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Cerebral regions and hemispheric specialization for processing spatial frequencies during natural scene recognition. An event-related fMRI study

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It has been suggested that visual scene recognition is mainly based on spatial frequency (Fourier) analysis of the image. This analysis starts with processing low spatial frequencies (LSF), followed by processing high spatial frequencies (HSF). Within the framework of the spatial frequency analysis, the right/left hemisphere would be predominantly involved in LSF/HSF analysis, respectively. The aim of this event-related fMRI study was to evaluate neural correlates and hemispheric specialization of spatial frequency analysis during recognition of nonfiltered (NF) and filtered, either in LSF or HSF, natural scenes. Comparing LSF or NF to HSF scene recognition, significant activation was obtained within right anterior temporal cortex and right parahippocampal gyrus. As these regions are known to be involved in scene processing, we interpret this result as suggesting that scene recognition is mainly based on LSF extraction and analysis. When LSF scene was compared to HSF scene recognition, supplementary activation was obtained within the right inferior parietal lobule that likely reflects attentional modulation on spatial frequency processing. A direct interhemispheric comparison for each particular band of spatial frequencies highlighted predominance within the early visual areas (such as the middle occipital gyrus) to the right for LSF processing and to the left for HSF processing. This result provides supplementary evidence for hemispheric specialization at early levels of visual analysis when spatial frequencies are processed.
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Introduction

Complex natural scenes are very quickly categorized, faster than 150 ms (Thorpe et al., 1996), suggesting a simple and efficient processing. There is considerable evidence suggesting that visual perception is fundamentally based on spatial image processing that may be characterized in terms of Fourier components: amplitude and phase spectra (roughly speaking, the amplitude spectrum summarizes the image in terms of spatial frequencies and orientations, and the phase spectrum describes spatial relationships between spatial frequencies) (Ginsburg, 1986; Hughes et al., 1996). On one hand, the primate primary visual cortex is widely dominated by complex cells that respond preferentially to orientation and spatial frequency (DeValois et al., 1982; Shams and von der Malsburg, 2002). On the other hand, simulation and psychophysical experiments showed that information from low/medium frequencies of amplitude spectrum is sufficient to allow scene categorization (Guyader et al., 2004; Torralba and Oliva, 2003). This functional viewpoint fits well the idea of a *coarse to fine* time course of spatial frequency processing in visual system as suggested by neurophysiological experiments in primates. That is, low spatial frequencies (LSF) conveyed by the magnocellular pathway would reach more rapidly higher order cortical areas (parietal and temporal cortex) than high spatial frequencies (HSF) conveyed by the parvocellular system (for further development see Bullier, 2001). The present experiment deals with this issue by studying in humans and using fMRI the cerebral substrate involved in spatial frequency processing during natural scene recognition and further investigate hemispheric specialization.

Many experimental studies evaluating hemispheric asymmetries of spatial frequency processing have suggested left hemispheric predominance for HSF processing and right hemispheric predominance for LSF processing. The hemispheric specialization was observed either by using a behavioral approach on

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healthy subjects (Kitterle et al., 1990; Peyrin et al., 2003; Sergent, 1982) and neurological patients (Lamb et al., 1990; Robertson et al., 1988; Robertson and Lamb, 1991), or using functional neuroimaging studies (Fink et al., 1996; Han et al., 2002; Heinze et al., 1998; Iidaka et al., 2004; Kenemans et al., 2000; Lux et al., 2004; Martinez et al., 1997, 2001; Yamaguchi et al., 2000). For assessing the hemispheric specialization, almost all authors used hierarchical forms (global form composed of several local elements, see Kinchla, 1974; Navon, 1977). For this type of stimuli, right hemispheric dominance was classically reported for global form recognition (attention focused on global elements) and left dominance for local form recognition (attention focused on local elements). As the global processing is mediated by low-pass spatial analysis and the local processing by high-pass spatial analysis (Badcock et al., 1990; Lamb and Yund, 1993; Schulman et al., 1986), the pattern of hemispheric specialization observed in global and local processing was interpreted as reflecting the hemispheric specialization for LSF and HSF, respectively.

With respect to cortical structures presenting hemispheric asymmetries, the neuroimaging studies have led to conflicting data. For instance, by using PET and hierarchical forms as stimuli, Fink et al. (1996, see also Fink et al., 1997) revealed the activation of the right lingual gyrus (BA 18) for global analysis and the left inferior occipital gyrus (BA 18, 19) for local analysis. Combining event-related potentials (ERP) and PET technique, Heinze et al. (1998) failed to observe cerebral asymmetry within the early visual areas. Rather, the ERP results of Heinze et al. (1998) showed long-latency asymmetries for global versus local processing (260–360 latency range). The authors concluded that spatial frequency processing is asymmetric only at higher levels of visual analysis.

Therefore, the hemispheric specialization hypothesis for spatial frequency processing has been widely inferred from hemispheric asymmetries in global and local processing rather than empirically demonstrated. However, in hierarchical forms the relationship between global/local and LSF/HSF, respectively, is far from univocal (Palmer, 1993). For instance, global information could be conveyed by not only LSF but also by HSF. Thus, it seems necessary to study hemispheric specialization for spatial frequency processing by explicitly manipulating spatial frequency spectrum. In our study, we have used natural scenes. Natural scenes are more ecological and complex stimuli that those usually used to investigate the hemispheric specialization (e.g., hierarchical stimuli, gratings) and allow an explicit change in the spatial frequency spectrum. Furthermore, natural scenes may be recognized in many frequency bands (i.e., whatever the type of filtering—low-pass, high-pass or pass-band), whereas hierarchical forms do not because a low-pass filtering cancels the local forms rendering the task impossible to be carried out.

Two aims were followed in the present event-related fMRI (ER-fMRI) performed in healthy subjects. The first aim was to investigate the cerebral regions involved in spatial frequency processing during recognition of complex visual stimuli. The second aim was to assess the hemispheric asymmetry underlying this process. For this purpose, a recognition task of low and high-pass filtered natural scenes was used. To estimate the effect of the amplitude spectrum manipulation on visual recognition process, we also included as stimuli, original nonfiltered (NF) natural scenes for which the whole frequency spectrum was present (LSF and HSF information).

Our hypotheses were the following. (1) If rapid visual recognition or categorization is mainly based on LSF analysis, we should obtain a greater activation of brain areas usually involved in scene recognition during LSF filtered scenes than during HSF filtered scenes processing. (2) Based on simulation and psychophysical experiments (Guyader et al., 2004; Torralba and Oliva, 2003), if NF natural scenes recognition is mainly based on LSF, we should observe a relatively similar neural network for NF and for LSF scene recognition, with respect to HSF scene recognition. (3) According to the hemispheric specialization hypothesis, the LSF filtered scene recognition would yield a greater involvement of the right hemisphere while the HSF filtered scene recognition would rather involve the left hemisphere.

Materials and methods

Subjects

Sixteen healthy male (mean age ± SD, 25.4 ± 3.2) volunteers were examined. All were right-handed as assessed by the Edinburgh inventory (Oldfield, 1971). All subjects had normal or corrected-to-normal vision and no history of neurological disorders. They gave their informed consent for the study.

Stimuli

Stimuli were built based on two images representing natural scenes, one belonging to “city” category and the other to “highway” category (see Fig. 1). Both had similar dominant orientations to avoid identification based on this information. They were black and white images (256 grey scales) sized 4° per visual angle. To facilitate the task execution, we choose only one scene by category, as in our recent behavioral study (Peyrin et al., 2003). For each scene, two types of stimuli were created, one represented by the original scene filtered in LSF (below 4 cycles per degree of visual angle) and the other one represented by the original scene filtered in HSF (above 6 cycles per degree of visual angle). Since at an equal level of contrast, LSF are more visible than HSF (Hughes, 1986), the HSF stimuli contrast was

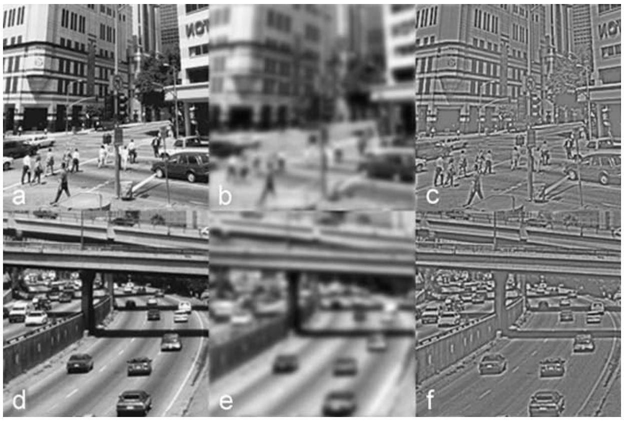

Fig. 1. Stimuli (six types) presented during the fMRI experiment. (a) nonfiltered (NF) city scene, (b) low spatial frequency (LSF) filtered city scene, (c) high spatial frequency (HSF) filtered city scene, (d) NF highway scene, (e) LSF filtered highway scene, (f) HSF filtered highway scene.

increased to match the LSF stimuli. This manipulation allows to investigate the cerebral organization of spatial frequency processing irrespective of perceptual salience (Fink et al. 1999). Thus, as presented in Fig. 1, for each natural scene, three types of stimuli were used (the original nonfiltered scene, the LSF filtered original scene and the HSF filtered original scene). To prevent retinal persistence of the scene, a mask was presented after each stimulus. 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 presented as stimuli. The stimuli were generated by means of Psyscope V.1.1 (Carnegie Mellon Department of Psychology, Cohen et al., 1993) on a Macintosh computer (Power Macintosh 9600). They were transmitted into the magnet using a video projector (Eiki LC 6000), a projection screen situated behind the magnet and a mirror centered above the participant's eyes.

Task

At the beginning of the fMRI experiment, all subjects viewed only the original black and white image of the highway and of the city scenes. Subjects were told that images could be presented either as those they have already viewed [i.e., nonfiltered (NF)] or "blurred" (i.e., filtered in LSF or HSF). Then, the status of target stimulus was attributed to one of the two scenes. The target stimulus was thus the city scene for half of the subjects or the highway scene for the half remaining. The target scene was shown in half of trials. The subjects were instructed to press a response key with the index finger of the dominant hand, each time and only when a stimulus was the "target" scene, that is, only for NF, LSF and HSF target scene (Go/NoGo task). The task to perform was the same in all conditions: NF scene processing, LSF scene processing and HSF scene processing. The motor responses were recorded and the task performance [accuracy and response time (RT)] evaluated.

Paradigm

A pseudorandomized ER-fMRI paradigm with six types of stimuli (city NF, LSF, HSF, highway NF, LSF, HSF) was used. Each type of stimuli was presented 24 times. Overall, 144 stimuli were presented during each functional scan. In addition 34 null events (10 of them at the end of the session) composed of a blank screen and a fixation cross on the center of the screen, were also included. A fixation cross was always presented between stimuli on the center of the screen (baseline condition). Each stimulus was projected onto the center of the screen for 100 ms. Each stimulus was followed by the mask presented for 40 ms. Interstimulus interval (ISI) varied for each type of stimuli but the averaged interval between two successive stimuli was 2.5 s. The total duration of functional scan was 6'02".

MR acquisition

Functional MR imaging was performed on a 1.5-T clinical MR imager (Philips NT) equipped with echo-planar (EPI) acquisition. A functional volume composed of 23 adjacent, axial slices (thickness 6 mm each) was imaged for 178 times. The imaging volume was oriented parallel to the bicommisural (AC-PC) plane. The positioning of cerebral volume was performed on scout images acquired in sagittal plane. The cerebral volume was measured 10 times in a dummy fashion before testing, so that system stability could be achieved. A T2*-weighted gradient echo sequence was used using the following MR acquisition parameters: TR=2 s, TE=45 ms, flip angle=90°, field-of-view=256 × 256 mm^2, imaging matrix=512 × 512, reconstruction matrix=128 × 128. Subsequent to the functional scan, a T1-weighted high-resolution three-dimensional scan (150 adjacent, axial slices, 1 mm thickness each) was acquired to provide high spatial resolution anatomical information about the volume previously functionally examined.

Data processing

Data analysis was performed based on the general linear model (Friston et al., 1995) for event-related designs, implemented in SPM-99 software (Wellcome Department of Imaging Neuroscience, London, UK) running on a Unix workstation under the MATLAB environment (Mathworks, Sherbon, USA).

Spatial preprocessing

MR images were processed using the following steps. First, during the slice timing step, the functional volumes were corrected for sampling bias effects caused by the different time acquisition of each slice composing the functional volume, relative to the hemodynamic response. In the second step, the realignment, motion correction was applied by using rotations and translations to realign each functional volume to the first acquired one. In a third step, the anatomical volume was spatially normalized into the Talairach and Tournoux (1988) reference space using as template a representative brain from the Montreal Neurological Institute. The anatomical normalization parameters were subsequently applied to functional volumes. Finally, in conformity with the assumption that data are normally distributed, the functional images were spatially smoothed by using a Gaussian filter (8 mm width).

Statistics

For each type of individual events, regressors of interest were created by convolving a delta function at each event onset with a canonical hemodynamic response function, and its two partial derivatives. To allow population inference, two-stage random-effect analyses were then performed. Linear contrasts of interest (see below), calculated for each subject, were entered into a one-sample t test. Clusters of activated voxels were then identified, based on the intensity of the individual responses ($P < 0.001$ uncorrected for multiple comparisons) and the spatial extent (clusters composed of at least four voxels).

Evaluation of cerebral substrates for spatial frequency processing

To assess the neural substrates involved in LSF processing with respect to HSF, the calculated contrast was LSF > HSF. Conversely, the contrast HSF > LSF was calculated to highlight regions significantly more activated during HSF with respect to LSF processing. To estimate if NF scenes are mainly recognized based on LSF rather than HSF, we also specified the following contrasts: NF > (LSF + HSF), NF > LSF, NF > HSF, (LSF + HSF) > NF, LSF > NF and HSF > NF.

Evaluation of the hemispheric predominance during LSF and HSF processing

We used a method allowing us to directly compare the activity of the two hemispheres (see Iidaka et al., 2004; Lux et al., 2004; Ward and Frackowiak, 2003). This method consists of comparing at both the individual and group level, two sets of functional volumes acquired during a functional scan. One set was represented by the functional volumes normalized in neurological convention (left is left) and the other set was represented by the same functional volumes normalized in radiological convention (left is right). The images belonging to the second set were "flipped" with 180° in the midsagital plane, such that they represent the "mirror" images of the first set. As the standard MNI template provided by SPM includes left–right morphological asymmetries that could bias the contrasts, a symmetrical template (built by averaging the standard template and its mirror about the midsagital plane) was used. At the individual level first, contrasts between unflipped and flipped images were calculated for each spatial frequency components of natural scenes. For instance, for assessing the hemispheric predominance for LFS processing, the following contrast was calculated: LSF_unflip > LSF_flip. Afterwards, random effect analyses were performed using a one-sample t test on contrast obtained in each subject for

Table 1
Activated regions obtained for (a) spatial frequency processing and (b) nonfiltered versus filtered natural scenes processing

Contrast	Region	H	BA	k	x	y	z	t
(a) Cerebral regions for spatial frequency processing								
LSF > HSF	*temporoparietal cortex (TPJ)*							
	inferior parietal lobule	R	40	4	40	−22	29	5.52
	temporal cortex							
	posterosuperior temporal gyrus	L	22	4	−51	−38	13	5.45
	posterosuperior temporal gyrus	R	22	8	59	−38	7	5.44
	anterosuperior temporal gyrus	R	38/21	24	32	−4	−10	4.81
	[anterosuperior temporal gyrus]		38		36	3	−15	4.77
	[hippocampal gyrus]/[amygdala]		–		28	−9	−20	4.36
	[parahippocampal gyrus]		28		20	−16	−14	4.06
	posterosuperior temporal gyrus	L	22	5	−48	−19	1	4.76
	striatum							
	putamen	L	–	24	−16	4	11	5.15
					−28	−11	6	4.70
					−28	8	5	4.43
HSF > LSF	*No significant voxel*							
(b) Cerebral regions for nonfiltered versus filtered natural scene processing								
NF > (LSF + HSF)	*frontal cortex*							
	medial frontal gyrus	L	10	9	−8	51	3	4.98
	[anterior cingulate gyrus]		32		−12	43	−2	3.92
	middle frontal gyrus	L	8	10	−24	33	43	4.61
	parietal cortex							
	postcentral gyrus	L	3	23	−55	−13	45	6.30
					−40	−17	51	4.54
					−44	−21	45	4.49
NF > LSF	*frontal cortex*							
	middle frontal gyrus	L	8	30	−24	37	42	7.14
					−12	37	42	4.95
NF > HSF	*temporal cortex*							
	anterosuperior temporal gyrus	R	38	8	44	11	−21	5.33
	parahippocampal gyrus/amygdala	R	–	5	28	−9	−15	4.56
	postero-superior temporal gyrus	L	21/22	4	−48	−23	1	4.44
	frontal cortex							
	supplementary motor area	L	6	9	−28	−16	67	4.94
		R	6	5	55	0	6	4.61
	medial frontal gyrus	L	10	6	−8	47	3	4.88
	parietal cortex							
	postcentral gyrus	L	3	10	−51	−13	45	5.37
(LSF + HSF) > NF	*No significant voxel*							
LSF > NF	*No significant voxel*							
HSF > NF	*No significant voxel*							

For each cluster, the region showing the maximum t value is listed first, followed by the other regions belonging to the cluster [between brackets]. The statistical significance threshold for individual voxels was set at uncorrected $P < 0.001$ (random-effect analysis). The Talairach coordinates (x, y, z) are indicated.

Abbreviations: Hemisphere (H), right hemisphere (R), left hemisphere (L), Brodmann area (BA), number of voxels in the cluster (k), low spatial frequency (LSF) filtered scenes, high spatial frequency (HSF) filtered scenes, nonfiltered (NF) scenes.

each spatial frequency components of natural scenes (NF, LSF and HSF).

Results

Behavioral results

Independently of spatial frequency, the mean error rate was very low when subjects recognized LSF filtered scenes (0.69%), HSF filtered scenes (0.69%) and NF scenes (0.63%). Therefore, an analysis of variance (ANOVA) was performed only on mean correct Reaction Times (mRT) with spatial frequency components as *within-subject* factor. There were no significant differences between LFS, HSF and NF scene recognition in terms of mRT [449, 439 and 438 ms, respectively; $F(2,30) = 1.98$, $P = 0.16$].

Cerebral activation results

Cerebral substrates for spatial frequency processing

Brain areas specifically involved in spatial frequency processing (LSF and HSF) are summarized in Table 1a. Figs. 2a–d show functional maps obtained during LSF scene recognition contrasted to HSF scene recognition (LSF > HSF). The activation from the group analysis is projected onto a 2D axial *b-single subject* template brain and presented at different levels with respect to the bicommissural plane. A significantly greater response to LSF than to HSF was observed within the right inferior parietal lobule (BA 40), the bilateral posterosuperior temporal gyrus (BA 22), the right anterosuperior temporal gyrus (BA 38), the anterior part of the right middle temporal gyrus (BA 21) and the medial part of the anterior temporal cortex (parahippocampal gyrus, BA 28) extending to the posterior part of the amygdala. No significant activation was obtained by contrasting HSF versus LSF (HSF > LSF).

Cerebral substrates for nonfiltered versus filtered natural scene processing

Brain areas specifically involved in nonfiltered versus filtered scene processing are summarized in Table 1b. No significant activation was obtained by contrasting filtered to nonfiltered scenes (LSF + HSF > NF, LSF > NF and HSF > NF contrasts). NF scene recognition generated stronger activation within the frontal (medial frontal gyrus, BA 10 and middle frontal gyrus, BA 8) and parietal (postcentral gyrus, BA 3) cortices relative to filtered scene recognition. The middle frontal gyrus activation was also obtained when NF were contrasted to LSF and the medial frontal and postcentral gyrus were activated when NF were contrasted to HSF. Importantly, the latter contrast also exhibited supplementary activations within anterior temporal cortex (see Fig. 2e), relatively similar to those provided by the contrast LSF > HSF. The right anterosuperior temporal gyrus (BA 38), the left posterosuperior temporal gyrus (BA 22) and the right parahippocampal gyrus (extending to the posterior part of the amygdala) all were significantly more activated during NF than during HSF scene recognition.

Hemispheric specialization for spatial frequency processing

The direct interhemispheric comparison for LSF, HSF, and NF scene recognition was done by contrasting LSF_unflip > LSF_flip, HSF_unflip > HSF_flip and NF_unflip > NF_flip. Activated regions provided by these contrasts are summarized in Table 2. The direct comparison of the hemispheres provided significant activation within the left primary motor and the occipitotemporal areas. The left primary motor cortex (BA 4) was significantly activated, independently of filtered (LSF and HSF) or nonfiltered (NF) scenes, related to the motor response given by subjects. Critically, a hemispheric specialization for spatial frequency processing was observed within occipitotemporal areas (see Fig. 3). Thus, the right middle occipitotemporal junction (BA 19/39) (peak coordinates, *x y z*, 32

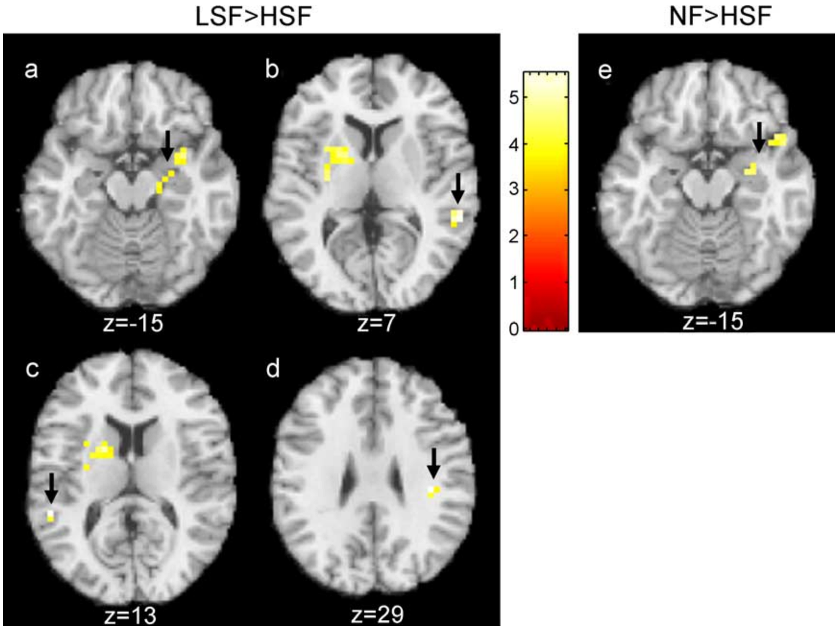

Fig. 2. Activated regions provided by the random effect group analysis by contrasting (a–d) LSF versus HSF filtered scenes (LSF > HSF) and (e) NF versus HSF scenes (NF > HSF). They are projected onto a 2D *b-single subject* template brain and represented in neurological convention (left is left). The colour scale represents the *t* value of activation ($P < 0.001$ uncorrected). The *z* value (mm) represents the slice level with respect to the bicommissural plane. The activated regions were the anterior temporal cortex (a and e), the bilateral superior temporal gyrus (b and c) and the right temporoparietal junction (d).

Table 2
Activated regions obtained for the LSF_unflip > LSF_flip, HSF_unflip > HSF_flip and NF_unflip > NF_flip contrasts ($P < 0.001$ uncorrected, random-effect analysis)

Contrast	Region	H	BA	*k*	*x*	*y*	*z*	*t*
LSF_unflip>LSF_flip	*motor areas*							
	primary motor area	L	4	70	−40	−17	56	7.51
					−36	−20	62	7.30
					−20	−20	67	5.24
					−51	−21	40	4.90
					−51	−17	51	4.80
	anterior cingulate gyrus	R	24	13	4	5	27	6.61
	putamen	L	–	4	−28	8	0	6.05
	caudate nucleus	R	–	6	32	−35	7	4.54
					36	−42	8	4.15
	occipitotemporal regions							
	middle occipitotemporal junction	R	39	11	32	−65	14	4.60
	[middle occipital gyrus]		19		28	−66	3	4.50
	[middle occipital gyrus]		19		32	−77	15	3.96
HSF_unflip>HSF_flip)	*motor areas*							
	primary motor area	L	4	39	−40	−16	62	9.34
					−48	−17	40	4.73
					−51	−22	23	4.30
	anterior cingulate gyrus	R	24	18	0	9	27	5.99
					8	2	33	4.70
	cerebellum	R	–	8	4	−39	2	4.75
	occipital cortex							
	middle occipital gyrus	L	19	4	−20	−81	15	4.97
NF_unflip>NF_flip	*motor areas*							
	primary motor area	L	4	85	−40	−17	56	6.63
					−55	−13	45	6.11
					−28	−16	67	4.96
	anterior cingulate gyrus							
		R/L	24	15	0	9	27	4.94
					0	16	16	4.43

Footnotes: Conventions and abbreviations are identical to those indicated for Table 1.

−65 14) was significantly more activated than its left homologue during LSF processing. By contrast, the left middle occipital gyrus (BA 19) (*x y z*, −20 −81 15) was significantly more activated than its right homologue during HSF processing. We did not obtain any significant activation within occipitotemporal regions during NF scene recognition as regarding the hemispheric dominance.

Discussion

The present event-related fMRI study aimed to assess cerebral regions and hemispheric dominance for spatial frequency processing during the recognition of natural scenes. Our study provided two main results. First, visual scene recognition is mainly based on

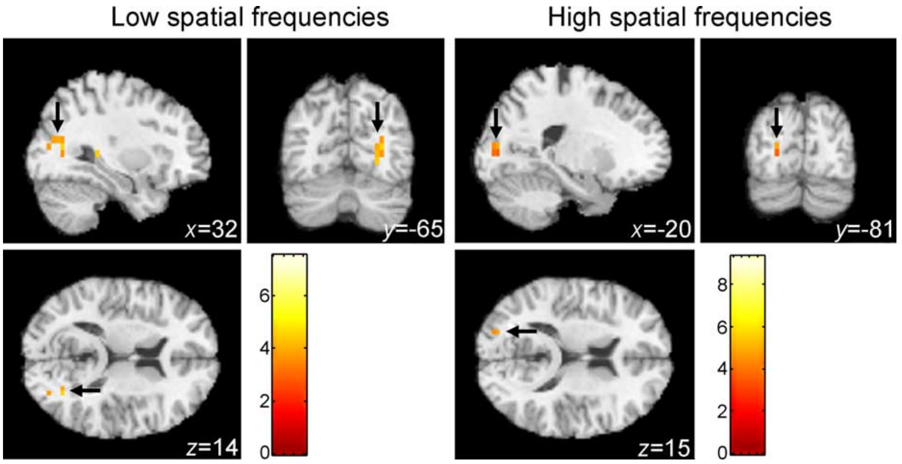

Fig. 3. Activated regions provided by the random effect group analysis by contrasting “LSF unflip versus LSF flip” and “HSF unflip versus HSF flip”. The Talairach coordinates (x, y, z) are reported. The activated regions were obtained within occipital-temporal areas (BA 39/19) for LSF processing and left middle occipital gyrus (BA 19) for HSF processing. Footnotes: Conventions are identical to those indicated for Fig. 2.

LSF information analysis. Second, there is a hemispheric specialization for processing spatial frequencies.

Spatial frequency processing

The comparison of HSF versus LSF did not show significant activation. The comparison of LSF versus HSF filtered scenes produced a significant activation of the right inferior parietal lobule (BA 40) within the temporoparietal junction (TPJ). TPJ has previously been described as mediating and sustaining the allocation of attentional resources to local and global information of hierarchical forms (Fink et al., 1996; Robertson and Lamb, 1991; Robertson et al., 1988). In our study, this activation could be interpreted as an attentional control mechanism exerted by the TPJ on visual areas responsible for processing low or high spatial frequencies. When subject do not know in advance in which spatial frequency band the natural scene will be displayed, the TPJ may constraint the right lower visual areas to emphasize LSF information by a low-pass-filtering and the homologous left areas to emphasize HSF information by a high-pass filtering. In an ERP study, Yamaguchi et al. (2000) showed temporoparietal cortex asymmetries during allocation of attention to global versus local information on hierarchical forms. Authors used a target letter which appeared either at global or at local level (divided attention task). Before a hierarchical form appears, the level of the target was cued by outward-pointing arrowheads for a subsequent global processing or inward-pointing arrowheads for a subsequent local processing. Yamaguchi et al. (2000) showed cerebral activity in the right temporoparietal area for a global attention shift (allocation of attention on LSF information) and activity in the left posterior temporal region for a local attention shift. However, in our fMRI study, we failed to observe hemispheric asymmetries of temporoparietal areas. We only showed a right inferior parietal lobule specialization for LSF (versus HSF) processing. A potential explanation could be that the attentional constraints involved in the filtered scene recognition were not as strong as those involved in a divided attention task on hierarchical forms. Alternatively, if scene recognition is mainly based on LSF rather than HSF analysis, the right inferior parietal lobule may maintain an attentional set to bias processing toward LSF.

With respect to HSF scene recognition, the LSF scene recognition also activated the bilateral posterosuperior temporal gyri (BA 22). This result is in disagreement with neuropsychological studies (Lamb et al., 1990; Robertson and Lamb, 1991; Robertson et al., 1988) which have shown that the right posterior superior temporal cortex is specialized in perceptual processing of global (LSF) information and the left in perceptual processing of local (HSF) information.

Importantly, LSF scene recognition also selectively activated the right parahippocampal gyrus. Bilateral parahippocampal activation was previously reported by Fize et al. (2000) during a rapid categorization task of natural images. Neuropsychological studies on patients with lesions within the parahippocampal cortex, suggest that this medial structure of the temporal lobe play an important role in spatial memory (Bohbot et al., 1998; Maguire et al., 1996; Ploner et al., 2000) and topographical information processing (Epstein et al., 2001; Habib and Sirigu, 1987). In addition, several neuroimaging studies showed that this region would be specifically involved in topographical information learning and retrieval during orientation and navigation in space (Aguirre et al., 1996; Maguire et al., 1997, 1998; Mellet et al., 2000), as well as in scene perception per se (Epstein and Kanwisher, 1998; Nakamura et al., 2000; Sato et al., 1999). The most commonly reported activation within the parahippocampal cortex, related to scene processing, was the PPA (Epstein and Kanwisher, 1998). PPA is specifically more activated when visual stimuli are represented by street, landscapes or buildings scenes for which spatial layout is a significant attribute of recognition, rather than for faces, objects or scrambled scenes. PPA activation was found even when subjects process the visual stimulus passively, without any navigational task (Epstein and Kanwisher, 1998). Finally, the PPA may play a key role in the encoding of new perceptual information about spatial layout (Epstein et al., 1999, 2001).

However, our activation within the right parahippocampal gyrus ($x\ y\ z$, 20 −16 −14) does not correspond to PPA activation reported by Epstein and Kanwisher (1998) ($x\ y\ z$, 20 −39 −5, peak coordinates reported in Epstein et al., 1999). Our activation is closer to those reported by Maguire et al. (1998) ($x\ y\ z$, 36 −12 −20) in task requiring the retrieval of topographical information in scenes. We suggest that our recognition task is based on information retrieval to match topographical information between stimuli and the “target” scene. In our study, the right parahippocampal cortex was more activated during LSF than during HSF, suggesting a possible “diagnostic spatial scale” role of LSF for processing topographical information. Furthermore, this activation extended slightly towards posterior amygdala. It has been suggested by Vuilleumier et al. (2003) that the subcortical route carrying visual inputs to amygdala via magnocellular tecto-pulvinar pathways is selectively tuned for LSF information. Our result suggests that during natural scene recognition, the right parahippocampal gyrus may receive LSF information from subcortical pathway.

The right anteriosuperior temporal gyrus (BA 38/21) was significantly more activated during LSF than during HSF scene recognition. It has been shown that the right anterior temporal region would be particularly sensitive to familiar versus unfamiliar faces and scenes (Nakamura et al., 2000). In our study, the right anterior temporal cortex activation probably reflects a familiarity effect since only two scenes were repetitively presented. Furthermore, this result could also suggest that visual information used in familiarity judgment of natural scenes would be preferentially conveyed by LSF.

In summary, relative to HSF, the LSF provided a stronger activation within brain areas involved in scene processing (anterior parahippocampal and temporal cortex). This result may be due to a property of spatial frequency per se, rather than to the evidence that rapid scene recognition is mainly based on LSF analysis. However, by contrasting filtered versus nonfiltered scene recognition, no significant activation was observed. This suggests that the amplitude spectrum manipulation had no notable effect on cerebral processing.

Furthermore, it has been shown that the task demands can be essential for choosing the preferential frequency band to be analyzed. For instance, in a recent fMRI study, Iidaka et al. (2004) used a “one-back task” where subjects had to judge whether two successive stimuli (either low-pass or high-pass filtered in distinct blocks) were identical or not. Whereas an activation of the left occipitotemporal cortex during HSF versus LSF condition was obtained, no significant activation was observed during the opposite contrast. The authors suggested that the “one-back task” was preferentially performed on local features, emphasized in HSF condition. Thus, their task should be mainly HSF-based. In addition, the influence of task demands on spatial frequencies preferentially process in faces has been largely demonstrated in several behavioral (Hellige and Sergent, 1986; Nasanen, 1999; Schyns and Oliva, 1999; Sergent, 1985) and fMRI studies (Vuilleumier et al., 2003; Winston et al., 2003). In our recognition task, while the anterior temporal cortex activation was observed during the LSF condition with respect to the HFS condition, no significant activation was observed during the HSF condition with respect to the LSF condition. This pattern of results could suggest that scene recognition is based on LSF processing. This pattern of results also supports the models proposing a prevalence of LSF information in recognition of natural scenes (Ginsburg, 1986; Hughes et al., 1996). Consequently, HSF information would be poorly emphasized, resulting in no differential activation when HSF were contrasted to LSF.

Finally, NF > HSF and LSF > HSF contrasts activated common cerebral regions within the right anterior temporal cortex (NF > HSF, $x\ y\ z$, 44 11 −21; LSF > HSF, $x\ y\ z$, 32 −4 −10) and right parahippocampal gyrus (NF>HSF, $x\ y\ z$, 28 −9 −15; LSF > HSF, $x\ y\ z$, 28 −9 −20). This pattern suggests that the spatial scale preferentially processed during NF scene recognition is rather low, in favor of LSF-based rapid scene recognition. By contrasting NF to filtered scenes, we also observed stronger activation within the medial frontal (BA 10) and middle frontal (BA 8) gyri. Frontal areas activation could be associated to mnesic processes (Cabeza and Nyberg, 2000; Nyberg et al., 2003) involved during processing of NF scenes, since only NF scenes were presented at the beginning of each fMRI session and subjects have to actively maintain them into the memory to perform the recognition task.

Hemispheric specialization for spatial frequency processing

In a recent behavioral study, we evaluated the hemispheric asymmetry in healthy subjects using natural scenes while manipulating spatial frequencies (Peyrin et al., 2003). Scenes were presented in divided visual fields. 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 suggest a right hemispheric superiority for LSF and left hemispheric superiority for HSF processing. They are consistent with Sergent's (1982) assumption that visual tasks needing LSF information to be processed (as for global letter identification in hierarchical stimuli) would result in a left visual field/right hemisphere advantage, whereas a task needing HSF information to be processed (as for local letter identification) would result in a right visual field/left hemisphere superiority. Based on this behavioral experiment, the present fMRI study also aimed at assessing regions specifically activated within each hemisphere during the processing of spatial frequencies in natural scenes.

Unlike previous fMRI studies (e.g., Han et al., 2002; Martinez et al., 1997), we did not observe a right occipitotemporal predominance in the LSF relative to HSF condition, nor a left occipitotemporal predominance in the HSF relative to LSF condition. Rather, we observed a stronger bilateral activation within the superior temporal gyrus (i.e., a region showing a hemispheric specialization based on neurological patients, Lamb et al., 1990; Robertson et al., 1988) for LSF > HSF and no significant activation for the opposite contrast (HSF > LSF). This result might be due to the LSF bias processing in our recognition task. To carry out any bias in spatial frequency processing for determining the hemispheric specialization, we directly compared the hemispheres by contrasting "unflip" to "flip" functional images for each particular spatial frequency band processing (LSF, HSF and NF). Using this method, we found that spatial frequency processing was associated with differential hemispheric activation within early visual areas. The middle occipitotemporal junction (BA 39/19) was significantly and predominantly activated within the right hemisphere during LSF scene recognition, whereas the middle occipital gyrus (BA 19) was significantly and predominantly activated within the left hemisphere during HSF scene recognition. These results suggest that right occipital areas (as the middle occipital gyrus) might be in charge of LSF emphasis while the left homologous, of HSF emphasis during natural scene recognition. No hemispheric asymmetry was observed during NF scene recognition. We could hypothesize that the whole frequency spectrum of NF scenes involved both low and high spatial frequencies emphasis (at relatively different degrees), activating middle occipital gyrus activation within each hemisphere.

The asymmetrical activations of the occipitotemporal cortices are in agreement with other studies that observed hemispheric specialization in spatial frequency processing at the earliest levels (occipital cortices) of visual analysis: for example, extrastriate areas (Fink et al., 1996), occipitotemporal areas (Martinez et al., 1997), occipital areas (Han et al., 2002), right lateral occipital areas in LSF processing (Kenemans et al., 2000) or left occipitotemporal areas in HSF processing (Iidaka et al., 2004). The right TPJ activation during LSF information selection indicates that this region could constraint the right middle occipital cortex to emphasize the LSF information. Thus, our results are in agreement with studies suggesting that hemispheric specialization in global/LSF versus local/HSF processing results from top-down influences of temporoparietal regions towards low-level regions of visual analysis (e.g., Fink et al., 1996). Our results do not confirm with studies proposing that spatial frequency processing is only asymmetric at higher levels of visual processing (e.g., Heinze et al., 1998).

Conclusion

In conclusion, our findings suggest that visual recognition of natural scenes is mainly based on LSF information extraction and analysis. Within this framework, LSF information would be preferentially conveyed to the right anterior parahippocampal and temporal cortex for an integrative visual recognition. Our results also suggest that activations within occipitotemporal cortex differed between the two hemispheres according to spatial frequency components of the scenes (LSF versus HSF). The right occipitotemporal areas were more activated than the left for LSF processing and the left middle occipital gyrus more than the right for HSF processing. We conclude that, at the occipital level, the visual system might be equipped with two perceptual filters, one within the right hemisphere for emphasizing LSF information and the other one within the left hemisphere for emphasizing HSF information. We also observed a right TPJ activation during LSF versus HSF processing, probably corresponding to a top-down control exerted by this region, on the low-pass filtering occurring in the right occipital cortex. Future studies in which attentional demands will be stronger than in our task (for instance, attentional resources divided between LSF and HSF information displayed simultaneously) would be useful to identifying which regions, in which hemisphere, exert top-down control on spatial frequency processing during the recognition of natural scenes.

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