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Research Report

Using spatial frequency scales for processing face features and face configuration: An ERP analysis

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ABSTRACT

In the present study we examined the influence of spatial filtering on the N170-effect, a relatively early face-selective ERP difference associated with face detection. We compared modulation of the N170-effect using spatially filtered stimuli that either facilitated feature analysis or impeded configural analysis. The salience of inner face components was enhanced by presenting them in isolation. Configural processing was manipulated by face inversion. The N170-effects elicited by upright faces and isolated inner components were similar across low- and high-spatial frequency scales. In contrast, the inversion effect (enhanced N170 amplitude for inverted compared with upright faces) was only observed with broadband and low-spatial frequency stimuli. These findings demonstrate that the N170-effect can be influenced by both low- and high-spatial frequency channels. Moreover, they indicate that different configural manipulations (isolated features vs. face inversion) affect face detection in distinct ways, consistent with separate processing mechanisms for different types of configural encoding.

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1. Introduction

All visual images in the natural environment are composed of a range of spatial frequencies (SFs), and the visual system filters incoming information via a number of SF channels (De Valois and De Valois, 1990). Perceptual demands such as stimulus characteristics and the task at hand can bias the spatial scale used during visual perception in any given instance (Davis, 1981; Davis and Graham, 1981). Consistently, psychophysical studies of face perception have reported that frequency channels are selectively used according to the task-determined type of categorization (Morrison and Schyns, 2001; Schyns and Gosselin, 2003; Schyns and Oliva, 1999; for a recent review see Ruiz-Soler and Beltran, 2006). In order to better understand how faces are processed by the visual system it is therefore necessary to determine what type of visual information is required for a given process and how this information is affected by different frequency scales.

Behavioral studies of face perception have revealed that normal recognition relies on the analysis of both the individual features in a face as well as their spatial configuration. Abundant research has revealed the importance of holistic processing of faces, that is, integrated processing of the features in conjunction. Research has also shown that face identification relies on computing spatial relations among inner face components, relative to each other and relative to

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the face contour, referred to as 2nd order configural processing (Maurer et al., 2002). This is distinct from 1st order configural processing, which refers to the processing of the global face shape (i.e., two eyes above a nose above a mouth), which allows for the basic level categorization of a face. Particularly relevant for face processing is behavioral evidence suggesting that global and configural processing in vision relies on relatively low spatial frequencies (LSFs) more than on relatively high spatial frequencies (HSFs; Badcock et al., 1990; Hughes et al., 1990; Lamb and Yund 1993; Shulman et al., 1986; Shulman and Wilson, 1987). Conversely, HSFs appear to be more important for local/feature processing (e.g. Shulman and Wilson, 1987). Since both details and their configuration are needed for different levels of face analysis, both LSF and HSF channels should be utilized during face perception. However, the relationship between global and local processing and low and high spatial frequency scales is not independent of task (see overview by Ivry and Robertson, 1998). The relative importance of different frequency scales is determined by the relative diagnostic value of the face components and global or configural shapes for the task at hand (Morrison and Schyns, 2001, see also Loftus and Harley, 2004).

Several studies have examined which spatial frequency scales are relevant for different face perception tasks. Generally speaking, these studies have found that high spatial frequencies are less critical for face identification than low spatial frequencies. They are also consistent with the importance of the spatial configuration of inner components for discriminating among individual faces and with the association between global vs. local analysis and the preferential processing of low vs. high spatial frequencies. For instance, face identification relies on a range of relatively low and mid SFs (~8–16 cycles/ image) while at higher SFs faces can lose their identity (Costen et al., 1996, Fiorentini et al., 1983; Hayes et al., 1986). Furthermore, Goffaux et al. (2005) directly linked 2nd order configural analysis with the processing of LSFs and feature analysis with the processing of HSFs in a face-matching task. In that study they manipulated either the spatial relations between the features of a face, or the features themselves, and found that frequencies below 1.86 cycles/ degree (8 cycles/image) were more important when faces differed on the basis of second-order configuration (that is, the relative location of the inner face components within the face contour; Maurer et al., 2002), while frequencies above 7.44 cycles/degree (32 cycles/image) were more important when matching required processing the feature properties. Other studies exploring face categorization have found that the frequency scale used depends on the nature of the categorization task. For example, deciding if a face is expressive or not requires LSFs (below 2 cycles/degree; 8 cycles/image), whereas categorization of particular expressions (such as happiness) seems to rely on higher SFs (above 6 cycles/degree; 24 cycles/image; Schyns and Oliva, 1999).

The spatial scales used during early stages of face perception were recently investigated by examining how SF affects the N170 component, an electrophysiological index of relatively early face processing. While all visual stimuli elicit negative or negative-going ERPs during this epoch (N1), the N170 is larger (more negative) in response to faces than to other objects, a difference referred to as the "N170-effect" (Bentin et al., 1996; George et al., 1996). There is evidence that the N170-effect is not modulated by face identity (Bentin and Deouell, 2000) and that it is at least as distinctive for isolated eyes as for full faces (Bentin et al., 1996; Itier et al., 2006), though there is also evidence for its sensitivity to the individuality of faces (Jacques and Rossion, 2006). Nonetheless, the N170-effect is insensitive to the configuration of the face features within or isolated from the face contour (Zion-Golumbic and Bentin, 2007). That is, the N170-effect is equally large in response to faces with normally-configured and spatially-scrambled inner components, albeit slightly delayed in the latter condition. Hence, Bentin et al. have claimed that the N170-effect is associated with base-level categorization (i.e., face detection) including the additional analysis of face features elicited by default when faces are detected. According to this view, the N170-effect is dissociated from neural events involving second-order configural processing. Rather, the mechanism manifested in the N170-effect is triggered by the occurrence of any type of physiognomic information in the visual field such as the global face contour (and 1st order configuration) as well as the presence of the features (Bentin et al., 2006; Sagiv and Bentin, 2001; Zion-Golumbic and Bentin, 2007).

If the N170-effect is associated with a face detection mechanism, reflecting base-level categorization as well as initial processing of face features, it should be relatively insensitive to frequency scale (within certain limits). This is because face detection may rely on analyzing the first-order configuration (which presumably relies preferentially on low spatial frequencies) as well as processing the features (which is presumed to rely more on high spatial frequencies). Hence, the difference between the N170 elicited by full-face and non-face objects could reflect either LSF information (supporting the global distinction) or HSF information (supporting the analysis of finer features). However, studies exploring the frequency scales that elicit the N170-effect have yielded mixed results.

Goffaux et al. (2003a) found that the N170-effect (face–car difference) was absent when spatial frequencies below 6.5 cycles/degree (32 cycles/image) were filtered out of the images (i.e., high pass). However, the task in that study was orientation judgment, which may have encouraged participants to adopt a strategy that diverted their attention from the face features. Supporting this notion, the N170-effect was not enhanced by face inversion, as commonly found in N170 studies (e.g. Rossion et al., 1999). The absence of this enhancement when using an orientation judgment task suggests that this task may have induced a different strategy than under conditions where participants are simply detecting or identifying faces. In a different paper, Goffaux et al. (2003b) found further evidence for the importance of task differences in determining the spatial scale eliciting the N170-effect. In a gender categorization task, they replicated their previous finding: the N170-effect was absent in high pass filtered images. However, in a familiarity task that required face recognition, they found similar N170-effects for low- and high-pass images. Another study examining processing of emotional faces also found no differential effects of frequency scale on the N170-effect (Holmes et al., 2005). Still another study using MEG found a reduction of the M170 only when the

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image was low-pass filtered (Hsiao et al., 2005). No similar decrease was found for mid-range or high-range.

That task demands modulate the use of spatial frequency scales begs the question: what is the default visual processing level for faces? That is, what spatial frequencies are used automatically when we are presented with a face, and before any specific task constraints are imposed? Given the evidence demonstrating the flexible use of spatial scales depending on task demands, in order to answer this question it is important to carefully select a task that minimizes external demands as

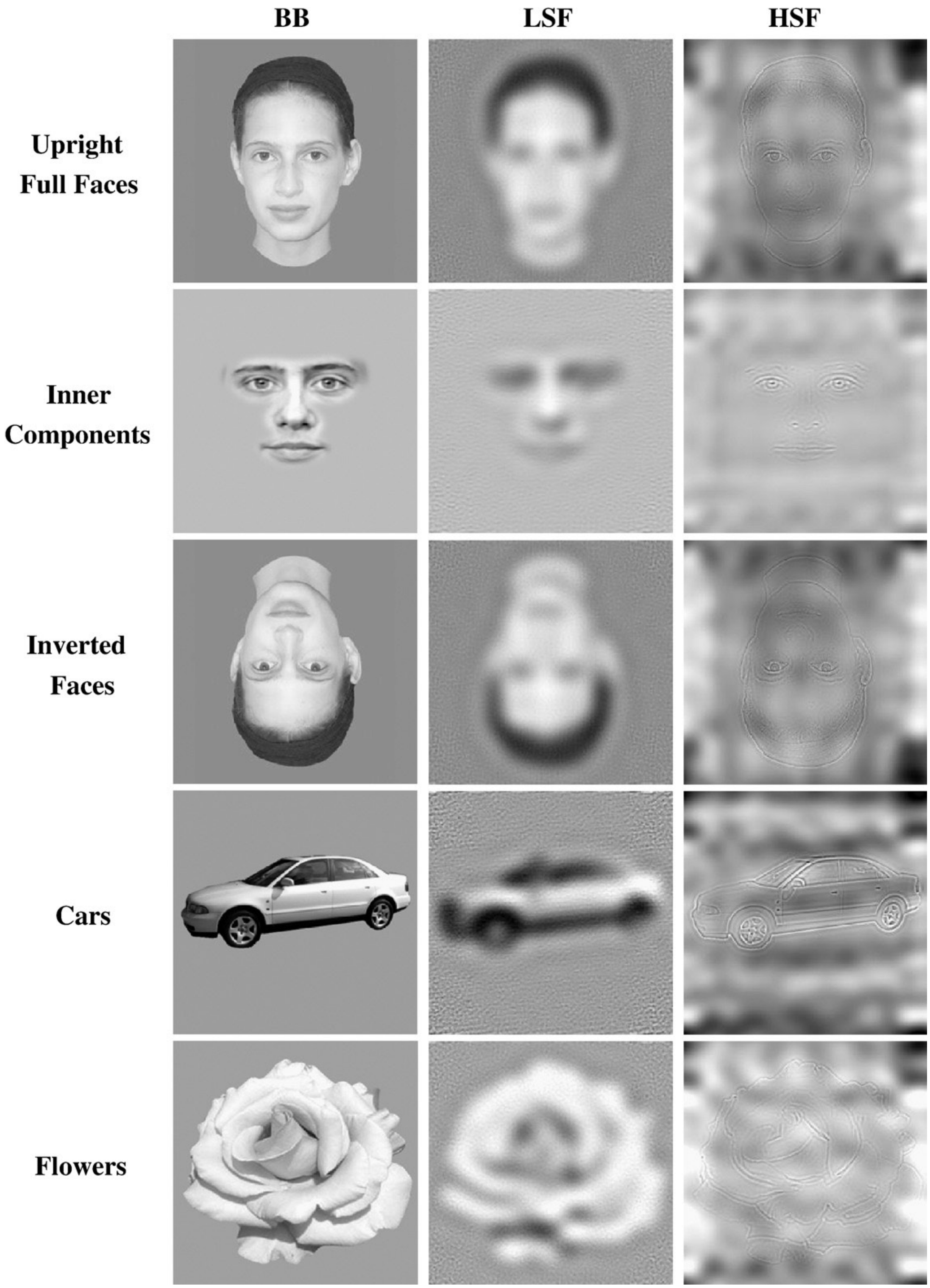

Fig. 1 – Examples of stimuli. Participants passively viewed stimuli and pressed a button every time a flower appeared on the screen. BB: broadband stimuli; LSF: low-pass spatially filtered stimuli; HSF: high-pass spatially filtered stimuli.

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much as possible. Assuming the N170-effect reflects a detection stage in face processing, one way to address this question is by determining the SF scales that elicit the N170-effect during a basic-level categorization task with minimum additional task constraints. In an attempt to address this question, Halit, de Haan, Schyns, and Johnson (2006) used a face detection task in which participants viewed spatially filtered stimuli that either contained a famous face in noise or noise alone. The stimuli were presented at brief exposure duration (120 ms) and participants were asked to indicate the presence or absence of a face embedded in the noise. In addition to low-pass (i.e., LSF) and high-pass (i.e., HSF) spatially-filtered faces, they included two conditions that contained both low and high SFs: a "high-low face" condition that contained the frequencies in both the LSF and HSF conditions (i.e., omitting the mid-range frequencies), and a broadband face condition which contained all the SFs in the image. The "noise-only" condition was a "high-low" condition in that it always contained both the LSFs and HSFs, omitting the mid-range frequencies. Although the N170-effect was greater for LSF faces than HSF faces, the HSF faces elicited a significantly greater N170 than high-low noise, suggesting that HSFs, in addition to LSFs, are useful during base-level categorization of faces. More importantly, the high-low face condition resulted in an even greater N170-effect than the LSF face condition, providing further evidence that HSFs are not redundant but important in eliciting the N170-effect. The N170 was greatest in response to broadband faces.

Although Halit et al. (2006) used a face detection task, the question of what SFs are used by default during face processing remains unanswered. Participants in their study were actively searching for faces in the stimuli, a task that proved to be more difficult in the HSF and high-low noise conditions than in the other conditions. Deciding if there is a face present in noise might engage different processes such as attention to face characteristics in the LSF range. Top-down mechanisms of this kind might not be used as extensively when faces are not masked.

In the present study we aimed to explore the SF scales used in early face processing when both faces and objects were task irrelevant. This was accomplished by asking participants to detect infrequently presented flowers among a stream of other items. Thus, unlike previous studies, we did not impose task constraints on the faces that might recruit the use of certain SFs not otherwise employed during base level categorization of faces.

In addition, we examined how the effects of different manipulations of face stimuli are modulated by spatial scale.

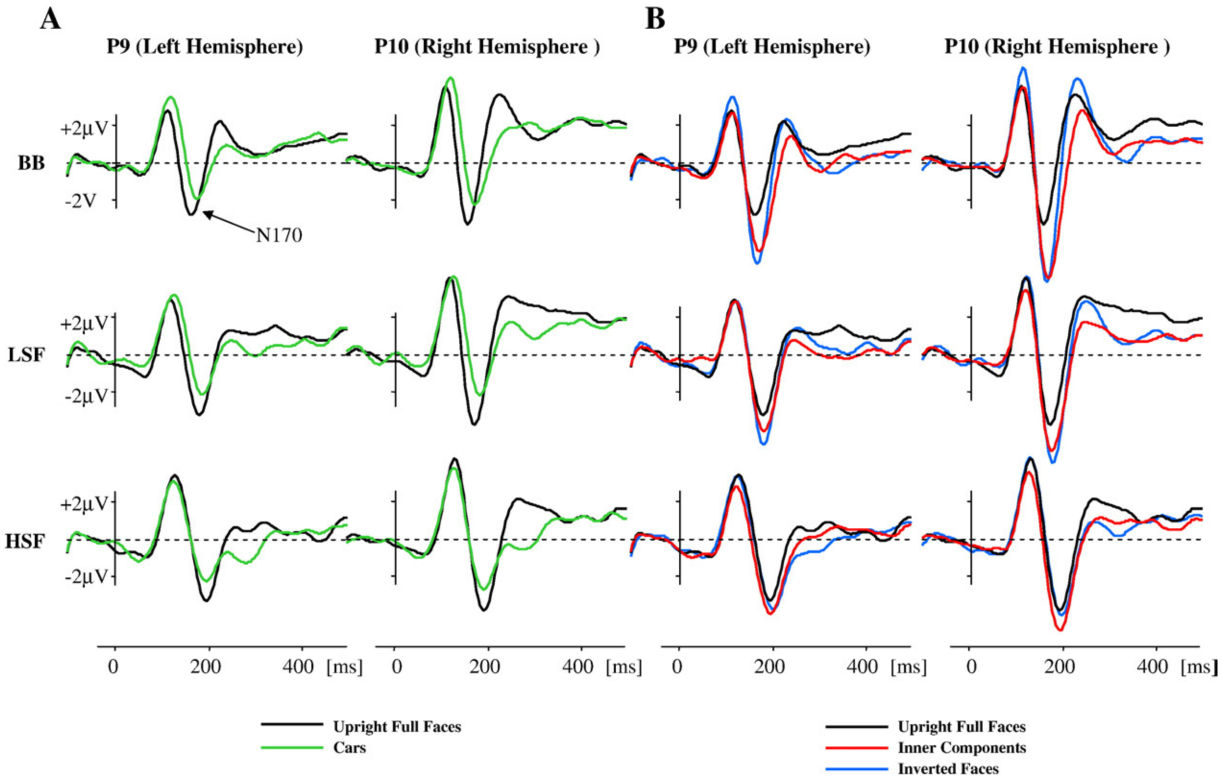

Fig. 2 – ERPs elicited by experimental stimuli in each filter condition. Note that these ERPs reflect the response to both the experimental stimulus (foreground figure) and the reciprocally filtered background texture, so comparisons across frequency scale should be made cautiously. The effect of the background texture was diminished in the analyses by subtracting the peak N170 amplitude elicited by cars from the peak N170 amplitude elicited by each face-related stimulus within each filter condition. BB: broadband stimuli; LSF: low-pass spatially filtered stimuli; HSF: high-pass spatially filtered stimuli. (A) The basic N170-effect (upright full faces vs. cars) is similar in each spatial frequency scale. (B) The enhancement of the N170 amplitude to isolated components is seen in all 3 spatial frequency scales, whereas the enhancement to inverted faces is only seen in broadband and LSF conditions.

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Assuming that face detection involves processing of some face features as well as the global structure, and that feature processing may rely more on high frequency scales than configural processing, it is important to determine the relative use of low- and high-spatial frequencies on processing face components. To this end, we presented participants with face stimuli that were canonical and intact, inverted and intact or without the global contour of the face. The saliency of the inner components was enhanced by presenting them in isolation (while sparing the internal but not the overall configuration), and we hindered overall configural analysis by face inversion (Fig. 1). We compared the influence of low-pass and high-pass spatial filtering with broadband stimuli (LSF, HSF, and BB, respectively) on the N170-effect across these different manipulations. Similar to Goffaux et al. (2003a,b) we equated overall spectral content across LSF and HSF conditions by adding a reciprocally filtered background texture to each filtered stimulus. That is, each LSF stimulus was combined with a HSF background texture and vice versa.

2. Results

The EEG data were processed and segmented individually for each stimulus type and experimental condition. Initial scrutiny of the waveforms showed a normal basic N170-effect across all spatial frequencies (Fig. 2A). It seems that the major effect of filtering on the N170-effect was a delay of the peak latency that was larger for the HSF than for the LSF conditions. However, note that the delay already started at P1, suggesting that it might reflect the influence of a visual process that is not specifically related to face processing (Fig. 3). Unlike the basic N170-effect (Fig. 2A), the effects of face inversion and isolating inner components were affected by filtering (Fig. 2B). Both effects were reduced for filtered stimuli relative to broadband. Comparing low- and high-pass filtered stimuli, there was no obvious difference between the LSF and HSF conditions for inner components (i.e., faces without contour), while the inversion effect was completely eliminated in the high frequency condition.

Table 1 – Mean amplitude difference (in μV) between the N170 elicited by each face-related stimulus and that elicited by cars

		Left Hemisphere Electrode Sites			Right Hemisphere Electrode Sites		
		P9	P7	P07	P10	P8	P08
Upright full faces	BB	−0.48	0.02	0.52	−0.62	−0.13	−0.18
	LSF	−0.12	−0.15	−0.81	−1.69	−1.84	−1.69
	HSF	−0.91	−0.06	0.11	−1.23	−0.40	−0.02
Inner components	BB	−2.41	−1.21	−1.05	−3.49	−2.64	−2.55
	LSF	−2.10	−1.59	−1.90	−2.64	−3.02	−3.20
	HSF	−1.48	−1.07	−0.89	−2.55	−1.72	−0.90
Inverted faces	BB	−3.06	−2.75	−2.79	−4.00	−3.90	−4.30
	LSF	−2.52	−2.99	−2.58	−3.66	−4.02	−3.73
	HSF	−1.44	−0.97	−0.27	−1.46	−0.77	0.09

BB: broadband stimuli; LSF: low-pass spatially filtered stimuli; HSF: high-pass spatially filtered stimuli.

Because the ERPs described above were elicited by a complex visual pattern that included a foreground meaningful image and a reciprocally filtered background texture, we sought to analyze these data after reducing the effect of the meaningless texture. This could be done with straightforward subtraction of the waveforms elicited by cars from those elicited by each face-related stimulus at each frequency scale, with the residual being the net face-specific effects. However, such a subtraction is meaningless in the present set of data due to the high variation in latency across frequency scales. We thus subtracted the peak N170 amplitudes elicited by cars from the peak N170 amplitudes elicited by the three face-related stimuli in each filter condition for each participant regardless of latencies and used this difference as our dependent variable in the statistical analyses. This subtraction also controlled for P1-related influences on the N170 (there was no main effect of filter on P1 amplitude [$F(2,48) < 1.00$]. These data are presented in Table 1 and Fig. 4.

The initial statistical evaluation of the N170-effects was based on repeated measures four-way ANOVA. The factors were Stimulus type (upright face, inverted face, inner

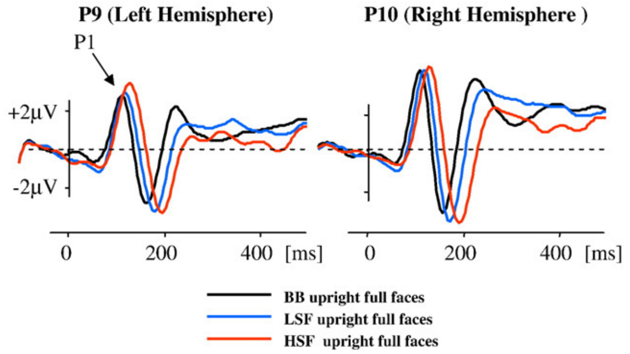

Fig. 3 – ERPs elicited by upright full faces in each frequency condition. BB: broadband stimuli; LSF: low-pass spatially filtered stimuli; HSF: high-pass spatially filtered stimuli. Note that the latency delay elicited by LSF and HSF stimuli relative to BB starts before the N170 at P1 (denoted by arrow).

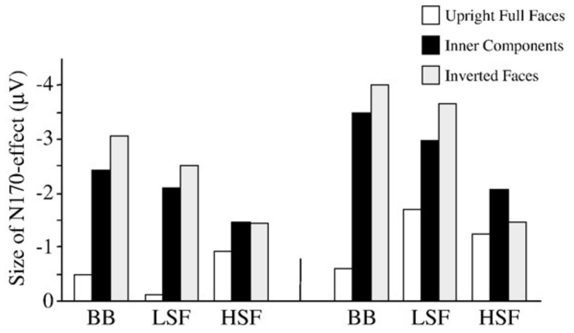

Fig. 4 – Mean amplitude difference between the N170 elicited by each face-related stimulus and that elicited by cars (N170-effect). Within each filter condition, comparison of the N170-effect for each face related stimulus. BB: broadband stimuli; LSF: low-pass spatially filtered stimuli; HSF: high-pass spatially filtered stimuli; P9: left hemisphere electrode site; P10: right hemisphere electrode site.

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components), Filter (BB, LSF, HSF), Hemisphere (left, right), and Site (P7/8, PO7/8, P9/10)[1], followed where indicated by post hoc contrasts. Whenever necessary, the degrees of freedom were adjusted using the Greenhouse–Geisser correction.[2] This analysis resulted in a significant main effect of Stimulus type [$F(2,48)=21.6$, $p<.001$], as well as of Filter [$F(2, 48)=11.1$, $p<.001$]. The effect of hemisphere only approached significance [$F(1,24)=3.5$, $p=.075$], with larger mean N170 amplitude effects over the right (−2.1 μV) than the left (−1.3 μV) hemisphere. The effect of site was also significant [$F(2,48)=3.7$, $p<.05$]. More revealing was the significant interaction between Stimulus type and Filter [$F(4,96)=9.0$, $p<0.001$] that was qualified by a tendency for a three-way interaction between Stimulus Type, Filter and Site [$F(8,192)=2.4$, $p=.061$]. In addition, there was a significant interaction between Filter and Site [$F(4,96)=5.6$, $p<.005$]. No other effects were significant, albeit there was a tendency for Hemisphere to interact with both Filter [$F(2,48)=2.6$, $p=.08$] and Stimulus type [$F(2,48)=2.6$, $p=.09$]. Analyzing the three-way interaction first, we found that the two-way interaction between Stimulus type and Filter were significant at all sites, albeit more conspicuous at P9 and P10 than at other sites. Based on this similarity, as well as on the previously established posterior lateral distribution of the N170-effect, we continued analyses with a focus on P9 and P10 only.

The factorial analysis at P9 and P10 mirrored the 4-way analysis. There was a significant main effect of Stimulus Type [$F(2,48)=23.2$, $p<.001$]. Post hoc contrasts showed that across filters the amplitude of the N170-effect elicited by upright faces was smaller (−1.0 μV) than for that elicited by inner components and inverted faces [−2.4 μV and −2.7 μV, respectively; $F(1,24)=52.1$, $p<.001$], with no significant differences between the latter two conditions. The main effect of Filter was also significant [$F(2,48)=5.4$, $p<.01$]. Post hoc contrasts showed no difference between the BB and LSF stimuli (−1.9 μV and −2.3 μV, respectively), both producing a significantly larger N170-effect than the HSF stimuli [−1.4 μV; $F(1,24)=9.8$, $p<.01$]. The main effect of Hemisphere showed a tendency for significance [$F(1,24)=3.9$, $p=.06$]. The only significant interaction was between Stimulus type and Filter [$F(4, 96)=9.1$, $p<.001$]. To explore this interaction we analyzed the Filter effect separately for each Stimulus type with the N170-effect as the dependent variable.

For upright faces the N170-effect was similar across filters [$F(2,48)=1.7$, $p=.19$], and across hemispheres [$F(1,24)=1.0$, $p=.32$]. There was also no interaction between the two factors [$F(2,48)<1.00$]. For inner components the main effect of Filter was significant [$F(2,48)=4.1$, $p<.05$]. Post hoc contrasts showed that the N170-effect for HSF stimuli was similar to LSF [$F(1,24)=2.8$, $p=.11$], but smaller than the effect elicited by BB stimuli [$F(1,24)=10.0$, $p<.01$]. The Hemisphere effect was significant [$F(1,24)=7.8$, $p<.01$], showing that the N170-effect for inner components was larger at P10 (−2.8 μV) than at P9 (−2.0 μV), and there was no interaction between the two factors [$F(2,48)<1.00$]. Finally, for inverted faces Filter had a significant main effect [$F(2,48)=19.7$, $p<.001$], while the Hemisphere effect was not significant [$F(1,24)=2.0$, $p=.09$], and neither was there an interaction between the two factors [$F(2,48)=2.4$, $p=.10$]. Post hoc contrasts showed that there was no difference between the N170-effect elicited by inverted faces in the BB and LSF conditions [$F(1,24)=2.0$ $p=.17$], which were both significantly larger than the N170-effect elicited by inverted faces in HSF [$F(1,24)=31.2$. $p<.001$].

Table 2 – Mean latency difference (in ms) between the peak N170 latency and the peak P1 latency for each stimulus condition

		Left Hemisphere Electrode Sites			Right Hemisphere Electrode Sites		
		P9	P7	P07	P10	P8	P08
Cars	BB	57.5	59.3	54.1	56.8	56.7	55.0
	LSF	60.8	64.8	61.1	58.1	57.8	57.8
	HSF	69.1	66.9	66.2	61.4	60.6	58.8
Upright full faces	BB	50.4	55.8	53.9	47.3	49.7	50.0
	LSF	58.3	62.2	58.3	50.6	51.2	50.1
	HSF	65.6	63.9	61.7	62.2	57.2	57.2
Inner components	BB	56.1	59.8	57.7	53.9	57.3	55.5
	LSF	60.1	60.3	58.3	53.9	59.2	56.6
	HSF	69.7	63.1	64.2	61.6	58.1	59.2
Inverted faces	BB	53.9	61.2	57.8	50.3	53.6	52.3
	LSF	61.1	64.5	63.2	55.2	60.8	58.6
	HSF	74.5	73.8	69.8	65.8	61.9	63.1

BB: broadband stimuli; LSF: low-pass spatially filtered stimuli; HSF: high-pass spatially filtered stimuli.

Analyses of the N170 peak latency differences were performed taking into account that these differences might have started earlier, at P1. Although the P1 amplitude was not affected by any of the independent variables, its latency was significantly affected by filter condition [$F(2,48)=44.3$, $p<.001$]. Moreover, as shown in Fig. 3, the sequence of P1 peaks in the different filter conditions was similar to the visible effect of filter on the N170 latency. Therefore, in order to isolate the experimental effects on the latency of the face-selective process reflected by the N170 we subtracted the P1 latency from the N170 latency. The ANOVA design for this analysis was similar to the one used for amplitude except that the Stimulus type factor included cars as one of 4 levels[3] (Table 2).

The 4-way ANOVA of the adjusted latencies revealed significant main effects of Stimulus type, Filter and Hemisphere [$F(3,72)=5.4$ $p<.01$; $F(2,48)=18.8$, $p<.001$; $F(1,24)=15.5$ $p<.001$, respectively]. The main effect of Site was not significant [$F(2,48)=1.5$, $p=.24$]. Post hoc contrasts showed that across filters the N170 elicited by cars peaked the latest but not significantly later than those elicited by inverted faces [$F(1,24)=1.0$], which peaked later than inner components [$F(1,24)=9.0$, $p<.01$], which in turn, were later than faces [$F(1,24)=10.2$ $p<.01$]. Post hoc analyses of the Filter effect showed that the N170 peaked earlier for BB than LSF stimuli [$F(1,24)=11.1$, $p<.01$], which in turn were earlier than for HSF stimuli. [$F(1,24)=21.6$, $P<.001$]. Importantly, the interaction

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[1] These sites were selected a-priori on the basis of previous studies.

[2] For clarity and brevity, the initial degrees of freedom will be reported.

[3] We included cars in the analysis of latency to assess the filter effects that were face-specific and those that were not.

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between Stimulus type and Filter was not significant [$F(6,144)=1.4$, $p=.22$), suggesting that the filter condition had similar effects on latency for all stimulus types. There was also no interaction between Stimulus Type, Filter and Site.

In summary, the results of this experiment showed that the size of the basic N170-effect (faces relative to cars) was similar across BB, LSF, and HSF filter conditions, while its latency (after controlling for P1 effects) was delayed by both filters relative to BB, but more so by the HSF than the LSF. Similarly, while both filters reduced the N170-effect for inner components relative to BB, there was no difference between the LSF and HSF, conditions. Yet, the latency of the N170 peak was delayed for inner components as for faces. In contrast, the amplitude enhancement of the N170-effect by face inversion, while similar for BB and LSF conditions, was not present in the HSF condition. That is, for HSF stimuli there was no difference between faces and inverted faces. Again, the latencies were shortest for BB stimuli, followed by LSF stimuli, and longest for HSF stimuli.

3. Discussion

The results of this study support other recent evidence suggesting that both HSFs and LSFs are used during early stages of face processing. Early evidence reported by Goffaux et al. (2003a) found that LSFs were sufficient to produce the N170-effect for upright faces. Later, Halit et al. (2006) showed that HSFs are not redundant but provide important information in eliciting the N170-effect when faces are targets. Our results extend their findings to demonstrate that the effect of spatial frequencies is not limited to conditions when attention is directed to faces, but is also evident even when faces are part of the distracter set. Moreover, while Halit et al. found LSF faces elicited a greater N170-effect than HSF faces, the results from our study demonstrate that the two scales are equally important when faces are not the targets. Although target relevancy is the most obvious difference between the study by Halit et al. and ours, there are also other differences that should be considered. For instance, Halit et al. used a higher high-pass filter (24 cycles/image rather than the 22 cycles/image in our experiment) and thus included less high frequencies that might help efficiency of face categorization. They also used a higher low-pass filter (8 cycles/image rather than the 5 cycles/image in our experiment), thus including higher low frequencies that may also increase efficiency of face categorization in their LSF condition. Whether or not these differences are substantial enough to account for the differences between our results and theirs, our data demonstrate that the distinction between faces and cars, as reflected by the N170-effect, is as efficient when based on high spatial frequency channels (above 5 c/d) as when it is based on low spatial frequency channels (below 0.9 c/d) (Fig. 2A). Relatively high- and low-spatial frequencies were automatically accessed during early face categorization.

Our findings also extend those of Goffaux et al. (2003a), who found that the N170-effect was only present when LSFs were included in the stimuli. Participants in a study by Goffaux et al. (2003a) were requested to determine the orientation of the stimuli (face and cars), again making faces task relevant. When faces are not task relevant, as was the case in the present study, both high and low frequency information is extracted, at least for upright faces. Although it might be expected that the N170-effect would be robust to task differences, the evidence together demonstrates that its interaction with the frequency spectrum is affected by top-down processes (Goffaux et al., 2003b). In the present study, we found no face inversion effects when the LSFs were excluded from the image. Again, there were differences between HSF filter cutoffs in ours and Goffaux et al's study. Specifically, in the HSF condition, they used a 32 cycles/image cutoff, which is considerably higher than those used either by Halit et al. or by us. Hence, it seems that excluding spatial frequencies below 22 cycles/image (the present study) leaves face processing as indicated by the N170-effect intact. Excluding spatial frequencies below 24 cycles/image (Halit et al's., 2006 study) reduces the efficiency of the system to distinguish between faces and cars (as reflected by a reduced N170-effect), while excluding spatial frequencies below 32 cycles/image (Goffaux et al's., 2003a study) eliminates the N170-effect entirely, although faces can still be detected in this range. The differences between these studies underline the importance of a systematic investigation of the SFs that are necessary to obtain the N170-effect and how the range of these frequencies is modulated by task demands.

The present results also revealed new effects of spatial frequency filtering on the N170 response to different face-related stimuli. In the BB condition, both inner components and inverted faces elicited and increased N170 amplitude relative to upright full faces. This effect was seen across both spatial scales for inner components but only in the LSF stimuli for inverted faces. Although both of these manipulations in BB stimuli have been described as affecting "configural" processing, they do so in different ways. The present results demonstrate that they are also sensitive to different frequency ranges, and these can be observed as early as the N170. Face inversion effects were driven entirely by the low spatial frequencies, while responses to inner components produced an increased N170 for BB, HSF and LSF stimuli. In other words the consequences of changing the face configuration by inversion and manipulating the salience of the inner components on passive face viewing are different.

It is particularly surprising that the inversion effect on the N170 was found in the low- and not high-spatial frequency condition because it is commonly assumed that inversion breaks the face configuration and triggers part-based processing (e.g., Bartlett and Searcy, 1993; Carey, 1978; Carey and Diamond 1977; Rhodes et al., 1993; Tanaka and Farah, 1993). For example, previous behavioral data have shown that while faces are recognizable as faces when blurred as well as when inverted, combining these two manipulations renders unrecognizable faces (Collishaw and Hole, 2000). This is presumably because blurring a face inhibits feature processing while inversion inhibits configural processing; while recognition was still possible when only one of these factors was present (i.e., blurring alone or inversion alone), it was not possible when both were present (i.e., blurring+inversion). If first-order configural processes that denote a potential face are inhibited when processing inverted faces, as has been argued, manipulations that change the ability to extract configural information should not be consequential. Specifically, the fact that

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HSFs disrupt configural processing, while LSFs do not, should not matter. In contrast, as previously reported (Goffaux et al., 2003a), the present results suggest that face inversion effects are absent in HSF while present in LSF stimuli. This suggests that, although extraction of configural information is much more difficult in an inverted than upright face, it is nevertheless attempted.

The similar response to inner components across LSF and HSF conditions provides additional evidence that high-frequency scales are used by face-selective mechanisms associated with the N170-effect. As with BB stimuli, the N170-effect was larger for inner components than for upright faces in both frequency scales, albeit peaking later in the HSF condition. Moreover, enhancement of the N170 elicited by inner components relative to full upright faces was equal in both the LSF and HSF conditions. As suggested by Bentin et al. in previous studies (e.g., Bentin et al., 2006) the enhancement of the N170 to inner components relative to the full face reflects particular sensitivity to features that produce the N170-effect. That is, removal of the face contour may enhance feature processing while reducing configural processing, leading to enhancement of the response. This enhancement was seen in both SF scales in the present study, suggesting that the common finding that inner components generate a greater N170 than full upright faces (in broadband) seems to be carried by both low- and high-spatial frequency information.

Finally, we should note that, unlike in many N170 studies, the manipulation of frequency range (and possibly the interaction of this manipulation with factors affecting the N170) had significant effects on the P1 component that precedes the N170 where selectivity to faces is not consistently found (cf. Itier and Taylor, 2004a,b). These effects were found here for P1 amplitudes but primarily on peak latencies. Although we took steps to alleviate the confound suggested by the P1 modulation between face-related and image-related effects by subtracting the P1 latency from the N170 latency, the robust effects on the P1 latency could have extended beyond its peak, and therefore the interpretation of the frequency-scale effects on the N170 latency should be considered cautiously. That said, it is apparent that, even after subtracting the P1 latency, the N170 latency was modulated by both stimulus type and frequency scale. The effect of stimulus type on the N170 latency conformed to a delay of this component for inverted faces and isolated components relative to upright faces. While the interpretation of this effect is still under debate, this discussion is outside the scope of the current paper. HSF delayed the N170 peak in all conditions across experiments, but it did not interact with inversion or components' isolation. The absence of this interaction makes it difficult to interpret these effects in terms of face processing mechanisms.

In conclusion, the current results suggest that multiple processes associated with face detection are reflected in the N170-effect, and that they flexibly use both low- and high-spatial frequency channels even when the basic-categorization of the face[4] is not task-relevant. Further research is required to clarify the nature of the difference between face inversion and other manipulations that may enhance feature processing (e.g., isolating the inner components). Yet, the current results indicate that these two manipulations are not simply two equivalent methods of decreasing the role of configural processing. Moreover, along with behavioral studies (e.g., Schyns and Oliva, 1999) the current findings point to a need for systematic investigations of interactions between the characteristic task demands and spatial frequency scales in ERPs as well as in psychophysical data.

4. Experimental procedure

Participants

The participants were 25 undergraduate students from the Hebrew University in Jerusalem with normal or corrected-to-normal vision. They received monetary compensation or course credit for their participation. All provided informed consent as approved by local committees and international standards before participation.

EEG recording and analysis

The EEG analog signals were recorded continuously by 64 Ag–AgCl pin-type active electrodes mounted on an elastic cap (ECI) according to the extended 10–20 system, and from two additional electrodes placed at the right and left mastoids, all reference-free. Eye movements, as well as blinks, were monitored using bipolar horizontal and vertical EOG derivations via two pairs of electrodes, one pair attached to the external canthi, and the other to the infraorbital and supraorbital regions of the right eye. Both EEG an EOG were sampled at 250 Hz using a Biosemi Active II digital 24-bits amplification system with an active input range of −262 mV to +262 mV per bit without any filter at input. The digitized EEG was saved and processed off-line.

The ERPs were analyzed with Analyze-Brain Products, Inc. The data were referenced to the tip of the nose. Blink artifacts were corrected by a subtraction of VEOG components with ICA. Additional EOG and EEG artifacts were removed monitoring the bipolar EOG derivations and the posterior lateral EEG sites P8, P10, P08, right mastoid, and the homologous sites over the left hemisphere. A change in voltage of more than 50 μV during a 100 ms epoch in any of these channels was considered an artifact and the EEG recorded in the interval 200 ms before and after the artifact was removed. Following this artifact removal procedure, more than 90% of the trials were preserved in each average. After removal of artifacts the EEG was digitally filtered between 0.8 and 17 Hz (12 dB), segmented and averaged separately for each stimulus type. An epoch of 100 ms prior to onset was used for baseline correction.

The peak latency and amplitude of the N170 component was extracted at the maximal negative amplitude between 150 and 220 ms at 6 posterior lateral sites: P8, P10, P08 and the homologous sites over the left hemisphere. These sites were selected a priori based on previous studies. Additionally, the peak latency and amplitude of the P1 component was extracted at the maximal positive amplitude between 75 and

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[4] Obviously, faces were categorized as “not flowers” but so were cars. Therefore, the base-level categorical distinction between faces and cars was incidental to the task.

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110 ms at the same sites. ANOVA with repeated measures and post hoc univariate contrasts were used to assess the statistical significance of the observed effects and, whenever necessary the degrees of freedom were adjusted using the Greenhouse–Geisser procedure.

Stimuli

The original stimuli were photographs that were digitally scanned and transformed into grayscale. None of the faces had glasses or jewelry. 76 different stimuli were presented in each condition. In order to equate overall stimulus size, the inner components were larger when presented in isolation than when embedded in the full face. Equating the size of the inner components within and outside the face context would have made the inner components stimuli significantly smaller than all other stimulus categories. We chose to equate overall stimulus size rather than inner component size, but previous experiments have found similar results under both circumstances (e.g., Zion-Golumbic and Bentin, 2007).

There were three filter conditions; broadband (BB), low-pass filter (LSF) and high-pass filter (HSF). The low-pass cutoff was 0.9 cycles/degree (c/d) and the high-pass cutoff was 5 c/d. Seen from a distance of 70 cm, these corresponded with 4 cycles/image and 22 cycles/image for the low and high cutoffs, respectively. As in Goffaux et al. (2003a,b) each filtered image was combined with a reciprocally filtered background texture so that the resulting hybrids were equated for spectral content across LSF and HSF conditions.[5] The broadband stimuli were presented as hybrids with the same background texture in its broadband version.

Using a house-made Matlab Algorithm we equated the luminance of all stimuli across all three filter conditions.

Procedure

Following electrode montage, participants were seated in an electrically shielded and sound attenuated booth. They were instructed to maintain central fixation and press a button every time a flower appeared on the screen. Examples of LSF and HSF flowers were shown to familiarize participants with the nature of the stimuli. A short practice block preceded the experimental blocks, which was identical to the experimental blocks but half the length. All filtered stimuli were intermixed and presented in random order, at a rate of approximately 1 stimulus/second, in four filtered experimental blocks with short breaks between blocks. Stimulus exposure time was 350 ms. The 4 filtered blocks were followed by a BB block, which was identical to the filtered blocks except that the stimuli were presented in their original BB versions.

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[5] We thank Prof. Philippe Schyns for providing us with the hybrid preparation Matlab algorithm.

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