

ATTENTIONAL MODULATIONS OF EVENT-RELATED BRAIN POTENTIALS SENSITIVE TO FACES

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Event-related brain potentials (ERPs) were recorded in response to centrally and peripherally presented faces and chairs under conditions where one stimulus category was attended and the other unattended. It was studied whether selective attention affects ERP components sensitive to the presence of faces. When compared with chairs, faces elicited larger N1 amplitudes at lateral temporal electrodes and a midline positivity in the same latency range. The latter effect was only found for central faces. Attention to centrally presented faces was reflected in enhanced posterior N1 amplitudes. This effect may be related to an attentional modulation of processing within face-specific brain areas. It was not elicited by chairs or peripheral faces. Beyond 200 msec post-stimulus, a category-unspecific attentional negativity was found at all recording sites for centrally and peripherally presented face and nonface stimuli.

INTRODUCTION

Evidence from numerous sources suggests that the perception of faces is qualitatively different from the perception of other types of objects. Whereas object recognition is assumed to proceed by decomposing objects into component parts on the basis of low-level edge and contour features (Biederman, 1987; Marr & Nishihara, 1978), face recognition seems to be based on more holistic representations. Object recognition is efficient with line drawings (Biederman & Ju, 1988), whereas face identification is impaired with line drawings as compared with photographs (Davies, Ellis, & Shepherd, 1978). Face recognition is more affected by object inversion than is the recognition of other object classes (face inversion effect: Valentine, 1988; Yin, 1969), which led Diamond and Carey (1986) to argue that face recognition depends on an analysis

of prototypical configurations of face components. Farah (1991) suggested that different types of representations underlie face and object recognition. In object recognition, representations are employed where wholes are decomposed into multiple simple parts, whereas face recognition depends on representations of complex wholes without part decomposition. Recent evidence for this comes from a neuropsychological case study of Moscovitch, Winocur, and Behrmann (1997), who studied a patient with severe object agnosia and dyslexia, with face recognition apparently spared. This patient performed normally in recognising photographs of famous people and caricatures, and in judging family resemblance. In contrast, when inverted or fractured faces were shown, recognition and perceptual matching performance was impaired. This suggests that a "holistic" face recognition system operates effectively in isolation upon

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upright (but not inverted) faces, and detects face identity by analysing the configuration of facial features.

If the processes underlying face and object recognition are qualitatively different, there may be brain areas exclusively devoted to the processing of faces. Evidence for this has been found in electrophysiological and brain imaging studies. Face-specific cells have been located in the macaque temporal cortex in the inferior temporal gyrus and on the banks and the floor of the superior temporal sulcus. These cells respond strongly to faces, but not to other types of objects (Perrett, Rolls, & Caan, 1982). Some cells respond equally well to filtered images of faces that do not share any spatial frequencies, to face images with changed or removed surface colours, and to images with different contrast levels, suggesting that they are truly face-selective, instead of responding to visual features common to all faces. The configuration of face components is critical for some face cells; their activity is reduced when face components are rearranged, or when only single facial components are presented (Desimone, Albright, Gross, & Bruce, 1984). Further evidence for the existence of face-specific brain areas comes from functional imaging studies in humans. In a PET study, Sergent, Ohta, and MacDonald (1992) found a bilateral, right predominant activation of the fusiform gyrus, of bilateral medial temporal areas, and of the right parahippocampal region in a face discrimination task. Kanwisher, McDermott, and Chun (1997) compared fMRI activity during passive viewing of faces or objects and located a fusiform region that was selectively activated when faces were presented. A similar pattern emerged when faces were compared to houses, scrambled faces, or hands. Since this "fusiform face area" responded to three-quarter views of faces with hair concealed, its activity seems largely viewpoint independent and is likely to be involved in face recognition rather than head detection.

If there is a brain region devoted to the processing of faces, an obvious question is whether this region will be automatically activated by the presence of face stimuli, or whether its activity is modulated by endogenous factors like selective

attention. If face-specific brain areas were activated pre-attentively, face stimuli should presumably pop out in visual search tasks against a background of nonface stimuli. Kuehn and Jolicoeur (1994) and Nothdurft (1993) tested this by presenting face targets simultaneously with a variable number of nonface distractors. Reaction time increased steeply with the number of distractors, indicating serial search. In contrast to the detection of low-level visual features, the detection of faces seems to require attention. Consistent with this, Wojciulik, Kanwisher, and Driver (1998) recently found attentional effects on face-specific fMRI activity of the fusiform face area (FFA). With retinal stimulation held constant, FFA activity was stronger when subjects were engaged in a face-matching task than when they had to match houses (see also Clark et al., 1997).

In the present experiment, event-related brain potentials (ERPs) were recorded from normal subjects in response to attended or unattended face and nonface stimuli. Previous studies found ERP modulations specifically related to the presence of faces, although these results are not fully consistent. Allison et al. (1994) recorded ERPs to faces and nonface stimuli intracranially and found that faces elicited a large-amplitude negativity with a latency of about 200msec in the left and right fusiform and inferior temporal gyri. Electrical stimulation of these areas resulted in a temporary inability to name familiar faces. Jeffreys (1996) reported a face-specific positive potential with a latency of 160msec that was maximal at Cz ("positive potential", VPP). A VPP was obtained in response to foveal faces, but not to faces presented with a horizontal distance of 3° or more from fixation. Bötzel, Schulze, and Stodick (1995) also found a VPP, and an additional negative peak at lateral temporal electrodes (T5, T6) in the same latency range. Based on dipole analyses, they suggested that the VPP may reflect hippocampal activity, whereas the lateral temporal negativity may be generated in the fusiform and lingual gyri. George, Evans, Fiori, Davidoff, and Renault (1996) observed positive potentials at midline sites and temporal negativities in response to faces as well as scrambled faces. In contrast to Bötzel et al. (1995), they argued that these effects

are caused by a single neural generator in the parahippocampal and fusiform gyri that is oriented in a way that produces a polarity reversal at the scalp surface between T5/T6 and Cz. Bentin, Allison, Puce, Perez, and McCarthy (1996) also recorded ERPs to face and nonface stimuli and found that faces elicited a negative potential with a latency of 170msec (N170) at lateral posterior temporal sites and a frontocentral positivity of slightly longer latency (P190). No N170 was triggered by cars, hands, furniture, or animal faces, nor, in contrast to George et al. (1996), by scrambled faces. According to Bentin et al. (1996), the N170 and the VPP are most likely to be caused by different generators, although their functional relationship is still unclear. Attentional modulations of these face-specific ERP components have not yet been investigated.

In the present experiment, ERPs were recorded in response to single centrally or peripherally presented face and nonface stimuli (chairs). Examples of these stimuli are shown in Fig. 1. The subjects' task was to attend to faces or chairs in order to detect target stimuli within this category (immediate repetitions of items in parts A and C, predefined target items in part B). Attention instructions were varied between blocks. In parts A and B, all stimuli were presented at fixation. In part C, stimuli were delivered in the left or right visual field centred about 3.5° horizontally displaced from fixation. In contrast to the Wojciulik et al. (1998) fMRI study, where attended and unattended stimuli appeared at different locations, so that some of the observed effects may have been due to location-specific sensory gating processes, all face and chair stimuli were presented in random sequence at fixation or unpredictably in the left or right visual field. Chairs were chosen as nonface items because within-category discrimination difficulties for face and nonface stimuli needed to be approximately equal. Similar to faces, the chairs employed in this study differed only with respect to the properties and configuration of their component parts.

The subsequent analyses consisted of two steps. First, ERPs elicited by face and nonface stimuli were compared to find out whether ERP components are selectively sensitive to the presence of

faces. Based on results of previous ERP studies, faces were expected to elicit enhanced negativities at lateral temporal electrodes and an enlarged positivity (VPP) at midline electrodes with a latency of 150–180msec post-stimulus. Such effects may, however, be restricted to faces presented at fixation, as Jeffreys (1996) found no VPP component for lateralised faces. Second, ERPs elicited in blocks where the respective stimulus category (face or chair) was relevant were compared to ERPs elicited by faces or chairs in blocks where the other category was relevant. If attention affected the processing of face stimuli within face-specific brain regions, this could be reflected in systematic attentional modulations of face-specific ERP responses. No such attentional effects should be observed for nonface (chair) stimuli. If attention affected object identification in an unspecific way, similar attentional modulations should be observed for face and nonface stimuli. An additional analysis was conducted in part B, where subjects had to detect a predefined target item. ERPs to male and female nontarget faces were compared between blocks where a face of the same sex or the opposite sex served as target. Differences between these waveforms would reflect effects of attention directed to male or female faces.

METHODS

Subjects

Thirteen paid volunteers participated in the experiment. One of them had to be excluded because of excessive eye blink activity. Thus 12 subjects (10 female), aged 19–36 years (mean age: 27.4 years) remained in the sample. All subjects were right-handed and had normal or corrected-to-normal vision.

Stimuli and Apparatus

Subjects were seated in a dimly lit, electrically shielded, and sound attenuated cabin, with response buttons under their left and right hands. A computer screen was placed 110cm in front of the

subject's eyes and the screen centre was positioned on the subject's horizontal straight-ahead line of sight. The stimuli were photographs of faces and chairs that were digitally scanned, processed by graphics software, and presented on a computer monitor in front of a white background (see Fig. 1 for examples). Fifteen images of chairs, and 9 images of male and female faces (resulting in a total of 18 face photographs) were used. All face images showed a frontal view, with eyes positioned in the middle of the image. Chair and face stimuli occupied a visual angle of approximately $3^\circ \times 4.5^\circ$. All stimuli were presented for 200msec, and successive stimulus presentations were separated by intertrial intervals of 1200msec. In the peripheral presentation condition (part C, see following), a small fixation cross (subtending a visual angle of about $0.2^\circ \times 0.2^\circ$) was continuously present at the screen centre. In parts A and B, all stimuli were presented at the centre of the screen. In part C, stimuli were presented in random order on the left or right side of the screen, with a horizontal distance of 3.5° from central fixation to the centre of the stimulus.

Procedure

The experiment consisted of 16 experimental blocks, divided into 3 experimental parts (A, B, and C). The order in which these parts were delivered was balanced across subjects. In all blocks, a sequence of 80 nontarget stimuli (faces and chairs) and a variable number of potential targets were presented and subjects were instructed to respond with a left or right button press to infrequently delivered relevant target items. Nontarget stimuli were selected randomly for each trial, and a total number of 20 male faces, 20 female faces, and 40 chairs was presented as nontargets. Part A consisted of four blocks, and the subjects' task was to attend to a stimulus category (faces or chairs) that was specified prior to the start of each block, in order to respond with a left-hand or right-hand button press to immediate repetitions of stimuli that belong to the relevant category. Repetitions of stimuli from the irrelevant category were to be ignored. Each of the four possible combinations of attended category

(faces, chairs) and response side (left, right) was realised in one block. In each block, 20 immediate stimulus repetitions occurred, with an average of 10 repetitions within the relevant category. Part B consisted of eight blocks, and the subjects' task was to remember a stimulus presented to them on the screen prior to the start of each block. A response was required whenever this stimulus was encountered in the course of a block. In four blocks the to-be-attended stimulus was a chair, in two blocks it was a male face, and in the remaining two blocks it was a female face. This critical stimulus was presented between 8 and 12 times in each block (10 presentations on the average), and subjects had to press the left or right button in blocks, respectively. Part C was identical to part A, except that all stimuli were presented horizontally displaced and in random order in the left or right visual field. Subjects were told that the position of a stimulus was irrelevant for their task of detecting immediate repetitions within the designated stimulus category.

Subjects were instructed to respond as quickly and accurately as possible to relevant target stimuli, to withhold responses to all other stimuli, and to maintain central eye fixation during the trials. To make subjects familiar with these task requirements and to ensure that all stimuli were encountered at least once before the start of the experimental blocks, one training block was run prior to each experimental part.

Recording

EEG was recorded with Ag-AgCl electrodes from Fz, Cz, Pz, T5, O1, T6, and O2 (according to the 10–20 system). EEG was measured relative to a reference electrode positioned on the tip of the nose. Horizontal EOG was recorded bipolarly from electrodes at the outer canthi of both eyes, vertical EOG was recorded from electrodes above and beside the right eye. Electrode impedance was kept below 5 k Ω . The amplifier bandpass was 0.10–40Hz. EEG and EOG were sampled with a digitisation rate of 200Hz, and stored on disk. The latency of manual responses (if present) was measured on each trial.

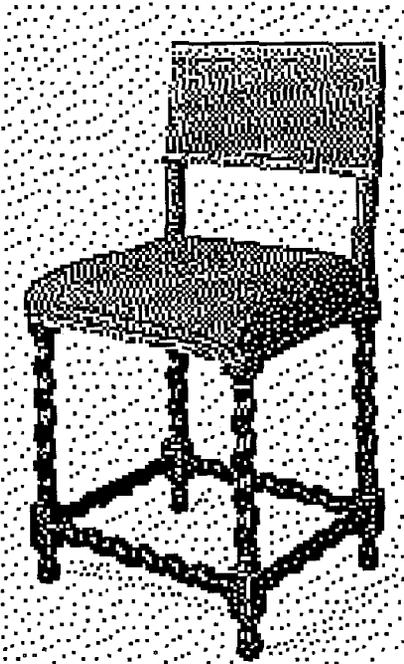
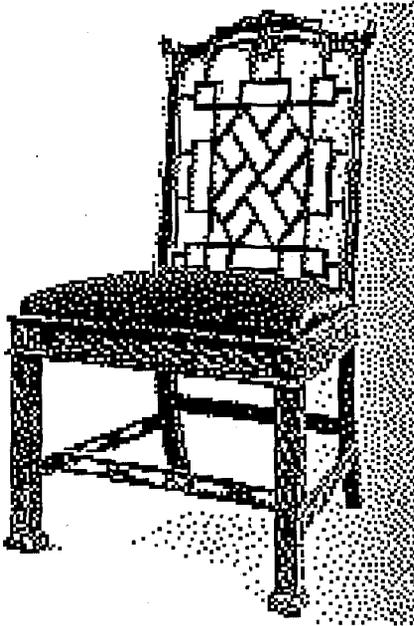


Fig. 1. Examples of chair and face stimuli used in the present experiment.

Data Analysis

EEG and EOG were epoched off-line into periods of 700 msec, starting 100msec prior to the onset of a stimulus, and ending 600msec, after stimulus onset. Trials with eyeblinks (vertical EOG exceeding 60 μV in the 600msec interval following imperative stimulus onset) or lateral eye movements (horizontal EOG exceeding $\pm 30 \mu\text{V}$ in the 600 msec interval following stimulus onset), response errors, or overt responses on nontarget trials were excluded from analysis. For the ERP analysis, only the data from nonrepetition trials (parts A and Q and nontarget trials (parts B) were analysed. EEG was averaged separately for the three experimental parts for all combinations of stimulus type (male, female, chair) attended category (attend face vs. attend chair), and stimulus side (left vs. right, part C). For part B, separate averages were computed for blocks where a male or a female face served as target stimulus. For all analyses except one, averages obtained to male and female face stimuli were collapsed.

All measures were taken relative to the mean voltage of the 100msec interval preceding stimulus onset. ERP effects of experimental variables were determined by conducting repeated measures analyses of variance on ERP mean amplitude values within three post-stimulus time windows (P1: 90–120msec; N1: 135–180msec; Nd: 200–260msec). Repeated measures ANOVAs were conducted separately for centrally presented stimuli (parts A and B) and laterally presented stimuli (part C) on ERP mean amplitude measures obtained at midline and lateral posterior sites. P1 effects were only analysed for lateral posterior electrodes. The following factors were included: stimulus category (face vs. chair), attention (attend face vs. attend chair), electrode location (temporal vs. occipital for lateral sites; frontal vs. central vs. parietal for midline sites), and recording side (left vs. right for lateral sites). For centrally presented stimuli, experimental condition (part A vs. part B), was included as a factor; for laterally presented stimuli, stimulus position (left vs. right) was included. When appropriate, additional ANOVAs were conducted for a single stimulus category or electrode location. For the ERPs elicited by faces in part B, an additional

analysis was conducted to investigate effects of attention directed to male or female faces. Reaction times (RTs) obtained in response to target stimuli were submitted to a repeated measures ANOVA with attention (attend face vs. attend chair) and experimental part (A, B, and C) as factors. Greenhouse-Geisser adjustments to the degrees of freedom were performed when appropriate.

RESULTS

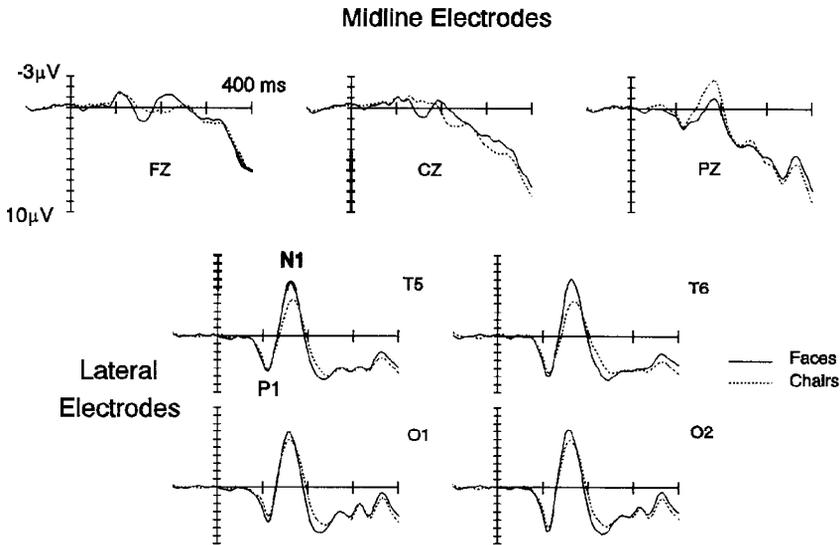
Behavioural performance

RTs to target stimuli were 487msec, 488msec, and 534 msec in parts A, B, and C, respectively. These differences were reflected in an effect of experimental part [$F(2,22) = 7.62$; $P < .008$; $\epsilon = 0.738$]. Additional t -tests revealed significant differences between the RTs obtained for peripheral targets (part C) and for central targets (parts A and B). RTs did not differ significantly for face and chair targets (488 vs. 487msec, 525 vs. 542 msec, for centrally and peripherally presented faces and chairs, respectively). Incorrect responses to nontarget stimuli were observed in less than 0.4% of all trials. Subjects missed 2.9%, 1%, and 6.1% of the targets in parts A, B, and C, respectively.

Event-related Brain Potentials: Centrally Presented Stimuli (Parts A and B)

Figure 2 (top) shows ERPs elicited by non-target faces and chairs at midline and lateral posterior sites, collapsed over parts A and B. The resulting face-chair difference waveforms are shown in Fig. 2 (bottom, solid lines) together with the difference waves obtained in the lateral presentation condition (part C). At lateral posterior sites, P1 amplitudes were slightly larger for faces than for chairs [$F(1,11) = 6.45$; $P < .027$], and an interaction between stimulus category and electrode location was obtained [$F(1,11) = 8.17$; $P < .016$]. Further analyses revealed that this P1 amplitude difference was significant at occipital electrodes [$F(1,11) = 9.12$; $P < .012$], but not at temporal sites. In the NI interval, mean amplitudes to face

Centrally Presented Stimuli



Difference Waveforms Faces - Chairs

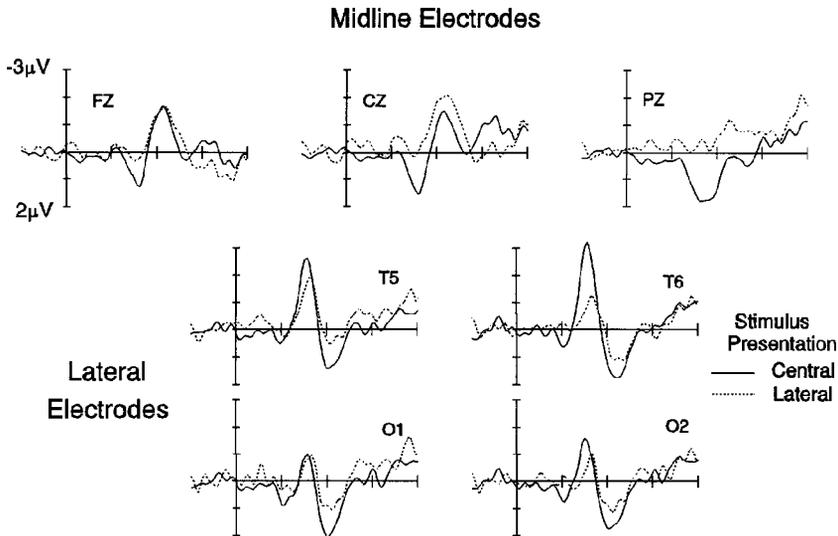


Fig. 2. Top: Grand-averaged ERPs recorded at midline and lateral posterior electrodes in response to faces (solid lines) and chairs (dashed lines) in the central presentation conditions (parts A and B). Bottom: Difference waveforms obtained by subtracting ERPs to chairs from ERPs to faces in the central presentation conditions (parts A and B, solid lines) and the lateral presentation condition (part C, dashed lines).

stimuli were more positive than ERPs to chairs at midline sites [$F(1,11) = 24.11$; $P < .001$]. At lateral sites, the effect of stimuli category approached significance [$F(1,11) = 4.05$; $P < .069$], and was accompanied by a significant category \times electrode location interaction [$F(1,11) = 27.79$; $P < .001$]. As can be seen from Fig. 2, faces elicited an enlarged NI as compared to chairs, and this effect was larger at temporal sites. Subsequent analyses revealed a significant effect of stimulus category at temporal electrodes [$F(1, 11) = 10.79$; $P < .007$] but not at occipital sites.

Figure 3 (top) shows ERPs elicited by face stimuli in blocks where faces were attended or unattended. Difference waveforms resulting from subtracting ERPs to unattended stimuli from attended-stimuli ERPs separately for faces and chairs are shown in Fig. 3 (bottom). All waveforms were collapsed over parts A and B. No effect of attention was obtained in the NI interval at midline electrodes. At lateral posterior sites, a main effect of attention approached significance [$F(1,11) = 3.77$; $P < .078$], and an interaction between stimulus category and attention was obtained [$F(1, 11) = 5.94$; $P < .033$]. As can be seen in Fig. 3, an enhanced negativity in the N1 time range was elicited at lateral electrodes by attended as compared to unattended faces. No such enhancement was present for chairs. This was confirmed by additional analyses of ERPs obtained at lateral posterior sites that were conducted separately for each stimulus category. For faces, attention affected N1 amplitude significantly [$F(1,11) = 7.16$; $P < .022$], and no interaction between attention and electrode location was obtained [$F(1,11) < 1$]. In contrast to the category-specific N1 effect that was largely restricted to temporal electrodes, the attentional N1 effect on face ERPs was present at temporal and occipital sites (see Fig. 3, bottom). No significant effects of attention were found in the N1 time range ERPs to chairs.

In the Nd interval (200–260msec), attention affected ERP amplitudes at midline electrodes as well as at lateral sites [$F(1,11) = 11.67$; $P < .006$; and $F(1,11) = 16.27$; $P < .002$, respectively], with enhanced negativities observed when a stimulus category was relevant. At midline sites, these effects

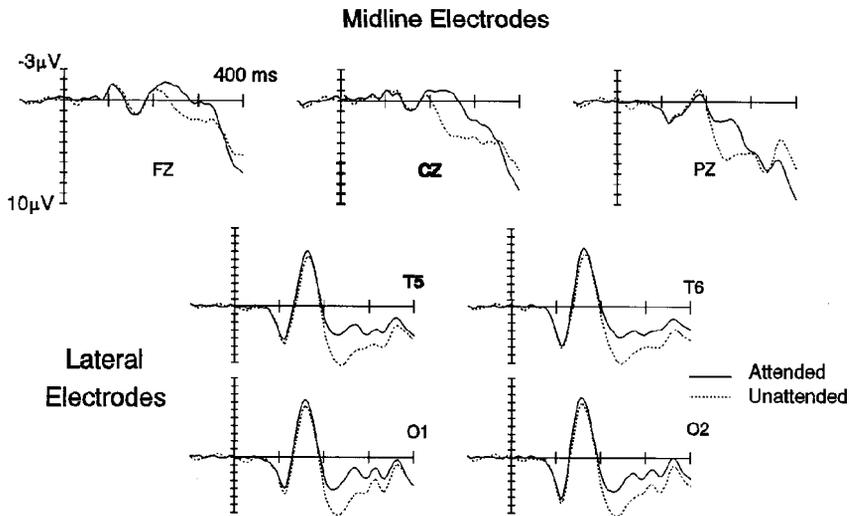
were larger for faces than for chairs (see Fig. 3, bottom), as evidenced by a stimulus category \times attention interaction [$F(1,11) = 10.09$; $P < .009$]. This interaction failed to reach significance at lateral posterior sites. At midline sites, an additional interaction between attention and electrode location was obtained [$F(2,22) = 5.31$; $P < .038$; $\epsilon = 0.544$], indicating that enhanced negativities for attended stimuli were larger at Cz and Pz than at Fz (Fig. 3, bottom). An interaction between experimental condition and attention that was significant at midline sites and almost significant at lateral electrodes [$F(1,11) = 5.04$; $P < .046$; and $F(1,11) = 4.73$; $P < .052$, respectively] indicated that these attentional effects tended to be larger in part B than in part A. Apart from this, no other interactions involving experimental condition and stimulus category and/or attention were obtained.

Figure 4 compares ERPs elicited by male and female nontarget faces when a same-sex or a different-sex face served as target. ERPs elicited by face stimuli of the attended sex were more negative than ERPs for unattended-sex faces, but these effects started later than the ERP effects of attention directed to faces as a category. No significant effects were found in the P1, N1, and Nd measurement window. An additional analysis was conducted on mean amplitude values obtained between 230msec and 300msec post-stimulus. An effect of attention to sex was found at lateral electrodes [$F(1,11) = 9.39$; $P < .011$], and subsequent analyses revealed significant differences between attended-sex and unattended-sex faces at all four lateral sites. At midline electrodes, this effect failed to reach significance [$F(1, 11) = 3.29$; $P < .097$].

Event-related Brain Potentials: Laterally Presented Stimuli (Part C)

Figure 5 (top) shows ERPs elicited by nontarget faces and chairs at midline and posterior sites ipsilateral and contralateral to the visual field of stimulus presentation. Face-chair difference waves are shown in Fig. 2 (bottom, dashed lines) together with the difference waves obtained in the central presentation condition. No effect of stimulus category on P1 amplitude was present. In contrast to

ERPs to Face Stimuli



Attended - Unattended Difference Waves

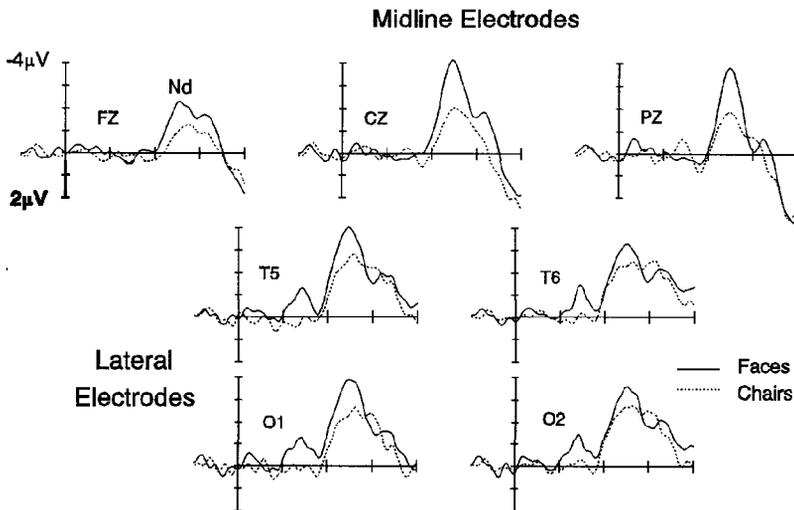


Fig. 3. Top: Grand-averaged ERPs recorded at midline and lateral posterior electrodes in the response to attended faces (solid lines) and unattended faces (dashed lines) in the central presentation conditions (parts A and B). Bottom: Difference waveforms obtained by subtracting ERPs to unattended stimuli from ERPs to attended stimuli in the central presentation conditions (parts A and B) separately for faces (solid lines) and chairs (dashed lines).

ERPs to Face Stimuli

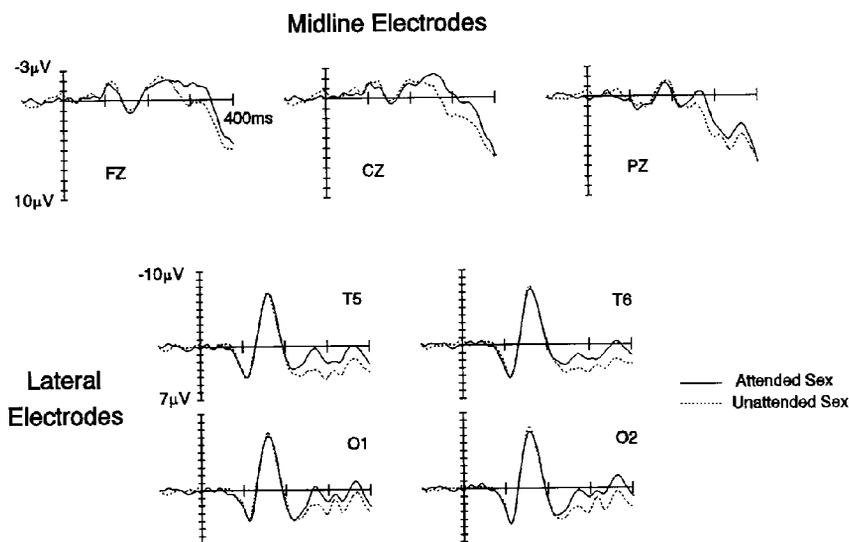


Fig. 4. Grand-averaged ERPs recorded in response to faces at midline and lateral posterior electrodes in part B in blocks where faces served as targets, displayed separately for faces of the same sex as the target (attended sex: solid lines) and faces of the opposite sex as the target (unattended sex: dashed lines).

the results obtained with central stimuli, no significant differences between faces and chairs were found in the N1 interval at midline electrodes, but face-specific N1 modulations similar to the central presentation conditions were present at lateral posterior electrodes (Fig. 2, bottom). A category \times electrode location interaction [$F(1,11) = 22.93$; $P < .001$] was obtained. N1 amplitude was significantly larger for faces than for chairs at temporal sites [$F(1,11) = 6.08$; $P < .031$], while this effect was not significant at occipital electrodes. A category \times recording side \times stimulus side interaction ($F(1,11) = 7.54$; $P < .019$) indicated that this temporal face-specific effect was larger contralateral to the visual field of stimulus presentation (Fig. 5, top).

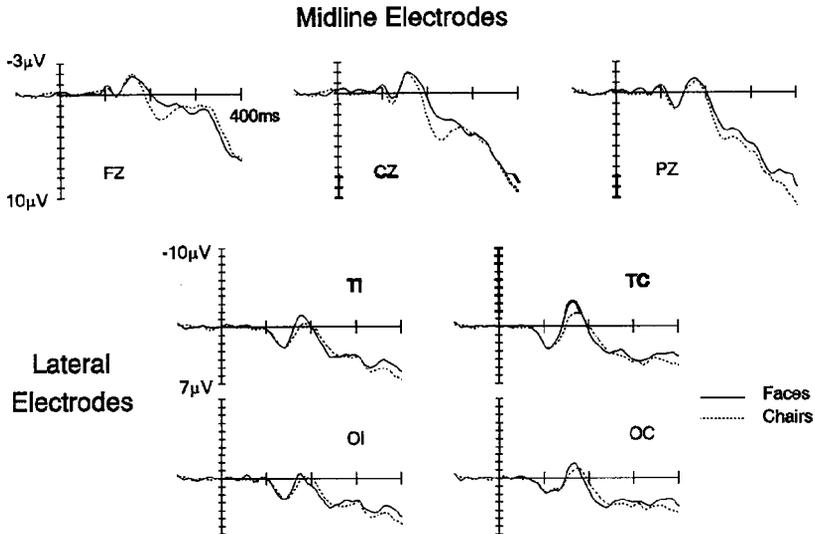
ERPs elicited by attended and unattended faces are shown in Fig. 5 (bottom). No significant attentional effects were found in the N1 interval. In the Nd interval, a main effect of attention at midline electrodes [$F(1,11) = 6.5$; $P < .027$] was accompanied by a category \times attention interaction [$F(1,11) = 10.67$; $P < .008$] reflecting enhanced

negativities for attended-category stimuli that were more pronounced with faces than with chairs. At lateral electrodes, a main effect of attention [$F(1,11) = 17.82$; $P < .001$] was present and no additional interaction was obtained.

DISCUSSION

The aim of the present study was twofold: First, we wanted to study differential effects of face and nonface stimuli on ERP waveforms, both for centrally presented and for lateral stimuli. Second, we wanted to investigate whether such effects would be modulated by selective attention. With respect to the first issue, the present results confirmed and extended previous findings. When compared with chairs, faces elicited an enhanced negativity at lateral temporal electrodes (T5, T6) and an enhanced positivity at midline sites in the N1 latency range (135–180 msec post-stimulus). The latter effect was observed for centrally presented faces, but not when faces were presented laterally. Jeffreys (1996)

Laterally Presented Stimuli



ERPs to Face Stimuli

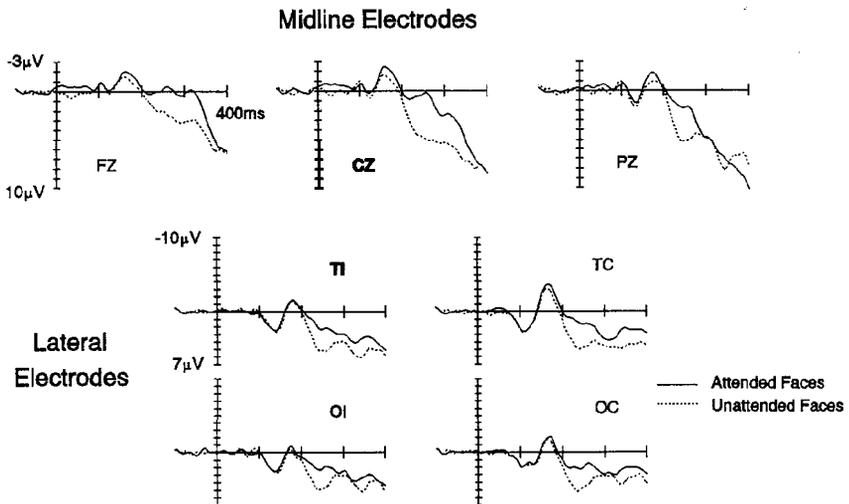


Fig. 5. Top: Grand-averaged ERPs recorded at midline and lateral posterior electrodes in response to faces (solid lines) and chairs (dashed lines) in the lateral presentation condition (part C). Bottom: Grand-averaged ERPs recorded at midline and lateral posterior electrodes in the response to attended faces (solid lines) and unattended faces (dashed lines) in the lateral presentation conditions (part C). Lateral posterior ERPs are shown for temporal and occipital electrodes ipsilateral (TI, OI) and contralateral (TC, OC) to the visual field of stimulus presentation.

reported a failure to obtain face-specific ERP effects (VPPs) for peripherally presented faces. Since his analysis was restricted to midline electrodes, he apparently missed the fact that similar to faces presented at fixation, peripheral faces elicit enhanced lateral temporal N1 amplitude. However, this effect seems to be considerably smaller for peripheral than for foveal faces (Fig. 2, bottom). The present study thus demonstrated that face-specific ERP modulations can be obtained in response to peripherally presented stimuli. The fact that face-specific temporal N1 enhancements were elicited by peripheral faces in the absence of any midline VPP may be seen as evidence against the idea that these two ERP effects reflect a unitary generator.

The face and nonface (chair) stimuli employed in the present study were presumably not completely equivalent with respect to their low-level visual features, which may explain why a slightly larger occipital P1 component was elicited by faces as compared to chairs in the central presentation condition (Fig. 2, top). It is, however, unlikely that such differences are responsible for the face-specific ERP effects observed in the present experiment. The effects reflected in the face-chair difference waveforms are very similar to face-specific ERP effects reported in previous studies where all sorts of different nonface stimuli were employed (Bentin et al., 1996; Bötzel et al., 1995; George et al., 1996). It is thus unlikely that these effects are primarily due to our specific choice of nonface stimuli. In subsequent, yet unpublished experiments in our lab, face ERPs were compared to ERPs elicited by different stimulus types (houses, objects, landscapes, human hands), and face-specific ERP effects were obtained that were highly similar to the effects reported here.

The second aim of the present study was to find whether face-specific ERP modulations are affected by selective attention. ERP effects of attention were present in the Nd time range (200–260msec) for faces and for chairs in the central and peripheral presentation conditions. In this interval, an enhanced negativity was elicited by items of the relevant category at midline and at lateral posterior electrodes. This effect is likely to reflect an

attentional selection negativity (Harter & Guido, 1980). Broadly distributed negativities are usually found in ERP studies of attentional selectivity and are presumably related to the detection and representation of task-relevant stimulus attributes (see Näätänen, 1990). The fact that similar Nd effects were observed for faces and chairs indicates that the underlying processes are not specifically related to face processing. Attention directed to male or female faces affected ERP waveforms obtained in part B in a similar way. Enhanced negativities were obtained for attended-sex faces beyond 230msec post-stimulus. This effect, which was significant at lateral posterior electrodes, may reflect the detection of features that differentiate between male and female faces (e.g. hair style).

Prior to these Nd effects, an attentional modulation of the N1 component was obtained at lateral posterior electrodes in the central presentation conditions. In contrast to the longer-latency effects of selective attention, this modulation was restricted to face ERPs, and was absent in the attended-unattended difference waveforms for chairs (Fig. 3, bottom). Since the lateral posterior N1 has been repeatedly shown to be selectively sensitive to face stimuli, the observation that its amplitude is affected by selective attention directed to or away from faces may be interpreted as further evidence for an attentional modulation of processing in face-specific brain areas, in line with the fMRI effects reported by Wojciulik et al. (1998). As an alternative, one could argue that the N1 amplitude differences between “detect faces” and “detect chairs” blocks are not specific to face processing, but rather reflect differences in task difficulty. For several reasons, this is not very likely. First, RTs were not significantly different for face and for chair targets. Second, if the N1 effects were an unspecific reflection of task difficulty, one should predict analogous effects for ERPs elicited by chairs, which was clearly not the case. Third, differential task requirements between conditions typically manifest themselves in ERP waveforms as sustained negativities with durations of at least 100–200msec. The posterior face-specific attention effects observed in the present experiment were clearly more transient in nature (Fig. 3, bottom). More problematic for the

idea that the attentional NI modulations obtained for centrally presented faces reflect the impact of selective attention on the processing of face-specific brain areas is the fact that these effects were equally large at temporal and occipital electrodes, whereas the face-specific ERP modulations were distributed temporally. Further experiments using more dense electrode arrays will be necessary to investigate the scalp distribution of these effects in more detail.

There were several other notable findings regarding the effects of category-specific attention on ERP waveforms. First, the two attentional manipulations for centrally presented items in parts A and B (detect repetitions of faces or chairs vs. detect face or chair targets) yielded equivalent attentional effects. There were no interactions involving experimental condition, except for the fact that attentional Nd effects beyond 200msec post-stimulus were larger in part B. Second, although centrally presented faces elicited enhanced N1 amplitudes at lateral temporal electrodes and a broadly distributed VPP at midline sites, early attentional effects were completely absent at midline sites. This apparent dissociation in the sensitivity of face-specific ERP components to attentional manipulations may be taken as additional evidence that the temporal negativities and the VPP do not reflect a unitary neuronal source. Third, no significant effect of selective attention on lateral posterior N1 amplitude was found for laterally presented faces. While this may indicate that selective attention affects the processing of foveal and peripheral faces differentially, such a conclusion may be premature. Similar to the fMRI activations reported by Wojciulik et al. (1998), face-specific effects were considerably smaller for lateral than for central stimuli (see Fig. 2, bottom). It is possible that any superimposed attentional modulations were simply too small to be reliably detected on the basis of the relatively small number of trials collected in part C.

In summary, the present experiment found enhanced NI amplitudes at lateral temporal sites and a broadly distributed VPP at midline electrodes specifically elicited by centrally presented faces. The former, but not the latter, effect was also pres-

ent for peripheral faces. Selective attention was reflected in a category-unspecific Nd effect starting around 200msec post-stimulus, and in an earlier modulation of the lateral posterior N1 that was only observed for centrally presented faces. This effect may be related to a selective attentional modulation of processing within face-specific brain areas.

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