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TIME COURSE OF SPATIAL FREQUENCY INTEGRATION IN FACE PERCEPTION: AN ERP STUDY

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Abstract

Face perception is based on the processing and integration of multiple spatial frequency (SF) ranges. However, the temporal dynamics of SF integration to form an early face representation in the human brain is still a matter of debate. To address this issue, we recorded event-related potentials (ERPs) during the presentation of spatial frequency-manipulated facial images. Twenty-six participants performed a gender discrimination task on non-filtered, low-, high-, and band-pass filtered face images, corresponding, respectively, to the full range, spatial frequencies up to 8 cycles/image, above 32 cycles/image, and from 8 to 16 cycles/image. Behaviorally, the task related-performance was more accurate and faster for non-filtered (NF) and mid-range SF (MSF) than for low SF (LSF) and high SF (HSF) stimuli. At both behavioral and electrophysiological levels, response to MSF contained in faces did not differ from the responses to full spectrum non-filtered (NF) facial images. In ERPs, LSF facial images evoked the largest P1 amplitude while HSF facial images evoked the largest N170 amplitude compared with the other three conditions. Since LSFs and HSFs would transmit global and local information respectively, our observations lend further support to the “coarse-to-fine” processing theory of faces. Furthermore, they offer original evidence of the effectiveness and adequacy of the mid-range spatial frequency in face perception. Possible theoretical interpretations of our findings are discussed.

Keywords: face processing; spatial frequency; mid-range spatial frequency; coarse-to-fine; event-related potentials

1. Introduction

1.1. *Time course of spatial frequency processing with gratings*

According to the spatial frequency theory, any visual object is first decomposed into multiple primitive components characterized by their spatial frequency spectrum (DeValois & DeValois, 1990). From retinal output to the visual cortex, spatial frequency processing is differentiated according to anatomic-functional segregations of the visual system (Livingstone & Hubel, 1988). In the lateral geniculate nucleus (LGN) especially, magnocellular cells are assumed to mainly convey low spatial frequency (LSF) information while parvocellular cells mainly convey high spatial frequencies (HSF) (De Valois, Albrecht, & Thorell, 1982; Hubel & Wiesel, 1977). The magnocellular pathway is known to transmit information faster than the parvocellular pathway (Bullier, 2001; Livingstone & Hubel, 1988; Nowak, Munk, Girard, & Bullier, 1995).

This differential time course has been verified in multiple studies using simple stimuli with easily controllable low-level characteristics such as gratings. In behavioral studies, several authors have reported longer response times to the perception of higher spatial frequency ranges alone compared with LSFs (Breitmeyer, 1975; Broggin, Savazzi, & Marzi, 2012; Lupp, Hauske, & Wolf, 1976; Mihaylova, Stomonyakov, & Vassilev, 1999; Musselwhite & Jeffreys, 1985; Vassilev & Mitov, 1976; Vassilev, Mihaylova, & Bonnet, 2002).

In the same way, electrophysiological studies have evidenced that early components of the visual evoked potential, such as the P1, have shorter latencies (Proverbio, Zani, & Avella, 1996; for a magnetoencephalography (MEG) study: Williamson, Kaufman, & Brenner, 1978), and larger amplitudes (Proverbio et al., 1996) in response to LSFs compared with HSFs. As a consequence, most studies using simple grating stimuli suggest the temporal precedence of LSF over HSF processing.

Concerning hemispheric asymmetry in SF processing, while the spatial frequency model of hemispheric asymmetry (Hellige, 1995; Reinvang, Magnussen, & Greenlee, 2002; Sargent, 1982) suggests that LSF are processed in the right hemisphere (RH) and HSF in the left hemisphere (LH), other studies did not evidence the same interaction (Grabowska & Nowicka, 1996; Boeschoten, Kemner, Kenemans, & van Engeland, 2005; Rebaï, Bernard, Lannou, & Jouen, 1998).

1.2. *From coarse-to-fine processing in face perception*

In contrast to gratings and other non-face objects, faces are much more complex visual stimuli that require the processing of two main sources of information to extract an integrated face percept, such as global/holistic information and finer featural information (for a review, see Maurer, Le Grand, & Mondloch, 2002). As such, face perception, more so than any other stimuli, is reliant

on spatial frequency processing (Collin, Liu, Troje, McMullen, & Chaudhuri, 2004; Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003; Goffaux, Gauthier, & Rossion, 2003; on the importance of spatial frequency processing for other objects, see Williams, Willenbockel, & Gauthier, 2009). These two types of facial information are believed to be contained in variable ranges of SF. It has been evidenced that low spatial frequency ranges (LSFs) convey holistic information while HSFs convey featural information about fine details (Goffaux et al., 2005; Goffaux & Rossion, 2006). Face perception is based mainly on global/holistic information (McKone & Yovel, 2009; Rossion, 2008) and is therefore believed to require LSF processing more specifically (Goffaux et al., 2003; Harel & Bentin, 2013). This assumption is supported behaviorally by the study by Parker, Lishman, & Hughes (1996, experiment 2), in which the presentation of low-to-high and high-to-low spatial frequency sequences revealed that it was the low-to-high sequence most closely resembled unfiltered presentation. The precedence of LSF over HSF face processing was also evidenced by Gao and Bentin (2011), who assessed the extraction of spatial frequency information from intact faces as well as their encoding in visual short-term memory.

Further evidence is provided by neuroimaging studies evaluating the activation of face-selective areas, such as the fusiform face area (FFA) and the occipital face area (OFA) (for reviews, see Haxby, Hoffman, & Gobbini, 2000; Kanwisher & Yovel, 2006; Duchaine & Yovel, 2015) by spatial frequency. It has been suggested that these areas may receive and process different ranges of spatial frequency input. LSF facial information is thought to activate the bilateral medial occipital gyri more strongly than HSF information, which is thought to activate the right inferior occipital gyrus and the left inferior temporal gyrus (Rotshtein, Vuilleumier, Winston, Driver, & Dolan; 2007). In addition, by varying the duration of face exposure (75, 150, or 300 ms), a fMRI study (Goffaux et al., 2011) showed that LSFs were extracted in most face-selective regions at shorter time latencies than HSFs, which required longer time exposure. In particular, LSF face images presented for 75 ms activated the right FFA (rFFA) more strongly than did HSF face images. Interestingly, while neural activity related to LSF face processing decreased over time, it increased for HSF face stimuli in the bilateral FFA and the right OFA. This pattern of results was congruent with the hypothesis of a coarse-to-fine sequence in face perception.

Owing to their high temporal resolution, electrophysiological investigations using event-related potentials (ERP) are particularly suitable for addressing the issue of the temporal dynamics of spatial frequency (SF) processing. Studies have focused on two early visual components: the P1 peaking at around 100 ms over lateral posterior regions and the N170 peaking at around 170 ms over occipito-temporal regions, in particular in the right hemisphere (Bentin, McCarthy, Perez, Puce, & Allison, 1996; Prete, Capotosto, Zappasodi, & Tommasi, 2018; Rossion & Caharel, 2011; Wyczesany, Capotosto, Zappasodi, & Prete, 2018). The P1 would be driven by low-level visual

cues (amplitude spectrum, contrast, color, etc.) (Rossion & Caharel, 2011; Rousselet, Macé, Thorpe, & Fabre-Thorpe, 2007; or at the level of the M1 for a MEG study: Tanskanen, Näsänen, Montez, Päällysaho, & Hari, 2005) and the face-sensitive N170 would reflect the perception of a face stimulus (Bentin et al., 1996; Bötzel, Schulze, & Stodiek, 1995; Rossion & Caharel, 2011; Rossion & Jacques, 2008; 2011). Regarding the modulations of the P1 as a function of spatial frequencies, its amplitude was consistently larger for LSF face images compared with that evoked by non-filtered (NF) full-spectrum face images (Nakashima et al., 2008; Obayashi et al., 2009), as well as with HSF face images (Obayashi et al., 2009). Although Nakashima et al. (2008) found no SF effect on P1 latency, Obayashi et al. (2009) found longer latency in response to LSF compared with HSF and NF face stimuli. Regarding the N170, the findings from the literature are somewhat contradictory. Whereas four studies reported larger N170 amplitude in response to HSFs than in response to NF full-spectrum face images (Nakashima et al., 2008; Obayashi et al., 2009) or LSFs (Obayashi et al., 2009; with non-frontal face: Mares, Smith, Johnson, & Senju, 2018; or at the level of the M170 for a MEG study: Hsiao, Hsieh, Lin, & Chang, 2005), two reported a smaller amplitude for HSFs compared with LSFs and NF face stimuli (Goffaux et al., 2003; Halit, de Haan, Schyns, & Johnson, 2006). In three of them, the N170 peak latencies were longer in response to HSFs compared with both NF stimuli and LSFs (Obayashi et al., 2009; Halit et al., 2006; with LSF only: Fievaris, Robertson, & Bentin, 2008) but in one (Hsiao et al., 2005) it was reported to be shorter for HSFs than LSFs and equal to NF face stimuli. In accordance with the coarse-to-fine theory, a recent EEG study (Petras, ten Oever, Jacobs, & Goffaux, 2019) revealed that LSF information would guide the processing of HSF information.

While overall these electrophysiological results tend to support the idea of the precedence of LSF information in face processing, their incongruences underline a critical aspect of the methodology pertaining to the importance of defining spatial frequency ranges that are sufficiently distinct to draw accurate conclusions on spatial frequency processing in faces. In this paper, we propose a redefinition of spatial frequency ranges, hoping to enable a clearer distinction between extreme spatial frequency ranges themselves (HSFs and LSFs) that involves excluding the band of MSFs from these ranges. Indeed, MSFs appear adequate to evoke a similar electrophysiological response to NF full-spectrum stimuli (Collin, Therrien, Campbell, & Hamm, 2012; Hsiao et al., 2005), thus altering the impact of ill-defined extreme ranges. We then propose a review of the few studies that compare the mid-range of spatial frequency with extreme spatial frequency ranges in face perception.

1.3. A review of studies using the mid-range of spatial frequency

The cut-off values chosen by the authors is an important factor when studying spatial frequency integration. They can use either two ranges, namely LSFs (fewer than 8, 5, or 4 cycles/image (c/img) depending on the study) and HSFs (above 30, 24, 22, or 15 c/img), or three with the addition of the MSFs. Most of the time this MSF range is commingled with the LSF and HSF ranges, inhibiting the assessment of a full spatial frequency range and the other two ranges. Nevertheless, the importance of the mid-range band of SF has been demonstrated (for a review, see Jeantet, Caharel, Schwan, Lighezzolo-Alnot, & Laprevote, 2018). In particular, Collin et al. (2012) showed that when participants had to adjust the “clarity” of the face image to resemble the filtered comparison faces, their response thresholds were situated within the 8-16 c/img mid-range band (MSF range) initially proposed by Costen, Parker, & Craw (1994). In Costen, Parker, & Craw’s study (1996), recognition accuracy was better for face images with a spatial frequency in the range from 4.5 c/img to 11.5 c/img and decreased outside this range. Later, Parker & Costen (1999) found that a mid-range band of 11.1 c/img enabled better and faster recognition compared with bands of 5.22 or 23.6 c/img. In addition, using more cut-off values, Collin et al. (2012) found that a non-face-relevant orientation discrimination task yielded a lower error rate as well as a shorter response time for mid-spatial frequency ranges (6.5-22.6 c/img) compared to other, more extreme values (ranging from 2.22 up to 45.25 c/img). Gaspar, Sekuler, & Bennett (2008), with a forced choice face recognition task, agreed with an optimal narrow band of MSFs within a range of 1.5 octaves from 8-10 c/img. An additional merit of this study is that the results were replicated with different viewpoints. Furthermore, in the study by Ojanpää & Näsänen (2003), participants needed longer search times to find faces when their phase was randomized at 8-11 c/img, around the central SF. Based on these multiple behavioral data, it appears that face processing is more reliant on MSFs than LSFs alone or even HSFs.

Further evidence has come from electrophysiological studies. In an orientation discrimination task, Collin et al. (2012) showed that MSF-filtered face stimuli between 6.73 and 32.0 c/img evoked a similar N170 component to NF full-spectrum faces. Moreover, these mid-range bands evoked higher amplitudes compared to extreme filtering values (LSFs and HSFs). Tanskanen, et al. (2005) provided further evidence of the importance of MSFs with the use of spatial frequency noise masks applied to face images in a face recognition task. At the level of the P1, the LSF noise mask (2 c/img) evoked the smallest peak of mid-occipital activity compared with the other 9 spatial frequency noise masks, including MSF noise. In contrast, at the level of the N170 occipito-temporal component, the pattern was reversed, with a smaller amplitude for the MSF noise (11.9 c/img). These results suggest that LSFs are actually important at an earlier stage of face processing but also that higher MSFs are integrated later. In a MEG study, Hsiao et al. (2005) showed that MSF (5-15

c/img) and HSF (> 15 c/img) face processing evoked similar latencies and amplitudes of the M170 component (the MEG counterpart of the N170) in the occipito-temporal regions, compared with non-filtered faces. This indicates that spatial frequency information from 5 to 15 c/img and above appears to be as useful and efficient as the full spectrum of NF faces. In view of all these findings, it thus appears self-evident that the MSF band merits an actual condition in the assessment of spatial frequency processing in faces.

1.4. Objectives and hypotheses of the present study

According to the literature, LSFs are generally observed to take precedence over HSFs in face processing in behavioral and electrophysiological studies. However, the incongruences observed between such studies may stem from differences in methodology, including the choices made for the cut-offs for various spatial frequency ranges. Furthermore, the review proposed here highlights the importance of the mid-range of spatial frequencies and the questions that appear to arise around its integration with LSFs or HSFs.

Taking into account these issues, the goal of the present study was to revisit the question of the time course of spatial frequency integration in face perception by recording ERPs during the presentation of face stimuli in four spatial frequency conditions, including the mid-range of spatial frequency (non-filtered NF, low spatial frequency LSF, mid-spatial frequency MSF, and high spatial frequency HSF). Based on a review of previous studies (e.g. Goffaux et al., 2003a; Goffaux et al., 2003b; Holmes, Winston, & Eimer, 2003; Tanskanen et al., 2005) and taking care to ensure that the spatial frequency ranges used did not overlap, cut-off frequencies were 8 cycles/image (c/img) for LSFs, 32 c/img for HSFs and 8-16 c/img for the band-pass filtered MSF faces. According to the coarse-to-fine theory (Flevaris, Bentin, & Robertson, 2011; Hegdé, 2008; Watt, 1987), the visual system is believed to allocate more resources to LSF processing in faces at short latencies after stimulus onset than at longer latencies during which HSF processing would be favored. Therefore, we expected that LSF face images would evoke a larger P1 component than HSF and non-filtered face images and conversely, that HSF face images would evoke a larger N170 than LSF and non-filtered face images. In contrast, MSF face images should yield similar electrophysiological and behavioral data to non-filtered face images. Behaviorally, we expected shorter response times for LSF than for HSF images, reflecting the precedence of LSF processing of faces.

2. Method

2.1. Participants

Participants were recruited by means of press advertising as well as oral inquiries as part of a larger study concerning the visual processing of cannabis users (for more detailed information on the recruitment process, see Schwitzer et al., 2016). Twenty-six participants (eight females, one left-handed, $M_{age} = 25.27$ years old, $SE = 0.85$ years) were included in the study. All participants had normal or corrected-to-normal visual acuity, as verified by the Snellen chart, with normal fundoscopic examination. For this study, approved by the Nancy University Hospital Ethics Committee (CPP 13-02-02, 2013-A00097-38), written informed consent was obtained from all participants prior to the experiment.

2.2. Stimuli

We used 32 original color photographs of full-frontal (16 female) faces without glasses, facial hair or make-up, and with neutral expression. Each picture was trimmed to remove the background, clothing, and the hairline and converted to grayscale. The resulting cropped faces were pasted onto a uniform grey background and Gaussian filtered using a Matlab program (similar to that used in Laprevote, Oliva, Delerue, Thomas, & Boucart, 2010). To avoid sharp edges around images, the background to filtered and non-filtered faces was then enlarged to fit the screen dimensions. Facial stimulus subtended a width of 6° of visual angle and a height of 9° of visual angle, eyes vertically adjusted to the center of the screen. Stimuli were presented in four spatial filtering conditions (non-filtered NF, low spatial frequency LSF, mid-spatial frequency MSF, and high spatial frequency HSF). Based on previous studies (e.g. Goffaux et al., 2003a; Goffaux et al., 2003b; Holmes et al., 2003; Tanskanen et al., 2005), LSF stimuli contained SFs below 8 cycles/image (c/img), HSF stimuli contained SFs above 32 c/img and the band-pass filtered MSF stimuli contained SFs above 8 c/img and below 16 c/img. Afterwards, images were normalized for contrast and luminance using the *Spectrum, Histogram and Intensity Normalization and Equalization* (SHINE) toolbox (Willenbockel et al., 2010) with MATLAB (version R2009a, The Mathworks Inc., 2009); see figure 1. This control was used to assess that only spatial frequencies would be responsible for the effects observed on variables.

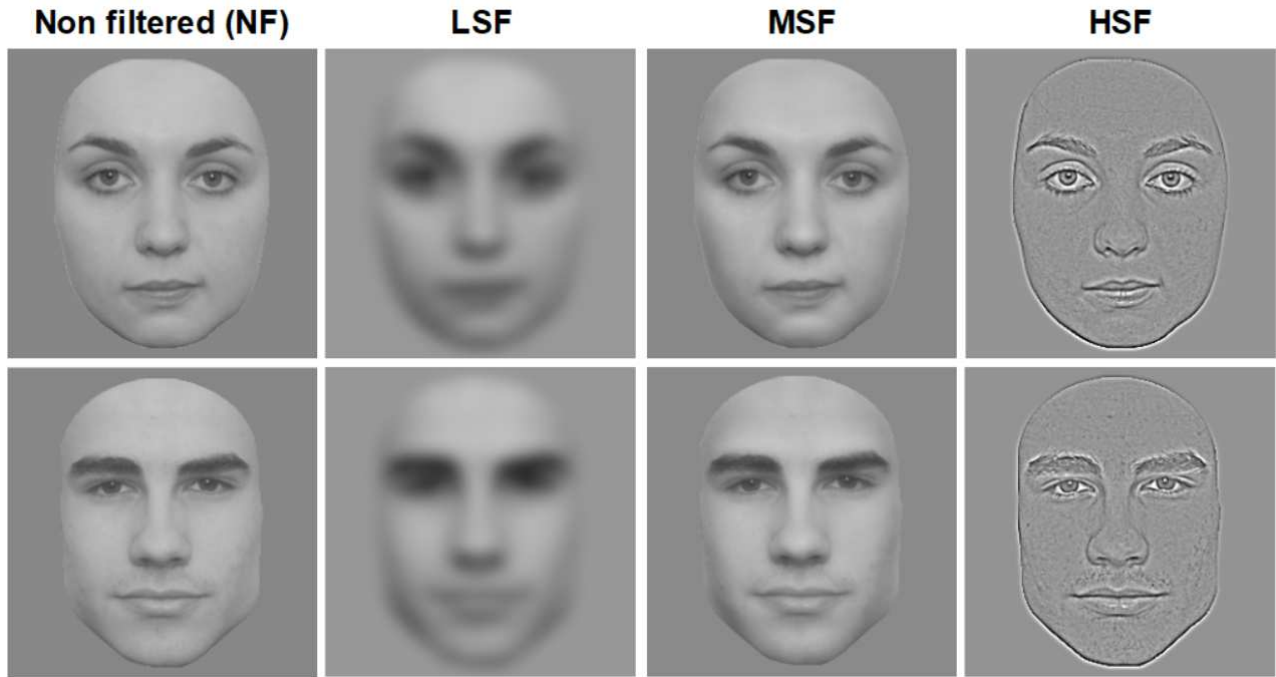


Figure 1. Examples of face stimuli after cropping, filtering and equalizing procedures. From left to right: non-filtered (NF), low-pass (LSF), band-pass (MSF), and high-pass (HSF) filtered face images.

2.3. Material and method

Participants were seated in a light- and sound- attenuated room. EEG recording took place inside an electrically isolated Faraday cage. The experiment, created on E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA), was presented on a CRT computer screen with a refresh rate of 120 Hz. The definition was set to 1024*768 and the resolution was 72 dpi. In each trial, a central fixation cross was shown for 500 ms, followed by a blank screen for approximately 200 ms (randomized between 100 and 300 ms), and then by the test stimulus, which was displayed for 500 ms. The offset of the stimulus was followed by a permitted response time of up to 1500 ms. Each trial ended with an inter-trial interval of about 1750 ms (randomized between 1500 and 2000 ms) (see Figure 2). Participants had to categorize faces by gender, and gave their response by pressing one of two keys with their dominant hand. This task was used to maintain participants' level of alertness throughout the experiment. They were instructed to maintain eye gaze fixation on the center of the screen throughout the whole of the trial and to give their response as accurately and as quickly as possible. Participants performed 6 blocks of 56 trials (336 trials in total with 84 trials per condition), presented in a randomized order within each block. Participants were provided with a familiarization block introducing the task (16 trials: 4 face images – not used in the evaluation session – with the 4 filtering conditions) before the evaluation session.

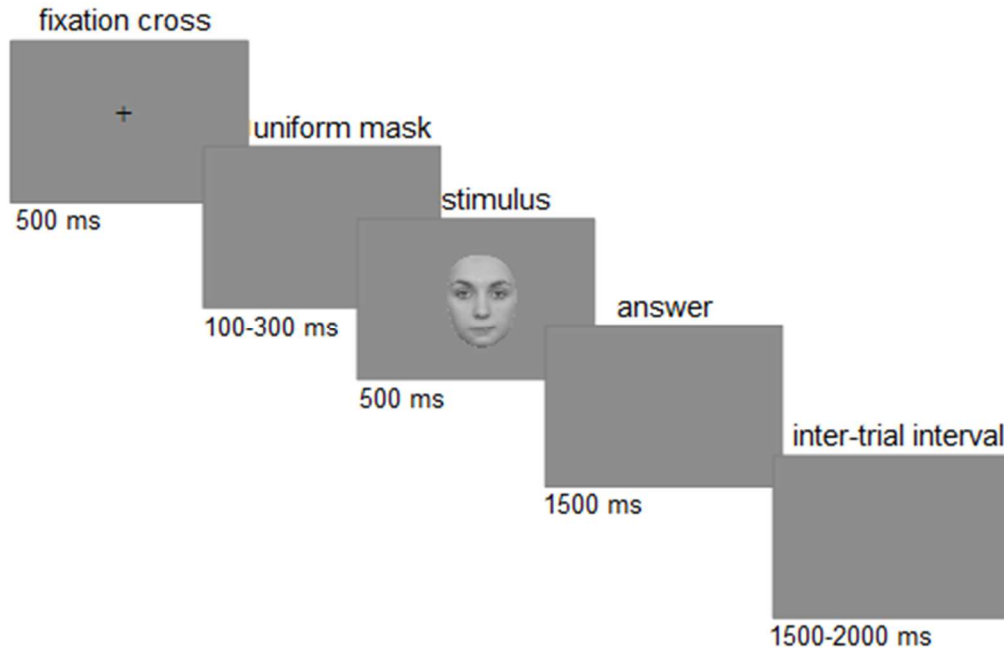


Figure 2. Timeline of stimulus presentation.

2.4. Electrophysiological data processing

An EEG was recorded from 64 electrodes according to the 10–10 classification system with a reference electrode placed on both earlobes and an earth electrode positioned on the C7 vertebra. Vertical and horizontal eye movements were monitored using four additional electrodes placed on the outer canthus of each eye and in the inferior and superior areas of the right orbit. Electrode impedance was maintained below 5 k Ω during the EEG recording. The EEG was amplified, digitized at a rate of 512 Hz, filtered and stored using MicromedTM software (Micromed S.p.A, Italy). EEG data were processed with Advanced Source Analysis ([ASA], version 4.7.3.1, ANT Software, 2016) and custom-made routines in Matlab 7.0 (R14 version, The Mathworks Inc., 2004). After a 0.1 - 30 Hz band-pass filtering of the raw EEG data, trials contaminated with eye movements or other artifacts ($\geq \pm 80 \mu\text{V}$ in -200 to 800 ms) were marked and rejected. When there were many eye-blink artifacts, a correction was applied using a principal component analysis method (Ille, Berg, & Scherg, 2002). Incorrect trials and trials containing EEG artifacts were removed. The mean number of trials remaining after EEG processing for all conditions confounded was of 77.7 ± 0.57 (SD) trials (NF: 77.3; LSF: 77.5; MSF: 77.4; HSF: 78.5 trials). Given these small variations between conditions, amplitude values were computed as the average value around the peak, a measure that is independent of small variations of SNR between conditions (Luck, 2005).

For each participant, averaged epochs ranging from -200 to 800 ms relative to the onset of the stimulus and containing no EEG artifacts were computed separately for each condition and

baseline-corrected using the 200 ms pre-stimulus time window. Participants' averages were then re-referenced to a common average reference and grand-averaged for data display of waveforms and topographical maps.

2.5. Statistical analyses

2.5.1. Behavioral data

Accuracy (percentages of correct responses) and mean correct response times were computed for each of the four conditions and were subjected to a repeated-measures analysis of variances (ANOVA) with Spatial Frequencies (NF, LSF, MSF, HSF) as within-subject factors, using the Statistica (version 7.0) software.

2.5.2. Electrophysiological data

Two clear visual ERP components were analyzed: the P1 (maximal at approximately 110 ms), and the N170 (maximal at approximately 160 ms). The amplitude values of these components were measured at different pairs of occipito-temporal electrodes in the left and right hemisphere where they were most prominent for both the P1 and the N170 (O1/O2, PO3/PO4, and PO7/PO8). Amplitudes were quantified for each condition as the mean voltage measured within 30 ms windows centered on the grand-average peak latencies of the components' maxima. Peak latencies for both components were extracted automatically at the maximum amplitude between 79 and 139 ms for the P1, and at the minimum value between 130 and 190 ms for the N170 at the same three pairs of occipito-temporal electrodes (O1/O2, PO3/PO4 and PO7/PO8) where these components were maximal (see for similar methodology, Barragan-Jason, Cauchoix, & Barbeau, 2015; Caharel & Rossion, 2011; Cauchoix, Barragan-Jason, Serre, & Barbeau, 2014).

The mean amplitude and peak latency values of each component were then subjected to separate repeated-measures analysis of variances (ANOVA) with Filtering (NF, LSF, MSF, HSF), Hemisphere, and Electrodes as within-subject factors, using the Statistica (version 7.0) software. Greenhouse-Geisser corrections (Keselman & Rogan, 1980) were applied with adjusted degrees of freedom, corresponding to the epsilon (ϵ) values. Post-hoc comparisons were performed with the Tukey test. Effect size was estimated with partial η^2 . The alpha significance value used was 0.05.

3. Results

3.1. Behavioral performance

3.1.1 Accuracy

Participants performed the gender discrimination task with a mean accuracy rate of 91% across the four SF conditions. However, there was a significant effect of *Spatial Frequency* ($F(3, 75) = 13.83$; $\epsilon = .57$, $p < .001$, $\eta^2 = .356$). Participants were more accurate with NF ($M = 94\%$, $SE = .72$) and MSF face images ($M = 94\%$, $SE = .85$) than with the extreme LSF ($M = 88\%$, $SE = 1.75$) and HSF face images ($M = 86\%$, $SE = 1.77$) (all $p < .001$). In addition, there was no difference between NFs and MSFs ($p = .752$), nor between LSFs and HSFs ($p = .119$).

3.1.2. Response times

The effect of *Spatial Frequency* on response times was also significant ($F(3, 75) = 31.63$; $\epsilon = .81$, $p < .001$, $\eta^2 = .559$). Corroborating the results for accuracy, participants answered faster for NF ($M = 555.78$ ms, $SE = 22.94$ ms) and MSF ($M = 562.30$ ms, $SE = 23.12$ ms) face images than for LSF ($M = 591.55$ ms, $SE = 24.34$ ms) and HSF images ($M = 586.64$ ms, $SE = 23.71$ ms) (all $p < .001$). Furthermore, and similarly to accuracy, no significant difference appeared between NFs and MSFs ($p = .146$), nor between LSFs and HSFs ($p = .273$).

3.2. Event-related potentials

Electrophysiological data time-locked to the presentation of the stimulus revealed the succession of the P1 and N170 event-related components usually observed following the presentation of a face. Each filtering condition (NF, LSF, MSF and HSF) evoked both components (see Figure 3).

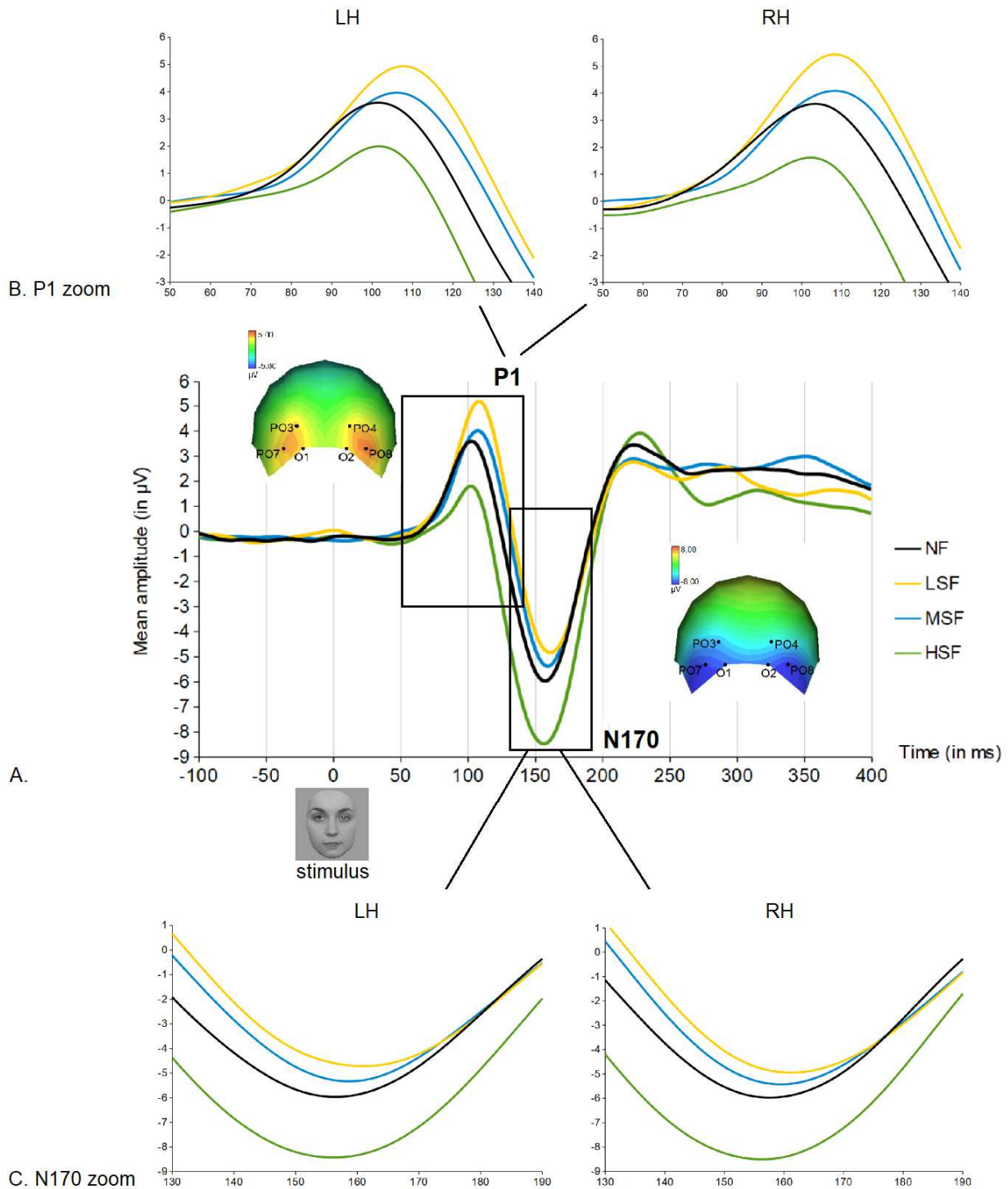


Figure 3. Electrophysiological data in response to non-filtered (NF), low spatial frequency (LSF), mid-spatial frequency (MSF) and high spatial frequency (HSF) face images. A) Grand average ERP waveforms at pooled occipito-temporal electrode sites (waveforms averaged for electrodes O1/O2, PO3/PO4, and PO7/PO8). The topographical maps, resulting from an average of all the conditions, represent the scalp distribution of the P1 and the N170 components. B) Magnified view of the P1 component at the pooled occipito-temporal electrode sites in the left (LH) and right (RH) hemisphere. C) Magnified view of the N170 component in the left (LH) and right (RH) hemispheres.

3.2.1. P1 amplitude and latency

The P1 amplitude was larger on the lateral (PO7/8) electrodes compared with the more medial O1/2 ($p < .0005$) and PO3/4 ($p < .05$) electrodes ($F(2, 50) = 11.89$; $\epsilon = .92$, $p < .001$, $\eta^2 = .322$), especially in the right hemisphere (Hemisphere x Electrodes interaction: $F(2, 50) = 4.33$, $\epsilon = .96$, $p = .019$, $\eta^2 = .148$). Most interestingly, a main SF effect ($F(3, 75) = 29.56$; $\epsilon = .52$, $p < .001$, $\eta^2 = .542$) was explained by a larger amplitude in response to LSF ($M = 4.35 \mu\text{V}$, $SE = 0.56 \mu\text{V}$) than to any of the other three conditions ($p < .05$). In addition, there was no difference in P1 amplitude between NF ($M = 2.95 \mu\text{V}$, $SE = 0.51 \mu\text{V}$) and MSF ($M = 3.28 \mu\text{V}$, $SE = 0.55 \mu\text{V}$) face images ($p = .77$). Of all three conditions (all $p < .001$), it was smallest for HSF ($M = 1.17 \mu\text{V}$, $SE = 0.66 \mu\text{V}$) (see Fig 3A and B). This SF effect was significant on the three pairs of electrodes but appeared greater on the O1/2 electrode pair ($p < .001$; $\eta^2 = .688$) than on PO3/4 ($p < .001$; $\eta^2 = .396$) and PO7/8 ($p = .002$, $\eta^2 = .232$), resulting from the interaction between Spatial Frequency and Electrodes ($F(6, 150) = 57.81$, $\epsilon = .29$, $p < .001$, $\eta^2 = .698$). Furthermore, post-hoc analyses suggested that this smaller SF effect on PO7/8 might be explained by the absence of difference in amplitude between the LSF and MSF only on this pair of electrodes ($p = .22$) (see Table 1).

In terms of latency, a main effect of Spatial Frequency ($F(3, 75) = 11.46$, $\epsilon = .66$, $p < .0001$, $\eta^2 = .314$) was also found (see Fig 3A and B). The P1 latency was shorter in response to the NF ($M = 102.55 \text{ ms}$, $SE = 1.71 \text{ ms}$) and HSF ($M = 103.17 \text{ ms}$, $SE = 1.58 \text{ ms}$) than to the LSF ($M = 108.67 \text{ ms}$, $SE = 1.60 \text{ ms}$) and MSF ($M = 107.13 \text{ ms}$, $SE = 1.77 \text{ ms}$) conditions (all $p < .05$). Furthermore, NF latency did not differ from HSF ($p = .960$) and MSF latency did not differ from LSF ($p = .608$). Analyses also revealed a Spatial Frequency x Electrodes interaction ($F(6, 150) = 4.20$, $\epsilon = .65$, $p < .005$, $\eta^2 = .144$) that would be explained by a stronger SF effect in O1/2 ($p < .0001$, $\eta^2 = .353$; PO3/4: $p < .005$, $\eta^2 = .207$; PO7/8: $p < .001$, $\eta^2 = .228$), and, in regard to post-hoc analyses, by a shorter latency for HSF than for MSF on O1/2 ($p < .0001$) (see Table 1), while these two conditions did not differ on PO3/4 ($p = .14$) and PO7/8 ($p = .09$).

All other effects or interactions on the P1 amplitude and latency were non-significant (all $p > .05$).

3.2.2. N170 amplitude and latency

A main effect of Electrodes ($F(2, 50) = 29.61$; $\epsilon = .89$, $p < .0001$, $\eta^2 = .542$) revealed that the N170 amplitude was larger on the O1/2 and PO7/8 electrode pairs (no significant difference between those, $p = .59$) than on the more superior and medial (PO3/4) electrodes (all $p < .0005$). Most importantly, a main effect of Spatial Frequency ($F(3, 75) = 32.26$, $\epsilon = .47$, $p < .001$, $\eta^2 = .563$) showed that, contrary to the P1, the N170 amplitude was larger in response to HSF ($M = -7.76 \mu\text{V}$,

$SE = .82 \mu V$) compared to any of the three other SF conditions (all $p < .0005$) but also larger for NF ($M = -5.25 \mu V$, $SE = .67 \mu V$) compared with LSF ($M = -4.17 \mu V$, $SE = .57 \mu V$) face images ($p < .05$). In addition, N170 amplitude did not differ between MSF ($M = -4.63 \mu V$, $SE = .62 \mu V$) with both NF and LSF conditions (respectively, $p = .408$ and $p = .669$) (see Fig 3A and C). This SF effect was significant on all three pairs of electrodes but appeared greater on the O1/2 ($p < .001$; $\eta^2 = .647$) than on PO3/4 ($p < .001$; $\eta^2 = .410$) and PO7/8 ($p < .001$, $\eta^2 = .466$) electrode sites, as announced by the Spatial Frequency x Electrodes interaction ($F(6, 150) = 34.90$, $\epsilon = .33$, $p < .001$, $\eta^2 = .583$). Besides, post-hoc analyses suggested that this greater SF effect on O1/2 might stem in particular from a significant difference between LSF and MSF conditions observed only on this electrode pair ($p < .0005$) (on PO3/4: $p = .714$; on PO7/8: $p = 1$).

Table 1. Mean P1 and N170 amplitudes and latencies (with SE in brackets) across conditions

	Amplitude (μV)						Latency (ms)					
	P1			N170			P1			N170		
	O1/2	PO3/4	PO7/8	O1/2	PO3/4	PO7/8	O1/2	PO3/4	PO7/8	O1/2	PO3/4	PO7/8
NF	2.46 (0.51)	2.82 (0.42)	3.57 (0.45)	- 5.57 (0.73)	- 3.62 (0.65)	- 6.65 (0.74)	102.73 (1.84)	101.80 (1.96)	103.11 (1.61)	157.05 (2.04)	159.11 (2.23)	156.60 (2.14)
LSF	4.89 (0.56)	3.94 (0.49)	4.21 (0.47)	- 3.67 (0.61)	- 2.87 (0.55)	- 5.98 (0.67)	110.06 (1.50)	107.65 (1.87)	108.29 (1.74)	162.04 (2.28)	162.99 (2.37)	160.69 (2.26)
MSF	3.03 (0.56)	3.09 (0.46)	3.73 (0.51)	- 4.71 (0.66)	- 3.25 (0.58)	- 5.92 (0.72)	107.99 (2.04)	106.19 (1.96)	107.21 (1.72)	158.02 (2.04)	160.35 (2.09)	157.23 (2.05)
HSF	- 0.87 (0.58)	1.60 (0.45)	2.78 (0.51)	- 9.37 (0.93)	- 5.29 (0.75)	- 8.62 (0.96)	101.26 (1.70)	103.68 (1.68)	104.56 (1.61)	153.61 (2.20)	158.92 (2.86)	160.69 (2.20)

At the level of the N170 latency, a main effect of Electrodes ($F(2, 50) = 4.60$; $\epsilon = .96$, $p < .05$, $\eta^2 = .155$) only evidenced a significantly longer latency on PO3/4 than on O1/2 ($p < .05$). Notably, a main effect of Spatial Frequency ($F(3, 75) = 5.32$, $\epsilon = .58$, $p < .05$, $\eta^2 = .175$) indicated a longer N170 latency in response to LSF stimuli ($M = 161.91$ ms, $SE = 2.24$ ms) compared to any of the three other SF conditions (NF: $M = 157.58$ ms, $SE = 2.07$ ms; MSF: $M = 158.54$ ms, $SE = 1.99$ ms; HSF: $M = 157.74$ ms, $SE = 2.20$ ms; all $p < .05$), which were otherwise equal (NF vs MSF: $p = .869$; NF vs HSF: $p = .999$; MSF vs HSF: $p = .918$). In addition, this SF effect only appeared on O1/2 ($p < .0001$, $\eta^2 = .267$) and PO7/8 ($p < .0005$, $\eta^2 = .271$) electrode sites (PO3/4: $p = .104$), as supported by the Spatial Frequency x Electrodes interaction ($F(6, 150) = 8.91$, $\epsilon = .34$, $p < .0005$, $\eta^2 = .263$). On these both electrode pairs, LSF stimuli evoked longer latency compared to both NF and MSF (all $p < .05$, see Table 1) and NF evoked similar latency compared to MSF (O1/2: $p = 1$;

PO7/8: $p = 1$). However, the N170 latency was shorter for HSF than for NF, LSF, and MSF conditions on O1/2 (all $p < .05$, see Table 1) but was conversely longer for HSF than for NF and MSF (all $p < .05$) and similar compared to LSF ($p = 1$) on PO7/8.

There was no other significant effect or interaction on the latency and amplitude of the N170 (all $p > .05$).

4. Discussion

How do various SFs contribute to the early extraction of face representations in the human brain? In the present study, we explored this issue by evaluating the modulations of early visual ERP components through SF filtering. Our ERP results indicate that, in the early stages, the earliest processing, which is associated with the P1 component, is more sensitive to LSF information contained in face stimuli whereas later processing, associated with the N170 component, is more sensitive to HSF information. Additionally, MSF information evoked similar P1 and N170 amplitudes to NF non-filtered images, revealing the importance of considering the mid-range band of SF as a potent and efficient range.

4.1 Coarse LSF to fine HSF face processing in successive P1 and N170 time windows

In this research, LSF face images evoked the largest P1 amplitude compared with any of the other three conditions (NF, MSF, and HSF), corroborating data from previous studies on low and high spatial frequency ranges (Nakashima et al., 2008; Obayashi et al., 2009). This early sensitivity to LSF could stem from the visual system's requirement to first extract global information about the configuration of visual objects. Indeed, coarse LSF information enables global processing of face characteristics, generating an initial, coarse representation of its configuration. However, the P1 component has not been specifically associated with face processing (Rossion & Jacques, 2008) and would more likely reflect the processing of psychophysical image characteristics (Bieniek, Pernet, & Rousselet, 2012; Puce et al., 2013; Rossion & Caharel, 2011; Rousselet, Macé, Thorpe, & Fabre-Thorpe, 2006; Tanskanen, Näätänen, Montez, Päällysaho, & Hari, 2005). In the present study, however, only face images were used, preventing any comparison with other complex visual objects. Thus, we cannot broaden the application of our results to other visual stimuli nor suggest face-sensitive reliance at this level.

Later, with regard to the N170 component, we observed an inverse modulation pattern depending on spatial frequency, with the largest amplitude in response to HSF stimuli compared with any of the other three conditions (NF, LSF, and MSF). This ERP component, which is sensitive to face processing (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000), is thought to

more particularly reflect the perceptual stage of information integration (Bentin & Deouell, 2000; Eimer, 2011) at the origin of the formation of a fully integrated percept of a face. The strong sensitivity to HSF during this stage could indicate the processing of detailed local information, refining the early representation of a face. This fine-grained information would therefore supplement and clarify the coarse global face representation built progressively from LSF information extracted previously at the level of the P1 component (Goffaux & Rossion, 2006). Thus, our observations provided further evidence of the temporal precedence of LSF over HSF processing in face perception (Goffaux et al., 2011; Parker, Lishman, & Hughes, 1996, experiment 2).

As mentioned in the introduction, the impact of SF on the amplitude modulations of N170 is controversial in the literature. Our results replicate those of several studies (Hsiao et al., 2005; Nakashima et al., 2008; Obayashi et al., 2009), although others, using different methodology, found contrasting results, with a larger N170 in response to LSFs (Goffaux et al., 2003; Halit, de Haan, Schyns, & Johnson, 2006). For instance, unlike our study and others besides (Hsiao et al., 2005; Nakashima et al., 2008; Obayashi et al., 2009), which presented face images on a uniform gray or black background, Goffaux et al. (2003) and Halit et al. (2006) chose to add the discarded ranges of spatial frequency in the form of a background in order to maintain a full spectrum of spatial frequency. However, another study that used this compensating background (Flevaris, Robertson, & Bentin, 2008) did not evidence any effect of spatial frequency on the N170 effect. Altogether, it is possible that the processing of spatial frequencies contained in faces might have been altered by this additional complementary spatial frequency information.

Moreover, cut-off values defining spatial frequency ranges might also be an explanatory factor in the variability of the observed results. In particular, for high-pass filtering conditions, some studies used relatively low cut-offs (16 c/img in Goffaux et al., 2003 and 24 c/img in Halit et al., 2006), compared with 32 c/img in our stimuli and in Nakashima et al. (2008) and Obayashi et al. (2009). Low high-pass values, approaching the MSF range, might have prevented the highlighting of specific processing of the HSF condition at the level of the N170 in these studies.

Finally, the task might be another methodological factor to take into account. Indeed, the task requirements could, if we consider task diagnosticity, lead to the processing of a favored range of spatial frequencies (Morrison & Schyns, 2001; Schyns & Oliva, 1999; Smith and Merlusca, 2014). For example, at behavioral level, it has been shown that discriminating face images based on ethnic group necessitates tuning to LSFs (Koyama, Gu, & Hibino, 2010) or that facial identity recognition required LSF information (Deruelle & Fagot, 2005). However, gender discrimination task, as used in the present study, has sometimes been linked to prioritized LSF processing (Deruelle & Fagot, 2005; Goffaux et al., 2003), sometimes to HSF processing (Koyama et al.,

2010), and even to neither of these ranges (Schyns & Oliva, 1999). Our behavioral results showed no preferential processing of either LSF or HSF, suggesting, like the last study (Schyns & Oliva, 1999), the non-diagnostics of spatial frequencies in the gender discrimination task. As Goffaux et al. (2003) found the task had an impact on ERP components, though, to rule out this potential impact on results, further studies would need to use two different tasks, or to use tasks that do not rely on the face stimulus (Nakashima et al., 2008; Obayashi et al., 2009).

Despite the dominant role of the right hemisphere in face perception, as supported by a wide range of evidence from divided visual field studies (Hillger & Koenig, 1991; Prete, Marzoli, & Tommasi, 2015; Yovel, Tambini, & Brandman, 2008), electrophysiological study (Bentin et al., 1996; Prete et al., 2018; Rossion & Caharel, 2011; Wyczesany et al., 2018) or neuroimaging (Kanwisher, McDermott, & Chun, 1997; Rossion, Dricot, Goebel, & Busigny, 2011; Sergent, Ohta, & Macdonald, 1992), in particular in global/ holistic face perception (Caharel, Leleu, Bernard, Viggiano, Lalonde, & Rebaï, 2003; Jacques & Rossion, 2009; Rossion et al., 2011; Sergent et al., 1992), our results did not reveal differential processing between the hemispheres for faces (e.g., N170) nor for the different ranges of spatial frequencies (see also for similar results, Collin et al., 2012; Flevaris et al., 2008; Halit et al., 2006; Hsiao et al., 2005; Obayashi et al., 2009). The task performed well in each filtering condition, thus ruling out a lack of face image processing by the participants. Though, one explanation may be related to the task demands, as no hemispheric asymmetry has been observed during a gender categorization task (Sergent, 1985; but see, Sergent et al., 1992). Also, given the evidence of a right-hemispheric superiority in recognizing female faces and a left-hemispheric superiority in recognizing male faces (Prete, Fabri, Foschi, Tommasi, 2016), the averaging of EEG data obtained from an equal number of female and male faces could have abolished any hemispheric asymmetry. The absence of hemispheric asymmetry for SF processing might find an answer in the hypothesis of SF processing being retinotopically mapped to the cortical cortex rather than hemispherically (Boeschoten et al., 2005; Kenemans, Baas, Mangun, Lijffijt, & Verbaten, 2000).

Consequently, on the whole, our observations, which reveal that LSFs take precedence over HSF information in the time course of face processing, lend some support to the view that face perception may rely on a “coarse-to-fine” mode of processing in which global, coarse information is processed before local, fine-grained information, with the former enabling the sharpening of the face percept (Bullier, 2001; Flevaris, Bentin, & Robertson, 2011; Hegdé, 2008; Watt, 1987). Indeed, the global information conveyed by a face, which is dependent on holistic processing, is believed to be transmitted by LSFs, while local information, which is dependent on analytical processing, is believed to be transmitted by HSFs (Goffaux, Hault, Michel, Vuong, & Rossion, 2005; Goffaux & Rossion, 2006). In other words, LSF information enables the building of a

framework, an overall structure of a visual object, while HSF information is integrated later, adding more details to this skeleton in order to form the final face percept.

Regarding the P1 and N170 latencies, our study did not provide substantial clarification to the diffuse data in the literature but nevertheless raised explanatory hypotheses. At the level of the P1, longer latencies in response to LSF and MSF face images compared with both NF and HSF images (in line with the only study available, Obayashi et al., 2009), did not substantiate either the early processing of LSF over HSF information (Goffaux et al., 2011) nor equivalent processing of NF and MSF face images (Collin et al., 2012; Hsiao et al., 2005). At the level of the N170, we observed a longer latency for LSF than for other SF filtering conditions and no difference between NF, MSF and HSF stimuli (for similar results, see: Hsiao et al., 2005, but see Collin et al., 2012; Halit et al., 2006; Obayashi et al., 2009). Again, our results on the N170 did not substantiate the precedence of LSF processing (Goffaux et al., 2011), but nevertheless indicated a similarity in NF and MSF processing (Collin et al., 2012; Hsiao et al., 2005). Additionally, the highlighting for the HSF condition of a shorter latency on O1/O2 and conversely of a longer latency on PO7/8 might support the retinotopically mapped hypothesis of SF processing (Boeschoten et al., 2005; Kenemans et al., 2000). However, the results concerning the latency should be approached with caution due to the time resolution (time resolution = $1 / \text{sampling rate}$) used in EEG recording. If the time resolution is too low with respect to the process' own dynamic scale (i.e., a recording every 4 ms, as with 250Hz sampling rate), statistics might reveal a significant difference of 2 ms when in fact, such a difference is not even recordable. Regrettably, currently published studies are disparate, with samplings ranging from 250 to 1333 Hz (250 Hz: Halit et al., 2006; 500 Hz in Collin et al., 2012; 512 Hz: present study; 600 Hz in a MEG study: Hsiao et al., 2005; 1333 Hz: Obayashi et al., 2009), preventing any reproducibility and comparison. Thus, one should be aware of this methodological factor when reviewing the divergent results observed in the literature.

4.2. Mid-range spatial frequency (MSF): an optimal information in early visual face processing,

Most importantly, the present study sheds light and definition on a poorly studied range of spatial frequencies: the mid-range spatial frequency. As expected, we found that P1 and N170 amplitudes, as well as N170 latency, evoked by NF did not differ significantly from that of MSF face images. These results suggest that the MSF range provides enough information to generate a similar processing to that of NF stimuli, containing the full spectrum of spatial frequencies. This can be explained as fairly efficient processing of the MSF range, to the extent that it would equate to the processing on full spectrum NF face images. Our observations therefore lend some support to the hypothesis of the effectiveness and adequacy of the mid-range of spatial frequency in face perception (Collin et al., 2012; Costen, Parker, & Craw, 1996; Fiorentini et al., 1983; Hsiao et al.,

2005; Parker & Costen, 1999). Again, since our experimental protocol only used pictures of faces, our results do not allow for the assessment of specific processing of MSF information for faces, which requires further exploration in the future. It has been shown, however, that MSFs seem to have a certain role in face processing, notably due to the visual system requirement that prioritizes processing of the eye region, which contains MSFs (Keil, 2008; Keil, Lapedriza, Masip, & Vitria, 2008; Sekuler, Gaspar, Gold, & Bennett, 2004). In our study, the effect of MSF could also be explained by the activation of both magno- and parvocellular pathways by MSF (Skottun & Skoyles, 2007), thus facilitating the visual processing because of the interactions between both pathways (Bar et al., 2006).

To our knowledge, just two studies have evaluated the influence of the MSF range on the N170 component. In line with our study, Collin et al. (2012) also found larger N170 amplitudes in response to MSF (< 6.73 c/img, < 11.71 c/img, and < 22.63 c/img) than to NF face stimuli, compared with the amplitudes for extreme HSF and LSF ranges. In a MEG study, Hsiao et al. (2005) evidenced M170 amplitudes that did not differ between NF, MSF (5-15 c/img), and HSF (> 15 c/img) face stimuli, and which were larger than those evoked by LSF stimuli. This finding could be explained by the fact that the HSF cut-off value in Hsiao et al. (2005) already includes the MSF range, thus hindering the discrimination of MSF and HSF conditions on the N170 shown in our study of ranges with better separation.

The early stages of face processing, reflected by the P1 and the N170 components, are responsible for the development and shaping of the facial representation which ultimately enables decision-making and the participant's behavioral response. Our behavioral results also confirmed the particular usefulness of MSFs. Indeed, in our study, the only availability of this MSF range delivered behavioral performances as good as those with NF face stimuli, in keeping with the literature (Costen, Parker, & Craw, 1996; Fiorentini, Maffei, & Sandini, 1983; Parker & Costen, 1999). In addition, all gender discrimination performance exceeded the chance threshold of 50% but did not evidence any ceiling effect of 100% accuracy, which would have indicated that the task was too easy.

4.3. Conclusion

To conclude, the present study assessed the relative contribution of different spatial frequency ranges to the extraction of early face representation in the human brain. We found a stronger sensitivity to LSF information in the P1 time window, followed by a stronger sensitivity to HSF information in the later N170 time window. These observations lend some support to the “coarse-to-fine” processing theory of faces (Goffaux et al., 2011; Parker, et al., 1996, experiment 2) as LSFs and HSFs respectively have been associated with global and local facial information

(Goffaux, 2009; Goffaux et al., 2005; Goffaux & Rossion, 2006). More importantly, this study offers novel data providing evidence for a clearer definition of the under-studied yet crucial band of mid-range spatial frequencies that we situated between 8 and 16 c/img. They demonstrate the effectiveness and adequacy of the mid-range of spatial frequency in face perception (Collin et al., 2012; Fiorentini et al., 1983; Hsiao et al., 2005; Parker & Costen, 1999; Costen et al., 1996) which is processed in a similar way to NF stimuli containing the full spectrum of spatial frequencies. These findings call for further experiments on the role and integration of this particular MSF range with other complex stimuli, to assess its specificity or lack thereof in face processing.

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