Effect of temporal constraints on hemispheric asymmetries during spatial frequency processing

Carole Peyrin [a,b,c,*], Martial Mermillod [c,d], Sylvie Chokron [c], Christian Marendaz [c]

[a] *INSERM U455, Hopital Purpan, Toulouse, France*
[b] *Laboratory for Neurology and Imaging of Cognition and Functional Brain Mapping Laboratory, Department of Neurosciences, University Medical Center, 1, rue Michel-Servet, CH-1211 Geneva, Switzerland*
[c] *Laboratoire de Psychologie et NeuroCognition, CNRS-UMR 5105/Université Pierre Mendès-France, BP 47, 38040 Grenoble Cedex 09, France*
[d] *Laboratoire de Psychologie Sociale et Cognitive (LAPSCO), CNRS-UMR 6024/Université Blaise Pascal, 34, av Carnot, 63037 Clermont-Ferrand, France*

Abstract

Studies on functional hemispheric asymmetries have suggested that the right vs. left hemisphere should be predominantly involved in low vs. high spatial frequency (SF) analysis, respectively. By manipulating exposure duration of filtered natural scene images, we examined whether the temporal characteristics of SF analysis (i.e., the temporal precedence of low on high spatial frequencies) may interfere with hemispheric specialization. Results showed the classical hemispheric specialization pattern for brief exposure duration and a trend to a right hemisphere advantage irrespective of the SF content for longer exposure duration. The present study suggests that the hemispheric specialization pattern for visual information processing should be considered as a dynamic system, wherein the superiority of one hemisphere over the other could change according to the level of temporal constraints: the higher the temporal constraints of the task, the more the hemispheres are specialized in SF processing.
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1. Introduction

Visual scenes are made up of several objects (e.g., houses, trees) themselves made up of smaller objects (e.g., windows, leaves). Convergent data from the functional neuro-anatomy of magnocellular and parvocellular visual pathways (Van Essen & DeYoe, 1995), neurophysiological recordings in primates (Bullier, 2001), and psychophysical results in humans (Ginsburg, 1986; Hughes, Nozawa, & Kitterle, 1996) suggest that visual analysis of this hierarchical information is critically dependent on spatial frequency (SF) processing of the image with a preferential coarse-to-fine (CtF) processing sequence. The low spatial frequencies (LSF), conveyed by fast magnocellular visual pathways, might activate the visual areas first allowing an initial perceptual parsing of a visual scene. This initial low-pass visual analysis might then be refined by high spatial frequencies (HSF), conveyed more slowly by parvocellular visual pathways.

Experimental evidence in support of a CtF processing hierarchy in human vision comes from psychophysical studies using gratings of different SF as stimuli. For example, Breitmeyer (1975, see also Breitmeyer and Ganz, 1977) showed that LSF channels have short latencies and short integration time, whereas HSF channels respond slowly and have a long integration time, suggesting thus that LSF are transmitted faster than HSF through the visual system. Additional evidence was provided by psychophysical studies using hierarchical forms, which are global forms composed of several local elements (see Navon, 1977). Classically, the global information is identified faster than the local elements. Based on the assumption that

* Corresponding author. Fax: +33476827834.
E-mail address: carole.peyrin@upmf-grenoble.fr (C. Peyrin).

global information is preferentially conveyed by LSF whereas local information by HSF (Badcock, Whitworth, Badcock, & Lovegrove, 1990; Hughes et al., 1996; Lamb & Yund, 1993), this global precedence effect has been interpreted as reflecting a fundamental principle of CtF analysis. Importantly, CtF analysis of SF was also demonstrated during the perception of more ecological visual stimuli, such as natural scene images. For example, Schyns and Oliva (1994) used a matching task with "hybrid" stimuli made of two superimposed images from natural scenes, belonging to different semantic categories and containing different SF-bands (e.g., a highway scene in LSF superimposed on a city scene in HSF). They showed that very brief presentation time of hybrids (30 ms) elicited matchings based on their LSF content while longer presentation time (150 ms) elicited matchings based on their HSF content. These results thus suggest a precedence of LSF on HSF over the course of scene recognition.

Within the framework of visual SF analysis, it has often been proposed that the right hemisphere (RH) might be predominantly involved in LSF information processing whereas the left hemisphere (LH) might be more involved in HSF processing. This assumption has been supported by numerous behavioural studies (Blanca, Zalabardo, Gari-Criado, & Siles, 1994; Chokron, Brickman, Wei, & Buchsbaum, 2000; Martin, 1979; Sergent, 1982) and neuro-imaging studies (Fink et al., 1996; Han et al., 2002; Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Lux et al., 2004; Martinez et al., 1997; Proverbio, Minniti, & Zani, 1998; Yamaguchi, Yamagata, & Kobayashi, 2000) conducted among healthy subjects, as well as neuropsychological observations (Lamb, Robertson, & Knight, 1990; Robertson & Lamb, 1991; Robertson, Lamb, & Knight, 1988) using hierarchical forms as stimuli. Typically, these studies observed a functional hemispheric specialization for global vs. local processing (i.e., a RH dominance for processing global information and a LH dominance for local information) that has been interpreted as reflecting a basic hemispheric specialization for low vs. high spatial frequency processing (see Grabowska & Nowicka, 1996; Ivry & Robertson, 1998; Sergent, 1982).

More direct evidence of hemispheric specialization in SF processing was provided by behavioural studies using gratings of different SF (Christman, Kitterle, & Hellige, 1991; Kitterle, Christman, & Hellige, 1990; Kitterle, Hellige, & Christman, 1992; Kitterle & Selig, 1991) or LSF and HSF natural pictures. Indeed, in recent divided visual field studies conducted on healthy participants, we addressed the issue of hemispheric specialization for SF processing by altering the frequency spectrum of natural scenes images (Peyrin, Chauvin, Chokron, & Marendaz, 2003; Peyrin et al., 2006). Our results showed that the two hemispheres differ significantly in the way they process SF. Results showed a left visual field/right hemisphere (LVF/RH) superiority during the recognition of LSF scene images, whereas a right visual field/left hemisphere (RVF/LH) superiority was observed during the recognition of HSF

scene images, thus supporting the hypothesis of hemispheric specialization in the processing of SF (Sergent, 1982). Recent functional brain imaging studies conducted on healthy subjects also support this pattern of functional cerebral organization (Iidaka, Yamashita, Kashikura, & Yonekura, 2004; Kenemans, Baas, Mangun, Lijffijt, & Verbaten, 2000; Peyrin, Baciu, Segebarth, & Marendaz, 2004; Peyrin et al., 2005).

The aim of the present study was to specify the pattern of hemispheric specialization for SF with respect to the CtF hypothesis among healthy participants. For this purpose, we aimed to investigate the influence of stimuli presentation time on the LVF/RH and RVF/LH advantage for respectively LSF and HSF natural scene images. A few studies dealing with hierarchical form processing have investigated the influence of exposure duration on hemispheric specialization. For example, in a divided attention task, Blanca et al. (1994) found a classical global/local hemispheric specialization for short (50 ms), but not for longer (100 and 200 ms) exposure duration of hierarchical forms. The authors concluded that hemispheric specialization during global and local information processing only appears when the stimulus visibility is limited. Differently, in a selective attention task, Boles and Karner (1996) found an unexpected RH dominance for local processing that was stronger for short (33 ms) than long duration (100 ms). The authors concluded that hemispheric asymmetries found for short exposure duration might reflect a basic RH predominance in the processing of degraded visual stimuli, irrespective of their SF content. More recently, Evert and Kmen (2003) using a larger sample of exposure duration in a selective attention task found more consistently a LH dominance for local processing than a RH dominance for global processing. Furthermore, this LH specialization was most commonly observed in the middle range of exposure durations tested (e.g., 53 and 67 ms). Thus, these studies led to conflicting hypotheses about the effect of exposure duration on hemispheric specialization for global and local processing. Furthermore, none of these experiments were designed with regard to the CtF analysis of natural scenes.

Therefore, in pilot work, we used the divided visual field task of LSF and HSF natural scene recognition (see Peyrin et al., 2003, 2006), in which we simply manipulated exposure duration of scene stimuli. Exposure durations were chosen on the basis of Schyns and Oliva's study (1994). Thus, scenes were displayed either for 30 ms (short presentation condition) or 150 ms (long presentation condition). However, results of this pilot work showed that filtered scenes briefly flashed for 30 ms in one visual hemifield were almost imperceptible for participants, suggesting that the task used was not appropriate to our investigations. Therefore, in the present study, we manipulated exposure duration independently of both SF content and visual field of presentation. For this purpose, we used matching task between two successive scene images. Based on Schyns and Oliva's works (1994), (Experiment 1), exposure

duration (either 30 or 150 ms) was manipulated on the first scene and always displayed in the central visual field (i.e., projected on both hemispheres). Based on our previous studies, the second scene was both filtered either in LSH or HSF and lateralized either in the LVF/RH or RVF/LH. Participants had to decide whether the two successive scenes were from the same category.

Our predictions were as follows: Under the hypothesis of hemispheric specialization for SF processing, we should observe a LVF/RH advantage when matching the second LSF scene and a RVF/LH advantage when matching HSF information. In addition, regarding the literature about CtF analysis of SF, variations in the presentation time of the first scene should change the SF band preferentially processed in the first non-filtered scene. Therefore, based on Schyns and Oliva's study (1994), for short presentation time (30 ms), we expected participants to use LSF information in the first non-filtered scene. This 'coarse' analysis may preferentially recruit the RH (specialized for LSF processing) and thus predominantly engage this hemisphere for the subsequent matching process with the second scene. Conversely, for longer presentation (150 ms), we expected them to use HSF information. This more 'fine' analysis may preferentially engage the LH (specialized for HSF processing) in the processing of the whole scene sequence. Therefore, our main prediction was that brief relative to long presentations should enhance the LVF/RH advantage when matching the second LSF scene, whereas long presentation should enhance the LH advantage when matching the second HSF scene. On the contrary, if temporal constraints applied on the processing of the first scene have no effect on the matching process, we should expect similar patterns of hemispheric asymmetries irrespective of the first scene exposure duration (30 vs.150 ms).

2. Method

2.1. Participants

Sixteen healthy undergraduate students of the Psychology from the Université Pierre Mendès-France in Grenoble (eight men and eight women) participated in the experiment for course credits. All were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants had normal or corrected-to-normal vision and they were not aware of the purpose of the experiment.

2.2. Stimuli

Stimuli were four black-and-white photographs (256 × 256 pixels, 256 grey-scales) of natural scene images: a city, a highway, a beach and a mountain (Fig. 1a). These scenes had been chosen in order to obtain pairs of scenes with similar dominant orientations in amplitude spectra (the city and highway pair, which had vertical and horizontal dominant orientations, and the beach and mountain pair, which had vertical dominant orientations in Fourier

domain, see Fig. 1b), so that their discrimination could not be made on the basis of this information. Stimuli were displayed against a grey background (68.8 cd/m^2), using E-prime software (E-prime Psychology Software Tools Inc., Pittsburgh, USA) on a computer monitor (17 in. TM Ultra Scan P790 monitor with a resolution screen of 1024 per 768 pixels; minimum luminance: 8.6 cd/m^2; maximum luminance: 115.6 cd/m^2) located 110 cm from the participant. Their angular size was thus of 4° of visual angle. For each scene, two additional filtered images were created, a LSF and a HSF stimulus (Fig. 1c–d). SF content of scenes was filtered by multiplying the Fourier transform of original images by Gaussian filters. The standard deviation of the Gaussian filter is a function of the SF cut-off, for a standard attenuation of 3 dB. We removed the SF content above 4 cycle/degree of visual angle (i.e., low-pass cut-off of 16 cycles per image) for LSF stimuli and below 6 cycles/degree (i.e., high-pass cut-off of 24 cycles per image) for HSF stimuli. In order to create stimuli that did not bias hemispheric dominance (see Christman, 1989), the total energy for LSF and HSF images was equalized for each scene.[1] A backward mask was used in order to prevent retinal persistence of the scene. The mask was built by the random sum of several natural scenes belonging to eight different categories. Therefore, the mean frequency spectrum of the mask was similar to natural scenes.

2.3. Procedure

Participants were tested individually in a darkened room. Head position was stabilized in a chin rest. An experimental trial consisted of an image-sequence during which two natural scenes were displayed in a rapid succession (see Fig. 1e). Each trial began with a central fixation point (in order to control the gaze direction to the centre of the screen) for 500 ms, immediately followed by the first scene of the sequence, then by the mask for 30 ms. At the offset of the mask, the second scene appeared and then a mask for 30 ms. The first scene in each sequence was always non-filtered, displayed in the central visual field and its exposure duration varied. Therefore, each participant performed two experimental sessions spaced out 1 week and counterbalanced across participants, one in which the first scene was always displayed for 30 ms and the other one for 150 ms. The second scene in each sequence was always filtered (in either LSF or HSF) and displayed in either the left visual field (LVF) or right visual field (RVF) for 100 ms. The inner and the outer edges of

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[1] The energy level for LSF and HSF stimuli was equalized for each scene as follow: If $LSF(i,j)$ and $HSF(i,j)$ represent the value of the pixel at position (i,j) of, respectively, the low and the high-pass filtered images of a scene, their energies are given by $E_{LSF} = \sum_{i,j} LSF(i,j)^2$ and $E_{HSF} = \sum_{i,j} HSF(i,j)^2$. The average energy between LSF and HSF stimuli is then given by $E_{AVR} = (E_{LSF} + E_{HSF})/2$. The stimuli are then normalized by the average energy, $LSF_{norm}(i,j) = LSF(i,j) E_{AVR}/E_{LSF}$ and $HSF_{norm}(i,j) = HSF(i,j) E_{AVR}/E_{HSF}$.
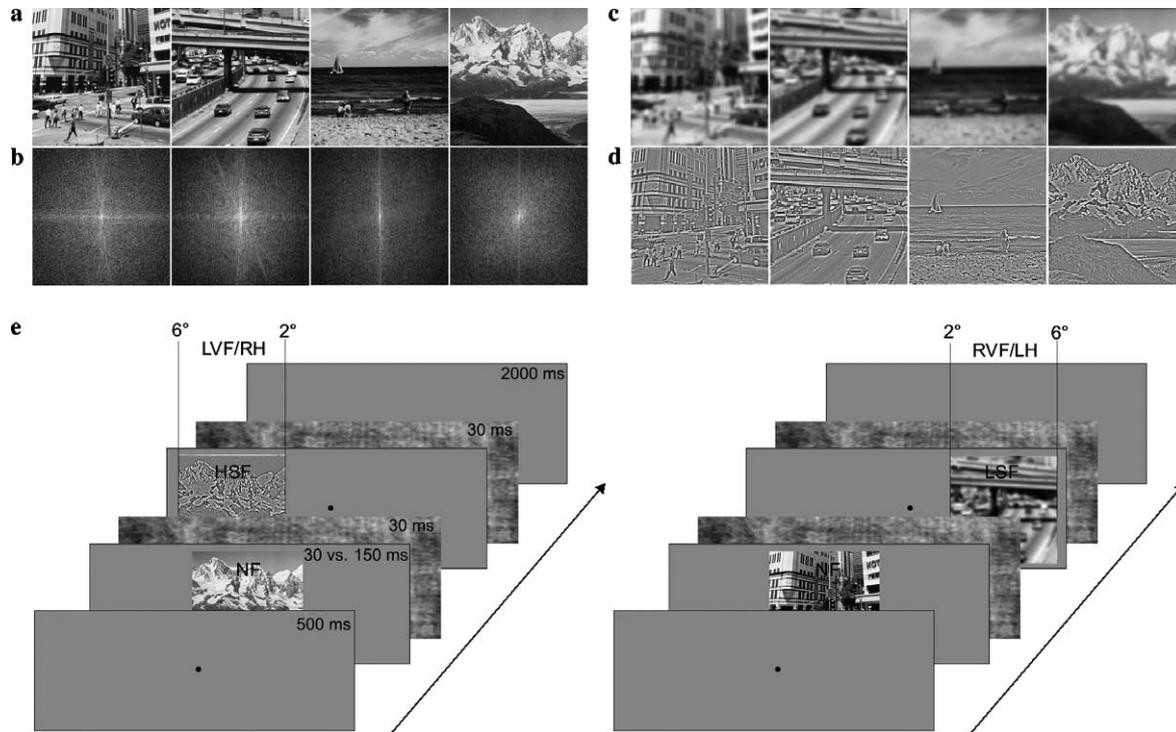
Fig. 1. (a) Scene images (a city, a highway, a beach and a mountain) used in the matching task and (b) their amplitude spectra. Each image was filtered in (c) low spatial frequencies (LSF, <4 cycles/degree) and (d) high spatial frequencies (HSF, >6 cycles/degree). (e) Each trial was composed of two successive scene images. The first scene was always non-filtered (NF), displayed in the central visual field for either 30 or 150 ms. The second scene was filtered either in LSF or HSF and lateralized to either the left visual filed/right hemisphere (LVF/RH) or right visual field/left hemisphere (RVF/LH) for 100 ms.

lateralized stimuli subtended a visual angle of 2° and 6° off centre, respectively. In each experimental session (30 and 150 ms), trials were presented in one experimental block in which both the SF content and the visual field of presentation of the second scene were randomly varied from trial to trial. Furthermore, in half of the trials, the two successive scenes in the sequence were the same exemplar, while in the other half, the two successive scenes were different.

Participants were asked to decide after the presentation of the second scene whether or not the two scenes were from the same exemplar (matching task). They were instructed to fixate the centre of the screen during the whole image-sequence, and to respond as quickly and accurately as possible by pressing a response button (located in the sagittal plane) with both index fingers each time and only when the two successive scenes were from the same exemplar (go/no-go response). This resulted in eight experimental conditions (containing 16 go trials and 16 no-go trials each): 30-LSF-RVF, 30-LSF-LVF, 30-HSF-RVF, 30-HSF-LVF, 150-LSF-RVF, 150-LSF-LVF, 150-HSF-RVF and 150-HSF-LVF. Before each session, lasting about 30 min, participants underwent a training session of eight practice trials using only the non-filtered version of scenes. After each experimental trial, reaction time (RT) was recorded to the nearest millisecond (ms) following the response, together with the response accuracy. The inter-trial interval was 2 s.

3. Results

Mean correct reaction times in milliseconds (mRT), standard deviations (SD), and mean error rate (mER) for each experimental condition (Exposure duration × SF content × Visual field of presentation) are reported in Table 1. To reduce the effect of extreme values in calculating mRT, RT for each subject's correct response in each condition was trimmed by removing responses inferior and superior to two standard deviations from the mean of each condition. This led to the exclusion of 4.49% of correct responses. A three-way analysis of variance (ANOVA) was then performed on mRT and mER with Exposure duration, SF content and Visual field of presentation as within-subject factors.

The error rate per condition and participant varied from 0% to 28.12%. In total, 5.13% errors were made. The ANOVA on mER revealed only a main effect of Exposure duration. Participants performed more errors when the first scene was displayed for 30 ms (8.06%) than 150 ms (2.20%) [$F_{1,15} = 10.80$, MSE = 101.73, $P < .005$]. The ANOVA on mRT revealed a main effect of Exposure duration of the first scene: RTs were slower for the 30 ms than the 150 ms condition [30 ms: 461 ms; and 150 ms: 418 ms, $F_{1,15} = 8.81$, MSE = 6534.70, $P < .01$]. There was no main effect of SF content [LSF: 439 ms; and HSF: 440 ms, $F_{1,15} < 1$] or Visual Field of presentation despite RTs being slightly faster when the second scene

Table 1
Mean correct reaction times in milliseconds (mRT), standard deviations (SD) and mean error rate (mER) for matching low (LSF) and high spatial frequency (HSF) scene, displayed either in the left visual field/right hemisphere (LVF/RH) or right visual field/left hemisphere (RVF/LH) according to the first scene exposure duration (30 and 150 ms)

| | 30 ms | | | | 150 ms | | | |
| | LSF | | HSF | | LSF | | HSF | |
	LVF/RH	RVF/LH	LVF/RH	RVF/LH	LVF/RH	RVF/LH	LVF/RH	RVF/LH
Correct mRT	447	471	471	455	410	429	413	421
SD	53	49	65	55	77	69	67	67
%mER	10.16	8.59	7.81	5.66	2.34	1.76	2.54	2.15

was displayed in the LVF/RH than the RVF/LH [LVF/RH: 435 ms; and RVF/LH: 444 ms, $F_{1,15} = 3.89$, MSE = 602.53, $P = .07$].

With regard to the hypothesis of hemispheric specialization, there was a significant SF content × Visual field interaction [$F_{1,15} = 20.83$, MSE = 253.66, $P < .0005$]. This interaction stemmed from the fact that the visual field of presentation significantly affected the matching of LSF but not of HSF scenes. RTs to LSF scenes presented in the LVF/RH (429 ms) were significantly faster than those in the RVF/LH (450 ms) [$F_{1,15} = 17.88$, MSE = 410.04, $P < .001$], while RTs to HSF scenes did not significantly differ between RVF/LH (438 ms) and LVF/RH (442 ms) [$F_{1,15} < 1$]. Interestingly, there was a significant Exposure duration × SF content × Visual field interaction [$F_{1,15} = 6.80$, MSE = 239.41, $P < .02$], suggesting that Exposure duration of the first scene affected the patterns of hemispheric dominances during the processing of different SF bands. Planned comparisons showed that hemispheric dominance patterns differed only when matching HSF information [Exposure duration × Visual field interaction: $F_{1,15} = 7.86$, MSE = 286.80, $P < .05$] but not when matching LSF information [Exposure duration × Visual field interaction: $F_{1,15} < 1$]. In order to specify the dynamics of hemispheric differences as a function of exposure duration, planned comparisons were performed for 30 and 150 ms conditions separately. These showed a significant SF content × Visual field interaction for 30 ms [$F_{1,15} = 24.69$, MSE = 258.85, $P < .0005$], but not for 150 [$F_{1,15} = 2.23$, MSE = 234.22, $P = .16$]. When examining the 30 ms condition, planned comparisons revealed the expected hemispheric dominances. RTs were significantly faster in the LVF/RH (447 ms) than RVF/LH (471 ms) for matching LSF scenes [$F_{1,15} = 23.18$, MSE = 195.61, $P < .0005$] and significantly faster in the RVF/LH (455 ms) than LVF/RH (471 ms) for matching HSF scenes [$F_{1,15} = 6.05$, MSE = 345.51, $P < .03$]. For the 150 ms condition, we observed a RH predominance for matching LSF scenes: RTs were significantly faster in the LVF/RH (410 ms) than RVF/LH (429 ms) [$F_{1,15} = 6.69$, MSE = 432.40, $P < .05$]. Interestingly, we observed here a RH dominance for matching HSF scenes (LVF/RH: 413 ms; and RVF/LH: 421 ms) but this difference was not significant [$F_{1,15} = 1.19$, MSE = 387.44, $P = .30$].

4. Discussion

The aim of the present study was to investigate whether the temporal properties of SF processing might influence hemispheric specialization. With regard to the CtF analysis of SF, we predicted that the RH dominance in LSF information processing might be enhanced by a brief presentation of visual information while a longer presentation might enhance the LH dominance for processing HSF.

However, contrary to our predictions, results showed a classic hemispheric specialization pattern for SF processing (i.e., a LVF/RH superiority when matching LSF information and a RVF/LH superiority when matching HSF information) when the presentation time of the first non-filtered scene was brief (30 ms), but only a LVF/RH advantage for matching LSF scenes when the presentation time was longer (150 ms). Furthermore, we observed a significant interaction between the exposure duration of the first scene and the visual field of presentation of the second scene only when the latter was filtered in HSF. This result suggests a shift in hemispheric dominance, from a left to a right hemisphere superiority, when matching HSF information as exposure duration increases, but no change in the RH dominance for LSF information as a function of exposure duration.

Our demonstration of hemispheric specialization for SF at brief (30 ms) exposure duration is consistent with Blanca et al. (1994) findings'. However, unlike Blanca et al. (1994) who did not find any difference between the two hemispheres at longer exposure durations (100 and 200 ms), we observed a trend for a RH advantage for matching filtered scenes, irrespective of their SF content, when exposure duration was increased (150 ms). Furthermore, our results do not confirm neither Boles and Karner (1996) study that showed RH dominance for local processing at brief (33 ms) exposure duration nor Evert and Kmen (2003) study that showed LH dominance for local processing at 53 ms exposure duration. The discrepancy between all these studies might be explained by methodological differences. For instance, in our study, as well as in the study of Blanca et al. (1994) on hierarchical forms, a divided attention task was used, i.e., a task that require participants to attend to both LSF/global and HSF/local information at the same time, while Boles and Karner (1996) and Evert and Kmen (2003) used a selective attention task on

hierarchical forms, i.e., a task in which attention is directed to one level of information (either global/LSF or local/HSF). As revealed by Yovel, Levy, and Yovel (2001), a selective attention task might be less sensitive than a divided attention task in detecting hemispheric specialization in global and local information processing. This may explain why Boles and Karner (1996) and Evert and Kmen (2003) failed to observe hemispheric specialization in global and local processing at short exposure duration.

As a whole, our results suggest that variations in exposure duration should affect the visual information extracted from the first central scene. However, contrary to our predictions, this extraction does not seem necessarily constrained by a CtF mode of processing (i.e., a temporal precedence of LSF on HSF) over the course of recognition. Indeed, our results suggest that HSF information could be available and used even at very brief presentations of visual stimuli. Along those lines, we hypothesized that the nature of visual information extracted from the first scene varies with the temporal constraints of the task. When temporal constraints are strong (i.e., decrease in exposure duration), recognition of the first scene seems to be mainly based on the whole SF content. In this view, both hemispheres should work in parallel, each one extracting what it can from the image. This extraction should depend on the specific abilities for SF processing of each hemisphere. LSF and HSF information should, respectively, be extracted by the RH and LH, favouring thus the RH over the LH during the subsequent matching process with a LSF scene, and vice-versa for a HSF scene. This functional explanation fits some models recently proposed in the field of natural scene categorization. According to these models, only the basic characteristics of signal, such as the energy spectrum (i.e., the 'rough abstract' of the image in terms of orientations and spatial frequencies), needs to be processed under high temporal constraints (for example, in subliminal priming tasks, see Guyader, Chauvin, Peyrin, Herault, & Marendaz, 2004). When more time is available to process the first non-filtered scene, participants might process the spatial properties of the image, such as the blobs or the lines, rather than explicitly identifying it (i.e., as the city, highway, beach or mountain scene). In this way, the task could be based on a simple perceptual matching between the spatial properties extracted from the first non-filtered and the second filtered scene (independent of both the SF content and the category of scene). This perceptual matching should thus involve visuo-spatial processing for which the RH is more efficient (see Corballis, 2003). This is consistent with neuropsychological data from callosotomy patients revealing a RH specialization in a spatial-matching task (Corballis, Funnell, & Gazzaniga, 1999).

Therefore, the present study suggests that the hemispheric specialization pattern for visual information processing should be considered as a dynamic system, wherein the superiority of one hemisphere over the other could change according to the level of temporal constraints: the higher the temporal constraints of the task, the more the hemispheres are specialized in SF processing. Alternatively, the dynamic of hemispheric specialization observed in the present experiment may correspond to some changes in the relative involvement of the two hemispheres occurring during the course of the first SF scene processing. In this view, our results could reflect the setting up of a callosal interhemispheric inhibition process (Cook, 1984) from the right to the left hemisphere: when there is a time limit in the visual processing of the stimulus (strong temporal constraints), the interhemispheric inhibition should not be efficient and the two hemispheres should work in parallel, depending on their specific SF superiority.

Finally, as previously suggested by Sergent and Hellige (1986), the present study underlines the need to control the duration of the stimulus presentation during experiments aiming to test the specific pattern of cerebral lateralization in visual tasks. As revealed by this study, time could be a crucial factor determining the pattern of cerebral specialization in natural scene recognition.

References

Badcock, J. C., Whitworth, F. A., Badcock, D. R., & Lovegrove, W. J. (1990). Low frequency filtering and the processing of local-global stimuli. *Perception, 19*, 617–629.

Blanca, M. J., Zalabardo, C., Gari-Criado, F., & Siles, R. (1994). Hemispheric differences in global and local processing dependant on exposure duration. *Neuropsychologia, 32*, 1343–1351.

Boles, D. B., & Karner, T. A. (1996). Hemispheric differences in global versus local processing: still unclear. *Brain and Cognition, 30*, 232–243.

Breitmeyer, B. G. (1975). Simple reaction time as a measure of the temporal response properties of transient and sustained channels. *Vision Research, 15*, 1411–1412.

Breitmeyer, B. G., & Ganz, L. (1977). Temporal studies with flashed gratings: inferences about human transient and sustained channels. *Vision Research, 17*, 861–865.

Bullier, J. (2001). Integrated model of visual processing. *Brain Research. Brain Research Review, 36*, 96–107.

Chokron, S., Brickman, A. M., Wei, T., & Buchsbaum, M. S. (2000). Hemispheric asymmetry for selective attention. *Cognitive Brain Research, 9*, 85–90.

Christman, S. (1989). Perceptual characteristics in visual laterality research. *Brain and Cognition, 11*, 238–257.

Christman, S., Kitterle, F. L., & Hellige, J. (1991). Hemispheric asymmetry in the processing of absolute versus relative spatial frequency. *Brain and Cognition, 6*, 62–73.

Cook, N. D. (1984). Homotopic callosal inhibition. *Brain and Language, 23*, 116–125.

Corballis, P. M. (2003). Visuospatial processing and the right-hemisphere interpreter. *Brain and Cognition, 53*, 171–176.

Corballis, P. M., Funnell, M. G., & Gazzaniga, M. S. (1999). A dissociation between spatial and identity matching in callosotomy patients. *Neuroreport, 10*, 2138–2187.

Evert, D. L., & Kmen, M. (2003). Hemispheric asymmetries for global and local processing as a function of stimulus exposure duration. *Brain and Cognition, 51*, 115–142.

Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1996). Where in the brain does visual attention select the forest and the trees? *Nature, 382*, 626–628.

Ginsburg, A. P. (1986). Spatial filtering and visual form perception. In K. Boff, L. Kaumann, & J. Thomas (Eds.), *Handbook of perception and human performance* (pp. 1–41). New York: Wiley.

Grabowska, A., & Nowicka, A. (1996). Visual-spatial-frequency model of cerebral asymmetry: a critical survey of behavioral and electrophysiological studies. *Psychological Bulletin, 120*, 434–449.

Guyader, N., Chauvin, A., Peyrin, C., Herault, J., & Marendaz, C. (2004). Image phase or amplitude? Rapid scene categorization is an amplitude based process. *Comptes Rendus Biologies, 327*, 313–318.

Han, S., Weaver, J. A., Murray, S. O., Kang, X., Yund, E. W., & Woods, D. L. (2002). Hemispheric asymmetry in global/local processing: effects of stimulus position and spatial frequency. *NeuroImage, 17*, 1290–1299.

Heinze, H. J., Hinrichs, H., Scholz, M., Burchert, W., & Mangun, G. R. (1998). Neural mechanisms of global and local processing. A combined PET and ERP study. *Journal of Cognitive Neuroscience, 10*, 485–498.

Hughes, H. C., Nozawa, G., & Kitterle, F. L. (1996). Global precedence, spatial frequency channels, and the statistic of the natural image. *Journal of Cognitive Neuroscience, 8*, 197–230.

Iidaka, T., Yamashita, K., Kashikura, K., & Yonekura, Y. (2004). Spatial frequency of visual image modulates neural responses in the temporo-occipital lobe. An investigation with event-related fMRI. *Cognitive Brain Research, 18*, 196–204.

Ivry, R. B., & Robertson, L. C. (1998). *The two sides of perception*. Cambridge, MA: MIT Press.

Kenemans, J. L., Baas, J. M., Mangun, G. R., Lijffijt, M. N., & Verbaten, M. N. (2000). On the processing of spatial frequencies as revealed by evoked-potential source modeling. *Clinical Neurophysiology, 111*, 1113–1123.

Kitterle, F. L., Christman, S., & Hellige, J. B. (1990). Hemispheric differences are found in the identification, but not the detection, of low versus high spatial frequencies. *Perception & Psychophysics, 48*, 297–306.

Kitterle, F. L., Hellige, J. B., & Christman, S. (1992). Visual hemispheric asymmetries depend on which spatial frequencies are task relevant. *Brain and Cognition, 20*, 308–314.

Kitterle, F. L., & Selig, L. M. (1991). Visual field effects in the discrimination of sine-wave gratings. *Perception & Psychophysics, 50*, 15–18.

Lamb, M. R., Robertson, L. C., & Knight, R. T. (1990). Component mechanisms underlying the processing of hierarchically organized patterns: inferences from patients with unilateral cortical lesions. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 471–483.

Lamb, M. R., & Yund, E. W. (1993). The role of spatial frequency in the processing of hierarchically organized stimuli. *Perception & Psychophysics, 54*, 773–784.

Lux, S., Marshall, J. C., Ritzl, A., Weiss, P. H., Pietrzyk, U., Shah, N. J., et al. (2004). A functional magnetic resonance imaging study of local/global processing with stimulus presentation in the peripheral visual hemifields. *Neuroscience, 124*, 113–120.

Martin, M. (1979). Hemispheric specialization for local and global processing. *Neuropsychologia, 17*, 33–40.

Martinez, A., Moses, P., Frank, L., Buxton, R., Wong, E., & Stiles, J. (1997). Hemispheric asymmetries in global and local processing: evidence from fMRI. *NeuroReport, 8*, 1685–1689.

Navon, D. (1977). Forest before trees: the precedence of global features in visual perception. *Cognitive Psychology, 9*, 353–383.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9*, 97–113.

Peyrin, C., Baciu, M., Segebarth, C., & Marendaz, C. (2004). Cerebral regions and hemispheric specialization for processing spatial frequencies during natural scene recognition. An event-related fMRI study. *NeuroImage, 23*, 697–706.

Peyrin, C., Chauvin, A., Chokron, S., & Marendaz, C. (2003). Hemispheric specialization for spatial frequency processing in the analysis of natural scenes. *Brain and Cognition, 53*, 278–282.

Peyrin, C., Chokron, S., Guyader, N., Gout, O., Moret, J., & Marendaz, C. (2006). Neural correlates of spatial frequency processing: a neuropsychological approach. *Brain Research*.

Peyrin, C., Schwartz, S., Seghier, M., Michel, C., Landis, T., & Vuilleumier, P. (2005). Hemispheric specialization of human inferior temporal cortex during coarse-to-fine and fine-to-coarse analysis of natural visual scenes. *NeuroImage, 28*, 464–473.

Proverbio, A. M., Minniti, A., & Zani, A. (1998). Electrophysiological evidence of a perceptual precedence of global vs. local visual information. *Cognitive Brain Research, 6*, 321–334.

Robertson, L. C., & Lamb, M. R. (1991). Neuropsychological contributions to theories of part/whole organization. *Cognitive Psychology, 23*, 299–330.

Robertson, L. C., Lamb, M. R., & Knight, R. T. (1988). Effects of lesions of temporal–parietal junction on perceptual and attentional processing in humans. *Journal of Cognitive Neuroscience, 8*, 3757–3769.

Schyns, P. G., & Oliva, A. (1994). From blobs to boundary edges: evidence for time- and spatial-scale-dependant scene recognition. *Psychological Science, 5*, 195–200.

Sergent, J. (1982). The cerebral balance of power: confrontation or cooperation? *Journal of Experimental Psychology: Human Perception and Performance, 8*, 253–272.

Sergent, J., & Hellige, J. B. (1986). Role of input factors in visual-field asymmetries. *Brain and Cognition, 5*, 174–199.

Van Essen, D. C., & DeYoe, E. A. (1995). Concurrent processing in the primate visual cortex. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 383–400). Cambridge, MA: MIT Press.

Yamaguchi, S., Yamagata, S., & Kobayashi, S. (2000). Cerebral asymmetry of the "top-down" allocation of attention to global and local features. *Journal of Neuroscience, 20*, RC72.

Yovel, G., Levy, J., & Yovel, I. (2001). Hemispheric asymmetries for global and local visual perception: effects of stimulus and task factors. *Journal of Experimental Psychology: Human Perception and Performance, 27*, 1369–1385.