

Research report

The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials

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Abstract

To investigate whether the processing of faces and emotional facial expression can be modulated by spatial attention, ERPs were recorded in response to stimulus arrays containing two faces and two non-face stimuli (houses). In separate trials, attention was focused on the face pair or on the house pair, and facial expression was either fearful or neutral. When faces were attended, a greater frontal positivity in response to arrays containing fearful faces was obtained, starting about 100 ms after stimulus onset. In contrast, with faces located outside the attentional focus, this emotional expression effect was completely eliminated. This differential result demonstrates for the first time a strong attentional gating of brain processes involved in the analysis of emotional facial expression. It is argued that while an initial detection of emotionally relevant events mediated by the amygdala may occur pre-attentively, subsequent stages of emotional processing require focal spatial attention. The face-sensitive N170 component was unaffected by emotional facial expression, but N170 amplitudes were enhanced when faces were attended, suggesting that spatial attention can modulate the structural encoding of faces.
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1. Introduction

Rapid awareness of impending danger is a crucial aspect of the interplay between humans and their environment, and neural systems have evolved to allow the expedient perceptual analysis of potentially aversive stimuli [10,23,32]. The tendency to prioritise threat-related information has been demonstrated in behavioural studies, including visual search [12,18,19,33,34] and modified dot probe tasks [26,27]. In these studies, negatively valenced stimuli are typically detected faster than neutral stimuli.

Numerous studies have established the importance of the amygdala in mediating responses to fear-eliciting stimuli, and have suggested that it might play a critical role in the detection of these stimuli. Studies of the monkey brain

[2,3] have revealed extensive reentrant projections from the amygdala back to occipital cortex. Through these projections, early visual processing of emotionally salient stimuli may be enhanced, leading to the selection of motivationally relevant stimuli. Functional neuroimaging studies in humans have provided evidence consistent with this view [4,22,30]. Emotionally charged stimuli, particularly fearful facial expressions, elicit specific neural responses in the amygdala and other connected limbic structures [24,29]. An amygdala response will occur even when the stimuli are masked and thus inaccessible to conscious awareness [31,43]. Enhanced amygdala activation, in turn, may give rise to greater neural activity in modality-specific sensory cortical areas [4,22,30], suggesting that connections between the amygdala and perceptual regions subserve a process by which emotionally significant stimuli receive high processing priority. This hypothesis is also supported by recent investigations of patients with unilateral neglect and visual extinction, disorders

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characterised by impaired mechanisms of spatial attention following damage to the parietal lobe. When presented in the affected visual hemifield, emotionally significant pictures were more likely to be detected than neutral pictures [40,41]. This suggests that the prioritising of stimuli due to their emotional value may operate partially independently of the fronto-parietal network implicated in spatial attention.

Recent event-related brain potential (ERP) studies have provided insights into the time course of emotional processing. A positive slow wave starting at about 300 ms after stimulus onset is elicited in response to pictures with emotional content [9,11], and has been interpreted as reflecting sustained selective attention directed to motivationally relevant input [9]. More recently, Eimer and Holmes [16] have shown that a larger positivity in response to fearful relative to neutral face stimuli is elicited over prefrontal areas within 120 ms after stimulus onset. This suggests that cortical circuits involved in the detection of emotionally significant events can be triggered rapidly by emotional facial expressions. A direct route linking the amygdala to orbitofrontal cortex could act as an early warning system, initiating autonomic responses, shifts of selective attention, and rapid action in response to emotionally salient stimuli (see also Ref. [20]).

While a substantial body of evidence exists concerning the selective modulation of neural activity by emotional stimuli, less is known about the influence of spatial attention on the processing of affective material. Recent neuroimaging studies have yielded conflicting findings: In one fMRI study, the amygdala response to fearful faces in humans was unaffected by spatial attention [42]. Similarly, an earlier PET study showed that amygdala activation by highly arousing emotional scenes was not affected by a secondary divided-attention task, whereas visual cortical activity was decreased by distraction [21]. These results suggest that emotional stimuli are detected pre-attentively, and may capture attention automatically, irrespective of the current focus of spatial attention. However, a recent fMRI study found that amygdala responses to both fearful and happy facial expressions were increased by focal attention [25], suggesting some modulation of responses to emotional stimuli by attentional processes. In addition, increased responses to attended fearful faces have been observed in other brain areas, including the anterior temporal pole and anterior cingulate gyrus [42].

The primary aim of the present ERP study was to further investigate the influence of attention on emotional processing, using stimuli and procedures similar to those employed in previous fMRI [42,44] and ERP [16] experiments. Participants were presented with arrays consisting of two faces and two houses arranged in horizontal and vertical pairs (see Fig. 1). The location of face and house pairs (vertical versus horizontal) and emotional facial expression (fearful versus neutral) varied randomly across trials. The task was to attend either to the two vertical or to the two horizontal locations (as indicated by a precue

presented at the beginning of each trial), in order to detect and respond to infrequent target stimuli (two identical photographs) at cued locations. Stimulus pairs at uncued locations could be entirely ignored.

ERP modulations sensitive to emotional facial expression were identified by comparing ERPs elicited by arrays containing fearful faces to ERPs in response to arrays with neutral faces. To investigate the impact of spatial attention on the processing of emotional facial expression, these comparisons were conducted separately for trials where faces were presented at cued (attended) locations, and for trials where houses were attended, and faces could be completely ignored. If emotional facial expressions are detected pre-attentively, and attract attention automatically, ERP responses to fearful versus neutral faces should be unaffected by the current focus of spatial attention. In contrast, if the processing of emotional faces is gated by spatial attention, ERP correlates of emotional face processing should be earlier and more pronounced on attend-faces trials than on attend-houses trials. Such a finding would cast doubt on the idea that the detection and processing of emotional facial expression is entirely independent of selective attention.

One additional aim of the present study was to investigate whether the face-sensitive N170 component, which is assumed to reflect the structural encoding of faces prior to face recognition [5,13,14], is affected by spatial attention. Earlier ERP studies have provided conflicting evidence as to whether the N170 is [15] or is not [8,38] modulated by selective attention. However, faces were always presented at fixation, and without competing distractor items in these experiments. In the present study, spatial attention was manipulated while presenting faces laterally and concurrently with non-face distractors, thus increasing the demands on attentional selectivity. Effects of spatial attention on the structural encoding of faces, as reflected by the N170 component, should result in enhanced N170 amplitudes on trials where faces are presented at attended locations relative to trials where faces appear at uncued positions.

2. Materials and methods

2.1. Participants

Twenty healthy subjects participated in this study. Two subjects had to be excluded because of excessive eye blinks, so that 18 subjects (11 female and seven male; 18–32 years old; average age: 23.7 years) remained in the sample. The experiment was performed in compliance with relevant institutional guidelines, and was approved by the School of Psychology ethics committee.

2.2. Stimuli

Photographs of faces of ten different individuals and of

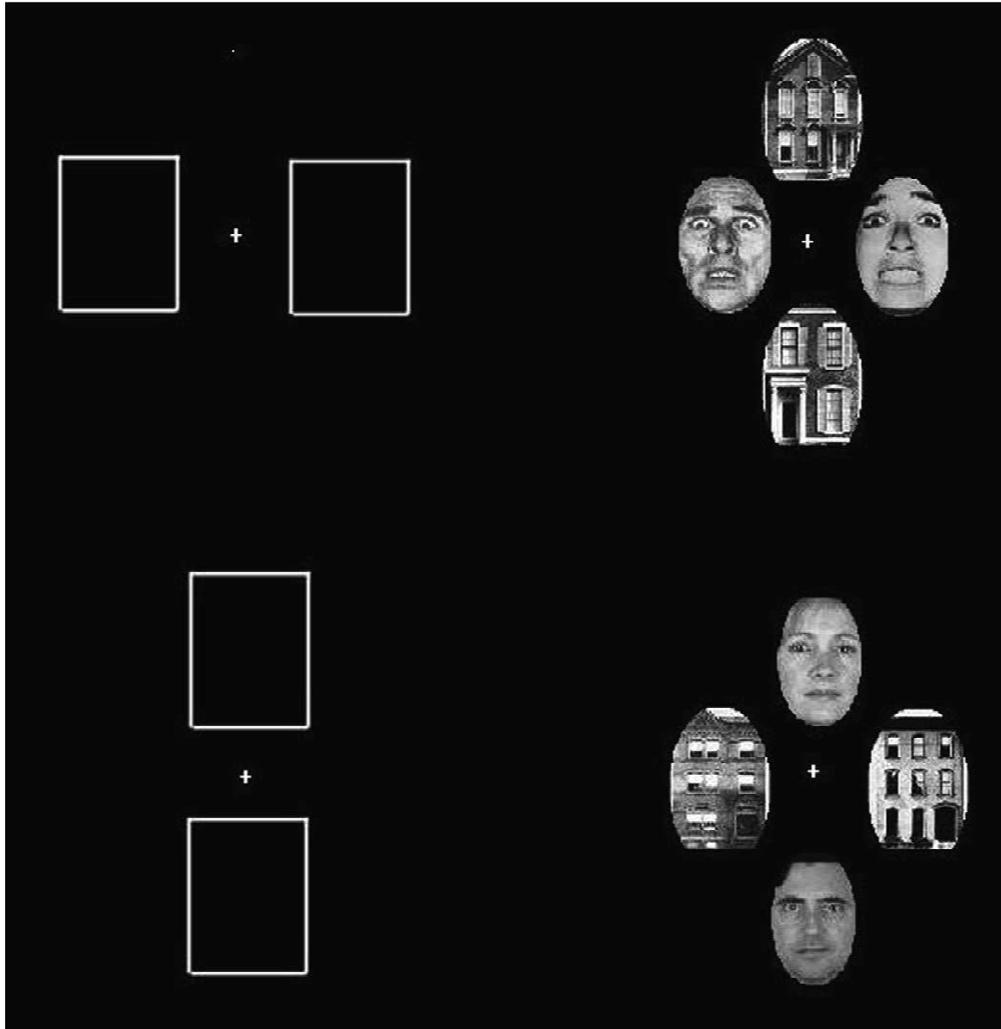


Fig. 1. Illustration of the stimulus presentation procedure used in this experiment. Each trial started with a cue (80 ms duration) directing attention to two horizontal (top left) or two vertical positions (bottom left). 720 ms after cue offset, a stimulus array consisting of two houses and two faces was presented for 300 ms. Face pairs were presented horizontally, and houses vertically (top right), or vice versa (bottom right), and faces were either fearful (top right) or neutral (bottom right). The figure shows non-target trials with non-identical fearful faces (top) or neutral faces (bottom) at cued (attended) locations. In target trials, identical stimuli were presented at cued locations.

ten different houses were used as stimuli. All faces were taken from a standard set of pictures of facial affect [17]. Facial expression was either fearful or neutral, resulting in a total of 20 different face stimuli. All stimuli covered a visual angle of about $2.5 \times 3.5^\circ$.

2.3. Procedure

Subjects were seated in a dimly lit sound-attenuated cabin, and a computer screen was placed at a viewing distance of 70 cm. The experiment consisted of ten experimental blocks, each containing 68 trials. In each trial, two face stimuli were presented together with two house stimuli, and stimuli from the same category were always arranged in vertical and horizontal pairs (see Fig. 1). The eccentricity of these stimuli (measured as the distance between the centre of each stimulus and the central fixation cross) was 2.5° , and all stimuli were

presented in front of a dark background. At the beginning of each trial, a precue was presented that instructed subjects to direct attention to the two vertically aligned or the two horizontally aligned positions. This cue consisted of two white rectangles ($3.0 \times 3.5^\circ$ visual angle) presented at either both horizontal or both vertical locations (Fig. 1). Each trial began with an 80-ms presentation of the attentional cue. Seven hundred and twenty milliseconds after the offset of the cue, the face/house stimulus array was presented for 300 ms. The interval between the offset of these stimuli and the beginning of the next trial was 1300 ms.

Subjects were instructed to direct their attention to the locations indicated by the cue, and to respond with a right-hand key press whenever they detected two physically identical stimuli at cued locations. Stimuli at uncued locations were to be ignored, regardless of their identity. Forty-eight trials per block were non-target trials, where

the stimulus array contained no identical stimuli. In these trials, paired faces and paired houses appeared randomly and with equal probability in the vertical and horizontal positions, and these positions were equally likely cued or uncued. Half of the faces were neutral, the other half were fearful. A total of six trials was presented per block for each of the eight possible combinations of stimulus location (faces horizontal/houses vertical, or vice versa), attentional focus (faces vs. houses at cued locations), and emotional facial expression (neutral vs. fearful). In the remaining 20 trials, one of the two stimulus pairs consisted of two identical stimuli. In eight of these trials, cued locations contained two identical faces (four trials with fearful or with neutral faces, respectively), and in four trials, they contained identical houses. A response was required only on these trials. In the remaining eight trials, identical face or house stimuli were presented at uncued locations, and these stimuli had to be ignored.

2.4. ERP procedures and data analysis

EEG was recorded with Ag–AgCl electrodes and linked-earlobe reference from Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, T5, P3, Pz, P4, T6, and Oz (according to the 10–20 system), and from OL and OR (located halfway between O1 and P7, and O2 and P8, respectively). Horizontal EOG (HEOG) was recorded bipolarly from the outer canthi of both eyes. The impedance for all electrodes was kept below 5 k Ω . The amplifier bandpass was 0.1 to 40 Hz, and no additional filters were applied to the averaged data. EEG and EOG were sampled with a digitisation rate of 200 Hz and stored on disk. Key-press onset times were measured for each correct response.

EEG and HEOG were epoched off-line into 1500-ms periods, starting 100 ms prior to cue onset and ending 600 ms after the onset of the subsequent imperative stimulus. Separate averages were computed for ERPs recorded in the cue–target interval (relative to a 100-ms baseline preceding cue onset), and for ERPs in response to imperative stimuli (relative to a 100-ms baseline preceding the onset of these stimuli). Trials with horizontal eye movements during the cue–target interval (HEOG exceeding ± 30 μ V), as well as trials with vertical eye movements, eyeblinks (Fpz exceeding ± 60 μ V), or other artefacts (a voltage exceeding ± 60 μ V at any electrode) measured after target onset were excluded from analysis.

The EEG obtained in response to imperative stimuli was averaged for non-target trials only, to avoid contamination by key-press responses. Trials where false-positive responses were recorded on non-target trials were excluded from analysis. Separate averages were computed for all combinations of stimulus position (faces horizontal/houses vertical, or vice versa), attention (faces-cued vs. houses-cued), and facial emotional expression (neutral vs. fearful), resulting in eight average waveforms for each electrode

and participant. Mean amplitude values were computed within four time windows. The first measurement interval was chosen to detect early frontal emotional expression effects [16], and was centred on the mean latency of the frontal N1 component (100–120 ms post-stimulus). The second latency window was centred on the mean latency of the face-sensitive posterior N170 component (160–200 ms post-stimulus). Two successive longer measurement windows (180–300 ms and 300–500 ms) were chosen to analyse expected sustained effects of emotional facial expression (cf. [16]).

Mean amplitude values obtained at lateral anterior sites (F7/8, F3/4, FC5/6), lateral central sites (T7/8, C3/4, CP5/6), lateral posterior sites (T5/6, P3/4, OL/R), and at midline electrodes (Fz, Cz, Pz) were submitted to separate analyses of variance (ANOVAs) with the factors electrode site, stimulus position, attention, and emotional expression. Additional analyses were conducted separately for faces-cued and houses-cued trials, omitting the factor attention. Analyses of attentional effects on the N170 component were restricted to lateral posterior electrodes T5/6 and OL/R. For key-press responses, repeated measures ANOVAs were performed on correct response latencies and on arcsin-transformed error rates for the factors target category (faces vs. houses) and target position (horizontal vs. vertical). Additional analyses were conducted to compare RTs in response to displays containing either fearful or neutral faces.

3. Results

3.1. Behavioural results

Responses to correctly detected identical stimulus pairs at cued locations were delayed for faces (721 ms) relative to houses (676 ms), resulting in a main effect of target category ($F(1,17)=24.7$; $P<0.001$). There was no effect of target position (horizontal versus vertical). RTs to cued face targets were not significantly influenced by their emotional expression, and RTs to target houses were not affected by the emotional expression of simultaneously presented distractor face pairs. Participants missed 31.5% of all cued identical faces, and 16.6% of cued identical houses (main effect of target category: $F(1,17)=16.7$; $P<0.001$). Targets were missed more frequently when presented vertically than horizontally (main effect of target position: $F(1,11)=31.3$; $P<0.001$), and this difference was more pronounced for faces (43% vs. 20% missed vertical and horizontal targets) than for houses (20.1% vs. 12.8%; target identity \times target position interaction: $F(1,17)=31.2$; $P<0.001$). The percentage of missed face targets or missed house targets was unaffected by facial emotional expression on target trials. False Alarms to non-target arrays were observed on 3.7% of trials where an identical stimulus pair was presented at uncued locations, and on 2.4% of trials

where no identical stimulus pair was present, and this difference was not significant. False Alarm rates were unaffected by the expression of non-target faces.

3.2. Electrophysiological results

Effects of attention directed to the location of faces or houses. Fig. 2 shows ERPs elicited in response to non-target arrays with faces at attended (cued) locations and houses at unattended (uncued) locations (solid lines), and to arrays where houses were attended and faces unattended (dashed lines). Fig. 3 shows ERPs elicited at lateral posterior electrodes, where the face-sensitive N170 component is maximal. Attention directed towards face pairs was reflected in an enhanced negativity at lateral posterior electrodes (Fig. 3), as well as an enhanced frontocentral positivity (Fig. 2), relative to trials where attention was directed towards houses. The face-sensitive N170 component was enhanced on trials where attention was focused on the face pairs relative to trials where faces were presented outside the attentional focus and could be ignored (Fig. 3). This was reflected in a main effect of attention at lateral posterior electrodes T5/6 and OL/R (both $F(1,17) > 11.8$; both $P < 0.003$) in the N170 analysis

ERPs for faces-cued and houses-cued trials

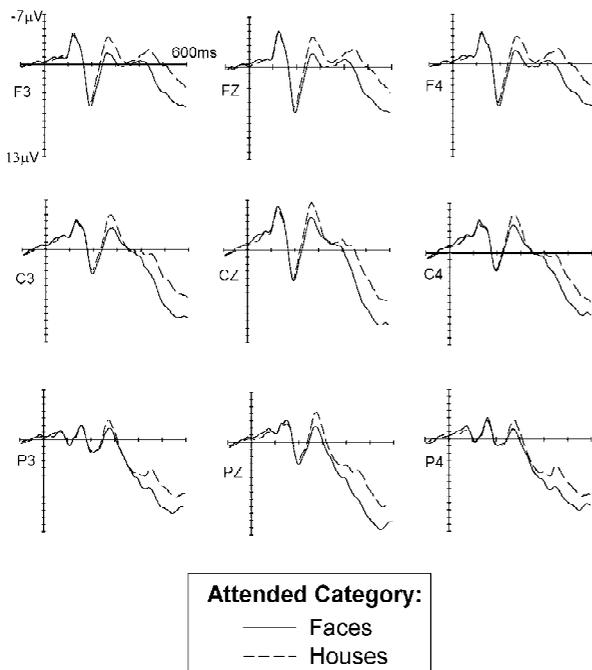


Fig. 2. Grand-averaged ERP waveforms elicited at midline sites and at lateral frontal, central, and parietal electrodes in the 600-ms interval following stimulus onset in response to non-target stimulus arrays containing face pairs at attended (cued) locations and house pairs at unattended (uncued) locations (solid lines), or vice versa (dashed lines), collapsed across stimulus positions (faces horizontal/houses vertical, and vice versa), and across trials where facial expression was neutral or fearful.

ERPs for faces-cued and houses-cued trials

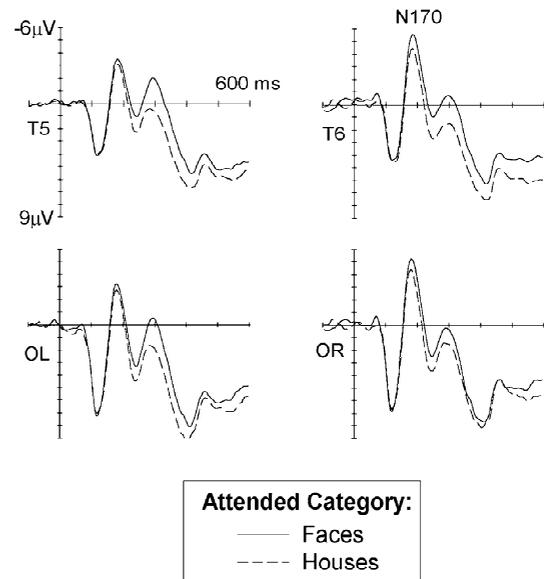


Fig. 3. Grand-averaged ERP waveforms elicited at lateral posterior electrodes T5/6 and OL/R in the 600-ms interval following stimulus onset in response to non-target stimulus arrays containing face pairs at attended (cued) locations and house pairs at unattended (uncued) locations (solid lines), or vice versa (dashed lines), collapsed across stimulus positions (faces horizontal/houses vertical, and vice versa), and across trials where facial expression was neutral or fearful.

window (160–200 ms). In contrast, no effects of attention were found at anterior, central, or midline electrodes within this latency range (Fig. 2). In the 180–300-ms and the subsequent 300–500-ms intervals, main effects of attention at lateral frontal, central, and midline sites (all $F(1,17) > 4.7$; all $P < 0.05$) were due to enlarged negativities for houses-cued trials relative to faces-cued trials (Fig. 2). The reverse pattern (enhanced negativities for faces-cued trials) was present at lateral posterior electrodes between 180 and 300 ms ($F(1,17) = 7.1$; $P < 0.018$; see Fig. 3),¹ but this effect failed to reach significance between 300 and 500 ms.

Effects of emotional facial expression and attention × emotional expression interactions. Figs. 4 and 5 show ERPs elicited in response to stimulus arrays containing fearful faces (solid lines) or neutral faces (dashed lines), displayed separately for trials where face pairs were presented at cued/attended locations (Fig. 4), and for trials where houses were presented at attended locations, and faces could be entirely ignored (Fig. 5). A consistent and sustained emotional expression effect was elicited when

¹The posterior negativity for faces-cued trials at lateral posterior electrodes in the 180–300 ms latency range may in principle be a carry-over effect from the earlier attentional modulation of the N170 component. This is, however, unlikely since the enhanced negativity for faces-cued trials observed at T5 and T6 between 180 and 300 ms was significantly larger than the enhanced negativity found at the same electrodes in the N170 time window (1.52 vs. 0.81 μV ; $t(17) = 3.17$; $P < 0.006$).

ERPs for faces-cued trials

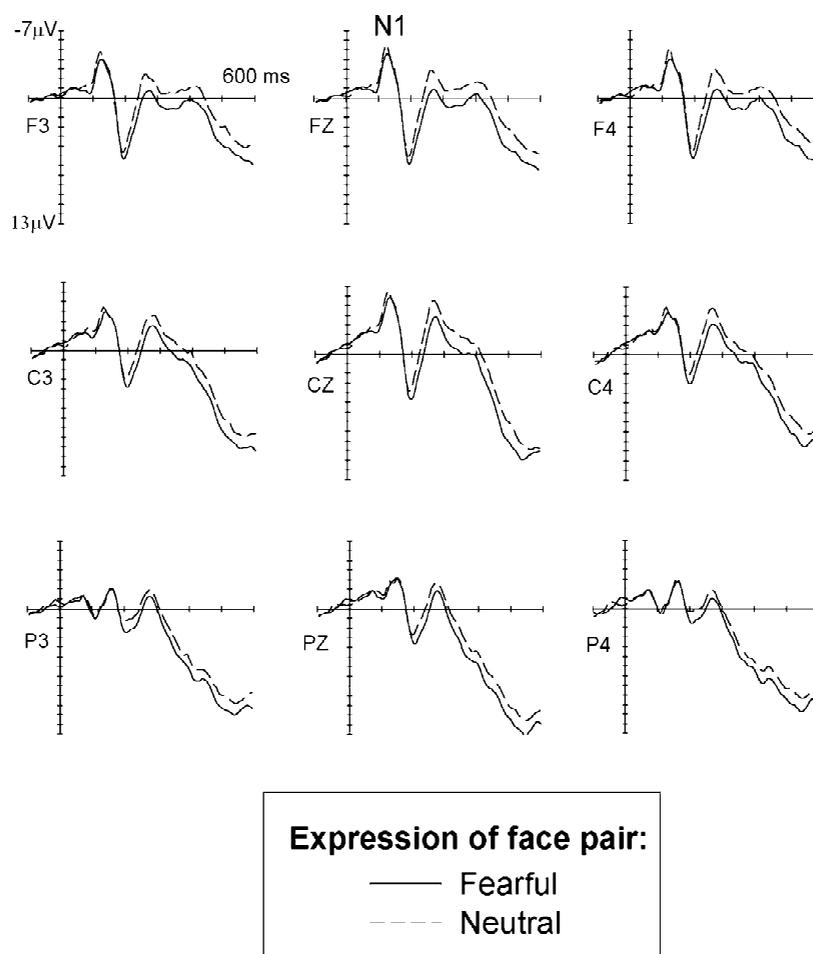


Fig. 4. Grand-averaged ERP waveforms elicited in the 600-ms interval following stimulus onset in response to non-target stimulus arrays obtained in trials where face pairs were presented at attended (cued) positions, collapsed across stimulus positions (faces horizontal/houses vertical, and vice versa). Solid lines represent ERPs in response to stimulus arrays including fearful faces, and dashed lines show ERPs in response to stimulus arrays with neutral faces.

faces were attended. Similar to earlier findings [16], a differential response, which can be described as an enhanced positivity (or reduced negativity), was triggered in response to fearful relative to neutral faces (Fig. 4). In contrast, this emotional expression effect appears to be completely eliminated in trials where faces were presented at unattended locations (Fig. 5).

These observations were substantiated by statistical analyses. An early emotional expression effect was obtained in the N1 time range (100–120 ms post-stimulus). Here, an attention \times emotional expression interaction was found at lateral anterior electrodes ($F(1,17)=4.9$; $P<0.05$). The anterior N1 component was significantly reduced in amplitude in response to attended fearful relative to neutral faces ($F(1,17)=5.5$; $P<0.05$). In contrast, no such effect was present for unattended faces. This early emotional expression effect was restricted to anterior sites during the N1 time window (see also Ref. [16]). In the subsequent 180–300 ms and the 300–500 ms measurement windows,

main effects of emotional expression (all $F(1,17)>4.7$; all $P<0.05$) at lateral anterior, lateral central, and midline sites were accompanied by significant attention \times emotional expression interactions at these sites (all $F(1,17)>6.8$; all $P<0.02$). Subsequent analyses conducted separately for faces-cued and houses-cued trials revealed larger positivities in response to stimulus arrays containing fearful as compared to neutral faces when faces were attended (all $F(1,17)>8.7$; all $P<0.01$; see Fig. 4). Most notably, and in marked contrast to the results for faces-cued trials, effects of emotional expression were entirely absent on houses-cued trials, where faces could be ignored (Fig. 5).

Fig. 6 shows ERPs elicited in response to arrays containing fearful and neutral faces at lateral posterior electrodes T5/6 during faces-cued trials (top) and houses-cued trials (bottom). Emotional expression effects were completely absent at lateral posterior electrodes, both for faces-cued or houses-cued trials. More specifically, the

ERPs for houses-cued trials

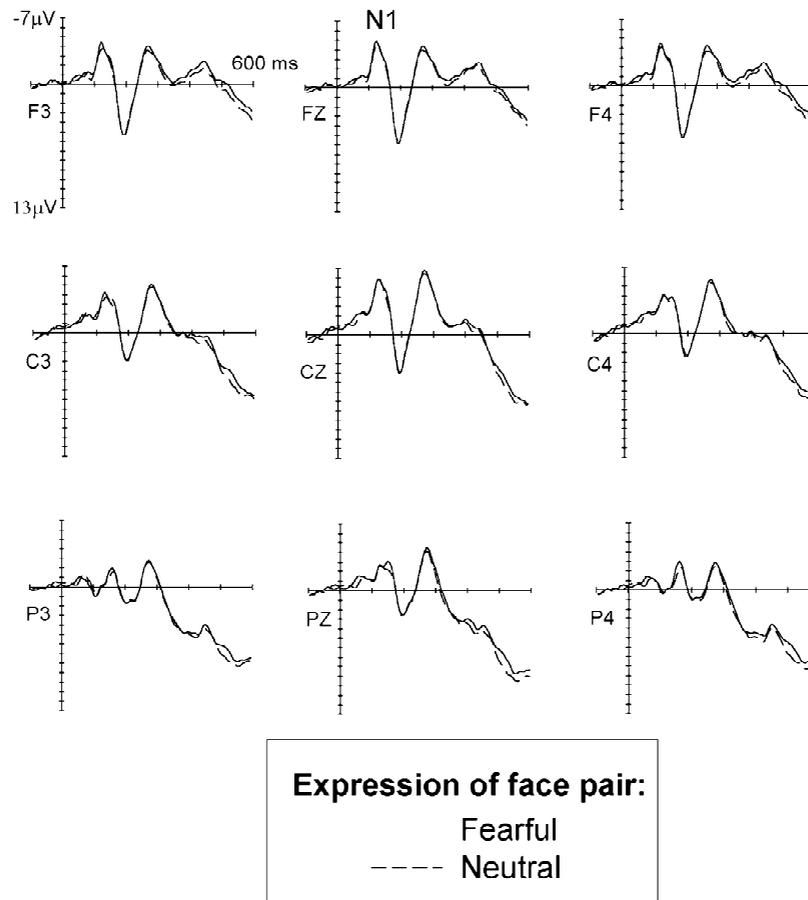


Fig. 5. Grand-averaged ERP waveforms elicited in the 600-ms interval following stimulus onset in response to non-target stimulus arrays obtained in trials where house pairs were presented at attended (cued) positions, and face pairs were uncued and could thus be ignored, collapsed across stimulus positions (faces horizontal/houses vertical, and vice versa). Solid lines represent ERPs in response to stimulus arrays including fearful faces, and dashed lines show ERPs in response to stimulus arrays with neutral faces.

face-sensitive N170 component at T5/6 was entirely unaffected by emotional facial expression (see Fig. 6).²

4. Discussion

The aim of the present study was to investigate whether the processing of faces and, more specifically, of emotionally relevant information conveyed by facial expression, is affected by spatial attention. ERPs were recorded in response to stimulus arrays containing two faces that could

either be fearful or neutral together with two houses. Face pairs and house pairs were presented with equal probability at cued (attended) and uncued (unattended) locations, under conditions where participants had to detect infrequent target stimulus pairs at cued locations, while ignoring stimuli at uncued locations.

To investigate effects of spatial attention on face-specific processing stages, ERPs elicited on faces-cued trials were compared to ERPs obtained on houses-cued trials, where faces were task-irrelevant and could be completely ignored. Attending to the location of faces versus houses produced a widespread modulation of posterior and anterior ERP components, in spite of the fact that visual displays were physically identical across attention conditions. The earliest effect of spatial attention was obtained at lateral posterior electrodes, where the face-sensitive N170 component, which is assumed to reflect the structural encoding of faces, was enhanced for faces-cued relative to

²Although Fig. 6 suggests that an enhanced negativity for fearful relative to neutral faces was elicited at electrodes T5/6 on houses-cued trials beyond 400 ms post-stimulus, this difference was not statistically significant within the 300–500 ms measurement window, nor within an additional later analysis period (400–600 ms post-stimulus).

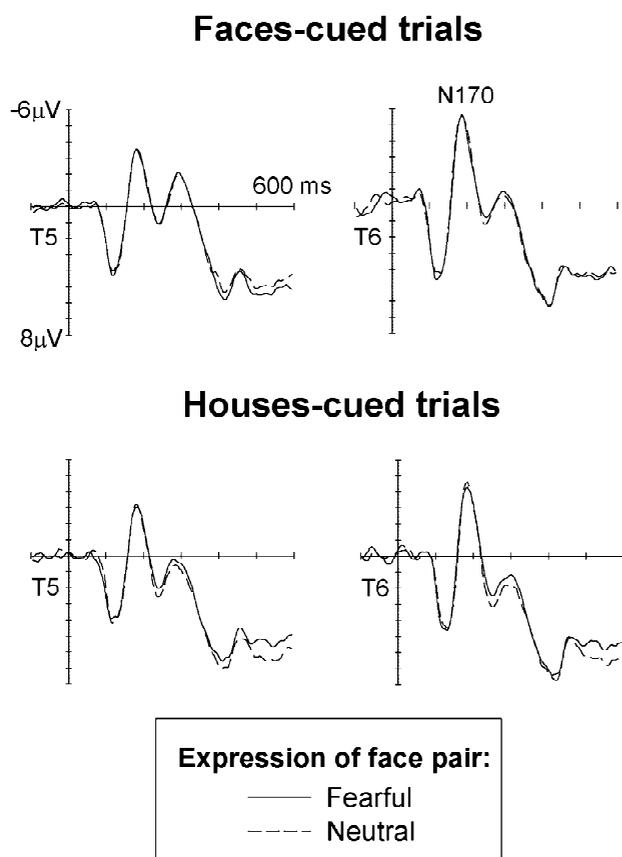


Fig. 6. Grand-averaged ERP waveforms elicited at lateral posterior electrodes T5/6 in the 600-ms interval following stimulus onset in response to non-target stimulus arrays containing fearful faces (solid lines), or neutral faces (dashed lines). Top panels: ERPs elicited for faces-cued trials. Bottom panel: ERPs elicited for houses-cued trials.

houses-cued trials (Fig. 3).³ This finding is consistent with fMRI results from studies using identical stimuli and a very similar paradigm [42,44], demonstrating an enhanced activity in face-sensitive fusiform areas during faces-cued trials. It should be noted that unlike previous ERP experiments which failed to obtain attentional effects on the N170 component [8,38], the present study manipulated spatial attention without changing the visual displays, where faces were presented laterally, and concurrently with distractors. The fact that N170 amplitudes were modulated by spatial attention under these conditions indicates that the structural encoding of faces can be affected by attention, provided that demands on attentional selectivity

³This N170 enhancement on faces-cued relative to houses-cued trials may primarily be a reflection of differences in task difficulty between these two types of trials. To investigate this possibility, a correlation was computed between the difference in N170 amplitudes for faces-cued versus houses-cued trials, as obtained at T5 and T6 for each participant, and the individual RT differences between these two types of trials (as a measure of the relative difference in task difficulty). These two measures turned out to be completely uncorrelated ($r=0.07$; $P=0.76$), which suggests that variations in task difficulty were at least not solely responsible for the observed effects of spatial attention on N170 amplitudes.

are sufficiently high. It should also be mentioned at this point that the design of this study precludes the testing of whether the N1/N170 component in response to houses was also modulated by spatial attention.

In addition to the attentional modulation of the face-sensitive N170 component, effects of spatial attention were also found at longer latencies. When compared to houses-cued trials, ERPs on faces-cued trials showed a sustained posterior negativity together with a frontocentral positivity. It is possible that these ERP modulations reflect a differential fusiform activity in response to attended versus unattended faces, as previously revealed by fMRI measures [42,44]. Longer-latency face-specific evoked components have also been observed in intracranial recordings from anterior fusiform gyrus [1], although the functional significance of these components is not yet clear. It should however be noted that the ERP differences between faces-cued and houses-cued trials obtained in the present study may at least partially be a reflection of differences in task difficulty between faces-cued and houses-cued trials. Similar to a previous fMRI study using the same stimulus material [42], reaction times and error rates indicated that target–non-target discriminations were somewhat more difficult in response to face pairs than to house pairs. This difference could have contributed to the ERP differences between faces-cued and houses-cued trials observed at longer latencies.

The central aim of the present experiment was to study interactions between spatial attention and emotional face processing, in order to find out whether the processing of emotional faces is affected by the current focus of spatial attention. ERPs in response to arrays containing fearful faces were compared to ERPs to arrays with neutral faces, separately for faces-cued and houses-cued trials. When faces were attended, fearful faces elicited a larger positivity as compared to neutral faces, thus confirming earlier observations [16,35,37]. Moreover, the present results replicate the finding that frontal emotional expression effects can be observed at very short latencies (between 100 and 120 ms post-stimulus; see [16]), and that these early frontal effects precede later, more broadly distributed emotional expression effects (Fig. 4). It is noteworthy that the early emotional expression effects we find here, as well as in our previous study [16], were generated prior to the peak of the face-sensitive N170 component. The N170 has been linked to ‘late’ stages of structural encoding [14], where representations of global face configurations are produced in order to provide a basis for further face recognition processing. It would appear therefore that facial expression is computed earlier and independently of global facial configuration, following a rudimentary encoding of face features. The extraction of information from an early stage of structural encoding for subsequent emotional expression processing is consistent with the face processing model proposed by Bruce and Young [7].

The critical new finding of the present study was that

these emotion-specific ERP modulations were strongly dependent on spatial attention. Both early as well as later emotional expression effects were completely eliminated on trials where faces were presented at unattended locations (Fig. 5). This marked and early effect of attention on ERP correlates of emotional face processing does not support the hypothesis that the detection and/or processing of emotional facial expression is entirely independent of the current focus of spatial attention. For example, if the rapid detection of emotional expression occurs pre-attentively, while its subsequent analysis may require focal attention, some ERP evidence for emotional face processing should be found at short latencies even when attention is directed away from the location of faces. The complete absence of any such effect on houses-cued trials thus provides evidence for a central role of attentional selectivity on the processing of emotionally relevant information—at least, when this information is provided outside of foveal vision—even at very short latencies after stimulus onset.

The conclusion from the present experiment that ERP modulations sensitive to emotional facial expression are gated by spatial attention, appears to contrast with results from a recent neuroimaging study using identical stimuli and similar procedures [42]. In this study, fear-related amygdala responses were elicited even when faces were located outside the current focus of attention (see also [31,43]).⁴ To resolve this apparent conflict between fMRI and ERP results, it should be noted that it is unlikely that the emotional expression effects observed in the present ERP study are generated in the amygdala, given its deep position and its nuclear structure of clustered neurones (unlike the regular alignment of neurones in layers of the neocortex). On the other hand, the fact that no ERP responses can be recorded from the amygdala because it is an electrically closed structure should not prevent it from modulating visual areas, as previous fMRI studies have shown [30]. It is therefore more likely that the discrepancy between the results observed here and in fMRI may instead be related to timing. Effects of emotional expression for unattended face stimuli may have taken place at very late stages of processing, beyond the post-stimulus recording window used here.⁵ It is possible that amygdala activations in response to emotional stimuli are unaffected by atten-

tional selectivity (but see Ref. [25]), while subsequent neocortical stages of emotional processing (as reflected by the emotional expression effects observed in the present study) are strongly dependent on focal attention. In line with the hypothesis that spatial attention affects emotional processing beyond the amygdala, interactions between emotional expression and spatial attention have in fact been demonstrated with fMRI measures in the anterior temporal pole and anterior cingulate gyrus [42]. The emotional expression effects observed in the present study might thus at least in part be generated in these areas, and/or in orbitofrontal cortex. Recently, short-latency emotion-specific single cell responses (120–160 ms) have been recorded in cortical areas connected with the amygdala, such as the orbitofrontal cortex [20]. These prefrontal responses may reflect emotional processing stages triggered by, and contingent upon, prior amygdala activations (see Refs. [36,23]).

Finally, another finding of the present study was that the face-sensitive N170 component was not modulated by emotional expression, irrespective of whether faces appeared inside or outside the focus of attention (Fig. 6). This replicates previous findings from depth electrodes [28] and scalp ERP [16], and thus provides additional evidence that the structural encoding of faces, as reflected by the N170, is certainly less sensitive to information derived from emotional facial expression than later recognition stages of face processing. However, activity within face-sensitive fusiform areas has been found to be modulated by emotional facial expression in several functional neuroimaging studies [4,6,21,42]. The fact that the N170 is insensitive to emotional expression could thus indicate that this component reflects facial processing at some earlier anatomical stage than fusiform gyrus proper (see also Ref. [5]). Alternatively, the N170 may reflect an early expression-independent stage of face processing in the fusiform gyrus. This early stage may be followed by further fusiform processing sensitive to emotional expression, perhaps mediated through re-entrant feedback signals from other brain areas (see Ref. [39]).

Overall, the present ERP results demonstrate that the processing of emotional expression is strongly modulated by selective spatial attention, and that this selective effect can be observed within 100 to 120 ms after stimulus onset. While there is substantial evidence for the obligatory and pre-attentive registration of emotional information in the amygdala [31,43], the present findings suggest that attentional gating processes play a crucial role during subsequent emotional processing stages. An adaptive advantage may be conferred by the fast and relatively automatic encoding of emotionally significant events occurring outside the focus of attention. Rapid fight, flight, or freezing behaviours may need to be primed in order to prepare the organism for dealing with environmental stressors. On the other hand, it is important that irrelevant affective stimuli do not continuously divert or ‘capture’ attention. Central

⁴The major difference between the design of the Vuilleumier et al. [41] and the present study is that blocked attentional cueing was employed in the former case, whereas trial-by-trial cueing was used here. If anything, trial-by-trial variation of attended locations might be expected to weaken spatial filtering, thus increasing rather than reducing the likelihood of emotional expression effects in the houses-cued condition. Furthermore, responses in the present study were required only to infrequent target pairs, as compared to each trial in the fMRI study [41]. This may have reduced the incentive to focus on cued stimuli further still. Nonetheless, the differential ERP modulations for faces-cued versus houses-cued trials demonstrate that participants did attend to cued locations.

⁵We would like to thank an anonymous reviewer for this suggestion.

mechanisms that allow distractibility to be minimised so that current goals and plans can be accomplished, are imperative to human functioning.

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