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On the Specific Role of the Occipital Cortex in Scene Perception

Carole Peyrin and Benoit Musel

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<http://dx.doi.org/10.5772/48438>

1. Introduction

In recent years there has been mounting scientific excitement about the perception of scenes containing more realistic and complex stimuli than simple objects or drawings. Visual recognition of scenes is a fast, automatic and reliable process. Experimental studies have shown that complex natural scenes can be categorized in a very short time (under 150 ms [1]), suggesting a simple and efficient coding process. Many studies have attested to the importance of the Fourier components of images in scene categorization. In terms of signal representation, an image can be expressed in the Fourier domain as amplitude and phase spectra [2-5]. The amplitude spectrum highlights the dominant spatial scales (spatial frequencies) and the dominant orientations of the image, while the phase spectrum describes the relationship between spatial frequencies. It is now well established that the primary visual cortex is mainly dominated by complex cells which respond preferentially to orientations and spatial frequencies [6-8]. Simulation and psychophysical experiments have shown that information from low/medium frequencies of the amplitude spectrum is sufficient to enable scene categorization [9, 10]. These data support current influential models of scene perception [11-14].

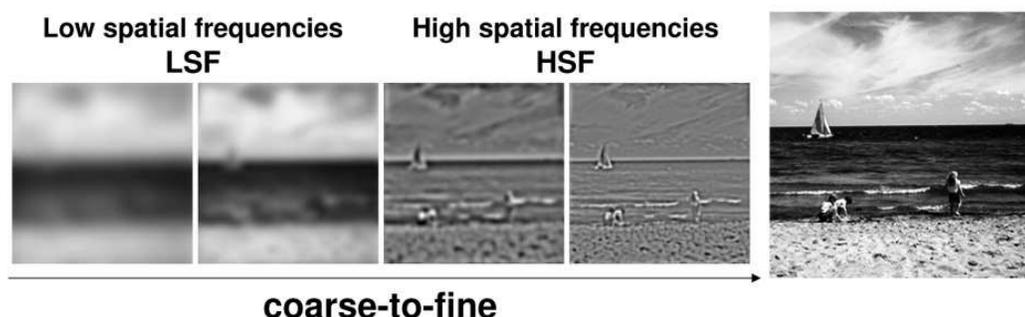


Figure 1. Coarse-to-fine sequence of spatial frequency processing (from low-to-high spatial frequencies) during scene perception

On the basis of convergent data from the functional neuroanatomy of magnocellular and parvocellular visual pathways [15], neurophysiological recordings in primates [12], and psychophysical results in humans [3, 4], these models have speculated that spatial frequency content may impose a specific temporal hierarchy on the processing of visual inputs. According to these models, visual analysis starts with the parallel extraction of different elementary attributes at different spatial frequencies, in a predominantly coarse-to-fine (low-to-high spatial frequencies) sequence which favours low spatial frequencies (LSF) in the initial stages of visual processing and high spatial frequencies (HSF) in the later stages (Figure 1). The LSF in a scene, conveyed by fast magnocellular visual channels, might therefore activate visual pathways and subsequently reach high-order areas in the dorsal stream (parietal and frontal) more rapidly than HSF, allowing an initial perceptual parsing of visual inputs prior to their complete propagation along the ventral stream (infero-temporal cortex) which ultimately mediates object recognition. This initial low-pass visual analysis might serve to refine the subsequent processing of HSF, which are conveyed more slowly by parvocellular visual channels to the ventral stream.

The majority of current visual models are, therefore, based on the neurophysiological properties of spatial frequency processing. However exactly how spatial frequencies are processed within the occipital cortex remains unclear. Initially, on the basis of neurophysiological recordings in nonhuman primates, Bullier [12] proposed that rapid LSF analysis, which takes place predominantly in the dorsal visual stream, might be “retro-injected” through feedback signals into low-level areas (e.g., primary visual cortex, V1), where it would influence subsequent HSF analysis and guide further processing through the ventral visual stream. The occipital cortex might therefore serve as an “active blackboard” integrating computations carried out by higher order cortical areas. Secondly, the issues of cerebral asymmetries and/or retinotopic organization of spatial frequency processing within the occipital cortex are still being debated in the literature. Many studies reveal retinotopic organization of spatial frequency processing in the occipital cortex [16-18]. HSF sinusoidal grating processing, for example, activates the foveal representation in all retinotopic areas (such as V1) of the occipital cortex, and LSF sinusoidal grating processing activates more peripheral representations in the same cortical areas. Despite studies showing retinotopic mapping of spatial frequency processing in the occipital cortex, many experimental arguments assume a certain hemispheric specialization of spatial frequency processing in the occipital cortex. The right occipital cortex appears to be preferentially specialized for LSF information processing, while the left occipital cortex seems to be preferentially specialized for HSF information processing [19-21]. It is, therefore, essential to determine whether hemispheric specialization and retinotopic processing can co-occur in the occipital cortex. While addressing this issue, the present chapter also aims to clarify the different attributes of the occipital cortex during scene recognition.

2. Coarse-to-fine analysis in visual perception

Results from various neurophysiological, computational, and behavioral studies all indicate that the totality of visual information is not immediately conveyed, but that information

analysis follows a predominantly coarse-to-fine processing sequence (LSF are extracted first, followed by HSF). The first experimental evidence in support of this type of coarse-to-fine processing sequence in human vision comes from psychophysical studies using hierarchical stimuli (global forms composed of several local elements [22, 23]). Usually, these forms represent a large global letter form made up of small local letters. The subject's task is to identify a target letter either at global level, at local level, or at both levels. Using this paradigm, two main findings have emerged. Firstly, global form identification is faster than local form identification. This phenomenon is known as the global precedence effect. Secondly, while inconsistent global information slows down local information identification, the identification of local information has no effect on global identification. This asymmetrical effect is known as the global interference effect. However, these effects decrease or even vanish when the hierarchical forms are high-pass filtered (i.e. LSF are cut off). They are also affected by a subject's adaptation to a given frequency band (low vs. high), suggesting that LSF carry global information, whereas HSF carry local information [24-26]. Based on the assumption that global information is preferentially conveyed by LSF, and that local information is conveyed by HSF, the global-to-local processing sequence has been interpreted as reflecting a fundamental principle of the coarse-to-fine processing sequence.

Additional evidence of a coarse-to-fine processing sequence was provided by psychophysical studies using more ecological stimuli, such as natural scenes and faces [14, 27-30]. Schyns and Oliva [14], for example, used hybrid stimuli consisting of two superimposed images of natural scenes, taken from different semantic categories and containing different spatial frequencies (e.g., a highway scene in LSF superimposed on a city scene in HSF). The perception of these hybrid scenes was dominated by LSF information when presentation time was very brief (30 ms). However when presentation time was longer (150 ms), perception was dominated by HSF information, suggesting precedence of LSF over HSF in the visual processing time-course. Furthermore, when two successive hybrids displayed a coarse-to-fine sequence for a given scene (e.g., the highway scene in LSF in the first hybrid and then in HSF in the second hybrid) and a fine-to-coarse sequence simultaneously for another scene (e.g., the city scene in HSF in the first hybrid and then in LSF in the second hybrid), scene perception was more frequently based on a coarse-to-fine rather than a fine-to-coarse sequence.

Quite exactly how and where in the brain LSF and HSF information is differentially analyzed and eventually merged during visual processing remains an unresolved question. Traditional models have generally assumed that different visual cues are combined at successive stages along the cortical hierarchy [31, 32], and suggest that LSF and HSF might converge only in higher-level visual areas in the inferior temporal cortex (such as the fusiform or parahippocampal cortex [33, 34]). However, drawing on evidence from neurophysiological recordings in nonhuman primates [35], Bullier [12] proposed that rapid LSF analysis, predominantly carried out in the dorsal visual stream, might be "retro-injected" through feedback signals into low-level areas (e.g., primary visual cortex) where it would influence subsequent HSF analysis, and guide further processing through the ventral

visual stream. The occipital cortex might therefore serve as an “active blackboard” integrating computations made by higher-order cortical areas. However, to date, the neural architecture and temporal dynamics of such top-down mechanisms have never been systematically investigated via direct testing of the preferential coarse-to-fine processing sequence during visual scene perception in humans.

3. Neural basis of the retro-injection mechanism during scene perception

In order to test the coarse-to-fine processing sequence and to identify its neural substrates in the human brain, we presented in rapid succession sequences of two spatial frequency-filtered scenes, with either an LSF image followed by an HSF image (coarse-to-fine sequence), or an HSF image followed by an LSF image (fine-to-coarse sequence) during fMRI and ERP recordings on the same participants [36]. Each scene in a sequence belonged to one of three categories (city, beach, or indoor). Half of the sequences displayed two scenes from the same category, and the other half displayed two scenes from different categories. Participants had to judge whether the two successive scenes belonged to the same category. This study also addressed the crucial issue of delayed “retro-injection” and spatial frequency integration in the occipital cortex.

Examination by fMRI showed selective increases in coarse-to-fine sequences (relative to fine-to-coarse sequences) in early-stage occipital areas, as well as in frontal and temporo-parietal areas. ERP topography and source analyses highlighted a similar network of cortical areas, but were in addition able to determine the time-course of activation in these regions, involving either LSF or HSF images in the different sequences. Higher-order areas in frontal and temporo-parietal regions responded more to LSF stimuli when these were presented first, whereas the occipital visual cortex responded more to HSF presented after LSF. More specifically, our results demonstrate that LSF in scenes (conveyed by fast magnocellular channels) can rapidly activate high-order areas, providing spatial (via the frontal eye fields) and semantic information (via the left prefrontal cortex and temporal areas), as well as attentional signals (via the temporo-parietal junction), all of which may promote the ongoing perceptual organization and categorization of visual input. This first coarse analysis may possibly be refined by further processing in the visual cortices of HSF in scenes (conveyed more slowly by the parvocellular channels). In order for this to occur, feedback from the first low-pass computations carried out in frontal and temporo-parietal areas might be “retro-injected” into lower level areas, such as the occipital cortex, at the level of the primary visual cortex, with a view to guiding the high-pass analysis and selecting the relevant finer details necessary for the recognition and categorization of scenes. These results provide critical support for recent models of vision, and for the retro-injection mechanism proposed by Bullier [12]. They also highlight the necessity for further investigation of the neural mechanisms of spatial frequency processing in the occipital cortex.

The majority of visual models assume, therefore, a predominantly coarse-to-fine sequence of spatial frequency processing in the whole brain, based on the functional properties of the

visual cortex. However, many studies have highlighted the fact that in humans, the left and right hemispheres do not deal with all aspects of visual information processing with equal ability. The two hemispheres might in fact make complementary contributions to the processing of LSF and HSF.

4. Hemispheric specialization of spatial frequency processing during scene perception

Many experimental arguments assume that spatial frequency processing is shared between the two hemispheres, with right hemispheric predominance for LSF processing and left hemispheric predominance for HSF processing. This hemispheric specialization has been observed either through behavioral studies on healthy subjects [21, 37-48] and neurological patients [49-51], or through functional neuroimaging studies [19, 20, 52-65]. However, the hemispheric asymmetries in question were largely inferred from studies assessing hemispheric specialization in global and local processing.

4.1. Behavioral arguments

Using hierarchical visual stimuli consisting of a global form made up of several local elements [22, 23] displayed either in the left or right visual field, Sergent [46] demonstrated that global forms were identified more quickly when they were presented in the left visual hemifield, projecting directly to the right hemisphere, while recognition of local forms was faster when they were presented in the right visual hemifield, projecting directly to the left hemisphere [52] (see also [38]). These results suggest right hemispheric dominance for the recognition of global forms, and left hemispheric dominance for the recognition of local forms. Since global processing can be considered to be mediated by low-pass spatial analysis, and local processing by high-pass spatial analysis [24-26], the hemispheric specialization patterns observed in global and local processing have been interpreted as reflecting the hemispheric specialization of LSF and HSF, respectively [46].

Unfortunately, the relationship between local and global information and spatial frequencies in hierarchical forms is far from univocal [66]. Global information could, for example, be conveyed not only by LSF but also by HSF. The hypothesis of hemispheric asymmetry in spatial frequency processing was subsequently directly tested by making explicit changes in the spatial frequency spectrum of stimuli, using sinusoidal gratings as stimuli [40-42], or more complex visual stimuli such as images of natural scenes [21, 43, 44]. It should be noted that hierarchical forms do not allow this type of manipulation, because low-pass filtering cancels out the local form, thus rendering execution of the task impossible. In a series of behavioral studies conducted by our team [21, 43, 44], we evaluated hemispheric asymmetry in healthy subjects using natural scenes, while manipulating the spatial frequency components of the scenes, which were presented in divided visual fields. In the princeps study [43], participants were asked to recognize either an LSF or an HSF filtered target scene (a city or a highway), displayed in either the left or the right visual field. Results showed that LSF filtered scenes were recognized more quickly when they were presented in the left

visual hemifield, projecting directly to the right hemisphere, while recognition of the HSF filtered scenes was faster when these were presented in the right visual hemifield, projecting directly to the left hemisphere. This study clearly demonstrated right hemispheric superiority for LSF and left hemispheric superiority for HSF processing, and therefore supports Sergent's assumption [46] that visual tasks which require the processing of LSF information (such as global letter identification in hierarchical forms) would result in a left visual field/right hemisphere advantage, whereas tasks requiring the processing of HSF information (such as local letter identification in hierarchical forms) would result in right visual field/left hemisphere superiority.

Following this, we examined whether the temporal characteristics of spatial frequency analysis (i.e. the temporal precedence of LSF over HSF as postulated by the coarse-to-fine processing sequence) might interfere with hemispheric specialization. We did this by manipulating the exposure duration of filtered natural scene images (30 vs. 150 ms [44]). Results showed the classical hemispheric specialization pattern for brief exposure duration (the right hemisphere was predominantly involved in LSF scene processing and the left in HSF scene processing), and a tendency towards right hemisphere advantage, irrespective of the spatial frequency content for longer exposure durations. These results suggest that the hemispheric specialization pattern for visual information processing ought to be considered as a dynamic system, within which 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 become specialized in spatial frequency processing. In a subsequent study [21], we provided evidence for hemispheric specialization in spatial frequency processing in men, but not in women. These results are consistent with studies showing that the functional cerebral organization of women is less lateralized than that of men [67, 68].

4.2. Neural correlates of hemispheric specialization

Neuropsychological and neuroimaging studies conducted on hierarchical visual stimuli have reported conflicting results on which cortical structures present hemispheric specialization. Robertson and collaborators [51] showed, for example, that unilateral damage of the temporo-parietal junction could impair patients' performance in the hierarchical form paradigm. Patients with a lesion in the left superior temporal gyrus thus exhibited a slowing down in local form identification, whereas the performance of patients with a lesion situated in the right temporo-parietal region was impaired during global form identification. These data suggest that two independent perceptual sub-systems may be involved; the right temporo-parietal junction which emphasizes global information, and the left temporo-parietal junction which emphasizes local information. However, using positron emission tomography, Fink and collaborators [53-55] reported cerebral asymmetries in the occipital cortex. The right lingual gyrus was more highly activated during the processing of global as opposed to local forms, while the left inferior occipital gyrus was more highly activated during the processing of local rather than global forms. Using electroencephalographic recordings, Heinze and collaborators [57, 60] failed to

demonstrate cerebral asymmetries in first-stage visual areas. Instead, their results, based on event-related potentials (ERPs), showed long latency asymmetries (260-360 latency range) for global versus local processing, suggesting that hemispheric specialization was present only in the higher levels of visual analysis.

Furthermore, some functional imaging data have revealed an attentional cortical mechanism which exerts control over the perceptual processes involved in global and local processing [50, 51, 53-55, 63-65]. This mechanism operates on the attentional selection of information presented either at global level, at local level, or at both levels depending on task constraints. This mechanism is located in the temporo-parietal junction. Using ERPs, Yamaguchi and collaborators [65] investigated the neural substrates of attentional allocation to global and local components of a hierarchical form. For this purpose ERPs were recorded while participants shifted their attention to the global or local level of a hierarchical form. Shift direction was controlled by a preceding cue stimulus. Hemispheric asymmetries arose not only during the task in which global–local processing was actually being performed, but also in the time interval during which attention was directed towards global or local levels by the cues. Therefore, in addition to hemispheric asymmetry during “bottom-up” processing, this study demonstrated the existence of neural substrates for a top-down mechanism of hemispheric asymmetry in global and local selection. ERPs to the cue showed greater amplitude in the right hemisphere during attentional allocation at global level, and greater amplitude in the left hemisphere during attentional allocation at local level. The neural activity in question was located in the right temporo-parietal junction for the global shift, and in the left temporo-parietal junction for the local shift. These electrophysiological results provided an asymmetrical neural basis for the “top-down” allocation of attention to global and local features, and revealed the contribution of the temporal-parietal cortex to this attentional mechanism.

On the whole, the imaging studies mentioned previously have provided conflicting results on hemispheric specialization using hierarchical stimuli. By directly manipulating the spatial frequency content of stimuli, subsequent studies revealed hemispheric specialization in certain occipito-temporal areas [19, 20]. In one fMRI study [20], we investigated the neural correlates and the hemispheric specialization of spatial frequency processing during the perception of scene stimuli which allowed an explicit change in the spatial frequency spectrum. For this purpose, we used a categorization task of small LSF and HSF scene images (at a visual angle of 4°).

By comparing LSF to HSF scene categorization (Figure 2a), we observed significant activation in the right anterior temporal cortex and the right parahippocampal gyrus. As these regions are known to be involved in scene processing, these results suggest that scene recognition is based mainly on LSF extraction and analysis, following a coarse-to-fine processing sequence. Significant activation was also obtained in the right inferior parietal lobule, and this probably reflects attentional modulation during spatial frequency selection. Compared to HSF scene recognition, LSF scene recognition also activated the bilateral posterior part of the superior temporal cortex. This result contradicts neuropsychological studies [49-51], which have shown specialization of the right superior temporal cortex in the

perceptual processing of global (LSF) information, and specialization of the left superior temporal cortex in the perceptual processing of local (HSF) information. Finally, comparisons between HSF and LSF scene categorization failed to show any significant activation, suggesting a bias towards the processing of LSF information.

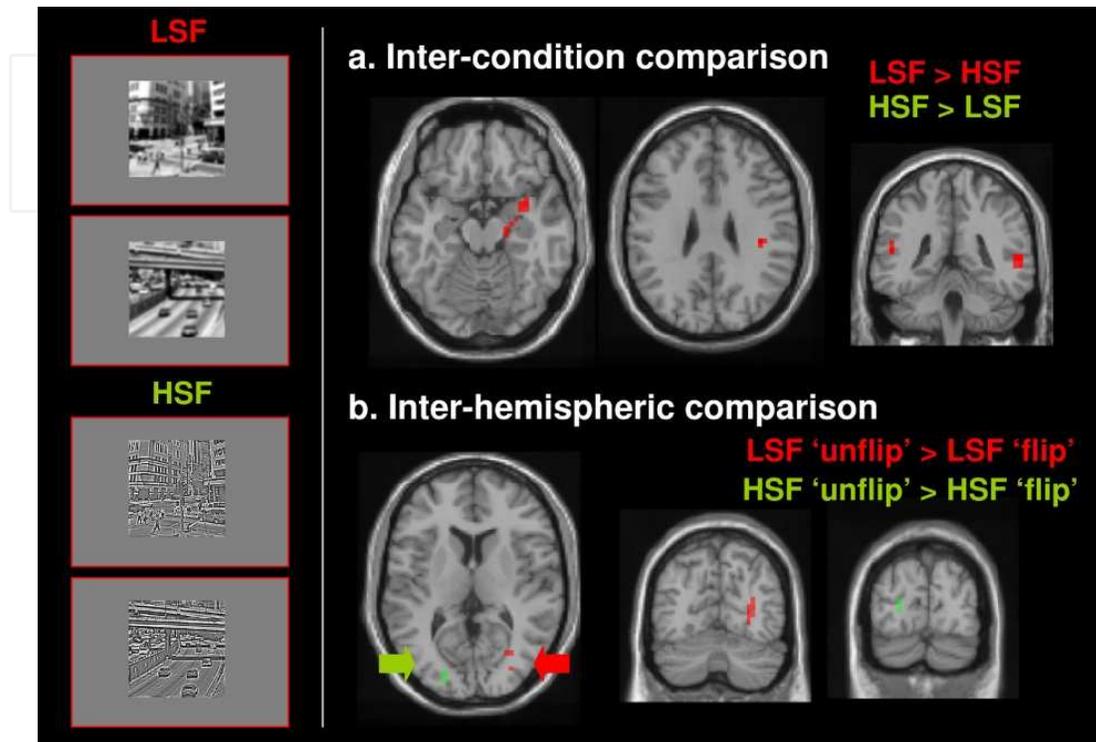


Figure 2. Hemispheric specialization of spatial frequency processing during scene perception

Based on behavioural experiments in which direct comparisons were made between the performances of the two visual fields [21, 40–44, 46], we suggested that any assessment of visual cerebral asymmetries must make direct comparisons between activation in the two hemispheres. In order to do so, we created a new method of fMRI data analysis. The method of direct inter-hemispheric comparison examines contrasts between “unflipped” and “left–right flipped” functional images from the same experimental condition (Figure 3), in order to compare activity in one hemisphere with activity in homologous regions of the other hemisphere [19, 20, 69, 70]. Using this method, we demonstrated higher levels of activation in the right middle occipital gyrus than in the left during the recognition of LSF scenes, and higher levels of activation in the left middle occipital gyrus than in the right during the recognition of HSF scenes (Figure 2b).

This result provides supplementary evidence for hemispheric specialization in the early stages of visual analysis when spatial frequencies are being processed. Another important point was that when analysing the fMRI data using a more traditional approach which contrasts spatial frequencies to one another, we observed stronger cerebral activation for LSF than for HSF scenes, while the reverse contrast did not reveal any significant activation. Results therefore differ according to the method of data analysis applied. A direct inter-hemispheric method of comparison seems more appropriate for the assessment of cerebral

asymmetries, since it allows the cancelling out of any main effect deriving from spatial frequency bias (i.e. stronger global cerebral activation for LSF than for HSF scenes).

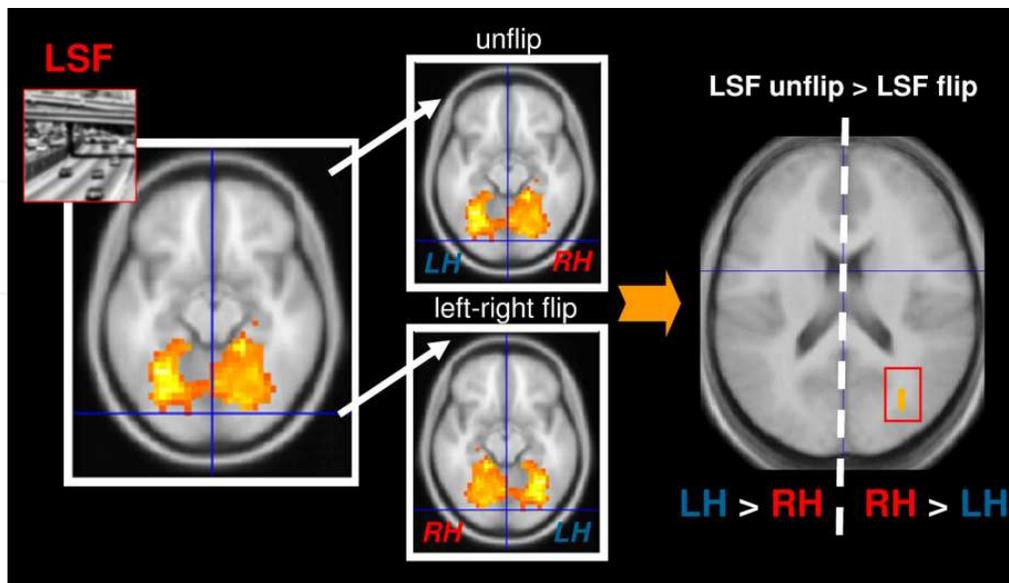


Figure 3. The method of direct inter-hemispheric comparison. In this method, two sets of functional volumes, obtained from functional scans, are compared at both individual and group level. One set is represented by functional volumes in accordance with neurological convention (the left hemisphere - LH appears on the left side of images) and the other set is represented by the same functional volumes this time in accordance with radiological convention (the right hemisphere - RH appears on the left side of images). Images from the second set were “flipped” by 180° in the midsagittal plane, thus providing “mirror” images of the first set. Contrasts between “unflipped” and “left-right flipped” images were then calculated for each of the spatial frequency components of natural scenes. In order to assess hemispheric predominance during the perception of LSF scenes, for instance, the following contrast was calculated: LSF unflip > LSF flip. Regions which were statistically more highly activated in the left hemisphere than in the right hemisphere appear on the left side, and regions which were statistically more highly activated in the right hemisphere than in the left hemisphere appear on the right side.

Using a neuropsychological approach [21], we further investigated the role of the right occipital cortex in LSF processing in a female neurological patient with a focal lesion in this region following the embolization of an arteriovenous malformation. As a result, she suffered from a left homonymous hemianopia. The study was conducted 1 week before and 6 months after the surgical intervention. As expected, after the embolization, LSF scene recognition was more severely impaired than HSF scene recognition. These data support the hypothesis of a preferential specialization of the right occipital cortex for LSF information processing, and suggest more generally a hemispheric specialization in spatial frequency processing in females, although this is difficult to demonstrate behaviourally in healthy women.

4.3. Cerebral asymmetries during coarse-to-fine analysis of scenes

What is important here is that although LSF information may be perceptually available before HSF, this does not necessarily imply that it is always used first to support visual

recognition in all tasks. Indeed, the global precedence effect can be turned into a local precedence effect by simple experimental manipulation (e.g., by changing the visual angle [22, 71] or the number of local elements [72]). In Schyns and Oliva's experiments [14], a substantial proportion (29%) of hybrid sequences were in fact categorized in accordance with a fine-to-coarse, rather than a coarse-to-fine sequence. Although the coarse-to-fine processing sequence appears to be the predominant way of operating, the processing sequence of spatial scale information has been found to be relatively flexible, and dependent on task demands [14, 29, 30]. A subsequent study by Schyns and Oliva [29] showed that the spatial scale preferentially processed in hybrid images can be constrained by a phase of prior sensitization which implicitly "primes" visual processing in favor of a particular scale (coarse or fine). After initial exposure to LSF information, the subsequent categorization of hybrid images was preferentially performed following LSF cues, whereas it was biased towards HSF information after priming by HSF. By using hybrid faces instead of scenes, Schyns and Oliva [30] showed that HSF information was preferentially used to determine whether a face was expressive or not, whereas LSF information was preferentially used to categorize emotion (e.g., happy, angry). The demands of a categorization task may, therefore, determine which range of spatial frequencies is extracted, and subsequently processed, from hybrid stimuli (even when using brief presentation times, such as 45 ms). In all, these studies suggest that all spatial frequencies were available at the beginning of categorization, and that both types of processing sequence may coexist in the visual system. The selection of spatial frequencies during the recognition of natural scenes may depend on dynamic interactions between the information requirements of a given recognition task and the perceptual information available. While a coarse-to-fine sequence of spatial frequency processing may preferentially arise for normal visual inputs containing both LSF and HSF information, our visual system should nonetheless be able to prioritize the processing of HSF in certain situations, such as when searching for a target known to be defined by specific local features rather than global visual properties (e.g., find something with a striped texture).

The cerebral occipital asymmetries observed in spatial frequency processing raise the fundamental question of the legitimacy of the coarse-to-fine sequence in the whole brain. It remains unclear whether coarse-to-fine analysis is used in both hemispheres and/or whether this sequence predominates in only one hemisphere. In an event-related fMRI experiment, we wondered whether hemispheric specialization of spatial frequency processing might underlie the flexibility of the temporal sequence used for spatial frequency analysis during scene perception [70]. In order to constrain spatial frequency processing according to different time-courses, we asked healthy participants to perform a matching task between two successive images of natural scenes (LSF or HSF), which were displayed either in a coarse-to-fine sequence (LSF scene presented first followed by HSF scene), or in a reverse fine-to-coarse sequence. Our direct inter-hemispheric comparison of the neural responses evoked by each spatial frequency sequence revealed greater activation in the right occipito-temporal cortex than in the left for the coarse-to-fine sequence, and greater activation in the left occipito-temporal cortex than in the right for the fine-to-coarse sequence. These fMRI

results therefore indicate that the hemisphere functionally specialized in the processing of the visual sequence of different spatial frequency inputs is the same hemisphere that is specialized in the processing of the first spatial frequency-band appearing in this sequence (i.e. right hemispheric dominance for coarse-to-fine, but also for LSF information analysis when presented alone; and conversely, left hemispheric dominance for fine-to-coarse, but also for HSF information analysis alone). This pattern suggests that the hemisphere preferentially engaged during the sequential processing of different spatial frequencies might be determined by the initial spatial frequency-band appearing in this sequence, and that both a coarse-to-fine and fine-to-coarse analysis might take place independently in both hemispheres. Our findings indicate that the visual system might be equipped with two types of cortical apparatus which are able to support scene perception differentially and flexibly, according to task demands or input sequence. The apparatus in the right occipital cortex would give priority to LSF analysis and the one in the left occipital cortex would give priority to HSF analysis. However, although a considerable number of studies postulate hemispheric specialization of spatial frequency processing in the occipital cortex, others highlight retinotopic processing of spatial frequencies.

5. Retinotopic organization of spatial frequency processing during scene categorization

The distribution of retinal photoreceptors and retinal ganglion cells is nonhomogeneous throughout the visual system [73, 74]. The density of cones and midget ganglion cells, which are used to process HSF information, is greatest in the fovea, while the density of rods and parasol ganglion cells, which are used to process LSF information, increase with foveal eccentricity. Different imaging data obtained from patients with cerebral lesions [75, 76] and from healthy participants [77, 78] show that the human primary visual cortex is retinotopically organized. Representation of the visual field ranges from the posterior to the anterior visual cortex, and shifts from the centre to the periphery. Since the fovea is represented in the posterior areas of the visual cortex, it could well be that HSF information (conveyed by the parvocellular pathway to the visual cortex) is predominantly processed in these areas, which are devoted to foveal vision. Similarly, since the peripheral retina is represented in progressively more anterior areas of the visual cortex, LSF information (conveyed by the magnocellular pathway to the visual cortex) might well be predominantly processed in these areas, which are devoted to peripheral vision.

5.1. Spatial frequency tuning in retinotopic visual areas

A large number of neurophysiological studies performed on cats [79, 80], primates [6, 81-84] and humans [16-18] have mapped representations of the different spatial frequencies in retinotopic areas. Using retinotopic encoding with achromatic sinusoidal gratings, Sasaki and collaborators [17] have, in particular, shown that LSF are mapped in occipital areas in accordance with the cortical representation of the peripheral visual field, whereas HSF are mapped in accordance with the central visual field. Other studies have demonstrated that

more complex cognitive functions, such as visual spatial attention, are also mapped consistently by cortical retinotopy [17, 85-89]. Using very large hierarchical visual stimuli in a block design fMRI study, Sasaki and collaborators [17] found evidence for retinotopic mapping of global and local attention in the occipital cortex. During “attend global” blocks, participants were required to deliberately focus their attention on the global form (at a visual angle of 29.4°) involving their peripheral vision, while during “attend local” blocks, they had to focus on local elements (at a visual angle of 2.4°), involving more foveal vision. fMRI data were analyzed using a traditional approach based on comparisons between local and global levels. Results showed that when attention was directed at local level (as opposed to global level), activation was consistent with the cortical representation of the fovea, which is also sensitive to HSF gratings. When attention was directed at global level (as opposed to local level), activation was consistent with the cortical representation of the periphery, which is also sensitive to LSF gratings.

The studies mentioned previously either postulate retinotopic processing of spatial frequencies [17], or demonstrate hemispheric specialization of spatial frequency processing in the occipital cortex [19, 20]. We conducted an fMRI study to reconcile the fact that spatial frequency processing could not only be retinotopically mapped, it could also be lateralized between both hemispheres.

5.2. How can retinotopy and cerebral asymmetries for spatial frequencies be reconciled?

The results obtained by Sasaki and collaborators [17] showed no hemispheric specialization for spatial frequency processing. However, the authors used a traditional method of data analysis, comparing global and local experimental conditions to one another, rather than the direct inter-hemispheric comparison method that we had used previously [20], and which had produced different results.

In a recent fMRI study, we used a categorization task (indoors vs. outdoors) of natural scenes filtered in LSF and HSF scenes, in order to evaluate, on the one hand the retinotopy, and on the other hand, functional lateralization in spatial frequency processing. With this aim in mind, we used larger scene images (at a visual angle of 24° × 18°) than in our previous studies (which used scenes with a visual angle of 4° × 4° [20, 21, 36, 43, 44, 70]), covering as broad a visual field as had Sasaki and collaborators [17]. We used a block-design fMRI paradigm, in which large LSF or HSF were displayed in separate experimental blocks. The retinotopy of spatial frequency processing was assessed using a traditional method of fMRI data analysis based on comparisons between LSF and HSF scene categorization. According to previous retinotopy studies, when processing spatial frequencies, the categorization of LSF scenes (compared to HSF) would recruit areas devoted to peripheral vision, whereas the categorization of HSF scenes (compared to LSF) would recruit areas devoted to foveal vision. Cerebral asymmetries were assessed using the inter-hemispheric comparison method. We expected a higher level of activation in right hemisphere than in the left during the processing of LSF, and more involvement of the left hemisphere during HSF processing.

Our results provided first of all evidence of retinotopic organization of spatial frequency processing in the human visual cortex. LSF (as opposed to HSF) scene categorization elicited medial occipital activation in the anterior half of the calcarine fissures in correspondence with the peripheral visual field, whereas HSF (as opposed to LSF) scene categorization elicited more lateral occipital activation in the posterior part of the occipital lobes in correspondence with the fovea, in accordance with retinotopic organization in visual areas (Figure 4a). By contrasting spatial frequency blocks to one another, we were, therefore, able to show that the processing of spatial frequencies is related to the organization of retinotopic eccentricity in the occipital cortex. In addition to the retinotopic activation obtained by contrasting spatial frequencies, cerebral asymmetries were also demonstrated. In order to identify cerebral asymmetries, we made direct comparisons between the two hemispheres by contrasting “unflipped” to “left-right flipped” functional images for each particular spatial frequency band (LSF and HSF). As expected from previous studies, and in accordance with our own previous results [20, 21], the inter-hemispheric method of comparison highlights occipital cortex predominance on the right (as opposed to on the left) for LSF scene categorization, and temporal cortex predominance on the left (as opposed to on the right) for HSF scene categorization (Figure 4b).

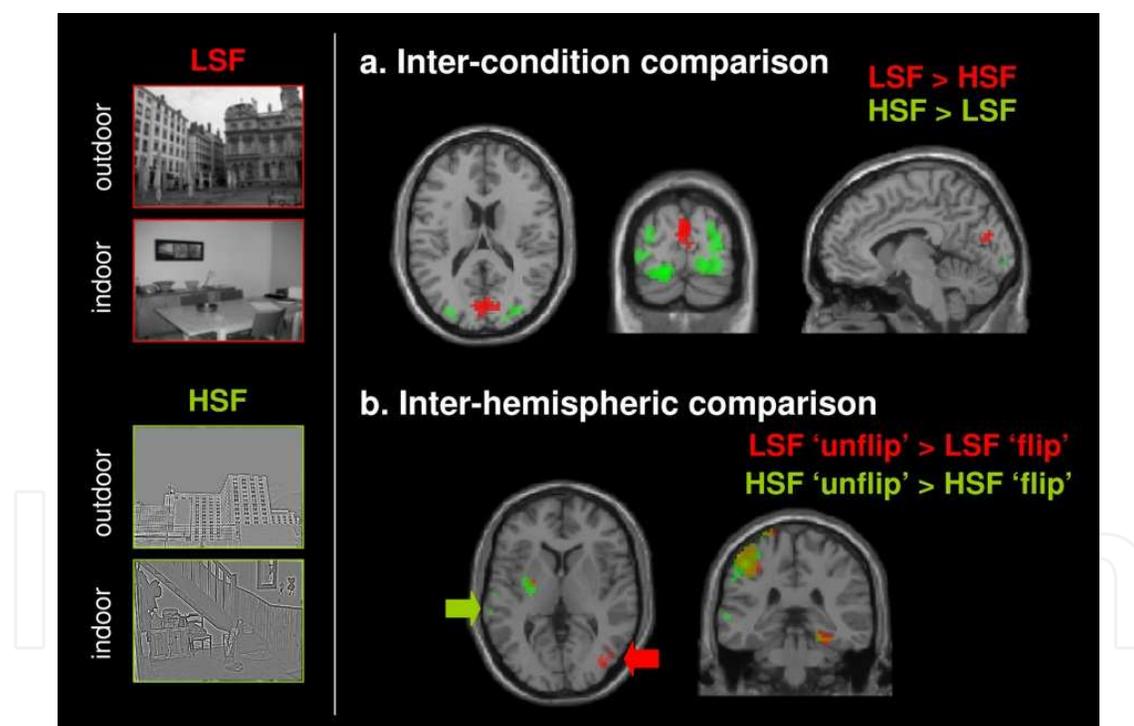


Figure 4. Retinotopic organization and hemispheric specialization of spatial frequency processing during scene perception

Using stimuli filtered in spatial frequencies covering a large part of the visual field, and depending on the method of data analysis used, we succeeded in showing that the processing of spatial frequencies is specifically organized in the visual areas of each hemisphere, as well as between the two hemispheres, according to functional lateralization. By using several different approaches on the same data, our results enabled us to reconcile

for the first time retinotopic and lateralized processing of spatial frequencies in the human occipital-temporal cortex.

In addition to neuroimaging studies on healthy subjects, patients with retinal disorders constitute pathological models which enable the specific investigation of retinotopic mapping of spatial frequency processing in the occipital cortex through the relationship between the position of the lesion on the retina and the processing of spatial frequencies. We specifically explored the relationship between central retinal lesions in age-related macular degeneration (AMD) patients and the processing of spatial frequencies during scene categorization.

5.3. Scene perception and spatial frequency processing in age-related macular degeneration

AMD, characterized by a central vision loss caused by the destruction of macular photoreceptors [90], is the primary cause of vision loss in the elderly population [91-93]. Owing to the central position of the retinal lesion, and the neurophysiology of the parvocellular and magnocellular pathways, AMD patients would be expected to be deficient in the categorization of HSF scenes compared to age-matched healthy participants. Many studies have demonstrated impairment of low-level visual processes in AMD patients (e.g., contrast sensitivity in gratings [94-96]). However, research on the ability of AMD patients to process and recognize complex visual stimuli filtered in LSF and HSF is scarce. Recent studies have shown impairment of scene perception in AMD patients [97-99]. In face perception tasks, AMD patients were able to identify facial emotions when the decision was thought to be based on LSF processing [100]. Perception of details in facial emotions, conveyed by HSF, was impaired. However, in this study, the HSF processing deficit was inferred rather than clearly demonstrated, because the spatial frequency content of faces was not manipulated explicitly. In order to test this assumption, we recently conducted behavioural experiments [101], in which AMD patients and healthy age-matched participants performed categorization tasks of large scene images (indoors vs. outdoors) filtered in LSF and HSF. The results showed that AMD patients made more non-responses and had longer reaction times for the categorization of HSF than for that of LSF scenes, whereas healthy participants' performance was not differentially affected by the spatial frequency content of scenes.

Furthermore, retinal lesions caused by AMD induce a lack of stimulation in the part of the visual cortex which is devoted to the processing of the central visual field, suggesting a reorganization of the human cortex. If HSF processing activates the foveal representation in the occipital cortex, the specific impairment of HSF processing in AMD may result in atypical occipital activation. Using our categorization task of LSF and HSF scenes under fMRI, we recently investigated the functional cerebral reorganization of spatial frequency processing in an AMD patient. The patient showed a deficit in the processing of HSF, linked with hypoactivation in the occipital cortex, compared to age-matched healthy participants (Figure 5). However, LSF processing was relatively similar in the AMD

patient and healthy participants, at both behavioural and neurobiological levels. The present findings point to a specific deficit in the processing of HSF information contained in photographs of natural scenes in AMD, linked with hypo-activation in the occipital cortex. LSF information processing was relatively well preserved. These results could also provide interesting perspectives for the diagnosis of AMD and monitoring of future treatments.



Figure 5. Hypoactivation in the occipital cortex during HSF scene perception in age-related macular degeneration (AMD)

6. Conclusion

Our findings demonstrate that LSF information may reach high-order areas rapidly to enable coarse initial parsing of the visual scene, which could then be retro-injected through feedback into the occipital cortex to guide a finer analysis based on HSF. Furthermore, spatial frequency processing may be retinotopically mapped and lateralized in the occipital cortex. Using stimuli filtered in spatial frequencies covering a large part of the visual field, and depending on the method of data analysis, we succeeded in showing that the processing of spatial frequencies is specifically organized in the visual areas of each hemisphere, as well as between the two hemispheres, according to functional lateralization. Critically, we provided evidence that a method of fMRI data analysis based on a direct inter-hemispheric comparison was more appropriate than the classical method of inter-condition comparison in the evaluation of hemispheric dominance. Using a method of inter-hemispheric comparison, we demonstrated greater activation in right occipital areas than in left during LSF scene perception, but greater activation in left than in right occipital areas during HSF scene perception, while the inter-condition comparison revealed retinotopic processing. HSF (compared to LSF) scenes activate the foveal representation in retinotopic areas of the occipital cortex, and LSF (compared to HSF) scenes activate more peripheral representations in the same cortical areas. Even if the hypothesis was not directly tested here, we suggest that retinotopic processing may result from bottom-up visual processes, while hemispheric specialization may be controlled by top-down attentional processes (in the temporo-parietal region). Finally, our findings indicate that in scene perception, the

predominantly coarse-to-fine analysis seems to be preferentially performed in the right hemisphere, from the occipital to the inferior temporal cortex.

Our findings also demonstrate that pathology constitutes an interesting way of investigating cognitive models of spatial frequency processing, both at behavioural and cerebral levels. Future studies conducted in patients with visual field defects (following peripheral or cerebral damage) are needed to fully investigate spatial frequency processing in the occipital cortex. Behavioural studies in hemianopic patients following occipital lobe damage would specifically allow the investigation of hemispheric specialization in spatial frequency processing. Categorization of LSF scenes ought to be more impaired in patients with left hemianopic (right occipital lesion), while categorization of HSF scenes ought to be more impaired in patients with right hemianopic (left occipital lesion). In a complementary way, studies conducted on patients with contrasting retinal diseases (e.g., AMD patients characterized by a central vision loss, and retinitis pigmentosa characterized by a peripheral vision loss) would allow further investigation of the retinotopic processing of spatial frequencies. We would expect to observe a differential reorganization of the occipital cortex depending on the retinal lesion site which mirrors the dissociation of the visual disorder in question. According to the retinotopy of spatial frequency processing, if HSF processing activates the foveal representation in the occipital cortex, a specific impairment of HSF processing in AMD may result in atypical activation in occipital areas corresponding to the fovea (compared to age-matched healthy participants). Similarly, a specific impairment of LSF processing in patients with retinitis pigmentosa may result in atypical activation in occipital areas corresponding to the periphery.

On the whole, the results obtained suggest that the occipital cortex could be the point of convergence of both afferent connections from the thalamus, and feedback connections from high-order visual areas. Coarse visual information would be rapidly forwarded to high level visual areas, more specifically to the frontal and temporo-parietal areas, via the magnocellular visual pathways. This information would provide the spatial and semantic characteristics required for the identification of the visual scene. Feedback connections from frontal and temporo-parietal areas to occipital areas might then modulate the processing of fine information, slowly conveyed by the parvocellular pathway. In the occipital cortex, the hemisphere preferentially involved in visual processing may depend on the spatial frequency band required in the task. In coarse-to-fine sequence processing, the right occipital cortex would in that case be more involved than the left. Visual information would then be sent through the right ventral visual stream, from occipital to infero-temporal areas. In tasks requiring the use of fine details, visual information would be sent preferentially through the left ventral visual stream. A more advanced analysis of the scene would be performed at the very end of the ventral visual stream (e.g., in the parahippocampal place area [102]). In addition, spatial frequencies in scenes were also retinotopically mapped in the occipital cortex. However, additional studies on the time course of activation induced by spatial frequencies are necessary to specify whether retinotopic and lateralized representations emerge from ascendant or descendant processes.

Author details

Carole Peyrin and Benoit Musel
Laboratoire de Psychologie et NeuroCognition, France

Acknowledgement

This work was supported by a research grant from the Fyssen Foundation to Carole Peyrin, by a doctoral fellowship from the Région Rhone-Alpes to Benoit Musel and by the National Centre for Scientific Research in France. The authors extend warm thanks to the "Délégation à la Recherche Clinique et à l'Innovation" of the University Hospital of Grenoble for sponsoring their work. We thank Catherine Dal Molin for the English revision of the manuscript.

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