulus materials

The face stimuli that were used in the ERP experiment were selected from a larger database that was created with EFIT-V software (VisionMetric Ltd). All faces from this database were Caucasian and were characterized by a neutral expression and a forward eye-gaze. The faces were cropped to remove hair and ears, leaving only a facial mask. All faces were presented in colour. Normative ratings were obtained online from independent male ($N = 30$) and female ($N = 46$) volunteers who fell within the same age-range as our target group (18–30 years). For each gender, initially 15 faces were selected of which five received high attractiveness ratings, five low attractiveness ratings and five average attractiveness ratings (seven point rating scale). The latter group of stimuli is referred to as reference faces. Table 1 provides descriptive values for the three experimental categories and examples of each can be seen in Figure 1.

Although overall the female faces received slightly higher attractiveness ratings [$F(1,24) = 3.42$, $P = 0.08$, $\eta_p^2 = 0.13$] there was no significant interaction between stimulus gender and stimulus category [$F(2,24) = 1.50$, $P = 0.24$, $\eta_p^2 = 0.11$) and the average difference between attractive and unattractive faces was comparable for male and female images. Both the attractive (mean 4.25; $P < 0.001$) and unattractive faces (mean 3.82; $P < 0.05$) were rated as more distinctive than the reference faces [mean 3.26; $F(2,24) = 12.23$, $P < 0.001$, $\eta_p^2 = 0.51$]. Because this 2:1 high/low-distinctiveness ratio may influence results, we included five more filler items for each gender that were comparable to the reference faces in terms of attractiveness ratings [mean 2.87, $t(18) = 0.54$, $P = 0.59$] and distinctiveness ratings [mean 3.32, $t(18) = 0.30$, $P = 0.77$]. Consequently, each participant was presented with 10 relatively high distinctive faces (5 attractive and 5 unattractive) and 10 relatively low distinctive faces (5 reference and 5 filler). Behavioural and ERP responses to the filler items, however, were not included in the analyses to avoid potential levelling effects due to larger numbers.

Table 1 Physical attractiveness ratings for the selected experimental stimuli based on an online normative rating study (normal print) and the post-experimental study (italics)

Stimulus gender	Stimulus category	Mean (s.d.)	Min	Max
Female	Attractive	4.84 (0.32)	4.53	5.30
		5.18 (0.30)	*4.95*	*5.65*
	Unattractive	1.94 (0.26)	1.57	2.23
		1.75 (0.22)	*1.40*	*1.95*
	Reference	3.08 (0.40)	2.50	3.60
		3.22 (0.32)	*2.95*	*4.30*
Male	Attractive	4.26 (0.24)	4.00	4.65
		4.87 (0.16)	*4.67*	*5.06*
	Unattractive	1.74 (0.21)	1.57	2.11
		1.82 (0.18)	*1.61*	*2.06*
	Reference	3.07 (0.82)	2.17	3.87
		3.35 (0.86)	*2.72*	*4.17*

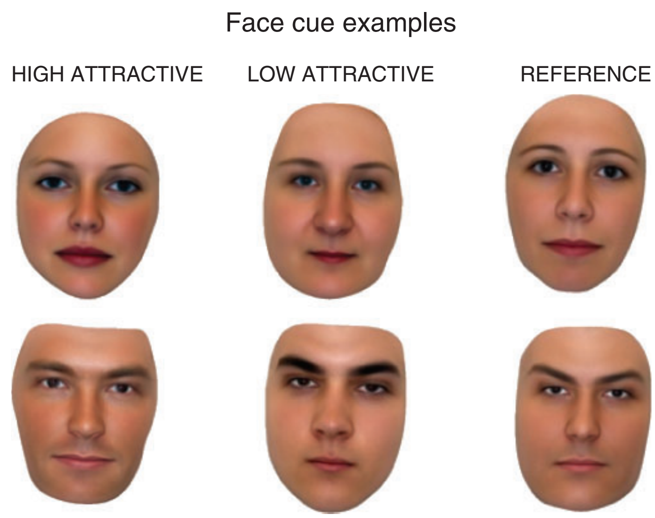

Fig. 1 Examples of the different stimulus categories.

Procedure

To increase the salience of a mating motive, participants were first asked to write down, in 3 min, how they would spend a romantic date with a highly desirable person of the opposite sex. Next, the covert orienting task was introduced, followed by 16 practice trials. Participants were exclusively presented with faces of the opposite sex to test our sexual strategy hypothesis. Figure 2 describes the sequence of events

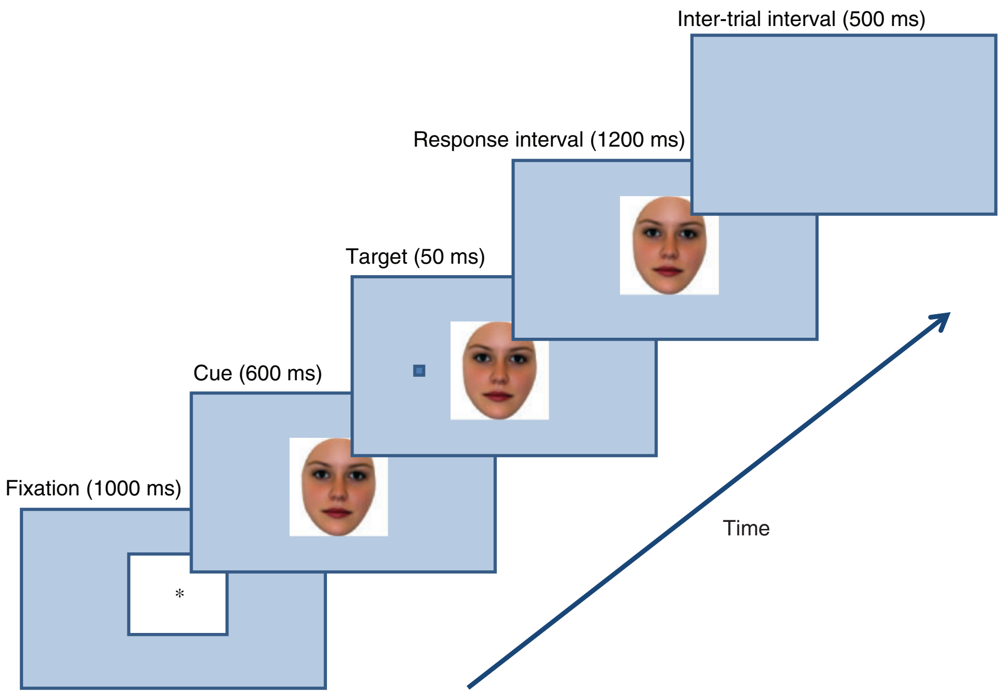

Fig. 2 Sequence of events in the covert orienting paradigm.

in the task modelled after Fox and colleagues (Fox *et al.*, 2001; Experiment 5). Each trial began with the presentation of a fixation cross (1000 ms). Then, a face cue was presented followed 600 ms later by a small target (square or cross, 50 ms), either 2 cm above, below, left or right of the face cue. Participants had to indicate as quickly as possible which target was presented by means of left/right button presses (button assignment counterbalanced between participants). Following target offset, the face cue remained on the screen for another 1200 ms. Each of the 20 opposite sex faces appeared once with each target in each target location ($20 \times 2 \times 4 = 160$ experimental trials). Trials were presented in random order with the restriction that the same face was not presented on consecutive trials. To validate the stimulus materials, participants were asked, after the experiment, to rate the faces for physical attractiveness similar to the online rating study that was used to create the database.

Electrophysiological recording and analysis

EEG data were recorded (average reference) from 19 standard Ag–AgCl electrodes mounted in an elastic cap (Easy Cap QA40) and from two ear-clip electrodes. Vertical eye movements and blinks were measured with two bipolar Ag–AgCl electrodes placed above and below the participants' left eye. EEG and EOG signals were amplified using a Quickamp 72 amplifier and Brain Vision Recording software (version 1.02). The data were recorded with a sample rate of 250 Hz and a bandpass filter of 0.01 and 35 Hz (24 dB). EEG data were corrected off-line for eye movements, re-referenced to a linked-ears reference and then filtered with a 25 Hz (24 dB) low-pass filter. EEG recordings were automatically screened for artefacts using the following criteria: (i) maximum allowed voltage step of 50 μV between two sample points, (ii) maximum allowed absolute difference of 80 μV over a 200 ms interval and (iii) lowest allowed activity of 0.5 μV over a 100 ms interval. EEG data containing artefacts in any of the recording channels were rejected from further analyses. ERP averages were calculated for each of the three stimulus categories, time-locked to cue-onset and with respect to a 100 ms pre-stimulus baseline. Data for one of the female participants had to be excluded from ERP analysis due to extremely high levels of alpha activity, leaving an insufficient number of artefact free EEG trials.

P2 peak detection was performed at Pz electrode and defined as the maximum local positive peak in the 120–220 ms time window. P2 peak amplitudes at other electrode positions were determined at the same latency as that the peak was detected at Pz. The subsequent slow wave was quantified as the mean amplitude of three consecutive 150 ms time windows starting 200 ms after cue onset. These amplitude measures at 9 electrode locations (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4) were subjected to 3 (stimulus category: attractive, unattractive, reference) × 3 (anterior–posterior position: frontal, central, parietal) × 3 (laterality: left, midline, right) repeated measures ANOVAs with participant gender (male, female) as a between-subjects factor. Effects with more than one degree of freedom were adjusted for sphericity violations using the Greenhouse Geisser method. Because of easier notification, however, uncorrected degrees of freedom are reported. If applicable, main effects were followed up by pairwise comparisons with Bonferroni correction. To avoid describing large amounts of statistical data concerning scalp distribution effects, only main effects of—or interactions with stimulus category and gender are reported.

RESULTS

Validation of stimulus materials

Averaged post-experimental attractiveness ratings are indicated in Table 1, together with those obtained from the stimulus selection study. Clearly, there was a high correspondence between the mean values of the two types of ratings. Importantly, there was also no overlap between the post-experimental ratings for each of the categories. A 2 (stimulus gender: male, female) × 3 (stimulus category: attractive, unattractive, reference) between subjects ANOVA showed a significant effect of stimulus category for the post-experimental attractiveness ratings [$F(2, 24) = 150.1$, $P < 0.001$, $\eta_p^2 = 0.93$], with all Bonferroni pairwise comparisons significant at $P < 0.001$. There were no significant effects for stimulus gender nor was there a significant interaction between stimulus gender and stimulus category. These results validated the classification of our stimulus materials.

ERP data

Figure 3A shows grand average ERP waveforms at midline electrode positions for male and female participants. As can be seen in this figure, the face cues elicited a clear N1–P2 complex, which was followed by a slow wave that was mainly positive over parietal electrode positions and negative over central and frontal ones. Visual inspection of Figure 3A shows that attractiveness level of the presented faces affected P2 amplitude in both male and female participants (larger amplitudes for the attractive and unattractive faces) and the amplitude of the subsequent slow wave in male participants only (more positive/less negative amplitudes for the attractive faces). Statistical analyses therefore focused on these two ERP components. There was no observable EPN effect.

P2 peak amplitude

Stimulus category significantly affected the P2 component [$F(2,74) = 6.54$, $P < 0.01$, $\eta_p^2 = 0.15$). Bonferroni pairwise comparisons showed that both attractive (mean 3.04 μV, $P < 0.01$) and unattractive faces (mean 2.52 μV, $P = 0.07$) elicited larger P2 peak amplitudes than reference faces (mean 1.56 μV). This means that more attention resources were allocated to perceptual processing of the attractive and unattractive faces than the reference ones. The gender × stimulus category interaction was not significant, revealing that this early attention bias was equally present in males and females. Participant gender, however, was found to interact with Anterior–posterior position [$F(2,74) = 5.81$, $P < 0.05$, $\eta_p^2 = 0.14$] and laterality [$F(2,74) = 4.08$, $P < 0.05$, $\eta_p^2 = 0.10$], revealing some gender-specific differences in early visual face processing that were not related to the attractiveness of the cues.

Late slow wave

Amplitude differences for the late slow wave were analysed for three consecutive 150 ms time windows to examine the time-course of this specific effect. Mean amplitude values as a function of stimulus category and gender are indicated in Table 2. For all three time windows significant effects of Stimulus category were found [200–350 ms: $F(2,74) = 5.10$, $P < 0.05$, $\eta_p^2 = 0.12$; 350–500 ms: $F(2,74) = 14.86$, $P < 0.001$, $\eta_p^2 = 0.29$; 500–650 ms: $F(2,74) = 3.80$, $P < 0.05$, $\eta_p^2 = 0.10$] revealing that, in general, the attractive faces elicited more positive (or less negative) amplitudes than the unattractive and reference faces (Table 2). For the first two time windows significant interactions between gender and stimulus category were present [200–350 ms: $F(2,74) = 4.58$, $P < 0.05$, $\eta_p^2 = 0.11$; 350–500 ms: $F(2,74) = 4.58$, $P < 0.05$, $\eta_p^2 = 0.11$] revealing that the stimulus category effects were primarily driven by the male participants. Indeed, separate analyses for each gender showed that Stimulus category reliably affected slow wave amplitudes in male participants [200–350 ms: $F(2,38) = 9.98$, $P < 0.001$, $\eta_p^2 = 0.48$; 350–500 ms: $F(2,38) = 21.31$, $P < 0.001$, $\eta_p^2 = 0.69$; 500–650 ms: $F(2,38) = 4.86$, $P < 0.05$; $\eta_p^2 = 0.20$] but not female participants. For male participants, Bonferroni comparisons showed that for each time window attractive faces elicited more positive (or less negative) amplitudes than the reference faces and the unattractive faces (Table 2). Mean amplitudes for the unattractive faces were not significantly different from those for the reference faces. These results suggest that, in agreement with our hypothesis, 'particularly' for men attractive opposite sex faces received more attention at post-perceptual stimulus evaluation stages. None of the interactions between stimulus category and anterior–posterior position were significant in any time window, indicating a wide scalp distribution of the attractiveness effect, albeit with a frontal maximum (Figure 3B).

Behavioural data

Accuracy and RT data were analysed with a 2 (participant gender: male, female) × 3 (stimulus category: attractive, unattractive, reference) mixed factorial ANOVA. Overall accuracy was very high (mean 0.93) and no significant main or interaction effects were found. Likewise, RTs were found to be similar for the targets paired with the three different stimulus categories (means: attractive 439 ms; unattractive 440 ms, reference 435 ms) and this was the same for both male and female participants.

DISCUSSION

Our ERP results are consistent with the common notion that opposite-sex faces with different levels of physical attractiveness also receive different levels of attention. Both early and late ERP attention effects were observed, which were

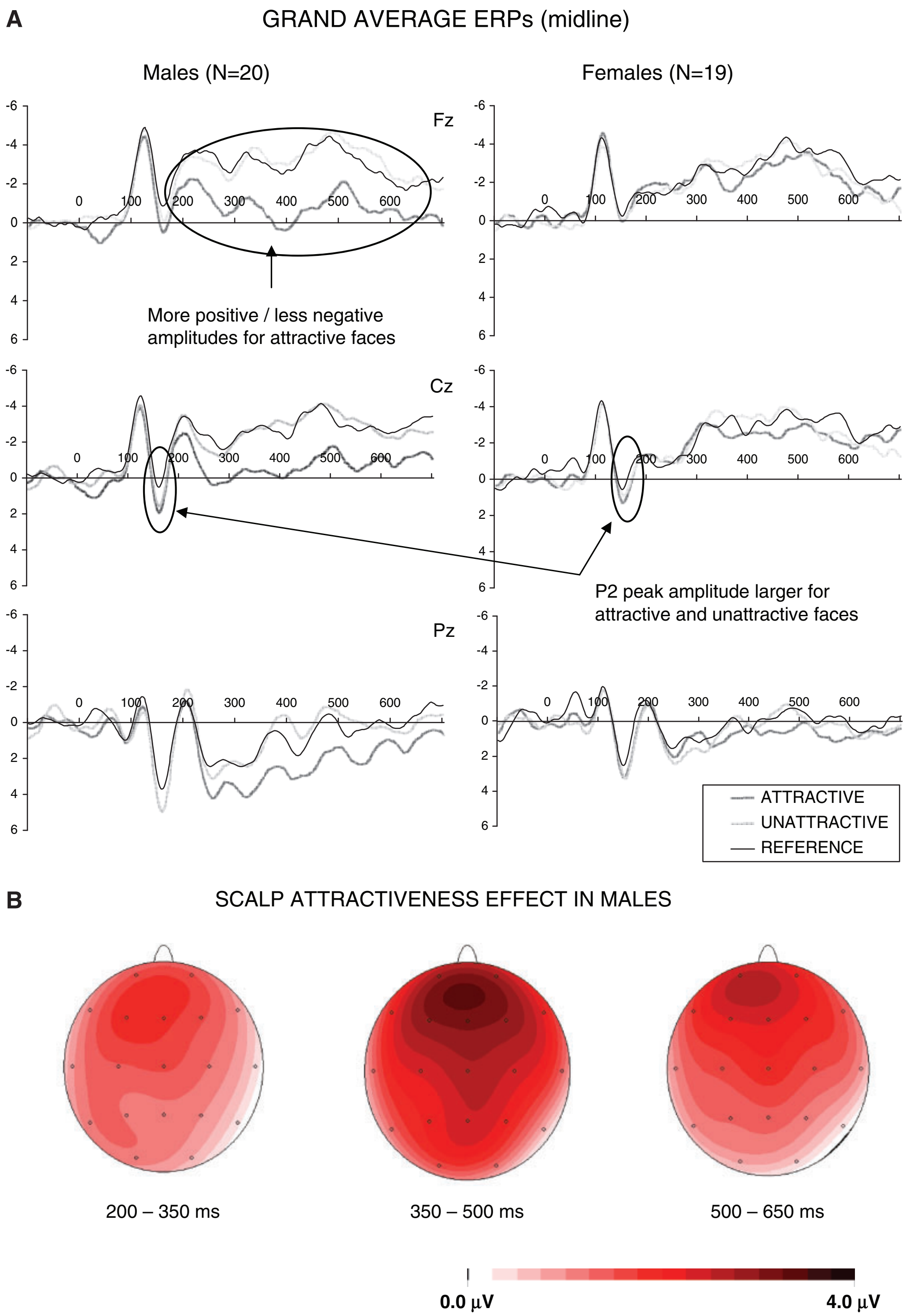

Fig. 3 (A) Grand average ERP waveforms for the midline electrode positions for male and female participants. *y*-axis: amplitudes in microvolt whereby positive is plotted downwards. *x*-axis: time in ms whereby the face cue was presented at time 0. (**B**) Scalp topographic maps for the three analysed time windows of the late slow wave effect in male participants (attractive minus unattractive face cues).

differently affected by attractiveness level of the presented faces and gender of the observer, demonstrating that they reflect separate aspects of facial attractiveness processing. Because we used a covert orienting paradigm, it is evident that these selective attention effects occurred spontaneously while participants held unrelated task goals in mind. Finally, consistent with sexual strategy theory, only male participants showed ERP evidence associated with heightened processing

Table 2 Mean amplitudes (averaged over the nine analysed electrodes, SE in parentheses) for the three time windows that made up the late slow wave as a function of stimulus category and participant gender

ERP amplitude	Stimulus category	All participants	Male participants	Female participants
Mean 200–350	Attractive	0.45 (0.39)	0.97 (0.54)	−0.08 (0.55)
	Unattractive	−0.32 (0.39)	−0.47 (0.55)**	−1.62 (0.56)
	Reference	−0.42 (0.37)*	−0.73 (0.52)**	−1.05 (0.53)
Mean 350–500	Attractive	−0.07 (0.41)	0.77 (0.57)	−0.92 (0.59)
	Unattractive	−1.72 (0.40)***	−1.76 (0.55)***	−1.68 (0.57)
	Reference	−1.49 (0.38)**	−1.47 (0.52)***	−1.50 (0.54)
Mean 500–650	Attractive	−0.45 (0.35)	0.07 (0.49)	−0.96 (0.51)
	Unattractive	−1.31 (0.45)	−1.62 (0.63)*	−1.00 (0.64)
	Reference	−1.48 (0.39)*	−1.39 (0.55)**	−1.56 (0.56)

Note: Significant differences of the Bonferroni pairwise comparisons with the attractive category are indicated with $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

and motivated attention towards attractive opposite-sex faces. Next, these results are discussed in detail with reference to the three aims of our study.

P2 and the time course of attention bias effects

In both men and women, P2 amplitudes were relatively larger for attractive and unattractive faces. Although initially linked to our negativity bias (e.g. Carretíe *et al.*, 2001), augmented P2 amplitudes have more recently been associated, like the EPN (Schupp *et al.*, 2004 and 2007a; Werheid *et al.*, 2007), with early, implicit selective attention to 'emotionally distinct' stimuli in general, to account for the fact that increased P2 amplitudes have been observed for pleasant as well as unpleasant pictures (Amrhein *et al.*, 2004; Carretié *et al.*, 2004). Because in our experiment the attractive and unattractive faces were both rated as being more distinctive than the reference faces (albeit that these ratings were not taken from the experimental sample), the P2 effect observed here may be interpreted more generally as reflecting some kind of 'stimulus-driven call for processing resources... which facilitates further sensory processing of the stimulus' (c.f. Öhman *et al.*, 2001, p. 466). Accordingly, we suggest that this triggering of attention is a fast and automatic process that primarily works on the basis of low-level stimulus features. The specific characteristics of these features and the way in which they relate to (un)attractiveness were not subjects of this study (and hence not systematically varied), but these could be very interesting topics for future research.

As far as our results concern, they suggest that the P2 effect was driven more by 'physical distinctiveness' rather than by attractiveness levels *per se*, because (i) P2 attention effects were comparable for high- and low-attractive faces (demonstrating no linear relationship between P2 amplitude and degree of attractiveness) and (ii) for P2 there was no attractiveness × gender interaction (suggesting no link with different mate selection motives in males and females). One complicating issue though, is the extent to which differences in stimulus probability may have contributed to the P2 amplitude differences, either directly or via perceived distinctiveness. Namely, although we took care to let the more distinctive, attractive and unattractive faces not stand out numerically as a 'combined' category, the attractive and unattractive faces each were presented with less frequency. Consequently, on the basis of our results the possibility cannot be excluded that the relative increase in P2 amplitude for attractive and unattractive faces was in part due to their lower occurrence frequency. Further research is needed to solve this issue.

Most interestingly, with respect to the time course of attention bias effects, observations (i) and (ii), as described above for the P2 component, did not apply to the subsequent slow wave (discussed in next section). Consequently, it is likely that the P2 and the PSW effects each reflect unique aspects of facial attractiveness processing. More specifically, whereas it seems that P2 amplitude reflects initial 'attention capture' of (physically) distinctive faces, amplitude of the late slow wave more likely reflects differences in 'elaborative processing' as a result of varying levels of motivational significance (for similar reasoning in the context of emotional picture processing, see Codispoti *et al.*, 2007; Foti *et al.*, 2009).

Late slow wave and automaticity of attention bias effects

Attractive opposite sex faces generated more positive ERP amplitudes in the 200–650 ms post cue period, but only in our male participants. This slow wave effect resembles the late positive effects, which in previous research have been found to be larger for arousing and/or rewarding pictures, including attractive faces (Johnston and Oliver-Rodriguez, 1997; Werheid *et al.*, 2007) and portraits of beloved ones (Langeslag *et al.*, 2007). In accord with these studies, the slow wave effect likely reflects heightened processing of the attractive opposite sex faces related to motivated attention. In addition, because the face cues in our study were unrelated to task goals, it appears that these extra processing resources were recruited automatically, albeit that our participants were primed with a mating motive. Maner *et al.* (2007a and b) found that such priming is vital for obtaining behavioural evidence for attention adhesion. It remains to be investigated, however, to what extent it is also needed to obtain ERP slow wave effects. Moreover, given our behavioural null results, it might be that the ERP slow wave is a more robust measure of automatic attention adhesion, which is less dependent on situational factors. This suggestion would be consistent with the observation that behavioural evidence for enhanced processing of threatening stimuli has been found primarily in high-anxious and not low-anxious participants (Bar-Haim *et al.*, 2007), while larger late positive potentials to such stimuli have been found regardless of participants' anxiety level (Olofsson *et al.*, 2008). Furthermore, because both male and female participants received the same treatment, the priming manipulation cannot be held responsible for the observed gender differences for the slow wave effects.

As far as our behavioural results concern, male and female participants performed equally well on all types of trials, suggesting that the observed ERP attention biases did not impact on the accuracy and speed of subsequent object identification. Tentatively, this could be due to the length of the interval between cue and target onset, which gave participants sufficient time to process the face cue and to prepare for target presentation. The relatively reduced stimulus category effect for the last slow wave time window (500–650 ms) supports this suggestion. Alternatively, the seizing of attention by attractive opposite sex faces might have been compensated by their higher reward value through selectively increasing task efforts on these trials (c.f. Hayden *et al.*, 2007). Whatever the reason, our results suggest that ERP measures might not only provide information about the temporal course of our attention bias towards distinctive and attractive faces but, as suggested above, they might also be more sensitive than behavioural ones.

Late slow wave and gender differences

As predicted, only in our male participants was the amplitude of the late slow wave modulated by attractiveness level of the presented opposite sex faces. In accord with sexual strategy theory (Buss and Schmitt, 1993), this confirms that attractiveness is a more salient feature of potential mates for men than for women. This finding is also consistent with results from Johnston and Oliver-Rodriguez (1997), who reported positive correlations between LPC amplitude and attractiveness level of female faces but not male faces. Interestingly, only male participants were included in their sample, who watched faces of both sexes. Unlike them, we used both male and female participants but they only watched faces of one sex (the one opposite to one's own). This design allowed us to examine the anticipated gender differences in connection with sexual strategy theory, but also placed some inferential limitations on the obtained data. For example, we cannot completely rule out the possibility that, compared to women, men are just more attentive to attractive faces in general. However, given that hetero-sexual men typically show a clear preference for looking at opposite-sex and not same-sex faces (e.g. Alexander and Charles, 2009; Levy *et al.*, 2008) this alternative explanation of the male-specific slow wave effect seems unlikely. Nevertheless, in another context it may be interesting to also examine responses to same-sex faces, for example, to better understand the reward value and aesthetic appreciation of beautiful faces (Senior, 2003) or to uncover potential attention biases towards sexual rivals (c.f. Maner *et al.*, 2007b).

One particular factor that may have contributed to the observed slow wave effect is the special reward value of the attractive faces for men. Using fMRI, Cloutier *et al.* (2008) found that multiple parts of the brain's reward circuit are activated by attractive faces in both men and women, but only in men this included the orbito-frontal cortex (OFC). They argued that this gender difference in OFC activation might be the reason why men attribute more value than women to attractive opposite sex faces. In our study, additional activation of the OFC may explain the more frontal scalp distribution of the slow wave effect compared to the typical centro-parietal LPC.

CONCLUSION

We successfully provided neurophysiological evidence for early, automatic attention biases that are relevant for mate selection. The observed time course of the ERP effects suggests that both men and women automatically select physically distinctive faces for prioritized processing, but, in accord with our evolutionary hypothesis, only in men was this followed by enhanced evaluative processing associated with motivated attention to attractive opposite sex faces. With reference to the question that inspired this research, these results suggest that, in addition to threat-related stimuli, other evolutionary relevant information is also prioritized by our attention systems. Overall, our results bring the integration between evolutionary social psychology and cognitive neuroscience one step further, which we believe is necessary to fully understand the adapted human mind.

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