

Research Report

The role of spatial frequency information for ERP components sensitive to faces and emotional facial expression

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Abstract

To investigate the impact of spatial frequency on emotional facial expression analysis, ERPs were recorded in response to low spatial frequency (LSF), high spatial frequency (HSF), and unfiltered broad spatial frequency (BSF) faces with fearful or neutral expressions, houses, and chairs. In line with previous findings, BSF fearful facial expressions elicited a greater frontal positivity than BSF neutral facial expressions, starting at about 150 ms after stimulus onset. In contrast, this emotional expression effect was absent for HSF and LSF faces. Given that some brain regions involved in emotion processing, such as amygdala and connected structures, are selectively tuned to LSF visual inputs, these data suggest that ERP effects of emotional facial expression do not directly reflect activity in these regions. It is argued that higher order neocortical brain systems are involved in the generation of emotion-specific waveform modulations. The face-sensitive N170 component was neither affected by emotional facial expression nor by spatial frequency information.

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1. Introduction

A growing literature exists on the ability of humans to rapidly decode the emotional content of faces [2,30]. Perceived facial expressions are important social and communicative tools that allow us to determine the emotional states and intentions of other people. Such skills are critical for anticipating social and environmental contingencies, and underlie various cognitive and affective processes relevant to decision-making and self-regulation [18,19,23].

Electrophysiological investigations have contributed in important ways to our understanding of the time

course of emotional facial expression processing in the human brain, with human depth electrode and magnetoencephalography (MEG) studies revealing discriminatory responses to emotional faces as early as 100 to 120 ms post-stimulus onset [34,35,43]. One of the most reliable findings from scalp electrode studies is that emotional relative to neutral faces elicit an early positive frontocentral event-related potential (ERP) component. This effect occurs reliably within 200 ms of face onset [7,27,28,37], and has been found as early as 110 ms in a study by Eimer and Holmes [27]. A more broadly distributed and sustained positivity has been identified at slightly later time intervals (after approximately 250 ms: [7,27,40,45,60]). Whereas the early frontocentral positivity may reflect an initial registration of facial expression, the later broadly distributed sustained positivity, or late positive complex (LPC), has been linked to extended attentive processing of emotional faces [27].

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In addition to findings relating to the temporal parameters of expression processing, neuroimaging and lesion studies indicate that distinct brain regions subserve facial emotion perception [1]. Amygdala, cingulate gyrus, orbito-frontal cortex, and other prefrontal areas are all activated by emotional expressions in faces [11,14,24,48,52]. Little is known, however, about the relationships between these brain areas and electrophysiological correlates of emotional expression analysis.

One compelling finding from neuroimaging is that amygdala and connected structures, such as superior colliculus and pulvinar, are preferentially activated by low spatial frequency (LSF), but not high spatial frequency (HSF), representations of fearful faces [64]. Selective activation from LSF stimuli is consistent with anatomical evidence that these brain areas receive substantial magnocellular inputs [9,42,61], possibly as part of a phylogenetically old route specialised for the rapid processing of fear-related stimuli [21,41,50,56,59].

Magnocellular cells are particularly sensitive to rapid temporal change such as luminance flicker and motion, and have large receptive fields making them sensitive to peripheral and LSF stimuli. They produce rapid, transient, but coarse visual signals, and have a potential advantage in the perception of sudden appearance, location, direction of movement, and stimuli signalling potential danger. Conversely, parvocellular neurons are responsive to stimuli of low temporal frequencies, are highly sensitive to wavelength and orientation, and have small receptive fields that show enhanced sensitivity to foveal, HSF information. Parvocellular channels provide inputs to ventral visual cortex, but not to subcortical areas, and are crucial for sustained, analytic, and detailed processing of shape and colour, which are important for object and face recognition [15,39,44].

Given the heightened sensitivity of amygdala and connected structures to coarse (LSF) signals, driven by magnocellular afferents, and the capacity for the amygdala to modulate activation in higher cortical brain regions [40,49], it is of interest to see whether the early face emotion-specific frontocentral positivity and subsequent LPC would also reveal this sensitivity. Differential sensitivities to emotional expression information at high and low spatial scales are also apparent in tasks examining facial expression processing, with LSF information found to be important for expression discrimination, and HSF information found to be important for emotional intensity judgements [17,62,64]. The dissociation of low relative to high spatial frequency components of faces is also evident in the production of rapid attentional responses to LSF but not HSF fearful facial expressions [38].

An ERP investigation into the differential tunings for LSF and HSF information in facial expression processing may provide further indications of the possible functional significance and time course of these processes. To examine this issue, ERPs were recorded while participants viewed

photographs of single centrally presented faces (fearful versus neutral expressions), houses, or chairs. Stimuli were either unfiltered and thus contained all spatial frequencies (broad spatial frequency or BSF stimuli), or were low-pass filtered to retain only LSF components (≤ 6 cycles/image; ≤ 2 cycles/deg of visual angle), or high-pass filtered to retain only HSF components (≥ 26 cycles/image; ≥ 4 cycles/deg of visual angle). To preclude possible confounds relating to differences between these stimuli in terms of their brightness or contrast, all stimuli were normalised for their luminance and average contrast energy.

If LSF cues are more important than HSF cues in producing ERP modulations to fearful facial expressions, ERP effects of emotional expression triggered by fearful relative to neutral LSF faces should be more pronounced than effects observed for HSF faces. LSF faces might even elicit emotional expression effects comparable to the effects observed with unfiltered BSF faces. Alternatively, if such ERP effects were dependent on the availability of full spatial frequency information, they should be present for BSF faces, but attenuated or possibly even entirely absent for HSF as well as LSF faces.

Another aim of the present study was to investigate effects of both spatial frequency and emotional facial expression on the face-sensitive N170 component, which is assumed to reflect the structural encoding of faces prior to their recognition [8,25,26,58]. One recent study [33] has found enhanced N170 amplitudes for faces relative to non-face objects with LSF, but not HSF stimuli, suggesting that face processing might depend primarily on LSF information. We investigated this issue by measuring the N170 as elicited by faces relative to houses, separately for BSF, LSF, and HSF stimuli. With respect to the link between the N170 and emotional processing, several previous ERP studies using BSF faces have found that the N170 is not modulated by emotional facial expression [27,28,36,37], consistent with the suggestion that the structural encoding of faces and perception of emotional expression are parallel and independent processes [16]. Here, we investigated whether emotional facial expression might affect N170 amplitudes elicited by faces as compared to houses at different spatial scales.

2. Materials and methods

2.1. Participants

The participants were 14 healthy volunteers (9 men and 5 women; 24–39 years old; average age: 30.6 years). One participant was left-handed, and all others were right-handed by self-report. All participants had normal or corrected-to-normal vision. The experiment was performed in compliance with relevant institutional guidelines, and was approved by the Birkbeck School of Psychology ethics committee.

2.2. Stimuli

The face stimuli consisted of forty gray-scale photographs of twenty different individuals (10 male and 10 female), each portraying a fearful and a neutral expression. All face photographs were derived from the Ekman set of pictures of facial affect [29] and the Karolinska Directed Emotional Faces set (KDEF, Lundqvist, D., Flykt, A., and Öhman, A.; Dept. of Neurosciences, Karolinska Hospital, Stockholm, Sweden, 1998). The face pictures were trimmed to exclude the hair and non-facial contours. All pictures were enclosed within a rectangular frame, in a 198×288 pixel array. Each face subtended 5×7.5 deg of visual angle when presented centrally on a computer monitor at a 57-cm viewing distance. The house stimuli consisted of twelve photographs of houses that possessed the same spatial dimensions as the faces. For each of the 40 original face and 12 original houses, we computed a coarse scale and a fine scale version (see Fig. 1). Spatial frequency content in the original stimuli (broad-band; BSF) was filtered using a high-pass cut-off that was ≥ 26 cycles/image (≥ 4 cycles/deg of visual angle) for the HSF stimuli, and a low-pass cut-off of ≤ 6 cycles/image (≤ 2 cycles/deg of visual angle) for the LSF stimuli. Filtering was performed in Matlab (The Mathworks, Natick, MA) using second order Butterworth filters, similar to previous studies [62,66]. All face and house stimuli were equated for mean luminance and were normalised for root mean square (RMS) contrast subsequent to filtering in Matlab. RMS contrast has been shown to be a reasonable metric for perceived contrast in random noise patterns [51] and natural images [10]. This was implemented by calculating the total RMS energy of each



Fig. 1. Example stimuli. Fearful (top row) and neutral faces, and houses (bottom row) with a normal (intact) broad spatial frequency (BSF) content (left column) were filtered to contain only a high range or low range of spatial frequencies (HSF or LSF; middle and right columns, respectively). Please note that in order to enhance the clarity of print, these images are not matched for luminance or contrast energy.

luminance-equated image, and then dividing the luminance at each pixel in the image by this value. A further set of ten chairs, with similar measurements to the face and house stimuli, was used as target stimuli. The chair images were also filtered to produce BSF, HSF, and LSF version.

2.3. Procedure

Participants sat in a dimly lit sound attenuated cabin, and a computer screen was placed at a viewing distance of 57 cm. The experiment consisted of one practice block and sixteen experimental blocks (99 trials in each). In 90 trials within a single block, single fearful faces (BSF, HSF, LSF), single neutral faces (BSF, HSF, LSF), and single houses (BSF, HSF, LSF) were selected randomly by computer from the different sets of images, and were presented in random order, with equal probability. In the remaining 9 trials, single chairs (BSF, HSF, and LSF) were presented. Participants had to respond with a button press to the chairs (using the left index finger during half of the blocks, and the right index finger for the other half of the blocks, with the order of left- and right-handed responses counterbalanced across participants), and refrain from responding on all other trials. Stimuli were presented for 200 ms and were separated by an intertrial interval of 1 s.

2.4. ERP recording and data analysis

EEG was recorded from 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 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. Key-press onset times were measured for each correct response.

EEG and HEOG were epoched off-line relative to a 100-ms pre-stimulus baseline, and ERP analyses were restricted to non-target trials only, to avoid contamination by key-press responses. Trials with lateral eye movements (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.

Separate averages were computed for all spatial frequencies (BSF, HSF, LSF) of fearful faces, neutral faces, and houses, resulting in nine average waveforms for each electrode and participant. Repeated measures ANOVAs were conducted on ERP mean amplitudes obtained for specific sets of electrodes within predefined measurement windows. One set of analyses focussed on the face-specific N170 component and its positive counterpart at midline

electrodes (vertex positive potential, VPP). N170 and VPP amplitudes were quantified as mean amplitude at lateral posterior electrodes P7 and P8 (for the N170 component) and at midline electrodes Fz, Cz, and Pz (for the VPP component) between 160 and 200 ms post-stimulus. To assess the impact of spatial frequency on the N170 and VPP components irrespective of facial emotional expression, ERPs in response to faces (collapsed across fearful and neutral faces) and houses were analysed for the factors stimulus type (face vs. house), spatial frequency (BSF vs. HSF vs. LSF), recording hemisphere (left vs. right, for the N170 analysis), and recording site (Fz vs. Cz vs. Pz, for the

VPP analysis). To explore any effects of emotional expression on N170 amplitudes elicited at electrodes P7 and P8, an additional analysis was conducted for ERPs in response to face stimuli only. Here, the factor stimulus type was replaced by emotional expression (fearful vs. neutral).

Our main analyses investigated the impact of emotional expression on ERPs in response to BSF, HSF, and LSF faces at anterior (F3/4, F7/8, FC5/6), centroparietal (C3/4, CP5/6, P3/4), and midline electrodes (Fz, Cz, Pz). These analyses were conducted for ERP mean amplitudes in response to faces elicited within successive post-stimulus time intervals (105–150 ms; 155–200 ms; 205–250 ms; 255–400 ms;

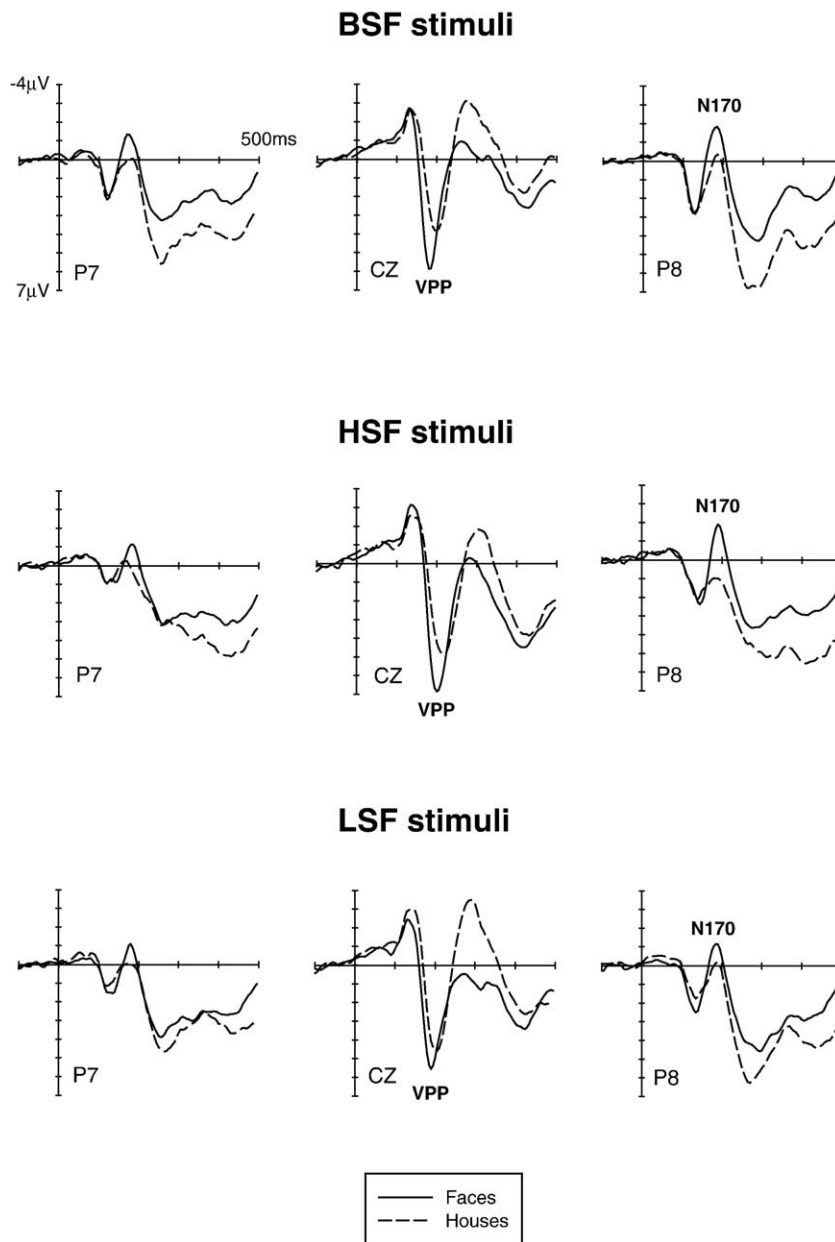


Fig. 2. Grand-averaged ERP waveforms elicited at lateral posterior electrodes P7/8 at and midline electrode Cz in the 500-ms interval following stimulus onset in response to faces (collapsed across neutral and fearful faces; solid lines) and houses (dashed lines), shown separately for broadband (BSF), high spatial frequency (HSF), and low spatial frequency (LSF) stimuli. A N170 component at lateral posterior electrodes is accompanied by a vertex positive potential (VPP) at Cz.

400–500 ms), for the factors spatial frequency, emotional expression, recording hemisphere (for lateral electrodes only), and electrode site. For all analyses, Greenhouse–Geisser adjustments to the degrees of freedom were performed when appropriate, and the corrected P values as well as ϵ values are reported.

3. Results

3.1. Behavioural performance

A main effect of spatial frequency ($F(2,26) = 32.4$; $P < 0.001$) on response times (RTs) to infrequent target items (chairs) was due to the fact that responses were fastest to BSF targets (360 ms), slowest to LSF targets (393 ms), and intermediate to HSF targets (376 ms). Subsequent paired t tests revealed significant differences between each of these stimulus conditions (all $t(13) > 3.6$; all $P < 0.003$). Participants failed to respond on 6.9% of all trials where a chair was presented, and this percentage did not differ as a function of spatial frequency. False Alarms on non-target trials occurred on less than 0.2% of these trials.

3.2. Event-related brain potentials

N170 and VPP components in response to faces versus houses. Fig. 2 shows the face-specific N170 component at lateral posterior electrodes P7 and P8 and the VPP component at Cz in response to faces (collapsed across fearful and neutral faces) and houses, displayed separately for BSF, HSF, and LSF stimuli. As expected, N170 amplitudes were enhanced for faces relative to houses, and this was reflected by a main effect of stimulus type on N170 amplitudes ($F(1,13) = 15.1$; $P < 0.002$). No significant stimulus type \times spatial frequency interaction was observed, and follow-up analyses confirmed the observation suggested by Fig. 2 that an enhanced N170 component for faces relative to houses was in fact elicited for BSF as well as for HSF and LSF stimuli (all $F(1,13) > 5.8$; all $P < 0.05$). An analogous pattern of results was obtained for the VPP component at midline electrodes. A main effect of stimulus type ($F(1,13) = 40.6$; $P < 0.001$) was due to the fact that the VPP was larger for faces relative to houses (see Fig. 2). As for the N170, no significant stimulus type \times spatial frequency interaction was obtained, and follow-up analyses revealed the presence of an enhanced VPP for faces relative to houses for BSF, HSF, and LSF stimuli (all $F(1,13) > 16.0$; all $P < 0.002$).

3.2.1. N170 components to fearful versus neutral faces

Fig. 3 shows ERPs to fearful faces (dashed lines) and neutral faces (solid lines), displayed separately for BSF, HSF, and LSF faces. No systematic differences between N170 amplitudes to fearful relative to neutral faces appear to be present for any stimulus frequency, thus again suggesting

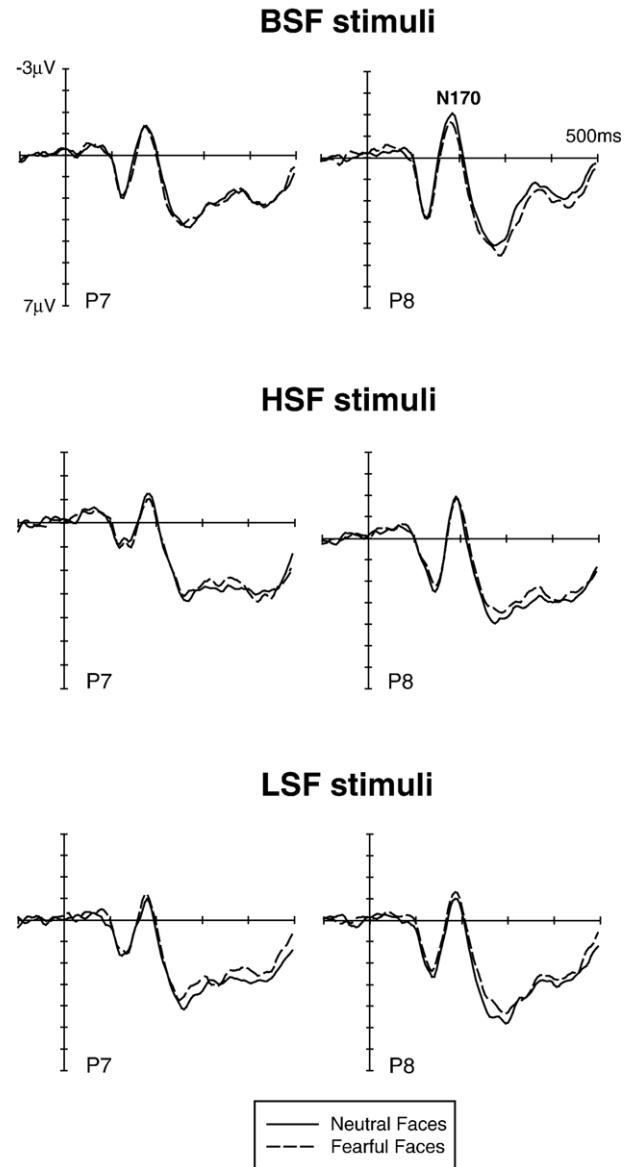


Fig. 3. Grand-averaged ERP waveforms elicited at lateral posterior electrodes P7/8 in the 500-ms interval following stimulus onset in response to neutral faces (solid lines) and fearful faces (dashed lines), shown separately for broadband (BSF), high spatial frequency (HSF), and low spatial frequency (LSF) stimuli.

that this component is insensitive to the emotional valence of faces. This was confirmed by statistical analyses, which found neither a main effect of emotional expression ($F < 1$), nor any evidence for an emotional expression \times spatial frequency interaction ($F < 2$).

3.2.2. Emotional expression effects

Figs. 4–6 show ERPs elicited at a subset of midline and lateral electrodes in response to fearful faces (dashed lines) and neutral faces (solid lines), separately for BSF faces (Fig. 4), HSF faces (Fig. 5), and LSF faces (Fig. 6). As expected, and in contrast to the absence of any effects of facial expression on the N170 component (see above), emotional

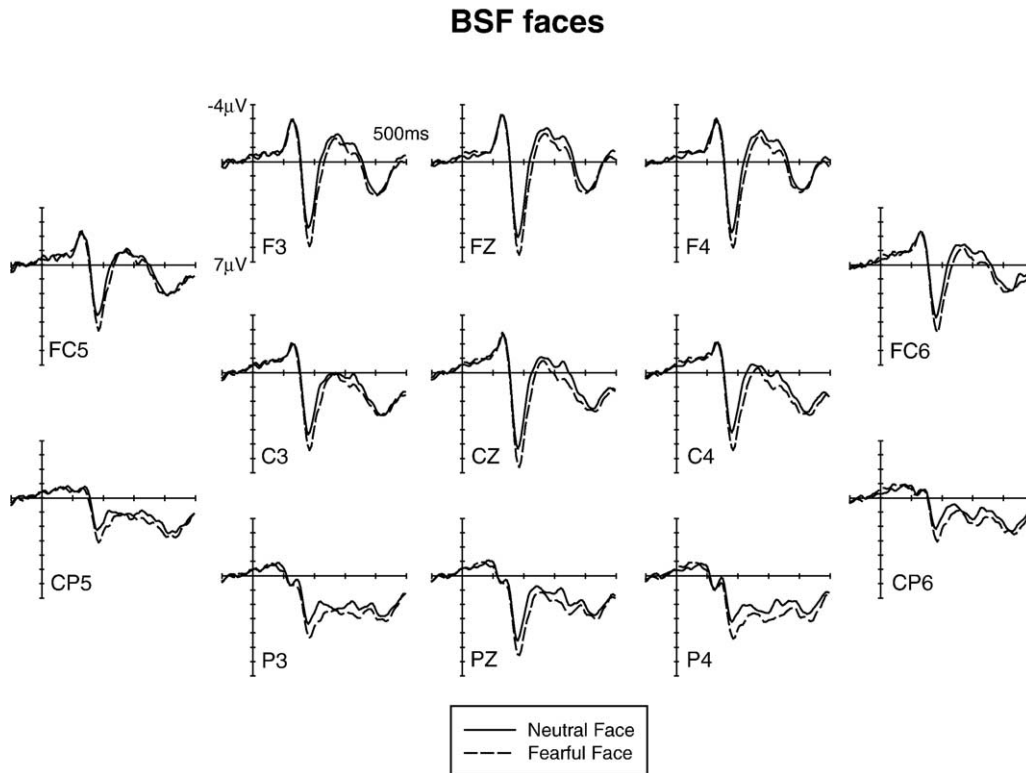


Fig. 4. Grand-averaged ERP waveforms elicited in the 500 ms interval following stimulus onset in response to neutral (solid lines) and fearful (dashed lines) broadband faces.

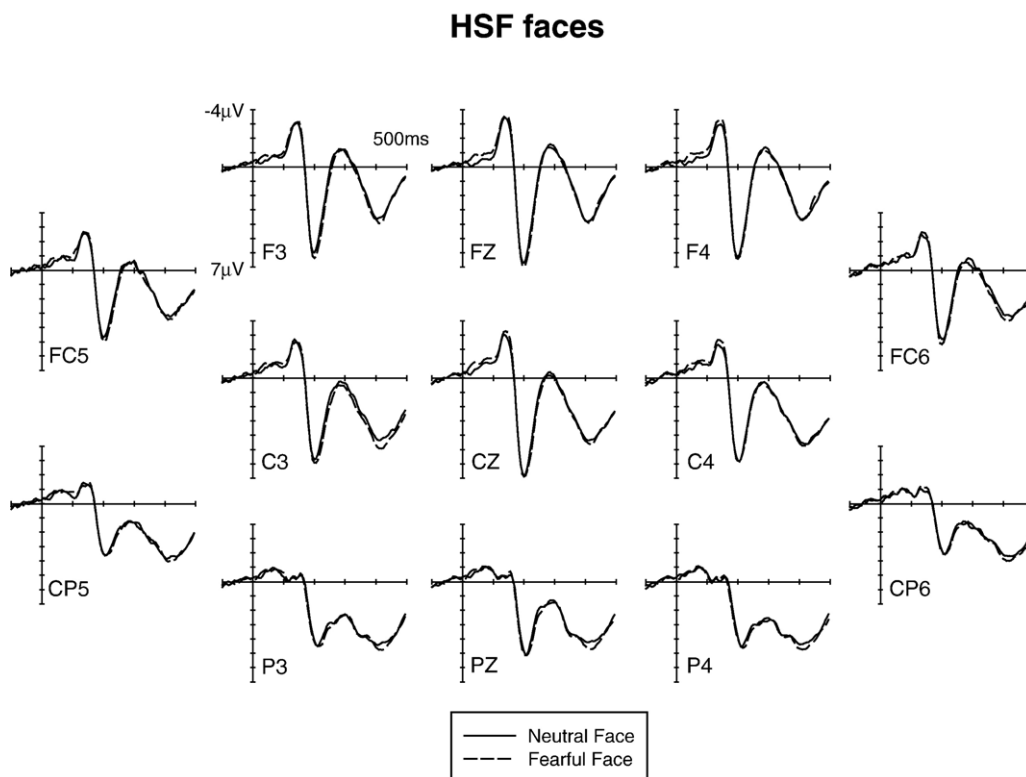


Fig. 5. Grand-averaged ERP waveforms elicited in the 500 ms interval following stimulus onset in response to neutral (solid lines) and fearful (dashed lines) high spatial frequency faces.

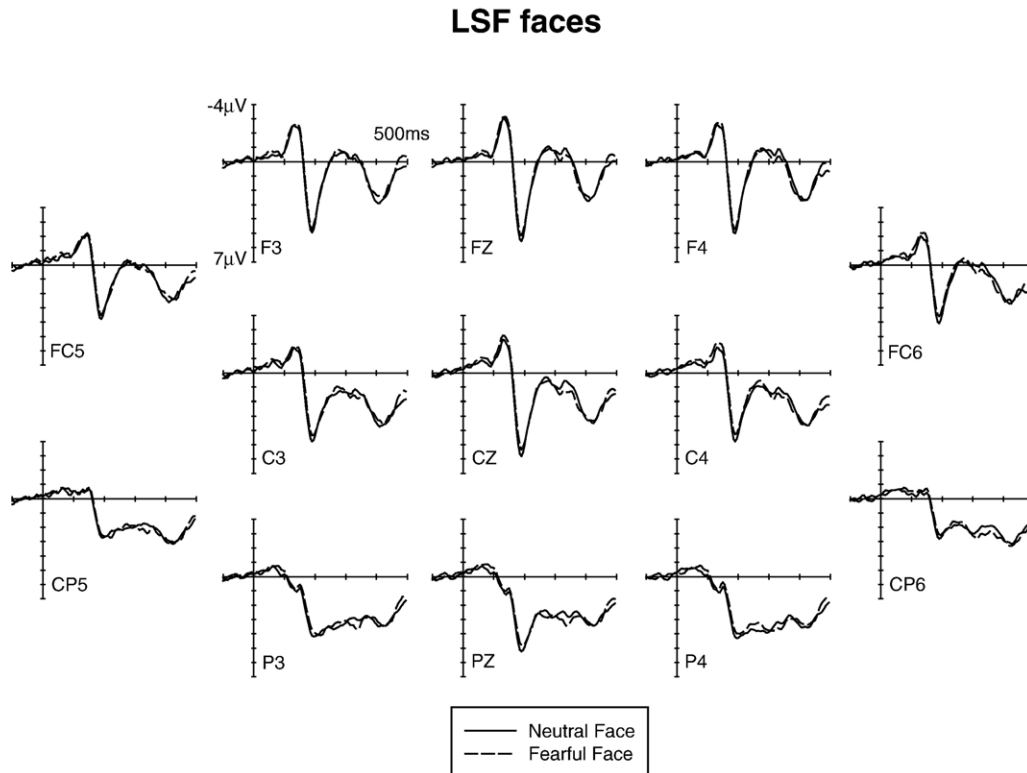


Fig. 6. Grand-averaged ERP waveforms elicited in the 500 ms interval following stimulus onset in response to neutral (solid lines) and fearful (dashed lines) low spatial frequency faces.

expression had a strong effect on ERPs elicited by BSF faces at these electrodes (Fig. 4). Here, a sustained enhanced positivity was elicited for fearful relative to neutral faces, which started at about 150 ms post-stimulus. In contrast, there was little evidence for a differential ERP response to fearful versus neutral faces for HSF and LSF stimuli (Figs. 5 and 6). This difference is further illustrated in Fig. 7, which shows difference waveforms obtained by subtracting ERPs to fearful faces from ERPs triggered in response to neutral faces, separately for BSF faces (black solid lines), HSF faces (black dashed lines), and LSF faces (grey lines). In these difference waves, the enhanced positivity in response to fearful as compared to neutral BSF faces is reflected by negative (upward-going) amplitudes, while there is little evidence for similar effects of emotional expression triggered by HSF or LSF faces.

These informal observations were substantiated by statistical analyses. No significant main effects or interactions involving emotional expression were observed between 105 and 150 ms post-stimulus. In contrast, significant emotional expression \times spatial frequency interactions were present between 155 and 200 ms post-stimulus at anterior, centroparietal, and at midline sites ($F(2,26) = 8.2, 7.3, \text{ and } 8.0$; all $P < 0.01$; $\epsilon = 0.77, 0.78, \text{ and } 0.83$, respectively). Follow-up analyses conducted separately for BSF, HSF, and LSF faces revealed significant emotional expression effects (an enhanced positivity for fearful relative to neutral faces) for BSF faces at all three sets of electrodes

(all $F(1,13) > 18.4$; all $P < 0.001$), whereas no such effects were present for either HSF or LSF faces.

A similar pattern of effects was present in the 205–250 ms post-stimulus measurement interval. Here, main effects of emotional expression at anterior, centroparietal, and midline sites ($F(1,13) = 15.0, 7.7, \text{ and } 9.5$; $P < 0.002, 0.02, \text{ and } 0.01$, respectively) were accompanied by emotional expression \times spatial frequency interactions ($F(2,26) = 8.6, 5.1, \text{ and } 6.6$; all $P < 0.02$; $\epsilon = 0.82, 0.89, \text{ and } 0.83$, respectively). Follow-up analyses again demonstrated significant emotional expression effects for BSF faces at all three sets of electrodes (all $F(1,13) > 31.7$; all $P < 0.001$). Again, no overall reliable ERP modulations related to emotional expression were observed for HSF and LSF faces. However, a marginally significant effect of emotional expression was found for HSF faces at anterior electrodes ($F(1,13) = 4.7$; $P < 0.05$).

No significant main effects of emotional expression or emotional expression \times spatial frequency interactions were obtained between 255 and 400 ms post-stimulus. However, despite the absence of overall significant interactions between emotional expression and spatial frequency, follow-up analyses showed that the enhanced negativity for fearful relative to neutral faces remained to be present for BSF faces in this measurement window at all anterior, centroparietal, and midline electrodes (all $F(1,13) > 5.0$; all $P < 0.05$). In contrast, no reliable ERP effects of emotional expression were present for HSF and LSF faces. Finally,

Difference Waveforms Neutral Faces - Fearful Faces

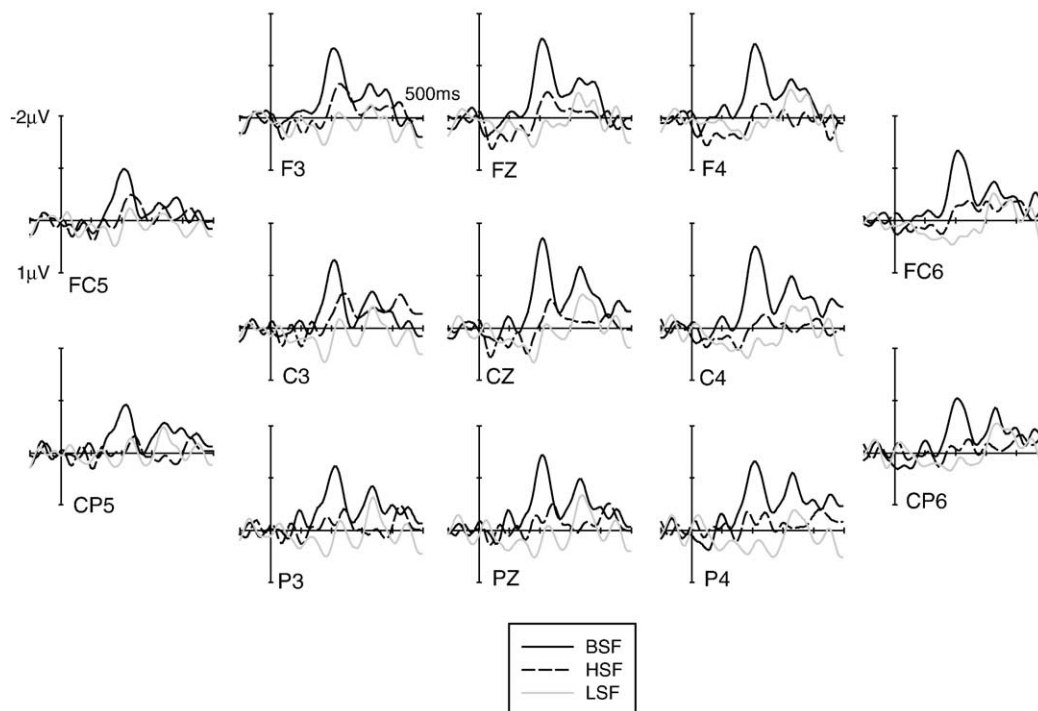


Fig. 7. Difference waveforms generated by subtracting ERPs to fearful faces from ERPs triggered in response to neutral faces, shown separately for broadband faces (BSF, black solid lines), high spatial frequency faces (HSF, black dashed lines), and low spatial frequency faces (LSF, grey lines).

between 400 and 500 ms post-stimulus, no significant emotional expression effects or interactions involving emotional expression were observed at all.

4. Discussion

The purpose of the present study was to examine the influence of spatial frequency information on face-specific and emotion-specific ERP signatures. ERPs were recorded to photographs of faces with fearful or neutral expressions, houses, and chairs (which served as infrequent target stimuli). These photographs were either unfiltered (BSF stimuli), low-pass filtered to retain only low spatial frequency components (LSF stimuli with frequencies below 6 cycles per image), or high-pass filtered to retain only high spatial frequency components (HSF stimuli with frequencies above 26 cycles per image).

To investigate effects of spatial frequency content on the face-specific N170 component, which is assumed to be linked to the pre-categorical structural encoding of faces, ERPs triggered by faces (collapsed across fearful and neutral faces) were compared to ERPs elicited in response to houses at lateral posterior electrodes P7/8, where the N170 is known to be maximal. N170 amplitudes were enhanced in BSF faces relative to BSF houses, thus

confirming many previous observations (c.f., [8,25,26]). More importantly, enhanced N170 amplitudes for faces relative to houses were also observed for LSF and HSF stimuli. The absence of any stimulus type \times spatial frequency interaction demonstrates that the face-specific N170 component was elicited irrespective of the spatial frequency content of faces, suggesting that the structural encoding of faces operates in a uniform way across varying spatial scales. This finding is consistent with a previous observation that the amplitude of the N200 component recorded subdurally from ventral occipitotemporal regions, which is also thought to reflect the precategorical encoding of faces [3], is relatively insensitive to spatial frequency manipulations of faces, although the latency of this component to HSF faces was found to be significantly delayed [46]. It should be noted that just like the N170, the VPP component triggered at midline electrodes was also not significantly affected by spatial frequency content, which is in line with the assumption that N170 and VPP are generated by common brain processes.¹

¹ The fact that the VPP is not affected by spatial frequency content, while the fronto-central positivity to fearful versus neutral faces is strongly modulated by spatial frequency, also suggests that although these two components are present within overlapping time windows, they are likely to be linked to different stages in face processing.

Our finding that the N170 is unaffected by the spatial frequency content of faces is at odds with the results from another recent ERP study [33], where a face-specific N170 was found only with LSF, but not with HSF, stimuli. There are several possible reasons for this discrepancy, including differences in the type of non-face stimuli employed, and the presence versus absence of a textured background. Whereas the overall power spectra were balanced in the Goffaux et al. study [33], they were not balanced in our own study. This is because we equalised the (RMS) contrast energy of the images, thereby circumventing one of the main problems with frequency filtering of natural stimuli, which is that contrast (power) is conflated with spatial frequency because the power of the image is concentrated at the low spatial frequencies. Differences between the studies in the low-pass and high-pass filter settings used to create LSF and HSF stimuli might account for the discrepancies between results. The fact that Goffaux et al. [33] failed to obtain a reliable face-specific N170 component in response to HSF stimuli containing frequencies above 32 cycles per image (6.5 cycles per degree of visual angle), while this component was clearly present in the current study for HSF stimuli with frequencies above 26 cycles per image (4 cycles per degree of visual angle), might point to a relatively more important role of spatial frequencies falling within the range of 26 and 32 cycles per image (4 and 6 cycles per degree of visual angle) for structural face processing.

We also investigated whether the face-specific N170 component is sensitive to fearful expressions at different spatial frequencies. In line with previous ERP studies using broadband photographic images (c.f., [27,36]), the present experiment confirmed the insensitivity of the N170 to emotional facial expression, not only for BSF faces (despite concurrent expression-related ERP deflections at more anterior electrode sites [see below]), but also for LSF and HSF faces. This finding further supports the hypothesis that facial expression is computed independently of global facial configuration, following a rudimentary analysis of face features, as proposed by Bruce and Young [16] in their influential model of face recognition.

The central aim of this experiment was to examine whether ERP emotional expression effects, as observed previously with unfiltered broadband faces [7,27,28,37], would also be present for LSF faces, but not for HSF faces, as predicted by the hypothesis that LSF cues are more important than HSF cues for the detection of fearful facial expressions. The effects obtained for fearful versus neutral BSF faces were in line with previous findings. Fearful faces triggered an enhanced positivity, which started about 150 ms post-stimulus. The onset of this emotional expression effect for BSF faces was slightly later in the present experiment than in our previous study where faces were presented foveally [27]. Here, an enhanced positivity for fearful as compared to neutral faces was already evident at about 120 ms post-stimulus.

A possible reason for this difference is that the BSF stimuli used in the present study had been equated with HSF and LSF stimuli for mean luminance and contrast energy, thereby rendering them lower in spectral power and therefore less naturalistic than the images employed in our previous study (unprocessed face stimuli usually have maximal power at low spatial frequencies).

As can be seen from the difference waveforms in Fig. 7, the early emotional ERP modulations observed with BSF faces almost returned to baseline at about 250 ms, again consistent with previous results [27], before reappearing beyond 300 ms post-stimulus in an attenuated fashion.² Early emotional expression effects, which are triggered within the first 150 ms after stimulus onset, have been attributed to the rapid detection of emotionally significant information. While such early effects appear to be only elicited when emotional faces are used as stimuli, longer-latency positive deflections have also been observed with other types of emotionally salient stimuli. These later effects have been linked with slower, top-down allocation of attentional resources to motivationally relevant stimuli [7,22,27], which may be important for the maintenance of attentional focus towards threatening information [31,32,67].

In contrast to the presence of robust effects of emotional expression for BSF faces, these effects were completely eliminated for HSF as well as for LSF faces, except for a marginally significant positive shift at frontal electrode sites between 205 and 250 ms for fearful relative to neutral HSF faces. The absence of any reliable effects of facial expression in response to LSF faces is clearly at odds with the hypothesis that these effects are primarily driven by LSF information. They also contrast with data from recent fMRI studies, which demonstrate that the classic emotion brain centres such as amygdala and related structures are selectively driven by coarse LSF cues, whilst being insensitive to fine-grained HSF cues [64,66]. This strongly suggests that the ERP emotional expression effects observed in the present and in previous studies do not directly reflect modulatory effects arising from emotional processes originating in amygdala and connected brain regions, but that they are produced by different brain systems involved in the detection and analysis of emotional information. Any amygdala or orbitofrontally generated effects on ERP responses would only be expected to arise through feedforward modulations of higher cortical areas. The amygdala, in particular, is an electrically closed structure positioned deep in the brain, and thus highly unlikely to produce EEG/ERP signatures that would be measurable with scalp electrodes. Some recent evidence consistent with this conclusion that the

² This was confirmed in a post hoc analysis conducted for ERP mean amplitudes between 250 and 280 ms post-stimulus. Here, no significant effects of emotional expression for BSF faces were obtained at all.

brain areas responsible for generating ERP emotional expression effects are distinct from the emotion-specific brain areas typically uncovered with fMRI comes from haemodynamic and electrophysiological investigations into interactions between attention and emotion processing. In contrast, amygdala and orbitofrontal areas appear to reveal obligatory activation to emotional facial expressions, irrespective of whether they fall within the focus of attention or not ([63]; but see also [54], for diverging findings). In contrast, both early and longer-latency effects of facial expression on ERP waveforms are strongly modulated by selective spatial attention [28,37], suggesting little direct involvement of the amygdala and orbitofrontal cortex. Such modulations of ERP emotional expression effects by selective attention were even elicited when using identical stimuli and similar procedures to the fMRI study conducted by Vuilleumier and colleagues [63]. In direct opposition to Vuilleumier and colleagues' [63] findings, Holmes et al. [38] found that effects of emotional expression on ERPs were entirely abolished when emotional faces were presented outside of the focus of spatial attention. Although by no means conclusive, this differential sensitivity of emotion-specific ERP and fMRI responses to attentional manipulations suggests that these effects may be linked to functionally separable stages of emotional processing.

The absence of any reliable effects of facial expression on ERPs in response to LSF faces in the present experiment, combined with previous demonstrations of the absence of such ERP modulations when faces are unattended, suggests that these effects are generated at stages beyond the early specialised emotional processing in amygdala and orbitofrontal brain areas. If the emotional expression effects observed in the present as well as in previous ERP studies are not linked to activity within these brain regions, then what is their functional significance? One possibility is there is a division of labour in the emotional brain, with mechanisms in amygdala and orbitofrontal cortex responsible for the pre-attentive automatic detection of emotionally salient events, and other cortical processes involved in the registration of emotional expression content in attended faces for the purposes of priming fast and explicit appraisals of such stimuli. The automatic and obligatory activation of amygdala and orbitofrontal cortex to emotionally charged stimuli, particularly fearful facial expressions [50,63,65], may be important in priming autonomic and motor responses [41,57], modulating perceptual representations in sensory cortices [40,49], and activating fronto-parietal attention networks [6,55]. These mechanisms confer evolutionary advantages, as unattended fear-relevant stimuli may be partially processed to prepare the organism for the occurrence of a potentially aversive situation. A number of behavioural and psychophysiological studies showing encoding biases for threat-related information are likely to reflect the operation of such initially preattentive processes [4,13,31,38,47,53]. Recently, a behavioural study by

Holmes and colleagues [37] showed that rapid attentional responses to fearful versus neutral faces were driven by LSF rather than HSF visual cues, in line with the role of amygdala and orbitofrontal cortex in the mediation of attention towards threatening faces.

However, areas beyond the amygdala and orbitofrontal cortex might be involved in a different type of emotional processing, which is aimed at an understanding and integration of salient social cues, such as facial expressions, within current environmental contexts. The accurate and rapid perception of social information is critical for our ability to respond and initiate appropriate behaviours in social settings [2,12,23], as well as for decision-making and social reasoning, and has been linked with processing in ventral and medial prefrontal cortices [5,20]. Information processing circuits in prefrontal cortices would be likely candidates for the elicitation of the early effects of emotional expression in response to fearful faces observed in the present and in previous ERP studies.

If this view was correct, the magnitude of these ERP effects might be determined by the amount of information contained in the face that is required for accurate emotional expression identification. Previous studies have found that fearful content in BSF and HSF faces is perceived more accurately and rated as more emotionally intense than fearful content in LSF faces [38,62,64]. In the present study, all stimuli were normalised for average luminance and contrast energy, after being filtered at different spatial scales. This procedure is likely to have made emotional facial expression more difficult to identify, especially for LSF faces. This fact, together with the general disadvantage for the recognition of fear in LSF faces reported before, may have been responsible for the absence of any ERP expression-related effects to LSF faces. A disadvantage for identifying LSF fear was also confirmed in a follow-up behavioural experiment, which examined the ability of participants ($N = 12$; mean age = 25 years) to identify fearful facial expressions of BSF, LSF, and HSF faces, using exactly the same stimulus set and presentation as in our main ERP study. Here, a one-way within-subjects analysis of variance (ANOVA) on identification accuracy revealed a significant main effect for the detection of fearful expressions ($F(2,22) = 12.36, P < 0.001$; means of 90.8%, 76.3%, and 66.3% correct responses for BSF, HSF, and LSF faces, respectively). While these results demonstrate that the identification of fear was most difficult for LSF faces, and more difficult for HSF than BSF faces, they also show that participants were still well above chance at categorising LSF fearful expressions (one-sample t test: $t(11) = 3.62, P < 0.005$). If the early frontocentral component observed in our ERP experiment was a direct correlate of emotional expression recognition performance it should have been delayed and/or attenuated, but not completely eliminated. An alternative interpretation of the present findings is that only faces approximating natural-

istic viewing conditions (i.e., BSF faces) are important for the elicitation of these emotional expression effects, which may prime processes involved in the rapid, explicit decoding of expression in other people's faces. Follow-up investigations systematically examining ERPs to faces presented at varying ranges of spatial frequencies will allow us to test this hypothesis.

It is also noteworthy that although early emotion-specific ERPs were mostly absent to HSF faces in our study, a marginally significant positivity to HSF fearful faces was evident at frontocentral sites between 205 and 250 ms after stimulus onset, possibly reflecting the enhanced ability of individuals to recognise fear conveyed in HSF, as compared with LSF, faces. Another possible reason for the transient frontocentral positive shift to HSF fearful faces is that participants may have been employing a strategy that favoured processing of HSF relative to LSF cues. The fact that participants were faster in the chair detection task to respond to HSF (376 ms) than LSF (393 ms) stimuli provides possible support for this argument. Any such strategy, however, should not prevent potential emotion-related effects as reflected in ERPs from being driven by LSF cues. For example, it was found by Winston et al. [66], who indirectly manipulated attention to high versus low spatial frequency attributes of fearful and neutral facial expressions, that LSF emotion effects were still evident within a number of different brain regions (including the amygdala), independent of this manipulation.

In sum, ERP differences in waveforms to fearful versus neutral facial expressions were evident for BSF face images. Replicating earlier findings, an enhanced positivity for fearful faces, which started at about 150 ms post-stimulus onset, was found in response to unfiltered faces. This emotional expression effect, however, was largely eliminated when faces appeared in low or high spatial frequencies, contrasting directly with recent fMRI studies showing enhanced amygdala activation to LSF fear faces. We conclude that the early emotional expression effect on ERPs obtained in response to BSF faces are likely to reflect mechanisms involved in the rapid priming of explicit social interpretative processes, such as decoding the meaning of a specific facial expression. Such ERP responses appear to depend on the presence of full spectral, naturalistic, visual spatial frequency information, and, as revealed in previous investigations, focal attention. In contrast, the preferential activation of amygdala and related structures to fearful faces is likely to represent the preparation of rapid autonomic, attentional, and motor responses to perceived threat. This amygdala response is selectively tuned to LSF visual information, and appears to be independent of the focus of current attention. Combined research into the relative contributions of different ranges of SF information in facial expression processing promises to yield valuable insights into the aspects of visual information that are important for different types of emotion processing.

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