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Task and Exposure Time Modulate Laterality of Spatial Frequency for Faces

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The present study psychophysically investigated the laterality of low spatial frequencies (LSFs) and high spatial frequencies (HSFs) during face recognition at different exposure times. Spatial frequency–filtered faces were presented in a divided visual field at high and low temporal constraints in 2 tasks: face recognition (Experiment 1) and face gender recognition (Experiment 2). Both experiments revealed general primacy in the recognition of LSF over HSF faces. In Experiment 1, LSF and HSF facial information was more efficiently processed in the right and left hemispheres, respectively, and exposure time had no effect. Experiment 2 showed right hemisphere asymmetry for LSF faces at a low temporal constraint. These results suggest that the spatial frequency processing for face recognition is lateralized in the brain hemispheres. However, the contributions of LSFs and HSFs depend on the task and exposure time.

Keywords: face perception, spatial frequency, hemispheric specialization, exposure duration, task influence

The human face provides much biological and social information and is the most expressive part of the human body. Humans are expert at being fast and accurate in recognizing faces because of their social and evolutionary relevance. Efforts have been made to understand the basis of human face perception. Studies have explored the role of low-level visual information regarding faces, especially spatial frequency (SF) content (i.e., periodic variations of luminance through space; e.g., Boutet, Collin, & Faubert, 2003; de Moraes Júnior, Sousa, & Fukusima, 2014; Gao & Maurer, 2011; Goffaux, Gauthier, & Rossion, 2003). Different SF ranges convey different types of facial information. Low spatial frequencies (LSFs) represent large-scale variations of luminance and convey coarse-resolution facial information. High spatial frequencies (HSFs) represent narrow-scale variations of luminance and convey fine-resolution facial information.

Some factors influence the extraction of SF in visual perception. Many studies have shown that the processing of SF is both time- and hemisphere-dependent. Regarding the time course of processing, the visual system does not extract the entire spectrum of SFs all at once. Instead, visual perception dynamic and progres-

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sively integrates different SF ranges. Coarse LSF information is conveyed by fast magnocellular pathways and extracted in the early stages of visual processing, initiating visual scene analysis. This low-pass scenario is then detailed by fine HSF information that is conveyed by slower parvocellular pathways (Bullier, 2001; Hegdé, 2008). Neurological and behavioral evidence of such coarse-to-fine information processing has been found for a wide variety of visual stimuli, including sinusoidal gratings (Breitmeyer, 1975), hierarchical forms (Navon, 1977), hybrid images (Schyns & Oliva, 1994), natural scenes (Peyrin et al., 2010), and human faces (de Moraes, Kauffmann, Fukusima, & Faubert, 2016). Studies have shown that, in addition to evidence that the processing of SF changes over time, SF bands are processed differently in the two brain hemispheres. Sergent (1982) postulated SF hemispheric specialization, which states that the right hemisphere (RH) is predominantly involved in LSF processing, and the left hemisphere (LH) is predominantly involved in HSF processing. This hypothesis was supported by studies that used different types of stimuli, including sinusoidal gratings (Proverbio, Zani, & Avella, 1997), natural scenes (Peyrin, Chauvin, Chokron, & Marendaz, 2003), and human faces (Keenan, Whitman, & Pepe, 1989). Additionally, the cognitive context modulates the extraction of SF in visual perception. Considering conditions that present the same visual stimuli, the visual system is tuned to input information that contains the most useful cues that are associated with a particular SF range in a given cognitive task (Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003; Schyns & Oliva, 1999).

The literature has supported the coarse-to-fine and hemispheric specialization hypotheses but has been unclear about the ways in which they are related (Goffaux etal., 2011). To our knowledge, no psychophysical study has considered both issues to assess the role of LSFs and HSFs in face recognition. One way to investigate stimulus-processing time and hence the coarse-to-fine hypothesis is to manipulate the duration of stimulus exposure. The observer's performance when perceiving a stimulus with a given exposure duration is related to the stimulus processing time, especially when it is backward-masked (Enns & Di Lollo, 2000; Keysers & Perrett, 2002). This method has been used in research on SF sensitivity and face perception (e.g., Goffaux et al., 2011; Schyns & Oliva, 1994). Regarding hemispheric specialization, a classic technique that is used to behaviorally assess laterality is the divided visual field approach (Bourne, 2006). The anatomical structure of the visual system validates this method, in which the RH initially processes a stimulus that is presented in the left visual field (LVF), and the LH initially processes a stimulus that is presented in the right visual field (RVF). Many investigations of SF processing and face recognition have also implemented this method (e.g., Cattaneo et al., 2014; Peyrin, Mermillod, Chokron, & Marendaz, 2006).

The present study examined hemispheric differences in the perception of LSF and HSF facial information by manipulating the stimulus presentation time. Faces that comprised LSFs, HSFs, and broadband spatial frequencies (BSFs) were presented in the LH/RVF and RH/LVF with high and low temporal constraints. We expected that, based on a coarse-to-fine and SF hemispheric specialization framework, with a high temporal constraint the coarse LSF information would be more efficiently processed when presented in the RH/LVF and that with a low temporal constraint HSF information would favor recognition in the LH/RVF. The cognitive context is another factor that modulates SF extraction from the visual input. We addressed this issue using two tasks: face recognition (Experiment 1) and face gender recognition (Experiment 2).

Experiment 1

In Experiment 1, participants performed a matching task that consisted of SF-filtered faces that were presented in a divided visual field with high and low temporal constraints. We investigated whether the stimulus presentation time affects SF sensitivity in the brain hemispheres in face recognition.

Method

Participants. Thirty students (15 female) from the University of São Paulo participated in the study (mean age = 25 years, *SD* = 4.4). The volunteers (a) were over 17 years old, (b) had normal or corrected-to-normal visual acuity (assessed by a Snellen chart) and were free from ocular diseases, (c) had no history of neurological disease, and (d) were right-handed (evaluated by the Edinburgh Inventory; Oldfield, 1971; mean score = 82.7, *SD* = 20.3). All of the participants read and signed a statement of consent that was approved by the local research ethics committee.

Stimuli. Fifty-two frontal images of Caucasian and Pardo (i.e., multiracial) faces (26 female) with a neutral expression of emotion were extracted from the face database of Mendes, Arrais, and Fukusima (2009). Using Adobe Photoshop 7.0 software, we attenuated striking facial attributes (e.g., wrinkles, blemishes, pimples, beard) and removed external features (e.g., hair, ears, neck) using an oval surrounding frame. The oval frame that was within the quadrant where the stimulus was inserted (256 × 256 pixels, equivalent to 5.8 × 5.8 degrees of visual angle) was filled with uniform medium gray. The faces were observed at 4 × 5.8 degrees of visual angle relative to the observer on a screen that was also filled with uniform medium gray on a 19-in. cathode ray tube monitor.

The filtering process was performed using MATLAB 7.9.0 software (Mathworks Inc., Sherborn, MA) as implemented by Goffaux et al. (2011). The quadrants were multiplied by Gaussian bandpass filters in the frequency domain. One filter preserved a wide range of the visual spectrum, which generated BSF faces (0–90 cycles per face [cpf], equivalent to 0–22.3 cycles per degree of visual angle [cpd]). Another filter preserved only LSF (0–7 cpf, 0–1.7 cpd). A third filter preserved only HSF (20–90 cpf, 5.1–22.3 cpd). Before and after spatial filtering, the luminance of the image set was normalized to global luminance (equal to 0), and the root-mean-square standard deviation of the contrast was equal to 1. The optimal bandwidth for face recognition did not overlap with the bandwidths that contained LSFs and HSFs, so we could maximize the differences between them (Gao & Maurer, 2011). Figure 1 (bottom) shows examples of the stimuli that were used.

Procedure and experimental design. The experimental procedure was performed in an individual and single session in a dark and adapted room in front of a computer using a chin and forehead rest. Instructions emphasizing the importance of fixating on the central fixation point during stimulus presentation were given to the participant by the researcher and the computer screen.

Each trial began by pressing a white key on the initial screen, which triggered a 1,200-ms presentation of a BSF target face. This was followed by a fixation point that was presented in the center of the screen for 500 ms. During the last 150 ms, the fixation point changed its color and shape (warning cue). The probe face

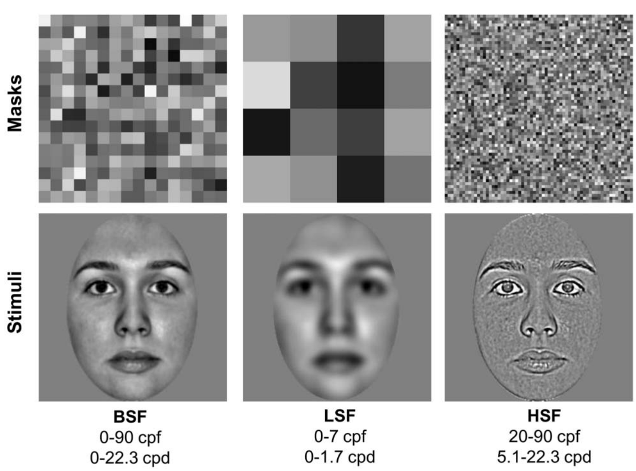

Figure 1. Examples of stimuli used in the experiment and their respective masks and spatial frequency cutoffs in cycles per face (cpf) and cycles per degree (cpd) of visual angle. BSF = broadband spatial frequency; LSF = low spatial frequency; HSF = high spatial frequency. Images are from Mendes, Arrais, and Fukusima (2009).

was then presented, lateralized in the RVF or LVF, with the face's inner edge at 2.5 degrees of visual angle from the fixation point. The face was presented in BSF, HSF, or LSF for six or 13 frames (approximately 71 and 153 ms, respectively; refresh rate = 85 Hz). The opposite hemifield was filled by a Gaussian noise mask (same size and eccentricity as the stimulus) that was presented during the same time as the probe. This procedure improves fixation control over trials by avoiding attention that is driven to a unilaterally presented stimulus that initiates a saccade toward it (Carpenter, 1988). Immediately afterward, the same Gaussian noise mask was applied in both hemifields for 200 ms to eliminate any persisting retinal image of the stimulus and limit processing time (Enns & Di Lollo, 2000; Keysers & Perrett, 2002). To maximize this effect, we built a noise mask that was adjusted for intermediate frequencies for each SF filter by varying the pixel cluster size: LSF mask (64 × 64 pixels; i.e., 4 cycles per image [cpi] in an image 256 × 256 pixels), BSF mask (16 × 16 pixels; i.e., 16 cpi), and HSF mask (4 × 4 pixels; i.e., 64 cpi). In every trial, the experimental program computed a new mask with rearranged clusters (see Figure 1, top, for examples of the masks). At mask offset, the participants had to respond whether the target and probe faces were from the same person. The answer was given by pressing a "yes" green button or "no" red button. When the response was given, the initial rest screen was presented again, starting the subsequent trial. Figure 2 (top) illustrates a trial.

The exposure times were based on those in a previous study that found a coarse-to-fine pattern for faces (Goffaux et al., 2011). In this study, the fusiform face area and other face-sensitive association cortical areas fired in re-

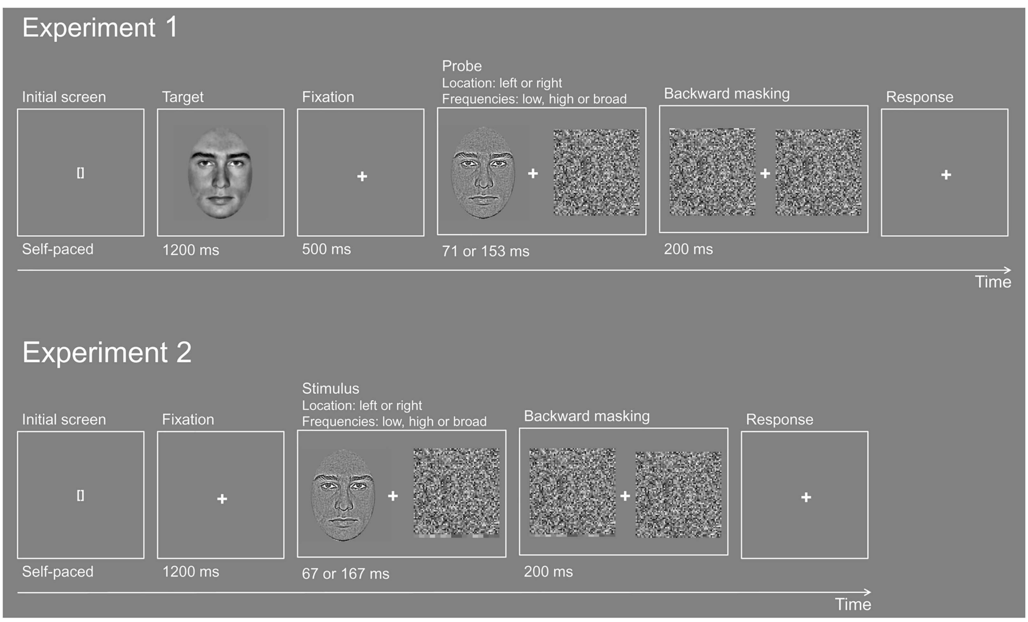

Figure 2. Illustration of one trial in Experiments 1 and 2. Each trial began after a key was pressed. In Experiment 1, this triggered presentation of the target face. A fixation screen followed the target. Subsequently, the probe face was presented and was immediately backward-masked. At mask offset, the participants had to respond whether the target and probe faces were of the same person. In Experiment 2, the initial screen was followed by a fixation screen. The stimulus was then displayed, which was backward-masked. At mask offset, the participants had to respond whether the face was male. In both experiments, the response was given by pressing yes–no buttons. The stimulus in Experiment 2 and probe face in Experiment 1 were presented (a) in the right or left visual hemifield; (b) in high, low, or broad spatial frequencies; and (c) with high or low temporal constraints. Images are from Mendes et al. (2009).

sponse to SF-filtered faces that were presented for 75, 150, and 300 ms and subsequently were backward-masked. Greater activation was found for LSF at 75 ms, and HSF elicited greater activation at 150 and 300 ms, depending on the cortical site. Additionally, an exposure time of up to 180 ms is recommended to avoid saccades when implementing the divided visual field (Bourne, 2006). Furthermore, a higher temporal constraint when presenting the stimuli is associated with the greater specialization of the brain hemispheres in processing SFs (Peyrin et al., 2006).

We employed a 2 (exposure duration) × 2 (visual field of presentation) × 3 (SF content) design with 52 trials per experimental condition: 26 same-face trials and 26 different-face trials. The same-face pairs were presented in each condition. The experiment had 624 trials that were randomly presented within and among conditions, plus 12 training trials at the beginning of the experiment. Each condition had the same number of male and female face trials for both same-face and different-face trial conditions. The entire experiment lasted approximately 45 min. Three predetermined rest intervals occurred during the experiment. Psychtoolbox 3 in MATLAB was used for Gamma correction, displaying the images, and collecting the data (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

Results

We used *z* scores from hit and false alarm rates for each participant to calculate the sensitivity parameter d'. A three-way repeated-measures analysis of variance (ANOVA; $\alpha = .05$) was used to analyze the data, with exposure duration (71 and 153 ms), SF content (BSF, LSF, and HSF), and visual field of presentation (LH/RVF and RH/LVF) as within-subject variables. We used Bonferroni adjustment for multiple comparisons and Greenhouse-Geisser correction (ε_{GG}) when the sphericity criteria were violated. The statistical analyses were performed using SPSS PASW 18 software (IBM – SPSS Inc., Hong Kong, China).

Figure 3 (top) shows the mean d' and standard error of the mean for each experimental condition. The ANOVA revealed a significant main effect of exposure duration, $F(1, 29) = 52.43$, $p < .001$, $\eta_p^2 = .64$, reflecting better recognition of faces that were presented for 153 ms ($d' = 1.52$) than for faces that were presented for 71 ms ($d' = .97$). There was also a significant main effect of SF content, $F(2, 58) = 44.04$, $p < .001$, $\eta_p^2 = .60$, indicating that BSF faces ($d' = 1.63$) were better recognized than were LSF ($d' = 1.24$) and HSF ($d' = .87$) faces, which in turn had a significant mean difference between them (all pairwise comparisons with $p < .001$). No main effect of visual field of presentation was found, $F(1, 29) = .34$, $p = .563$, $\eta_p^2 = .01$, and no Exposure Duration × Visual Field of Presentation interaction, $F(1, 29) = .17$, $p = .680$, $\eta_p^2 = .01$, or Exposure Duration × SF Content interaction, $F(2, 58) = 2.01$, $p = .143$, $\eta_p^2 = .07$. No Exposure Duration × SF Content × Visual Field of Presentation interaction was observed, $F(2, 58) = .45$, $p = .588$, $\eta_p^2 = .02$, $\varepsilon_{GG} = .77$. However, a significant Visual Field of Presentation × SF Content interaction was found, $F(2, 47) = 5.93$, $p = .008$, $\eta_p^2 = .17$, $\varepsilon_{GG} = .81$.

To reveal the source of such interactions, we performed Bonferroni post hoc tests to analyze differences among SF conditions in the LH/RVF and RH/LVF when the exposure duration variable was not considered. In the LH/RVF, observers performed better in recognizing BSF faces ($d' = 1.70$) than LSF ($d' = 1.38$, $p < .001$) and HSF ($d' = .95$, $p < .001$) faces, and the d' for LSF and HSF was significantly different ($p = .049$). These LH/RVF results followed the same pattern as those for the main effect of SF content. However, when presentation occurred in the RH/LVF, BSF ($d' = 1.56$) and LSF ($d' = 1.34$) faces were recognized with similar efficiency by the visual system ($p = .111$) and more efficiently than were HSF faces ($d' = .78$; both *p*s $< .001$). We also performed Bonferroni post hoc tests to analyze differences between the visual hemifields for each SF condition. No difference was observed between the RH/LVF and LH/RVF in recognizing BSF faces ($p = .160$). Notably, a marginally significant difference was found for LSF faces, favoring recognition in the RH/LVF compared with the LH/RVF ($p = .05$). The recognition of HSF faces also supported the functional asymmetry of SF, in which the participants more efficiently recognized HSF faces that were presented in the LH/RVF than in the RH/LVF ($p = .035$).

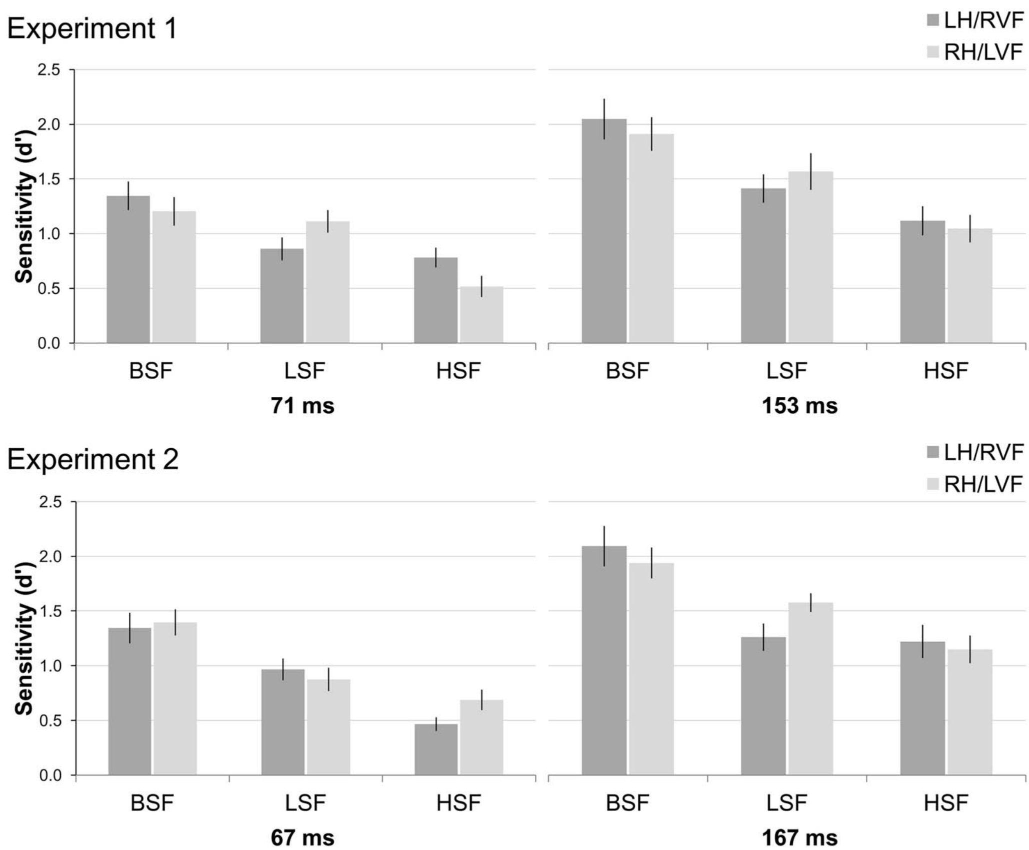

Figure 3. Average d' for faces presented in broadband (BSF), high (HSF), and low (LSF) spatial frequencies in the left hemisphere–right visual field (LH/RVF) and right hemisphere–left visual field (RH/LVF). The faces were presented with high (left) and low (right) temporal constraints in Experiment 1 (top) and Experiment 2 (bottom). Error bars indicate the standard error of the mean. Significant interactions were evaluated by analysis of variance ($\alpha = .05$). In Experiment 1, the Visual Field of Presentation × SF Content interaction indicated better performance in recognizing LSFs than did HSFs in the RH/LVF and better performance in recognizing HSFs than did LSFs in the LH/RVF. When analyzing differences between the visual hemifields for each SF condition, we found that participants more efficiently recognized LSF faces in the RH/LVF than in the LH/RVF and more efficiently recognized HSF faces in the LH/RVF than in the RH/LVF. In Experiment 2, a significant Exposure Duration × Visual Field of Presentation × SF Content interaction was found, with a significant Visual Field of Presentation × SF Content interaction only in the 167 ms condition. Low spatial frequency faces were more efficiently recognized than were HSF faces in the RH/LVF. When analyzing differences between the visual hemifields in each SF condition, we found that participants more efficiently recognized LSF faces in the RH/LVF than in the LH/RVF.

Discussion

We investigated the ways in which the brain hemispheres use LSF and HSF information over time during early stages of visual processing in a face recognition task. Thus, we performed a matching task that consisted of SF-filtered faces in a divided visual field with high and low temporal constraints. The exposure time had no effect on the results of Experiment 1, which did not confirm our initial hypothesis that we would observe LSF–RH asymmetry at high temporal constraints and HSF–LH asymmetry at low temporal constraints. However, our results supported the literature on face perception and the functional asymmetry of SF. The analysis of d'

suggested that LSF information was more important for recognizing faces when the hemifield of presentation was not considered. Additionally, LSF and HSF facial information was more efficiently processed in the RH and LH, respectively.

Considering the general advantage of LSF over HSF, previous studies have indicated that LSFs are more important than HSFs for face perception. A previous event-related potential (ERP) study reported a larger amplitude of the face-specific N170 component in response to LSF faces than to LSF cars and no amplitude difference between HSF faces and HSF cars (Goffaux, Gauthier, & Rossion, 2003). More directly related to our task, some evidence has suggested that LSFs are more important for face recognition than are HSFs. Deruelle and Fagot (2005) performed a matching task in which a target face was followed by two probe faces (Experiment 1). Their study had two types of trials: (a) In SF-filtered trials, a high-pass or low-pass target face was derived from one of two different unfiltered probe faces; (b) in hybrid trials, a high-pass–low-pass hybrid target face was created by superimposing the two different probe faces, one containing HSFs and the other containing LSFs. The analyses of error rates in the SF-filtered trials and analyses of response choices in the hybrid trials showed that the participants relied primarily on LSFs.

In the present study, the results showed that, in addition to the predominance of LSF over HSF, the participants more efficiently recognized BSF faces than HSF and LSF faces. The BSF filter that we used contained intermediate SFs that constitute the optimum range for face recognition, which conveys coarse and fine facial information cues (Morrison & Schyns, 2001; Parker & Costen, 1999).

Regarding hemispheric differences, our results showed that the sensitivity to SF bands was hemispheric-dependent. Low spatial frequency facial information is better processed in the RH, and HSF information is better processed in the LH. Previous studies that used spatial filtered stimuli have supported the SF hemispheric specialization hypothesis (Coubard et al., 2011; Peyrin, Baciu, Segebarth, & Marendaz, 2004; Peyrin et al., 2003). One previous study performed three tasks to evaluate face perception: identification, categorization of gender, and categorization of membership of the subject's department (Sergent, 1984). The faces were broad-pass-filtered (0–32 cpd; used to access HSF) and low-pass-filtered (0–2 cpd) and presented lateralized for 100 ms (Experiment 2). The face-identification and member-categorization tasks indicated LH asymmetry for broad-pass faces, and the three tasks indicated RH asymmetry for LSFs. However, even when considering the technical difficulties in processing stimuli at the time this study was performed, one can conclude that the broad-pass filter that was used comprised both coarse and fine cues for face recognition. The unidirectional RH asymmetry for LSFs that was found in the male–female categorization task is consistent with Experiment 2 in the present study. Another behavioral study also supported the differential processing of SF between the brain hemispheres. Perilla-Rodríguez, de Moraes, and Fukusima (2013) presented memorized and distractor faces in a divided visual field using LSF, HSF, and unfiltered versions. The signal detection parameters showed that LSF faces were better recognized than were HSF faces in the RH/LVF, and HSF faces were better recognized in the LH/RVF.

We can assume that, based on our results, LSFs contain more diagnostic cues that are important for face recognition than do HSFs. Furthermore, fine gradients of luminance variation of the facial pattern are more efficiently processed in the LH, whereas a coarse resolution analysis is more efficiently processed in the RH.

Experiment 2

The processing of facial SF information is modulated by the specific task. In Experiment 2, we investigated whether SF asymmetry effects and their timing are affected by the task. The same type of stimuli (i.e., neutral faces) and response modality (i.e., yes–no) that were employed in Experiment 1 were used in the face gender recognition task in Experiment 2. We also increased the experimental control by monitoring the participant's gaze location using an eye tracker.

Method

Participants. Thirty students (18 female) from the University of Montreal participated in the study (mean age = 26 years, *SD* = 5.2).

Laterality was assessed by the Edinburgh Inventory (mean score = 81.3, *SD* = 22.4). We followed the same ethical and methodological criteria of Experiment 1.

Stimuli and apparatus. Fifty-two frontal images of Caucasian faces (26 female) with a neutral expression of emotion were extracted from the Karolinska Directed Emotional Faces database (Lundqvist, Flykt, & Öhman, 1998) and used in Experiment 2 because this set was more suitable for the Canadian sample. The image treatment and presentation and spatial filtering were similar to those used in Experiment 1, in which faces were observed at 4 × 5.8 degrees of visual angle relative to the observer on a 23-in. LED monitor.

FaceLAB 5 (Seeing Machines Inc., Canberra, ACT, Australia) monitored the fixation locations at a sampling rate of 60 Hz, with accuracy error of .5 to 1 degree of visual angle. The eye-tracking device comprised two infrared cameras, one infrared light, and EyeWorks software (EyeWorks Inc., San Diego, CA). Inhouse code that was written in MATLAB recorded temporal markers to analyze the gaze location between stimulus onset and offset.

Procedure and experimental design. The experimental procedure was again performed by each participant alone and in a single session in a dark room in front of a computer using a chin and forehead rest. The eye tracker was calibrated for each participant using a standard 9-point grid. Instructions emphasizing the importance of fixating at the central fixation point during stimulus presentation were given to the participants by the researcher and the computer screen.

Each trial began by pressing a white key on the initial screen, which triggered a 1,200-ms presentation of the fixation point, which changed its color and shape in the last 250 ms. A face was then presented in the LVF or RVF, with the face's inner edge at 3 degrees of visual angle from the fixation point. The face was presented in BSF, LSF, or HSF for four or 10 frames (approximately 67 and 167 ms, respectively; refresh rate = 60 Hz). The opposite hemifield was filled by a Gaussian noise mask with the same size and exposure duration as the stimulus. We varied the size of the mask's pixel cluster for each SF condition as in Experiment 1. The same Gaussian noise was then applied for 200 ms as backward masking in both hemifields. At mask offset, the participants had to respond whether the face was male. The answer was given by pressing a "yes" green button or "no" red button. When the response was given, the initial rest screen was presented again, which started the subsequent trial. Figure 2 (bottom) illustrates a trial. The choice of male faces as "signal" and female faces as "noise" was arbitrary, and we did not counterbalance the female faces as the signal across participants, to avoid differences in sensitivity and response criteria. We also preferred a yes–no signal detection task rather than a categorization task because the latter is more common in the literature. The use of d' as the performance parameter allowed us to better compare the results with Experiment 1 and avoid possible bias that may result from the response modality.

All of the stimuli set were presented in each condition. We employed a 2 (exposure duration) × 2 (visual field of presentation) × 3 (SF content) design, with 52 trials per experimental condition, for a total of 624 trials that were randomly presented within and among conditions, plus 12 training trials at the beginning of the experiment. The entire experiment lasted approximately 45 min, and three predetermined rest intervals occurred. Psychtoolbox 3 in MATLAB was used to display the images and collect the data.

Results

An offline analysis eliminated trials in which the participants switched their gaze to the left or right 1.5 degrees of visual angle away from the central fixation point during stimulus presentation. One participant had more than 30% of the trials invalidated and was excluded from the sample. Altogether, 8.38% of the trials were excluded because of inaccurate gaze. As in the Experiment 1 procedure, we calculated the sensitivity parameter d'. Two cases were excluded because they were outside the boundaries of 3.5 *SD*s within their experimental condition and because each isolated case was responsible for significant effects. Both cases were replaced by the mean of the condition. The statistical analyses were performed exactly as in Experiment 1.

Figure 3 (bottom) shows the mean d' and standard error of the mean for each experimental condition. The ANOVA revealed a significant main effect of exposure duration, $F(1, 28) = 133.81$,

$p < .001$, $\eta_p^2 = .83$, indicating that increasing the exposure time from 67 ms ($d' = .96$) to 167 ms ($d' = 1.54$) resulted in a greater d'. We also found a main effect of SF content, $F(2, 26) = 53.95$, $p < .001$, $\eta_p^2 = .66$. Similar to Experiment 1, BSF faces ($d' = 1.69$) were better recognized than were LSF ($d' = 1.17$) and HSF ($d' = .88$) faces, which in turn had a significant mean difference between them (all pairwise comparisons with $p \leq .001$). No main effect of visual field of presentation was found, $F(1, 28) = .66$, $p = .425$, $\eta_p^2 = .02$. None of the two-factor interactions were significant: Exposure Duration × Visual Field of Presentation, $F(1, 28) = .09$, $p = .766$, $\eta_p^2 < .01$; Exposure Duration × SF Content, $F(2, 26) = .58$, $p = .563$, $\eta_p^2 = .02$; and Visual Field of Presentation × SF Content, $F(2, 26) = 1.11$, $p = .338$, $\eta_p^2 = .04$. However, there was a significant Exposure Duration × Visual Field of Presentation × SF Content interaction, $F(2, 26) = 5.74$, $p = .005$, $\eta_p^2 = .17$.

To elucidate the dynamics of hemispheric differences as a function of exposure duration, we divided the ANOVA into the two exposure duration conditions, revealing a significant Visual Field of Presentation × SF Content interaction for the 167 ms condition, $F(2, 26) = 5.01$, $p = .010$, $\eta_p^2 = .15$, but not for the 67 ms condition, $F(2, 26) = 1.85$, $p = .167$, $\eta_p^2 = .06$. We then examined differences among SF conditions in the LH/RVF and RH/LVF for the 167 ms condition. Pairwise comparisons (Bonferroni-corrected) showed that the participants more efficiently recognized BSF faces ($d' = 2.09$) than LSF ($d' = 1.26$, $p < .001$) and HSF ($d' = 1.22$, $p < .001$) faces in the LH/RVF. Likewise, they also more efficiently recognized BSF faces ($d' = 1.94$) than LSF ($d' = 1.58$, $p = .043$) and HSF ($d' = 1.15$, $p < .001$) faces in the RH/LVF. Low spatial frequency faces were more efficiently recognized than were HSF faces in the RH/LVF ($p = .013$) but not in the LH/RVF ($p > .999$), thus revealing RH–LSF asymmetry. We also performed Bonferroni post hoc tests to analyze differences between the visual hemifields for each SF condition. No difference was found between the RH/LVF and LH/RVF when recognizing BSF faces ($p = .280$) or HSF faces ($p = .419$). However, the recognition of LSF faces was more efficient in the RH/LVF than in the LH/RVF ($p = .021$), supporting the RH–LSF asymmetry for faces in the 167 ms condition.

Discussion

Experiment 2 investigated the ways in which the brain hemispheres use SF information over time during early stages of visual processing in a male–female facial recognition task. We used stimuli and a response modality that were similar to those used in Experiment 1 to investigate whether the task modulates the laterality and temporal processing of SF in face encoding. Our results showed better general sensitivity for LSF, RH asymmetry for LSF faces at low temporal constraints, and no HSF preferences. These results suggest that gender facial information is more efficiently driven by LSFs in the RH.

Previous experiments have supported the notion that gender facial information is mostly conveyed by LSF cues. A behavioral study investigated the perception of identity, gender, and emotion in adults and children using LSF–HSF hybrid faces (Deruelle & Fagot, 2005). In one session in Deruelle and Fagot's (2005) Experiment 2, the participants were asked to categorize the gender of the face that was displayed in the center of the screen for 400 ms (for children) or 100 ms (for adults). The number of low-pass choices showed a LSF bias for children and adults (Deruelle & Fagot, 2005). However, no SF bias was found in a gender-categorization task using hybrid faces (Schyns & Oliva, 1999). More behavioral evidence came from a study that used SF filtered faces rather than hybrids (Aguado, Serrano-Pedraza, Rodríguez, & Román, 2010). The faces were displayed until a response was emitted by the participants or until 2,000 ms elapsed. In the gender-categorization task that utilized expressive faces (Experiment 1) and neutral faces (Experiment 3), HSF faces had a greater error rate than did LSF faces, although the response latencies for LSF faces were slower than for HSF faces (Aguado et al., 2010). In Goffaux, Gauthier, & Rossion, (2003) ERP study, participants performed gender and familiarity tasks by responding male–female and familiar–unfamiliar after a training phase. The face-sensitive N170 component had a larger amplitude in the gender task than in the familiarity task for LSF faces only. The gender task showed a different N170 amplitude between LSF and HSF faces. Additionally, the behavioral data showed less accurate and slower responses to HSF faces compared with LSF faces in the gender-categorization task.

In addition to demonstrating LSF primacy for the processing of face gender information, our Experiment 2 also highlighted RH asymmetry for LSF faces, which was expected when considering the hypothesis of SF hemispheric specialization (Sergent, 1982). Our results are consistent with those in previous work. This study presented lateralized broad-pass- and low-pass-filtered faces for 100 ms in three tasks: identification, membership categorization (the participant's department), and male–female categorization. Unlike identification and membership categorization, which indicated double asymmetry for SFs as described in the Discussion section for Experiment 1, the gender categorization showed RH asymmetry for only LSFs (Sergent, 1984). This may reflect the absence of an HSF-lateralized process for gender recognition because HSFs do not appear to contain the most diagnostic cues for such a task.

We were expecting to observe RH–LSF asymmetry in the high temporal constraint condition because coarse information is conveyed faster than is fine information. In the study by Aguado et al. (2010) cited earlier, responses to LSF faces had longer latencies in the male–female categorization tasks, although LSF faces yielded fewer errors. These authors proposed an interpretation that was based on a speed–accuracy trade-off. In short, the efficiency of processing LSF faces was not followed by (a) faster processing, reflected by response time (Aguado et al., 2010), or (b) better sensitivity in the RH in the high temporal constraint condition (Experiment 2 in the present study). We propose an alternative explanation of this issue that is distinct from the speed–accuracy trade-off. New evidence has suggested that the initial LSF input rapidly reaches high-order areas that feedback to low-level areas to modulate visual processing (see Kauffmann, Ramanoël, & Peyrin, 2014). Task demands may modulate this rapid top-down analysis of LSF and influence subsequent SF processing.

We propose that, based on our results, HSFs are not as critical as LSFs to recognize the gender of a face. Furthermore, the RH appears to play a major role in this task. Top-down processes may modulate the asymmetrical sensitivity of LSFs in the RH and its occurrence in later stages of visual processing.

General Discussion

We investigated the ways in which the visual system processes LSFs and HSFs in the left and right brain hemispheres under conditions of high and low temporal constraints in a face recognition matching task (Experiment 1) and male–female recognition task (Experiment 2). Our results showed that SF bands were differentially processed by the brain hemispheres and that the presentation time and task influenced SF hemispheric specialization.

Regarding the influence of the task, behavioral studies have shown that both visual input properties and the task modulate the LSF and HSF processing of facial information (for examples of tasks and stimuli that modulate SF processing, see Awasthi, Sowman, Friedman, & Williams, 2013; Rotshtein, Schofield, Funes, & Humphreys, 2010; Schyns & Oliva, 1999). In the present study, we further evaluated the role of the task in the processing time course and asymmetry effects. By comparing Experiments 1 and 2, we observed different patterns of functional asymmetry. In Experiment 2, the stimulus presentation time influenced emergence of the asymmetry effect. Considering that both experiments used neutral faces[1] and yes–no responses, we attribute the different results to the tasks that the participants performed.

Our results provide evidence that visual perception is flexible even for high expertise-based stimuli such as faces, adapting its spatial and temporal processing to demands of the cognitive context. Cognitive top-down factors may modulate the extraction of SF content in face perception, selecting the most important information for a given high-level process. Therefore, our data argue against the cognitive impenetrability hypothesis, which states that there are no cognitive influences over perceptual pro-

[1] We used different face databases in the two experiments. Although the same database would be used in a more controlled scenario, we avoided cultural bias because the participants were from two different countries. People are generally better at recognizing same-race faces than cross-race faces (i.e., the so-called cross-race effect; for review, see Meissner & Brigham, 2001). In practical terms, however, faces from the two databases were very similar after digital treatment (i.e., reducing size from the original, inserting into a quadrant, hiding external features with an oval-shaped mask, and smoothing facial features) and spatial filtering (including luminance and contrast control).

cesses (Pylyshyn, 1999). We demonstrated that SF sensitivity is modulated by the cognitive context, functional asymmetries, and their timing. However, the direction of functional asymmetry appears to be unidirectional. When information selection favors LSFs, processing is performed mostly in the RH. When information selection favors HSFs, processing is performed mostly in the LH.

Several studies have investigated facial recognition regarding SF sensitivity, temporal processing, hemispheric specialization, and task influence. In the present study, we combined all of these variables to better comprehend the interactions between them. Furthermore, unlike previous behavioral studies that used classic performance indices, such as accuracy and error rate, we used d' from signal detection theory as the sensitivity parameter. Signal detection measures are uncontaminated by response bias; therefore, variability in the measured sensitivity is reduced because there is no variability that is caused by changes in the decision criteria (Pastore & Scheirer, 1974; Stanislaw & Todorov, 1999).

Additionally, the present results may be helpful for researchers who are interested in the high-level integration of information. Influential models assume that visual perception begins with SF analysis (Bar, 2003; Bullier, 2001; Hegdé, 2008; Schyns & Oliva, 1994). There is extensive literature on the processing of SFs by specialized cells in the retina to the primary visual cortex (De Valois, Albrecht, & Thorell, 1982; Livingstone & Hubel, 1988). However, the way in which this information is integrated in higher order cognitive representations is unclear (Goffaux et al., 2011). The present study provides insights into the ways in which cognitive representations of the human face rely on SF information in the left and right brain hemispheres and such factors as the task and exposure time.

In summary, we investigated the ways in which the brain hemispheres process LSF and HSF information under conditions of high and low temporal constraints in a face recognition task (Experiment 1) and face gender recognition task (Experiment 2). We initially established a general hypothesis based on coarse-to-fine and hemispheric specialization assumptions: RH asymmetry for LSFs at high temporal constraints and LH asymmetry for HSFs at low temporal constraints. The results did not confirm this initial hypothesis, but interesting interactions emerged from the data. Both experiments demonstrated general primacy in the recognition of LSF over HSF faces, indicating that LSF bands conveyed more diagnostic cues in the tasks that were performed herein. In Experiment 1, LSF and HSF facial information was more efficiently processed in the RH and LH, respectively, and exposure time had no effect. In Experiment 2, the results showed RH asymmetry for LSF faces at low temporal constraints. We conclude that LSF and HSF processing is lateralized in the RH and LH, respectively, for face recognition. However, their contribution depends on the task and exposure time.

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