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Research Report

Neural correlates of spatial frequency processing: A neuropsychological approach

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ARTICLE INFO

Article history:
Accepted 8 December 2005
Available online 27 January 2006

Keywords:
Hemispheric specialization
Spatial frequency
Natural scene
Gender difference
Occipito-temporal cortex
Arterioveinous malformation

Abbreviations:
SF, spatial frequency
HSF, high spatial frequency
LSF, low spatial frequency
LVF, left visual field
RVF, right visual field
LH, left hemisphere
RH, right hemisphere
AVM, arterioveinous malformation

ABSTRACT

We examined the neural correlates of spatial frequency (SF) processing through a gender and neuropsychological approach, using a recognition task of filtered (either in low spatial frequencies/LSF or high spatial frequencies/HSF) natural scene images. Experiment 1 provides evidence for hemispheric specialization in SF processing in men (the right hemisphere is predominantly involved in LSF analysis and the left in HSF analysis) but not in women. Experiment 2 aims to investigate the role of the right occipito-temporal cortex in LSF processing with a neurological female patient who had a focal lesion of this region due to an embolization of an arterioveinous malformation. This study was conducted 1 week before and 6 months after the surgical intervention. As expected, after the embolization, LSF scene recognition was more impaired than HSF scene recognition. These data support the hypothesis that the right occipito-temporal cortex might be preferentially specialized for LSF information processing and more generally suggest a hemispheric specialization in SF processing in females, although it is difficult to demonstrate in healthy women.

1. Introduction

When we look straight on, the global visual scene that we see (for example, a city) is made up of objects (houses) themselves made up of smaller objects (windows). In this hierarchically organized visual word, each cerebral hemisphere seems to play a differential role for visual recognition. The right hemisphere might be predominantly involved in global

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doi:10.1016/j.brainres.2005.12.051

information analysis whereas the left hemisphere might be more involved in the relative local information analysis. This assumption has been supported by behavioral studies (Blanca et al., 1994; Chokron et al., 2000; Martin, 1979; Sergent, 1982; Van Kleeck, 1989; Yovel et al., 2001) and neuroimaging studies (Evans et al., 2000; Fink et al., 1996, 1997, 1999; Han et al., 2002; Heinze et al., 1998; Lux et al., 2004; Martinez et al., 1997; Proverbio et al., 1998; Yamaguchi et al., 2000) conducted among healthy subjects and brain-damaged patients (Delis et al., 1986; Doyon and Milner, 1991; Lamb et al., 1990; Rafal and Robertson, 1995; Robertson and Lamb, 1991; Robertson et al., 1988).

Interestingly, recognition of global and local aspects of visual stimuli can be linked to different spatial frequency (SF) analysis (Badcock et al., 1990; Hughes et al., 1996; Lamb and Yund, 1993). Global information would be preferentially conveyed by low spatial frequencies (LSF) whereas local information by high spatial frequencies (HSF). Therefore, data obtained on hierarchical forms (i.e., a global form composed of several local elements; see Navon, 1977) have been assumed to reflect a basic hemispheric specialization in SF processing (Ivry and Robertson, 1998; Sergent, 1982). This assumption has been corroborated by behavioral studies conducted on healthy participants using LSF and HSF gratings in identification tasks (see Kitterle and colleagues' psychophysical experiments; Christman et al., 1991; Kitterle and Selig, 1991; Kitterle et al., 1990, 1992), but not by studies using similar gratings in simple detection tasks (Kitterle et al., 1990; Peterzell et al., 1989) or filtered hierarchical letters in global and local letter identification tasks (Hübner, 1997) (for reviews, see Grabowska and Nowicka, 1996; Ivry and Robertson, 1998). Recently, we also addressed the issue of hemispheric specialization by using natural scene images as stimuli in a divided visual field recognition task (Peyrin et al., 2003). Natural scene images represent more ecological and complex stimuli than those usually used to investigate hemispheric specialization (i.e., hierarchical forms, gratings) and can be recognized in many frequency bands (low-pass and high-pass). Our previous results with these kinds of stimuli suggested that the two hemispheres differ significantly in the way they process SF. We thus have demonstrated a left visual field/right hemisphere (LVF/RH) dominance during the processing of LSF information, whereas a right visual field/left hemisphere (RVF/LH) dominance was observed for the processing of HSF.

Importantly, it is thought that gender may affect the patterns of visual field/hemispheric dominance (for reviews, see McGlone, 1980; Voyer, 1996). Indeed, although contradictions exist (e.g. Eviatar et al., 1997; Frost et al., 1999; Hellige et al., 1994), a large number of studies have showed that patterns of functional cerebral asymmetry are more pronounced in men than in women (they tend to be more symmetrical in the latter). For instance, men are more strongly lateralized to the left hemisphere than women in various language functions (Baxter et al., 2003; Boles, 1984; Cormier and Stubbert, 1991; Inglis et al., 1982; Kansaku et al., 2000; McGlone, 1977; Piazza, 1980; Pugh et al., 1996; Rossell et al., 2002; Schlosser et al., 1998; Shaywitz et al., 1995) and to the right hemisphere in more visuospatial functions (Chiarello et al., 1989; Corballis and Sidey, 1993; Hausmann and Gunturkun, 1999; Inglis et al., 1982; McGlone and Kertesz, 1973; Rizzolatti and Buchtel, 1977; Tucker, 1976). For these reasons, to avoid any sex effect, most studies, including ours, evaluating cerebral asymmetries in SF processing have been restricted to male participants.

In Experiment 1, we aimed to further investigate the hemispheric specialization by directly testing the effect of sex on SF processing. For this purpose, we presented a divided visual field task of LSF and HSF natural scene recognition to male and female healthy participants. Our previous experiments (Peyrin et al., 2003, 2004) show that this task is suitable for assessing hemispheric differences in SF processing. Under the hypothesis of hemispheric specialization in SF processing, we should observe LVF/RH dominance for the processing of LSF information and RVF/LH dominance for HSF information. In addition, regarding the literature about gender effect on hemispheric specialization, we predict a greater hemispheric specialization for male than female participants.

Besides the question of the hemispheric specialization for SF, an additional question remains, which concerns the intra-hemispheric region where this specialization may occur. Using hierarchical forms as stimuli, functional imaging data have suggested that such hemispheric specialization could appear at early levels of visual analysis. For instance, by using PET, Fink et al. (1996) revealed greater activations within the right lingual gyrus for global analysis and within the left inferior occipital gyrus for local analysis. Supplementary arguments for early hemispheric specialization were provided by fMRI studies that found hemispheric asymmetries within the occipito-temporal junction (Martinez et al., 1997) and within the occipital cortex (Han et al., 2002). The few neuroimaging studies that have explicitly manipulated the SF spectrum of visual stimuli (Iidaka et al., 2004; Kenemans et al., 2000) converge also towards a hemispheric specialization, which could be present at the very early stages of visual analysis. Using LSF and HSF filtered natural scenes in an event-related fMRI study, we recently provided new evidence of hemispheric specialization at the level of the right occipito-temporal junction for LSF processing and left occipital cortex for HSF processing (Peyrin et al., 2004). Studies on unilateral brain-injured patients also constitute an important source of information concerning the neural substrates involved in this hemispheric specialization. Neuropsychological studies using hierarchical forms as stimuli have revealed that the right posterior superior temporo-parietal cortex could be involved in global information, i.e., LSF, processing, and the homologous left hemisphere region in local information, i.e., HSF (for a review, see Robertson and Lamb, 1991). In this way, studies on patients suffering from left or right occipito-temporal cortex lesion should allow us to thoroughly investigate the role played by this specific cortical region in SF processing.

For this reason, Experiment 2 aimed to further investigate the role of the right occipito-temporal cortex in SF processing. For this purpose, we compared the performance of a female neurological patient who underwent an embolization of this critical cerebral region, before and after the surgical intervention. If, as we hypothesize, the right occipito-temporal cortex is preferentially involved in LSF scene recognition, the patient performance for this SF range should be selectively impaired by the surgical intervention. Since it was conducted on a female patient, Experiment 2 could provide complementary information to the investigation of hemispheric specialization in women.

2. Experiment 1

In Experiment 1, we investigated the hemispheric specialization in SF processing across gender using a recognition task of filtered (either in LSF or HSF) natural scenes images. Scenes (a city and a highway) were displayed either in the LVF or in the RVF (Fig. 1). At the beginning of the experiment, male and female healthy participants viewed the original black and white image of scenes. They were told that images will be "blurred" (i.e., filtered in LSF or HSF) during the experiment. Then, one of the two scenes was designed to be the target scene. The target stimulus was thus the city scene for half of the participants or the highway scene for the half remaining. All participants were instructed to press a response button each time and only when a stimulus was the "target" scene, whatever its SF content. We measured accuracy and reaction times.

2.1. *Results*

Mean correct reaction times in milliseconds (mRT), standard deviations (SD), and mean error rate (mER) for each experimental condition (Gender of participants × Target scene × SF content of scenes × Visual field of presentation) are reported in Table 1a (Fig. 2). A four-way ANOVA was performed on mRT and mER with Gender and Target scene as between-subjects factor, and Visual field of presentation and SF content as within-subject factors.

The error rate per condition and participant varied from 0% to 15.63%. In total, 2.38% errors were made. The ANOVA on mER revealed neither main effects due to Gender ($F_{1,20} < 1$),

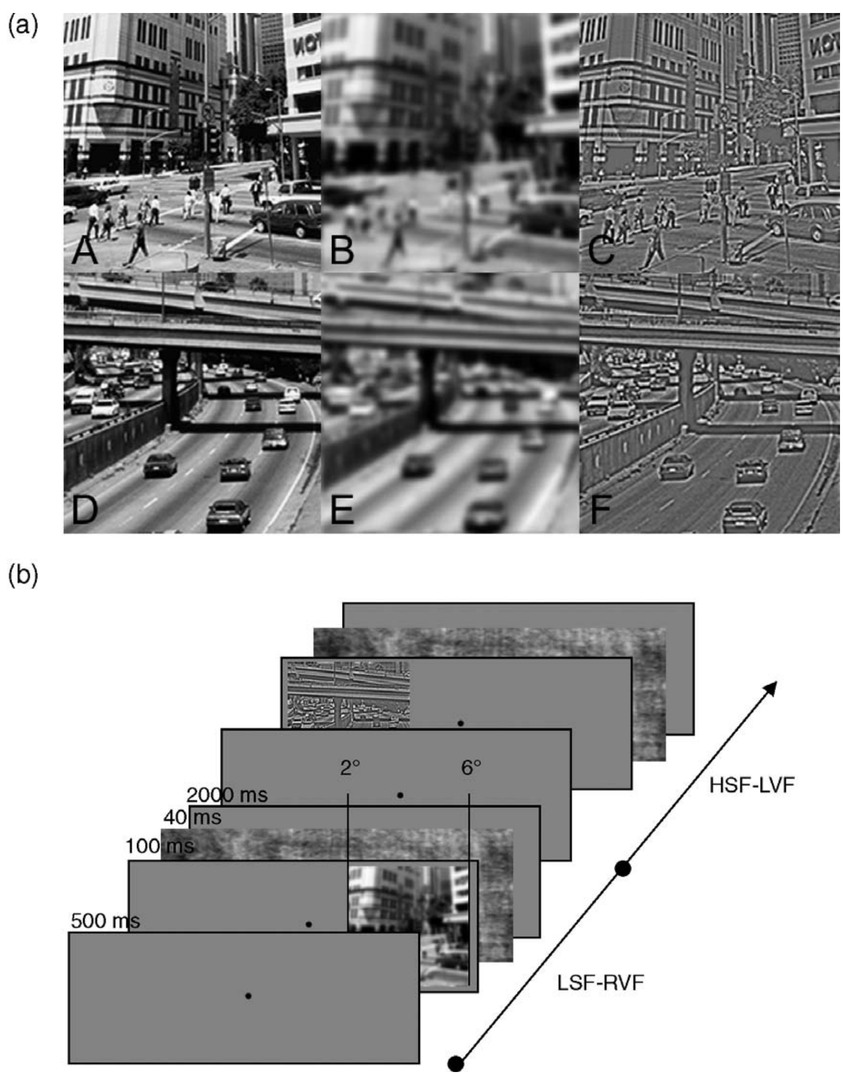

Fig. 1 – (a) Stimuli: original gray-level city scene (A), low spatial frequency (LSF) filtered city scene (B), high spatial frequency (HSF) filtered city scene (C), original gray-level highway scene (D), LSF filtered highway scene (E), and HSF filtered highway scene (F). (b) Example of trials: stimuli, either in LSF or HSF, were presented either in the right visual field/left hemisphere (RVF/LH) or the left visual field/right hemisphere (LVF/RH).

Target scene ($F_{1,20}$ = 1.29, MSE = 17.72, P = 0.27), SF content ($F_{1,20}$ = 5.43, MSE = 15.20, P = 0.23), or Visual field ($F_{1,20}$ = 1.54, MSE = 5.35, P = 0.23), nor interaction between factors (all factors, $F_{1,20} < 1$). The ANOVA on mRT did not reveal significant differences between males and females (416 vs. 442 ms, respectively, $F_{1,20} < 1$), or between the LSF and HSF processing (436 vs. 422 ms, respectively, $F_{1,20}$ = 3.31, MSE = 1464.17, P = 0.08), or between an LVF/RH and RVF/LH presentation (429 vs. 429 ms, respectively, $F_{1,20} < 1$). However, RTs to the city target scene were significantly slower than those of the highway target scene (466 vs. 391 ms, respectively, $F_{1,20}$ = 7.99, MSE = 16757.17, $P < 0.02$). Furthermore, there was an unexpected Target scene × SF content interaction ($F_{1,20}$ = 6.45, MSE = 1464.17, $P < 0.02$). Planned comparisons revealed a HSF processing bias only for the recognition of the city target scene. Indeed, RTs were significantly slower for LSF (483 ms) than HSF (450 ms) city target scenes ($F_{1,20}$ = 9.50, MSE = 1464.17, $P < 0.006$), while RTs did not significantly differ between LSF (388 ms) and HSF (394 ms) highway target scenes ($F_{1,20} < 1$).

With regard to the hypothesis of hemispheric specialization, we observed the expected SF content × Visual field interaction ($F_{1,20}$ = 24.51, MSE = 125.12, $P < 0.0001$). This interaction stemmed from the fact that the visual field of presentation significantly affected the processing of HSF but not of LSF. RTs to HSF target scenes presented in the RVF/LH were significantly faster than those in the LVF/RH (416 vs. 427 ms, respectively, $F_{1,20}$ = 4.85, MSE = 301.03, $P < 0.05$), while RTs to LSF target scenes did not significantly differ between RVF/LH and LVF/RH (442 vs. 430 ms, respectively, $F_{1,20}$ = 3.035, MSE = 530.66, P = 0.10).

Interestingly, there was a significant Gender × SF content × Visual field interaction ($F_{1,20}$ = 12.06, MSE = 125.12, $P < 0.003$), suggesting that participant gender affected the patterns of hemispheric dominances during the processing of different SF bands. In order to examine the hemispheric differences for each gender, planned comparisons were performed for males and females separately. These showed a significant SF content × Visual field interaction for males ($F_{1,20}$ = 35.47, MSE = 125.12, $P < 0.0001$), but not for females ($F_{1,20}$ = 1.09, MSE = 125.12, P = 0.31). When the performances of males participants were examined, RTs were significantly faster in the RVF/LH (399 ms) than LVF/RH (419 ms) during the recognition of HSF target scenes ($F_{1,20}$ = 7.81, MSE = 301.03, $P < 0.02$). Although RTs were faster in the LVF/RH (413 ms) than RVF/LH (432 ms) during the recognition of LSF target scenes, this difference did not reach significance ($F_{1,20}$ = 3.94, MSE = 530.66, P = 0.06). Unlike male participant RTs, RTs of females participants did not significantly differ between the LVF/RH and the RVF/LH during both the LSF (447 vs. 451 ms, respectively, $F_{1,20} < 1$) and HSF (435 vs. 433 ms, respectively, $F_{1,20} < 1$) target scene recognition.

Table 1 – Mean correct reaction times in milliseconds (mRT), standard deviations (SD), and mean error rate (mER) for low (LSF) and high spatial frequency (HSF) city and highway scenes (a) displayed either in left visual field/right hemisphere (LVF/RH) or right visual field/left hemisphere (RVF/LH) for healthy men and women in Experiment 1, and (b) displayed in the RVF/LH for the patient and healthy control participants in Experiment 2

		Target scene		LSF		HSF	
				LVF/RH	RVF/LH	LVF/RH	RVF/LH
(a) Experiment 1							
Healthy men		Highway	mRT	351	362	374	350
			SD	63	53	54	42
			mER	1.04%	2.60%	1.56%	2.60%
		City	mRT	475	501	464	448
			SD	82	56	75	63
			mER	4.17%	2.08%	2.60%	2.08%
Healthy women		Highway	mRT	410	430	427	425
			SD	39	74	62	77
			mER	2.08%	3.65%	1.04%	0.52%
		City	mRT	483	472	443	441
			SD	88	100	68	78
			mER	2.08%	5.21%	2.08%	2.60%
(b) Experiment 2							
Healthy control women	Session 1 (preembolization)	Highway	mRT	–	343	–	357
			SD		16		25
			mER	–	2.5%	–	2.5%
	Session 2 (postembolization)	Highway	mRT	–	350	–	348
			SD		12		25
			mER	–	0.63%	–	0%
Patient	Session 1 (preembolization)	Highway	mRT	–	398	–	404
			SD		40		39
			mER	–	0%	–	0.63%
	Session 2 (postembolization)	Highway	mRT	–	458	–	436
			SD		57		25
			mER	–	0%	–	0%

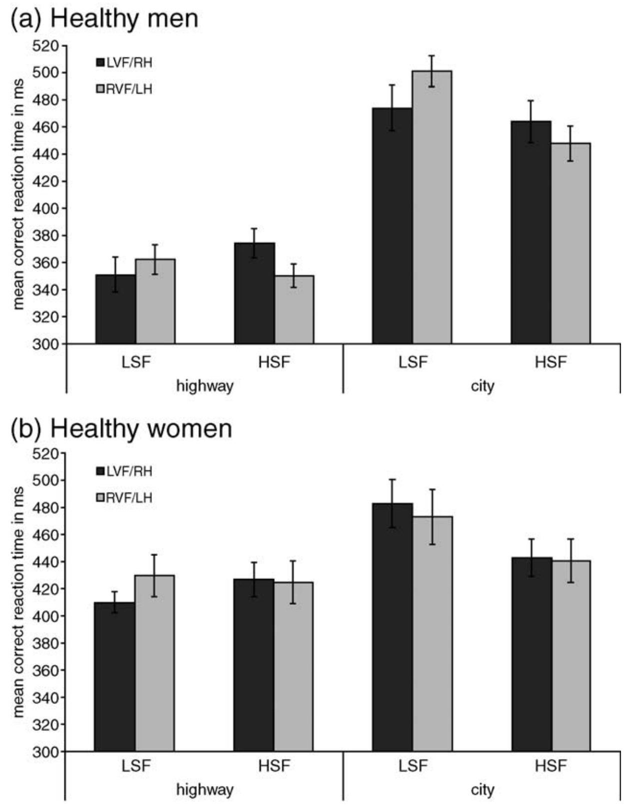

Fig. 2 – Mean correct reaction time in milliseconds to recognize the target (LSF and HSF natural scenes) for healthy men and women in Experiment 1.

Finally, the analysis showed a slightly Gender × Target scene × SF content × Visual field interaction ($F_{1,20}$ = 4.26, MSE = 125.12, P = 0.05). Planned comparison revealed that Gender interacted with the pattern of cerebral asymmetries for the city target scene (Gender × SF content × Visual field, $F_{1,20}$ = 15.32, MSE = 125.12, P < 0.001), but not for the highway target scene ($F_{1,20}$ < 1). Furthermore, Target scene interacted with the pattern of cerebral asymmetries for women (Target scene × SF content × Visual field, $F_{1,20}$ = 5.32, MSE = 125.12, P < 0.04), but not for men ($F_{1,20}$ < 1). More precisely, for women, we observed a significant SF content × Visual field interaction for the highway target scene ($F_{1,20}$ = 5.62, MSE = 125.12, P < 0.03), even though the LVF/RH dominance for LSF ($F_{1,20}$ = 2.20, MSE = 530.66, P = 0.15) and RVF/LH dominance for HSF ($F_{1,\ 20}$ < 1) processing did not reach significance. Conversely, we did not observe any significant SF content × Visual field interaction for the city target scene ($F_{1,20}$ < 1).

2.2. *Discussion*

The main result of Experiment 1 is that women are less lateralized than men in SF processing. Precisely, the results for men show that the two hemispheres differ significantly in the way they processed SF, according to a classical hemispheric specialization. There was an RVF/LH superiority in HSF scene processing, whereas an LVF/RH superiority was observed for LSF scenes. This result is in agreement with our previous behavioral studies exclusively conducted on male healthy participants (Peyrin et al., 2003). On the contrary, the visual field of presentation of scenes did not influence SF processing in women, confirming thus that the functional cerebral organization of women is less lateralized than one of men (McGlone, 1980; Voyer, 1996).

However, women's results are controversial. Indeed, the target scene interacted significantly with the hemispheric processing of SF. More precisely, results showed a significant interaction between SF and visual field for the highway target scene, in favor of a hemispheric specialization even though visual field/hemispheric dominance did not reach significance. On the other hand, visual field did not interact with SF for the city target scene. Interestingly for the understanding of these results, RTs were slower for the city than the highway target scene, irrespective of gender. This is due to the fact that despite their global similarity in the Fourier domain (energy spectra), in the spatial domain, the highway scene has a simpler organization of its visual features (blobs, lines, objects) than the city scene. This result suggests that to perform the task efficiently, participants needed more time to process visual information contained in the city than the highway image. A longer processing time did not affect hemispheric specialization for men but it did for women. We suggest that this longer visual processing may have disturbed the detection of cerebral asymmetries in female behavioral measures (see General discussion). However, as mentioned in the Introduction, looking at focal unilateral brain-injured patient performance constitutes an alternative approach to the investigation of the neural basis of SF processing. In Experiment 2, we therefore investigated the functional specialization of the right occipito-temporal cortex during SF processing in a neurological female patient.

3. Experiment 2

The patient suffered from an occipito-temporo-parietal arterioveinous malformation (AVM) in the right hemisphere (Fig. 3) which induced a left inferior lateral quadranopia. She underwent an embolization of this region. As a consequence, she suffered from a left homonymous hemianopia. The

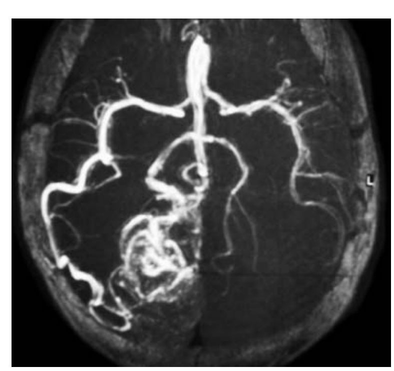

Fig. 3 – Angiography revealing a right occipito-temporo-parietal arterioveinous malformation (image represented in radiological convention).

patient was tested twice, before and 6 months after the surgical intervention, using an adapted version from the recognition task of filtered scene images used in Experiment 1. Indeed, to avoid any disturbance related to the presence of the left visual field defect (quadranopia at the preoperative session and hemianopia at the postoperative session), the scenes were only presented in the right (healthy) visual field. We hypothesize that if there is a right occipito-temporal cortex specialization for processing LSF information, as we previously observed in an fMRI study (Peyrin et al., 2004), then LSF scene recognition should be more impaired than HSF scene recognition after the embolization. Experiment 2 constitutes also a main source of information concerning the hemispheric dominance for SF processing in women.

In addition to the patient, healthy control women participated in the experiment. In order to control that the patient's performance cannot be attributed to the repetition of the experiment or to the time between experimental sessions, control participants were also tested two times spaced out 6 months. All participants were instructed to press a response button each time and only when a stimulus was the highway scene, whatever its SF content. This choice was guided by the observation in Experiment 1 that RTs are significantly slower for the LSF than HSF city scene. RTs recorded on the city scene thus should not be appropriate for assessing the hypothesized selective slowing down of the patient in LSF processing.

3.1. *Results*

Mean correct reaction times in milliseconds (mRT), standard deviations (SD), and mean error rate (mER) for patient and control participants are reported in Table 1b. Mean error rate was very low (0.10% for the patient and 1.88% for control participants). Reaction times on correct responses were entered in an ANOVA with Participant group (patient vs. controls), SF content (LSF vs. HSF), and Experimental session as within-subjects factors. ANOVA was run on individual RTs per participant group, per experimental condition, and therefore constitutes an items analysis. This method allowed a direct comparison of performance between the patient and the controls.

RTs were significantly slower for the patient than control participants (424 ms and 350 ms, respectively; $F_{1,15}$ = 116.29, MSE = 1522.83, P < 0.0001). There was a significant interaction between Participants and Experimental sessions ($F_{1,15}$ = 11.34, MSE = 1607.56, P < 0.01). Planned comparisons showed that the patient responded faster before than after the embolization (401 vs. 447, respectively, $F_{1,15}$ = 10.93, MSE = 3135.13, P < 0.005), whatever the SF content of scenes (LSF: 398 vs. 458, respectively, $F_{1,15}$ = 11.89, MSE = 2436.75, P < 0.005; HSF: 404 vs. 436, respectively, $F_{1,15}$ = 6.62, MSE = 1267.26, P < 0.05), whereas no difference was observed between the two experimental sessions for controls (350 vs. 349, respectively, $F_{1,15}$ < 1; LSF: 343 vs. 350, respectively, $F_{1,15}$ = 1;38, MSE = 228.88, P = 0.26; HSF: 357 vs. 348, respectively, $F_{1,15}$ = 1.55, MSE = 436.50, P = 0.23).

Critically, the patient showed a significant interaction between Experimental session and SF content ($F_{1,15}$ = 5.43, MSE = 568.87, P < 0.05) indicating that she was more impaired in LSF than HSF processing after her embolization (Fig. 4). More precisely, during the preembolization session, the patient's RTs did not differ significantly between LSF and HSF target scenes (398 ms and 404 ms, respectively; $F_{1,15}$ < 1). However, during the postembolization session, the LSF target scene was recognized significantly slower than the HSF target scene (458 ms and 436 ms, respectively; $F_{1,15}$ = 5.06, MSE = 739.92, P < 0.05). For control participants, Experimental sessions did not significantly interacted with SF content ($F_{1,15}$ = 3.87, MSE = 417.72, P = 0.07).

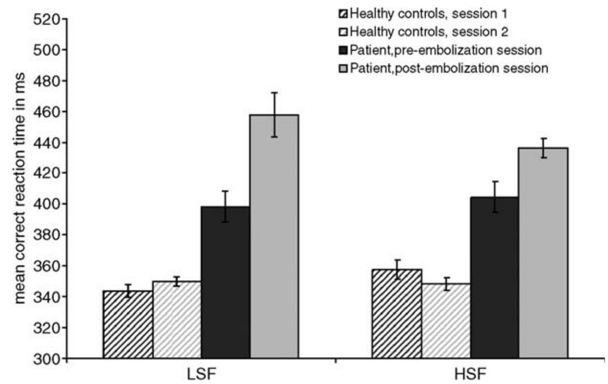

Fig. 4 – Mean correct reaction time in milliseconds to recognize the target (LSF and HSF natural scenes) for patient and healthy control women in each experimental session in Experiment 2.

3.2. *Discussion*

Experiment 2 aimed to assess the contribution of the right occipito-temporal cortex to SF processing. For this purpose, we compared the performances of a female patient who underwent an embolization of this critical cerebral region and of healthy control participants. In addition, by testing the patient before and after the surgical intervention, we were able to directly estimate the consequences of a right occipito-temporal cortex lesion on SF processing.

Firstly, results showed that scene recognition was slower for the patient than for control participants, whatever the experimental session and the SF content of the target scene. Secondly, the patient's performance was systematically slowed down after the embolization. Since control participants did not show any significant variation in RTs between the first and the second testing, the patient's performance variability can be attributed neither to the experiment design nor to the time between experimental sessions. Critically, after the right occipito-temporal cortex embolization, LSF target recognition was more impaired than HSF recognition, thus suggesting the major contribution of the right occipito-temporal cortex for LSF analysis. As mentioned above, after embolization, the patient was also impaired for HSF recognition (but to a lesser degree than LSF processing). However, contrary to a low-pass filtering that provides information about the global structure and impairs seriously the perception of local elements, a high-pass filtering provides information not only about local, but also about global structure by grouping local elements (see Schulman et al., 1986).

Neuropsychological studies have shown a global processing deficit in right hemisphere-damaged patients (Robertson and Lamb, 1991; Robertson et al., 1988). Therefore, we hypothesize that this global processing, likely impaired by the embolization of the right occipito-temporal cortex, might disturb HSF scene recognition. Finally, as natural scenes were always displayed in the right visual field, i.e., projected on the healthy left hemisphere, our results suggest that LSF information needs to be transferred to the right occipito-temporal cortex to be optimally processed.

4. General discussion

In the two experiments reported here, we investigated neural correlates of SF processing by focusing successively on hemispheric specialization across gender (Experiment 1) and the deficits in SF processing following right occipito-temporal lesion (Experiment 2).

In Experiment 1, men showed a greater hemispheric specialization in SF processing than women. For healthy male participants, our results showed that LSF filtered scenes were recognized faster when they were presented in the left visual hemifield, projecting directly to the right hemisphere, while the HSF filtered scenes were recognized faster when they were presented in the right visual hemifield, projecting directly to the left hemisphere. These results, which replicate the findings of earlier work (Peyrin et al., 2003), thus suggest a right hemispheric dominance for LSF and a left hemispheric dominance for HSF processing. Furthermore, they are consistent with Sergent's assumption (Sergent, 1982) that visual tasks needing LSF information to be processed (such as global letter identification in hierarchical stimuli) would result in an LVF/RH dominance, whereas when HSF information is needed for the task to be processed (such as local letter identification), one should observe an RVF/LH dominance. For healthy female participants, the existence of hemispheric specialization for SF is surrounded by controversy. Indeed, woman performance tends to be only lateralized in the highway target scene condition. RTs being slower for the city than the highway target scene, we suggested that the required time to perform a visual task might dramatically disturb the detection of hemispheric specialization in women. Data obtained in Experiment 2, showing a worse performance in LSF scene recognition in a female patient having a postsurgical lesion of right occipito-temporal cortex, corroborate this idea. The critical question is thus why healthy women should be more sensitive to the temporal timing of hemispheric processing than men.

We propose that gender differences in hemispheric specialization might be partially based on sex differences in the shape and surface of the corpus callosum. Such a difference has previously been suggested based on postmortem morphological studies (DeLacoste-Utamsing and Holloway, 1982; Holloway and DeLacoste, 1986) and magnetic resonance images examination (Allen et al., 1991). For example, the splenium, an anatomical structure of the corpus callosum connecting the visual areas of both hemispheres, may be larger in women than men relative to brain weight. Therefore, because more connections between the hemispheres may be present in women, this may enable a fast transfer of information to the specialized hemisphere when initially projected to the non-specialized hemisphere, removing visual field differences. Furthermore, the longer the processing of visual information, the more the communication between the two hemispheres could take place, removing visual field differences. In addition to these anatomical sex differences, gender differences in visuospatial performance are also assumed to result from differences in sex hormone levels. Indeed, in women, cerebral asymmetries might change throughout the menstrual cycle (Altemus et al., 1989; Hausmann and Gunturkun, 2000; Hausmann et al., 2000, 2002; Heister et al., 1989). In the present study, women were selected irrespective of the phase of the menstrual cycle. Therefore, shifts of functional cerebral asymmetries during the menstrual cycle could, in part, underlie the absence of hemispheric specialization for SF processing in women as a group.

While Experiment 1 allowed us to examine the neural correlates of SF processing through hemispheric specialization and gender effect, Experiment 2 aimed to investigate the particular role of the right occipito-temporal cortex in SF processing through the behavioral consequences of its damage. This study was conducted on a female patient having a focal lesion of the right occipito-temporal cortex subsequent to embolization of an AVM. As predicted, LSF was more impaired than HSF scene recognition after the embolization. This result, in agreement with several functional brain imaging studies showing a right hemispheric specialization for global/LSF information processing at the earliest levels of visual analysis (Fink et al., 1996, 1997; Han et al., 2002; Kenemans et al., 2000; Lux et al., 2004; Martinez et al., 1997; Peyrin et al., 2004), supports the hypothesis that the right occipito-temporal cortex might be preferentially specialized in LSF information processing.

In addition, the patient's performance was generally poorer than healthy control women's performance in Experiment 2, even before surgical embolization. This observation is consistent with her neurological deficit, i.e., a left inferior lateral quadranopia, before embolization. One might think that patient's performance was worsened when she suffered from a left lateral homonymous hemianopia (after the embolization), relative to a left inferior lateral quadranopia only. However, as for control participants, the patient's performance did not significantly differ between LSF and HSF before embolization when she suffered from quadranopia. Furthermore, the stimuli were systematically presented in the right healthy visual field, in the preoperative as well as in the postoperative session, precisely to avoid any disturbance related to the presence of the left visual field defect. These data suggest that quadranopia and hemianopia did not disturb the processing of LSF relative to HSF before and after the embolization, respectively. Considering that the patient had developed with the presence of a right temporo-occipital AVM, her visual behavior before embolization might reflect the interaction between cortical maturation and plasticity. On the contrary, the embolization might induce a cortical lesion leading to qualitatively and quantitatively different mechanisms of cortical reorganization (Pizzamiglio et al., 2001). Therefore, the decrease in the patient's performance between the two sessions should not be due to the aggravation of the left visual field defect but might be rather linked to the disturbance in LSF processing after the right occipito-temporal lesion. This latter result emphasizes the need to disentangle between visual field defects and other visual functional deficits, as for example here in SF processing, in patients suffering from an occipital lesion. Pambakian et al. (2000) studied the natural scene processing of lateral homonymous hemianopic patients and showed that LSF filtered natural scenes recognition was impaired in patients compared with healthy control subjects. As they were not interested in hemispheric specialization for SF processing, neither the effect of the occipital lesion lateralization nor the recognition of high-pass filtered scenes was investigated. However, their study suggests that the primary visual cortex might be at least involved in LSF processing. Taken together, the study of Pambakian and colleagues as well as the present one demonstrates that testing hemianopic patients should provide more information concerning the understanding of the hemispheric specialization in SF processing.

In conclusion, the neuropsychological approach we adopted to study the neural correlates of SF processing provided two main findings. First, our results bring evidence for hemispheric specialization in SF processing on men. We argue that this hemispheric specialization might be more difficult to detect in healthy women because of interfering factors (e.g., fast callosum transfer, hormonal level fluctuations over the menstrual cycle). However, the deficit in LSF processing observed in the female patient we tested suggests that the right occipito-temporal cortex is involved in LSF processing even in females, although it is difficult to observe in normal subjects. Our findings thus point out the need to study males and females together as well as both normal and brain-damaged patient performance in order to establish the neural correlates of visual function.

5. Experimental procedures

5.1. Experiment 1

5.1.1. Participants

Twenty-four healthy undergraduate students of Psychology from the Université Pierre Mendès-France in Grenoble (12 men, mean age ± SD, 21.3 ± 2.6; 12 women, 20.3 ± 2.4) 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.

5.1.2. Stimuli and procedure

Stimuli were two black-and-white photographs (256 × 256 pixels, 256 grey-scales) of natural scene images: a city and a highway (Fig. 1a). They had similar dominant orientations so that their identification could not be made on the basis of this information (Guyader et al., 2004). Stimuli were displayed 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 screen resolution of 1024 by 768 pixels) located 110 cm from the participant. Their angular size was thus 4° of visual angle. For each scene, two types of image were created, an LSF and HSF image (Fig. 1a). 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, the total energy for LSF and HSF images was equalized for each scene. Furthermore, averaged stimuli luminance was relatively similar (LSF city, LSF highway, HSF city, and HSF highway: 129, 132, 136, and 136 on a 256 gray-level scale). 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.

Participants were tested individually in a darkened room. Head position was stabilized by a chin rest. For each trial, the stimulus display was preceded by a fixation point (in order to keep the gaze direction at the center of the screen) during 500 ms and followed by the mask for a duration of 40 ms, then by a 2 s blank interval after the response was made. The stimulus display was presented for 100 ms against a gray (128 gray-level scale) background. Stimuli were displayed either in the LVF or in RVF. The inner and the outer edges of these lateralized stimuli subtended a visual angle of 2° and 6° off center, respectively. For each trial, participants judged whether the scene was the city or the highway. They were instructed to press a response button (located in the sagittal plane) with the index finger of the dominant hand, each time and only when a stimulus was the "target" scene (go/no go response), whatever its SF content. The target scene was the city for half of the participants or the highway for the half remaining and was present in half of the trials. This resulted in four experimental conditions (containing 16 go trials and 16 no go trials each): LSF-RVF, LSF-LVF, HSF-RVF, and HSF-LVF (see Fig. 1b). After each experimental trial, reaction time (RT) was recorded to the nearest millisecond (ms) following the response, together with the response accuracy. Before the experiment, lasting about 30 min, participants underwent a training session of 8 practice trials using only the non-filtered version of scenes. The order of the experimental trials was pseudorandom (i.e., no more than three consecutive trials with the same scene in the same filtering).

5.2. Experiment 2

5.2.1. Patient and healthy participants

Our patient was a 19 year-old right-handed woman who presented a left inferior lateral quadranopia. She did not suffer from other any neurological disorder. Angiography revealed a large occipito-temporo-parietal AVM in the right hemisphere (Fig. 3). AVM was treated inside the blood vessels using a first sitting of endovascular embolization within the right occipito-temporal cortex. While the endovascular therapy allows the reduction of the size of the nidus, particularly within the postero-intern component of the AVM, the patient then suffered from a complete left lateral homonymous hemianopia (without hemineglect). In addition to the patient, five healthy right-handed control women (mean age ± SD, 24.6 ± 2.3) participated in the experiment. They had normal or corrected-to-normal vision and they were not aware of the purpose of the experiment.

5.2.2. Method

The patient and control participants performed the same task as in Experiment 1, except for the visual field of presentation of scenes. Scenes were only presented in the RVF. The inner and the outer edges of the lateralized scenes subtended a visual angle of 2° and 6° off center, respectively. All participants were instructed to press a response button (located in the sagittal plane) with her index finger of the dominant hand, each time and only when the stimulus (LSF or HSF) was the highway scene (go/no go response). The experimental paradigm was presented to the patient 1 week before the embolization (preembolization session) and 6 months after (postembolization session). Control participants were also tested two times spaced out 6 months. In each session, the experiment, lasting about 15 min, consisted of 8 practice trials, in which only non-filtered version of scenes was displayed, followed by 64 experimental trials (16 by condition) displaying filtered scenes. The same pseudorandom experimental trial order was used for all participants and all experimental sessions.

Acknowledgments

The authors wish to thank Patrik Vuilleumier and Alex Lewis for their assistance. This research was funded by the National Centre for Scientific Research and Pierre Mendès France University. Carole Peyrin was funded by a PhD Grant from the *Ministère de l'Education Nationale, de la Recherche et de la Technologie*, France, and by a postdoctoral fellowship from the *Fondation Fyssen* in the University of Geneva.

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