



Hemispheric specialization of human inferior temporal cortex during coarse-to-fine and fine-to-coarse analysis of natural visual scenes

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Received 2 March 2005; revised 30 May 2005; accepted 1 June 2005

Recent models of visual recognition have suggested that perceptual analysis may start with a parallel extraction of different spatial frequencies (SF), using a preferential coarse-to-fine (low-to-high SF) sequence of processing. A rapid extraction of low spatial frequency (LSF) information may thus provide an initial and crude parsing of the visual scene, subsequently refined by slow but more detailed high spatial frequency (HSF) information. However, the sequence of SF analysis could be flexible, a high-to-low (HtL) being sometimes preferred to a low-to-high (LtH) SF sequence depending on task demands. Furthermore, it has also been suggested that the right vs. left hemisphere might be differentially specialized in LSF vs. HSF analysis, respectively. By manipulating the temporal succession of LSF and HSF stimuli, the present fMRI study investigated whether such hemispheric specialization may underlie the flexible use of different time-course in SF analysis. Participants performed a matching task between two successive images of natural scenes (LSF or HSF) that were displayed either in an LtH (LSF scene presented first and HSF scene second) or in a reverse HtL sequence. A direct inter-hemispheric comparison of the neural responses evoked by each SF sequence revealed greater activations within the right occipito-temporal cortex for the LtH sequence and within the left occipito-temporal cortex for the HtL sequence. These fMRI results suggest that the hemisphere preferentially engaged during the sequential processing of different SF might be determined by the initial SF-band appearing in this sequence, and that both a coarse-to-fine and fine-to-coarse analysis might independently take place in the two hemispheres.

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Keywords: Visual recognition; Natural scene; Spatial frequency; Cerebral asymmetry; Occipito-temporal cortex; Event-related fMRI; Coarse-to-fine; Fine-to-coarse

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Available online on ScienceDirect (www.sciencedirect.com).

Introduction

On the basis of convergent data from the functional neuroanatomy of magnocellular and parvocellular visual pathways (Van Essen and DeYoe, 1995), neurophysiological recordings in primates (Bullier, 2001), and psychophysical results in humans (Ginsburg, 1986; Hughes et al., 1996), several recent models of visual recognition (e.g., Bullier, 2001; Bar, 2003) have suggested that the visual analysis of a scene may start with a parallel extraction of different elementary attributes at different spatial scales (or spatial frequencies, SF), but with a predominant coarse-to-fine processing sequence. Accordingly, low spatial frequencies (LSF) in a visual scene might be conveyed by the fast magnocellular visual pathways and thus rapidly reach higher-order areas in the visual system, not only in parietal and frontal cortices (Bullier, 2001; Bar, 2003) but also in inferotemporal regions (Sugase et al., 1999), allowing an initial perceptual parsing of the visual scene. This first coarse analysis might then be refined by higher spatial frequency information (HSF) that is conveyed more slowly to the cerebral cortex by the parvocellular pathway.

Experimental evidence in support of a low-to-high SF processing hierarchy in human vision comes from psychophysical studies using global forms composed of several local elements (see Navon, 1977). Typically, the global information is identified faster than the local elements (global precedence effect), and global processing interferes with local processing (global interference effect). Together, these two behavioral effects suggest that global information is processed *before* local information. Based on the assumption that global information is preferentially conveyed by LSF whereas local information is conveyed by HSF (see Badcock et al., 1990; Hughes et al., 1996; Lamb and Yund, 1993; Schulman et al., 1986), the global-to-local processing sequence has been interpreted as reflecting a fundamental principle of low-to-high SF analysis. Additional evidence was provided by psychophysical studies of Schyns and

Oliva (1994) who used “hybrid” stimuli made of two superimposed images from natural scenes, belonging to different semantic categories and containing different SF-bands (e.g., a highway scene in LSF superimposed on a city scene in HSF). The perception of these hybrid scenes was dominated by LSF information when their presentation time was very brief (30 ms), but by HSF information when their presentation time was longer (150 ms), suggesting a precedence of LSF on HSF in the visual processing time-course. Furthermore, when two successive hybrids displayed a coarse-to-fine sequence for a given scene and simultaneously a fine-to-coarse sequence for another scene, scene perception was more frequently based on the coarse-to-fine than the fine-to-coarse sequence.

However, the fact that LSF information can be perceptually available before HSF 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 with simple experimental manipulations, e.g., by changing the visual angle (Kinchla and Wolfe, 1979; Lamb and Robertson, 1990) or the number of local elements (Martin, 1979). Furthermore, in a Schyns and Oliva (1994) study, a substantial proportion (29%) of hybrid sequences were in fact categorized according to a fine-to-coarse rather than a coarse-to-fine time-course, and subsequent studies (Oliva and Schyns, 1997) demonstrated that the spatial scale preferentially processed in hybrid scenes can be constrained by a previous sensitization phase implicitly “priming” the visual processing in favor of a particular spatial scale. Thus, after initial exposure to LSF information, the subsequent categorization of hybrid images was preferentially made on LSF cues, whereas it was biased toward HSF information after priming by HSF. When using hybrid faces instead of scenes, Schyns and Oliva (1999) also showed that HSF information was preferentially used to judge whether a face is expressive or not, whereas LSF information was preferentially used to classify expression in discrete categories. These findings suggest that the demands of a categorization task might determine which range of SF is extracted and perceived from hybrid visual stimuli (even when using brief presentation times, i.e., 45 ms). Taken together, these results suggest, first, that the low-to-high time-course of SF analysis may constitute a general default strategy, rather than a unique fixed process; and second, that the selection of SF during the recognition of natural scenes may depend on dynamic interactions between the information needs for a given recognition task and the perceptually available information. Whereas a low-to-high sequence of SF processing may preferentially arise for normal visual inputs containing both LSF and HSF information (see Bar, 2003), our visual system should nonetheless be able to prioritize the processing of HSF in certain situations, for instance, during search for a target known to be defined by specific local features rather than global visual properties (e.g., find something with a striped texture).

Importantly, in the framework of visual SF analysis, it has often been proposed that the right vs. left hemisphere might be predominantly involved in LSF vs. HSF processing, respectively. This hemispheric specialization has been supported by numerous behavioral studies in healthy subjects using lateralized presentation of visual stimuli (e.g., Blanca et al., 1994; Chokron et al., 2000; Christman et al., 1991; Kitterle and Selig, 1991; Kitterle et al., 1990, 1992; Martin, 1979; Peyrin et al., 2003; Sergent, 1982; Van Kleeck, 1989; Yovel et al., 2001), by functional neuroimaging studies in healthy subjects (e.g., Evans et al., 2000; Fink et al., 1996, 1997, 1999; Han et al., 2002; Heinze et al., 1998; Lux et al., 2004; Martinez et al., 1997; Proverbio et al., 1998; Yamaguchi et al., 2000), and by neuropsychological observations in brain-

damaged patients (e.g., Delis et al., 1986; Doyon and Milner, 1991; Lamb et al., 1990; Rafal and Robertson, 1995; Robertson and Lamb, 1991; Robertson et al., 1988). In a recent event-related fMRI study, we also found evidence for such hemispheric specialization during a visual recognition task using filtered natural scenes, presented either in LSF or HSF alone (Peyrin et al., 2004). In this previous study, hemispheric specialization was assessed by a method of direct inter-hemispheric comparison (see Baciú et al., in press; Iidaka et al., 2004; Lux et al., 2004), allowing us to examine contrasts between “unflipped” and “left–right flipped” functional images from the same experimental condition, in order to compare activity in one hemisphere with activity in homologous regions of the other hemisphere. Using this approach, we were able to demonstrate a greater activation in the right than the left occipito-temporal areas for LSF scenes, but greater activation in the left than the right middle occipital gyrus for HSF scenes.

In the present event-related fMRI experiment, we asked whether the hemispheric specialization for SF processing might underlie the flexibility of the temporal sequence used for SF analysis during visual recognition. To constrain the SF processing according to different time-courses, we presented healthy observers with two successive images of natural scenes (each filtered in either LSF or HSF) appearing in either a low-to-high (LtH, i.e., LSF scenes first and HSF scenes second) or a reverse high-to-low (HtL) sequence. Observers had to decide whether the two successive scenes belonged to the same category. This task ensured that participants attended to the whole SF sequence, and did not concentrate on one SF-filtered image only. In addition, the first image in each sequence was displayed either in the central visual field (CVF) or lateralized in either the left visual field (LVF) or the right visual field (RVF). This manipulation of the side of presentation allowed us to test whether the SF analysis in either type of sequence might be determined, or modulated, by the hemisphere to which the visual information was projected first; and also to include trials in which the two scenes within a sequence were not overlapped at the same location, thus preventing the use of simple retinotopic cues in the image for the matching task.

Our critical question was whether each type of stimulus sequence would engage one hemisphere more than the other, depending on the SF-band presented first and/or the visual hemifield stimulated first. When visual recognition is performed according to an LtH time-course, the initial LSF information might preferentially activate the right hemisphere (specialized for LSF analysis), such that this hemisphere might subsequently dominate during the processing of the whole visual sequence. Conversely, during HtL processing, the initial HSF information may first activate the left hemisphere (specialized for HSF analysis) and thus predominantly recruit this hemisphere in the processing of the whole stimulus sequence. Therefore, our main hypothesis was that right-hemisphere visual areas might show greater involvement during the LtH analysis, whereas left-hemisphere visual areas should preferentially contribute to the HtL analysis instead.

Method

Subjects

Fourteen healthy male volunteers (age range 20–38, mean age $27.7 \pm SD 5.7$) 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 according to the ethical regulation of the Geneva University Hospital. Our study was restricted to male participants in order to avoid sex differences in functional hemispheric asymmetries that could interfere with hemispheric specialization in SF processing (for a meta-analysis on gender differences in hemispheric lateralization, see Voyer, 1996).

Stimuli and procedure

Stimuli were 54 black-and-white photographs (256×256 pixels, 256 gray scales) of natural scene images classified in three distinct categories (18 cities, 18 beaches, and 18 indoors). Stimuli were displayed using E-prime software (E-prime Psychology Software Tools Inc., Pittsburgh, USA) and projected onto a mirror mounted on the MRI head coil ($\sim 15.2 \times 11.4$ degrees of visual angle). For each scene, an LSF and an HSF stimulus were created (Fig. 1). We removed the SF content of images above 4 cycles/degree of visual angle for LSF stimuli, and below 6 cycles/degree for HSF stimuli, by convolving gaussian filters to the Fourier transform of the original images. The average energy level for LSF and HSF stimuli was equalized for each scene, in order to avoid some biases due to contrast and luminance which are known to influence hemispheric differences in visual processing (e.g., Christman, 1989), and to minimize intrinsic visual differences between these two types of stimuli. Overall, averaged stimuli luminance did not differ between LSF and HSF stimuli (118 and 120, respectively, on a 256 gray-level scale, $F_{1,51} < 1$), or between cities, beaches, and indoors (116, 126, and 117, respectively, $F_{2,51} = 1.76$, $P = 0.18$).

One experimental trial consisted of an image sequence during which two natural scenes (in either LSF or HSF) were displayed in a rapid succession, following either an LtH or HtL sequence. In half of the trials, the two successive scenes in the sequence were

the same exemplar from the same category, but with inverse SF content, while in the other half of trials, the two successive scenes belonged to different categories. Note that the same/different image condition was orthogonal to our critical manipulation of SF sequence and not further considered in our analyses. More importantly, the first image in each sequence was displayed either at the center of the screen (central visual field, CVF), in the left visual field (LVF), or right visual field (RVF). This resulted in six experimental conditions (containing 36 trials each) of particular interest for the purposes of the current study: LtH-CVF (see Fig. 1, left panel), LtH-LVF, LtH-RVF (see Fig. 1, right panel), HtL-CVF, HtL-LVF (see Fig. 1, central panel), and HtL-RVF.

Each trial began with a central fixation point for 500 ms, immediately followed by the first filtered scene for 100 ms, then a new central fixation point reappeared for 400 ms, followed in turn by the second filtered scene for 100 ms. Note that since the two scene images appeared in brief succession over less than 600 ms, the resulting hemodynamic responses measured by fMRI were modeled as one single composite event in our analyses. The average inter-trial interval was 2 s. Onset of trials was jittered with respect to scan repetition ($TR = 2.5$ s) to allow for better sampling of the hemodynamic response across the whole brain (Josephs and Henson, 1999). Thirty-six null trials were also randomly intermixed with image sequence in order to provide an appropriate baseline measure (Friston et al., 1999).

Participants were asked to decide after the presentation of the second scene whether or not the two scenes were from the same category (city, beach, or indoor). They were instructed to fixate the center of the screen during the whole image sequence, and to respond as quickly and accurately as possible by pressing one of two response buttons. Half of the participants responded with their right index finger for ‘Same’ and right middle finger for ‘Different’, and vice versa for the other half. Reaction time (RT) and response accuracy were recorded. Each participant performed

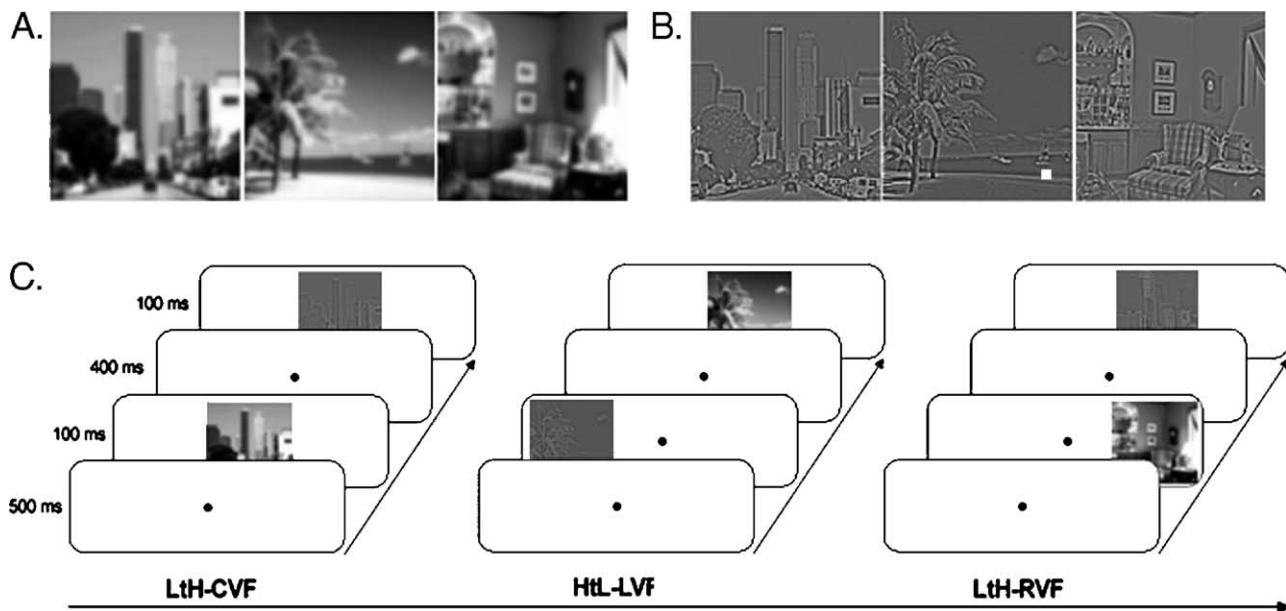


Fig. 1. Examples of stimuli used in the matching experiment ($N = 54$). Each image of a natural scene (either a city, a beach, or an indoor) was filtered in (A) low spatial frequencies (LSF, < 4 cycles/degree) and (B) high spatial frequencies (HSF, > 6 cycles/degree). (C) Each trial was composed of two successive filtered scenes presented either a low-to-high (LtH) or a high-to-low (HtL) sequence. In one experimental session, the first scene in the sequence was always presented in the central visual field (CVF); whereas it was pseudorandomly lateralized to either the left (LVF) or right visual field (RVF) in two other experimental sessions.

one session in which the first scene was always displayed in the center of the screen, and two lateralized sessions in which the first scene was randomly displayed either in the LVF or in the RVF. When lateralized, the inner and the outer edges of scenes subtended a visual angle of 2° and 6° off center, respectively. The order of the experimental trials was pseudorandom (i.e., no more than three consecutive trials of the same sequence type, or visual hemifield for lateralized sessions) and the order of the experimental sessions was counterbalanced across participants. Before the experiment, subjects underwent a training session outside the scanner, with different scene stimuli.

MR acquisition and data analysis

Whole-brain functional MR imaging was performed using echo planar imaging (EPI) on a 1.5-T whole-body INTERA system (Philips Medical Systems), equipped with a standard head coil configuration. The imaging volume was oriented parallel to the bi-commissural (AC–PC) plane. Functional volumes composed of thirty 4-mm adjacent, axial slices were acquired using a gradient echo-planar T2*-weighted sequence (TR = 2.5 s, TE = 40 ms, flip angle = 80°, matrix size = 128 × 128, FOV = 250 mm, in-plane voxel size = 2 × 2 mm). After discarding the four initial scans, a total of 180 scans were acquired for each participants in each experimental session (7.5 min each). Subsequent to the functional scans, a T1-weighted high-resolution three-dimensional volume (130 adjacent, axial slices, 1.25 mm thickness; in-plane voxel size = 1 × 1 mm) was acquired.

Data analysis was performed using the general linear model (Friston et al., 1995) for event-related designs in SPM2 (Wellcome Department of Imaging Neuroscience, London, UK, www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (Mathworks Inc., Sherborn, MA, USA). Individual scans were realigned, time-corrected, normalized to the MNI space and spatially smoothed by an 8-mm FWHM (Full Width at Half Maximum) Gaussian kernel. Time-series for each voxel were high-pass filtered (1/128 Hz cutoff) to remove low-frequency noise and signal drift.

To evaluate hemispheric asymmetries during LtH and HtL analyses, we used an approach allowing direct inter-hemispheric comparisons according to the following procedure (Peyrin et al., 2004; see also Baciú et al., in press; Iidaka et al., 2004; Lux et al., 2004). First, to avoid left–right morphological asymmetries that could bias our comparisons, a symmetrical template was built by averaging the standard EPI template provided by SPM and its mirror about the midsagittal plane, which was then used during the normalization of individual subject's data. Then, two sets of functional volumes were contrasted, one corresponding to the functional volumes in neurological convention (left is left) and the second set corresponding to the *same* functional volumes flipped 180° with respect to the midsagittal plane (left is right), such that the second set represented “mirror” images of the first set. These comparisons were performed both at the individual and group level, as described in more details below.

Six conditions of interest (LtH-CVF, LtH-LVF, LtH-RVF, HtL-CVF, HtL-LVF, and HtL-RVF) were modeled as 6 regressors convolved with a canonical hemodynamic response function (HRF) for both unflipped and flipped images normalized to the symmetric template. Movement parameters derived from realignment corrections (3 translations and 3 rotations) were also entered in the design matrix as additional factors of no interest. Two-stage random-effect analyses were performed. Individual contrasts were first created by

comparing unflipped and flipped images for each image-sequence condition, irrespective of the visual field of presentation of the first image: LtH_unflip > LtH_flip and HtL_unflip > HtL_flip contrasts. Thus, these contrasts allowed us to identify any cerebral regions more activated in one hemisphere than in the other during the processing of a particular image sequence. At the second random-effect level, linear contrasts from all individual subjects were analyzed using one-sample *t* tests. Clusters of activated voxels were then identified using an empirically defined threshold ($P < 0.005$ uncorrected, $T > 3.01$, cluster size ≥ 30 voxels), and all major peaks were significant at $P < 0.001$ (see Table 1). To facilitate comparisons with other studies, a transformation of MNI into Talairach and Tournoux (1988) coordinates was performed using the MNI2TAL function (created by Matthew Brett, available at <http://www.mrc-cbu.cam.ac.uk/Imaging>).

During fMRI scanning, eye position was monitored on-line on eight participants by an infrared eye-tracker (ASL Model 504, Applied Science Group). A repeated-measure ANOVA on mean eye position data recorded along the vertical axis during the first image of sequence (~100 ms period) showed no significant differences due to the visual field of the first image presentation (CVF, LVF, and RVF [$F_{2,14} < 1$, $P > 0.95$]).

Results

Behavioral results

Reaction times (RTs) for correct responses from eleven participants (data from 3 subjects were lost due to technical

Table 1

Hemispheric asymmetries during visual processing of low-to-high and high-to-low spatial frequency sequences

Area	Side	BA	<i>k</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>T</i>
<i>Low-to-high analysis</i>							
Primary motor cortex	L	4	401	−48	−20	59	6.85*
Opercular precentral gyrus	L	6	44	−48	0	6	6.25*
Inferior temporal gyrus	R	37	32	53	−53	−2	6.13*
Lingual gyrus	R	19/37	71	21	−56	−12	6.02*
Occipito-parietal junction	R	19/39	54	30	−68	34	5.22*
[Middle occipital gyrus]				21	−66	23	5.17*
[Inferior parietal lobule]				36	−71	39	3.44
<i>High-to-low analysis</i>							
Primary motor cortex	L	4	397	−48	−15	48	7.26*
Posterior cingular gyrus	R	30/23	35	6	−57	22	6.61*
Occipito-temporal junction	L	37/19	43	−39	−56	−5	6.25*
[Inferior temporal gyrus]			37	−45	−70	1	3.91*
[Middle occipital gyrus]			19	−48	−64	−4	3.84
Lingual and fusiform gyrus	R	19/37	121	24	−57	−15	5.62*
[Parahippocampal gyrus]				27	−42	−18	3.36
Occipito-parietal junction	R	19/39	50	33	−68	34	5.49*
[Middle occipital gyrus]				24	−66	25	4.21*
[Inferior parietal lobule]				36	−71	42	3.27
Pulvinar	L	−	36	−27	−6	−7	5.09*

For each cluster, the region showing the maximum *T* value is listed first, followed by the other sub-regions belonging to the same cluster [between brackets].

Abbreviations: R = right hemisphere; L = left hemisphere; BA = Brodmann area; *k* = number of voxels in the cluster.

* $P < 0.001$.

problems) were collapsed over the 3 experimental sessions and submitted to a repeated-measure analysis of variance (ANOVA) with Sequence (LtH vs. HtL), Visual Field of the first image in the sequence (LVF vs. CVF vs. RVF), and the Matching response (Same vs. Different) as within-subject factors. This ANOVA revealed only a significant main effect of the Matching response: RTs were faster for same than different images (same: $619 \text{ ms} \pm 68$; and different: $672 \text{ ms} \pm 75$, $F_{1,10} = 6.08$, $P < 0.04$). There was no main effect of the critical factors of Sequence (LtH: $650 \text{ ms} \pm 73$; and HtL: $640 \text{ ms} \pm 72$, $F_{1,10} = 1.79$, $P = 0.21$) or Visual Field, despite responses being slightly faster when the first scene was displayed centrally than lateralized (LVF: $659 \text{ ms} \pm 75$, CVF: $624 \text{ ms} \pm 59$ and RVF: $654 \text{ ms} \pm 82$, $F_{2,20} < 1$, $P > 0.44$). No other interaction was significant. The mean error rate was generally low ($<10\%$), without any main effect or interaction due to Sequence, Visual Field, or Matching [all $F_{2,20} = 2.56$, $P > 0.10$].

fMRI results

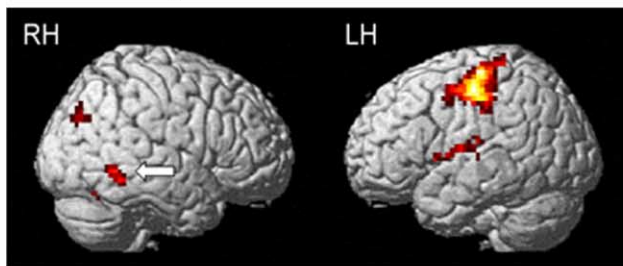
A direct inter-hemispheric comparison for the LtH and HtL sequences was done by contrasting LtH_unflip > LtH_flip and

HtL_unflip > HtL_flip, respectively. Such comparisons should identify any areas that were more activated in one hemisphere relative to the other during the same experimental conditions (high-to-low or low-to-high). Activated regions identified by these two contrasts between flip and unflip images are listed in Table 1 (the same results were obtained when including all 14 participants or after excluding the three subjects without behavioral data).

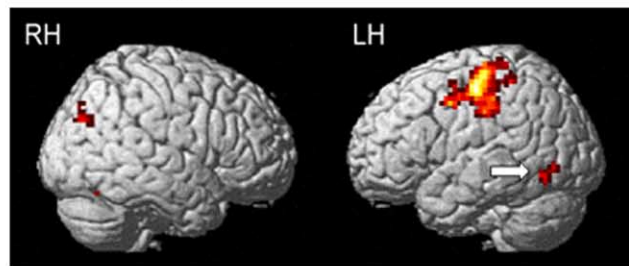
First, this direct comparison of the two hemispheres revealed significant asymmetries in the activation of several areas that arose irrespective of the type of visual sequence (LtH and HtL). Such asymmetries therefore probably reflect common processes engaged by the visual stimuli and the task demands in all conditions (see Fig. 2A). These common regions included the left primary motor cortex (BA 4), the right anterior lingual and fusiform gyrus (BA 19/37) extending into the posterior part of the right parahippocampal gyrus, as well as the right occipito-parietal junction (BA 19/39). These activations indicate functional hemispheric asymmetries during the task that were independent of the sequence of SF-filtered images.

More critically, additional hemispheric asymmetries that depended on the type of SF sequence arose selectively within

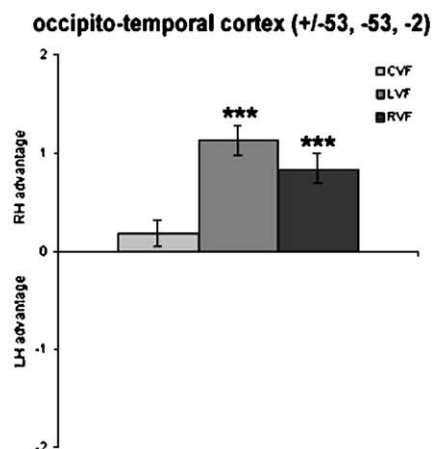
A. LtH sequences



B. HtL sequences



C. fMRI response - LtH



D. fMRI response - HtL

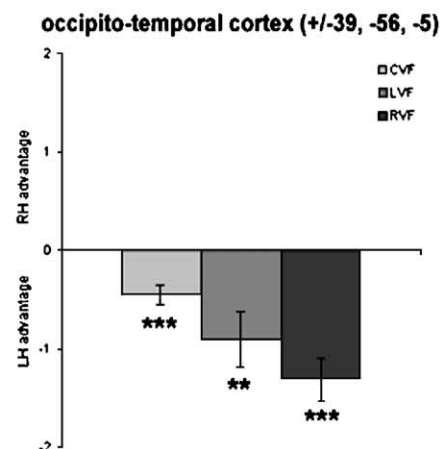


Fig. 2. Hemispheric asymmetries within the occipito-temporal cortex. During (A) the low-to-high (LtH) sequence of spatial-frequency analysis, left motor cortex, right occipito-parietal, and inferior temporal regions were more activated than homologous regions in the opposite hemisphere. (B) Similarly, during high-to-low (HtL) sequences, left motor cortex and right occipito-parietal regions also showed increased activity relative to homologous regions in the opposite hemisphere, while left occipito-temporal regions were selectively more activated in this condition. Therefore, some regions were more activated in the left or right hemisphere irrespective of the spatial-frequency sequence, while other regions were differentially activated in the left or right hemisphere as a function of the sequence type. (C and D) Difference (\pm SE) between the average parameter estimates of the fMRI responses calculated from unflipped and flipped functional images are shown for the occipito-temporal cortex activity in the right (C) and left (D) hemisphere. There was greater occipito-temporal activity in the right hemisphere during the LtH analysis (C), particularly when the first SF-filtered image was lateralized (but irrespective of visual hemifields); and greater activity in the left hemisphere during the HtL analysis (D), again irrespective of the visual hemifield of the first image.

occipito-temporal cortical areas (see Table 1). The right inferior temporal gyrus (BA 37, peak coordinates, x, y, z : 53, -53, -2, $T = 6.13$) was significantly more activated than its left homologue during the LtH sequence of processing (Fig. 2A). By contrast, left occipito-temporal regions (BA 37/19, x, y, z : -39, -56, -5, $T = 6.25$), including the inferior temporal gyrus and the middle occipital gyrus, were significantly more activated than their right homologue during the HtL analysis (Fig. 2B).

Parameter estimates of event-related responses were then extracted from the clusters activated during the LtH_unflip > LtH_flip contrast, as well as from those activated during the HtL_unflip > HtL_flip contrast, and these values were submitted to separate repeated-measure ANOVAs with Hemispheric Flip (unflipped vs. flipped side) and Visual Field of the first image in the sequence (LVF, RVF, or CVF) as within-subject factors.

First, we examined the parameter estimates from the (right) occipito-temporal cluster differentially activated during the LtH analysis. The ANOVA confirmed a main effect of Hemispheric Flip, indicating significantly greater activation of this occipito-temporal region on the right (unflipped) than on the left (flipped) side of the brain ($F_{1,13} = 48.22, P < 0.001$). There was no main effect of Visual Field ($F_{2,26} = 1.25, P > 0.30$). However, the Visual Field interacted with Hemispheric Flip ($F_{2,26} = 14.16, P < 0.001$). Planned comparisons between the flip and unflip brain sides for each visual field condition revealed a significant dominance of the right over the left side when the first scene was lateralized, irrespective of whether it projected to the LVF ($F_{1,13} = 53.36, P < 0.0001$) or to the RVF ($F_{1,13} = 28.86, P < 0.0002$), whereas this difference did not reach significance when images were presented centrally ($F_{1,13} = 1.86, P > 0.2$) (Fig. 2C). Despite the right hemisphere dominance being slightly stronger when the first scene was presented in the LVF than in the RVF (Fig. 2C), this difference did not reach significance (Hemispheric Flip \times LVF/RVF: $F_{1,13} = 2.73, P > 0.12$).

Second, we considered the (left) occipito-temporal activation found during the HtL analysis. The ANOVA confirmed a main effect of Hemispheric Flip, indicating a greater increase in this region within the left (unflipped) than within the right (flipped) brain side ($F_{1,13} = 8.04, P < 0.001$). There was also a main effect of Visual Field ($F_{2,26} = 8.04, P < 0.001$) due to the fact that the left occipito-temporal cortex was generally more activated when the first scene was lateralized rather than presented at the center of the screen ($F_{1,13} = 14.88, P < 0.0001$). Furthermore, Visual Field interacted with Hemispheric Flip ($F_{2,26} = 8.04, P < 0.002$). Planned comparisons showed that the left occipito-temporal cortex (unflipped brain images) was generally more activated when the first scene was lateralized than presented centrally ($F_{1,13} = 34.82, P < 0.001$), although overall the left side dominance was significant irrespective of the location of the first image in the sequence (LVF: $F_{1,13} = 10.22, P < 0.008$, CVF: $F_{1,13} = 19.92, P < 0.001$, RVF: $F_{1,13} = 37.03, P < 0.001$). Once again, even though the left hemisphere dominance appeared stronger when the first scene was presented in the contralateral RVF than in the ipsilateral LVF (Fig. 2D), this difference did not reach significance (Hemispheric Flip \times RVF/LVF: $F_{1,13} = 8.84, P > 0.07$). Taken together, these results clearly indicate that a differential activation arose in temporo-occipital region of the right or left hemisphere as a function of the SF sequence in visual stimuli, regardless of which visual field was initially stimulated at the time of the first image.

Finally, we also performed an ANOVA on parameters of activity from the (right) occipito-parietal junction activated in both

the LtH and HtL image sequence. This analysis showed a significant Hemispheric Flip \times Visual Field interaction (LtH: $F_{2,26} = 8.07, P < 0.002$; HtL: $F_{2,26} = 9.18, P < 0.001$), reflecting that activation of this region was higher in the right hemisphere when the first scene was lateralized rather than when it was presented centrally (LtH: $F_{1,13} = 6.46, P < 0.03$; HtL: $F_{1,13} = 8.04, P < 0.02$), but this effect was independent of the Visual field side (Hemispheric Flip \times RVF/LVF, all $F < 1$).

Discussion

Several models of visual recognition have proposed that a global analysis of visual stimuli may first take place based on coarse/LSF information in the image, preceding a more detailed local analysis based on fine/HSF processing (Bar, 2003; Bullier, 2001). This general framework is supported by psychophysical (Ginsburg, 1986; Hughes et al., 1996; Navon, 1977) and electrophysiological results (Livingstone and Hubel, 1988; Munk et al., 1995; Nowak et al., 1995), showing that LSF information can be processed faster and become perceptually available in the visual system before HSF information. We have also recently found both fMRI and EEG evidence suggesting greater activation of early visual areas and frontoparietal attentional networks when LSF visual inputs precede HSF inputs, relative to the reverse sequence (Peyrin et al., 2005). Importantly, because of this temporal precedence of LSF on HSF processing in the visual system, coarse-to-fine or low-to-high SF sequence might constitute the more efficient, and therefore the predominant sequence for processing visual inputs, particularly during very rapid recognition of visual stimuli (e.g., with natural scenes; Parker et al., 1992; Schyns and Oliva, 1994). Nevertheless, some psychophysical studies in humans have clearly shown that visual recognition is not always strictly constrained by these basic functional properties (for review, see Schyns and Oliva, 1997). The perceptual precedence of LSF on HSF information may not necessarily ensure that LSF information is used before HSF in order to perform a visual recognition or categorization task. Indeed, the sequence of spatial scale information processing has been found to be relatively flexible, depending on the demands of the current task.

Here, we hypothesized that this flexibility might be related to the distinct sensitivities of the right and the left hemispheres for processing different SF ranges. The present event-related fMRI study directly tested for hemispheric asymmetries during the analysis of different SF sequences involving images of natural scenes, displayed in either an LtH succession (where an LSF scene is presented first and an HSF scene second) or a reverse HtL succession (LSF is presented first and HSF scene second). To determine such hemispheric dominance during sequential SF processing, we used a method allowing a direct comparison of neural activity between homologous areas of the two hemispheres (Baciu et al., in press; Iidaka et al., 2004; Lux et al., 2004; Peyrin et al., 2004). Unlike traditional imaging analyses examining each hemisphere separately when contrasting two conditions of interest, here we compared activity within homologous areas of the two hemispheres on a voxel-by-voxel basis, by contrasting “unflipped” to “flipped” functional images of the brain for each experimental condition. Using this method, we observed a clear hemispheric dominance for the primary motor cortex, which was significantly more activated on the left than the right side/

hemisphere regardless of the SF sequence (LtH and HtL) of the visual stimuli. We expected such an asymmetry due to the motor response given by participants who used their right (dominant) hand across all stimulus conditions. This finding also demonstrates the reliability of our direct inter-hemispheric comparison in revealing asymmetric activations in homologous brain regions during the same condition.

Similarly, we observed increased activation of lingual and fusiform gyri in the right hemisphere (including the “lingual landmark area”, Aguirre et al., 1998) extending anteriorly into the adjacent right parahippocampal gyrus (including the “parahippocampal place area”, Epstein and Kanwisher, 1998), independent of the SF sequence. These areas have previously been reported to be involved in the recognition and categorization of natural visual scenes, as shown by several imaging studies (e.g., Aguirre et al., 1998; Epstein and Kanwisher, 1998; Fize et al., 2000; Maguire et al., 1998; Nakamura et al., 2000; Sato et al., 1999) and neuropsychological studies (Habib and Sirigu, 1987; Landis et al., 1986). Such activation of the right lingual and parahippocampal regions in the present study might therefore reflect the stimulus category and the task used here. More interestingly, these results provide new evidence for a significant hemispheric asymmetry of the lingual and parahippocampal gyri during natural scene perception, with clear dominance in the right hemisphere. Such asymmetry has previously been suggested based on neuropsychological data from brain-damaged patients (Habib and Sirigu, 1987; Landis et al., 1986). In addition, the occipito-parietal junction was also found to be more strongly activated in the right than the left hemisphere, during both the LtH and HtL stimulus conditions. This result might partly reflect some general demands of the current task, requiring category matches that could potentially bias subjects toward a global processing strategy (i.e., to extract the global spatial configuration of scenes), for which the right occipito-parietal junction might be specialized (Robertson et al., 1988). In addition, however, this activation was more pronounced when the first image was lateralized (irrespective of the visual hemifield side) rather than centrally presented. A right-dominant activation of the occipito-parietal junction might therefore also be consistent with classical hemispheric asymmetries in the control of visual attention (Heilman et al., 1993; Mesulam, 1985), and perhaps reflect the greater demands on spatial attention shifts in the matching task when the first image was lateralized.

Critically, using our direct inter-hemispheric comparison method, we could establish that the visual analysis of different image sequences was associated with differential hemispheric activation in posterior brain regions in the occipito-temporal cortex. These posterior inferior temporal regions are thought to be essential for visual recognition in both humans and monkeys (Grusser and Landis, 1991; Mishkin et al., 1983; Tanaka, 1996). Here, we found a greater activation of inferior temporal cortex in the right than left hemisphere during LtH visual analysis, but greater activation in the left than right hemisphere during HtL visual analysis. This double dissociation between the functional properties of homologous regions in each hemisphere is unlikely to reflect any primary structural asymmetries of the human brain, since all functional and structural MRI scans, flip and unflipped versions, were normalized to the same symmetrical brain template. Importantly, these differences could not be due to any differences in visual stimulation since our approach

involved a comparison of hemispheres during the same visual events. Taken together, our results therefore reveal a striking functional asymmetry in the human extrastriate cortex related to the temporal sequence of SF analysis during visual scene perception.

These results go beyond a simple main effect of LSF or HSF producing distinct hemispheric activations (e.g., Peyrin et al., 2004), since here hemispheric asymmetries were contingent on the SF content of the first image. This lateralization cannot be explained by a general preference for LSF in the right hemisphere, as opposed to a general preference for HSF in the left hemisphere, because the same (bilateral) amount of activation should then occur during all trials irrespective of the HSF/LSF or LSF/HSF combination of stimuli in the sequence. Rather, the hemispheric asymmetry probably resulted from cortical processes that took place during the first picture and then determined the subsequent dynamics of processing during the second picture.

Importantly, we could also demonstrate that this hemispheric specialization was not restricted to visual stimuli that were first presented to the contralateral visual hemifield, although functional asymmetries in temporal cortex were generally stronger when the first scene in the sequence was lateralized rather than centrally presented. This difference between central and peripheral presentation may be due to the fact that, when the two scenes were presented in the CVF, the matching task could be performed not only by explicit categorization of the scenes (i.e., as a distinct beach, city, or indoor scene), but also to some extent by more simple perceptual detection of overlapping features and contours in LSF and HSF information. Using such a perceptual strategy on some trials with CVF presentations could explain why the hemispheric dominance was generally weaker in temporal cortical areas involved in visual recognition.

Our fMRI results therefore indicate that the hemisphere functionally specialized for processing a visual sequence of different SF inputs is the same hemisphere that is specialized for processing the first SF-band appearing in this sequence (i.e., right hemispheric dominance for LtH, but also for LSF information analysis when presented alone; and conversely, left hemispheric dominance for HtL, but also for HSF information analysis alone). This pattern suggests that the hemisphere mainly involved in the analysis of a specific SF sequence might be selected, or pre-activated, by the first SF-band extracted from this sequence. Furthermore, even though there was a trend for these hemispheric dominances to be strongest when the first image was presented in the contralateral visual hemifield, specific ANOVAs conducted on parameter estimates of activity in these regions showed that the hemispheric dominance did not significantly differ between trials where the first scene was presented to the LVF or RVF, suggesting that these hemispheric asymmetries were not simply produced by a pre-activation based on contralateral peripheral inputs. These data converge with other recent evidence from neuroimaging studies indicating that visual information may be preferentially processed by specialized networks in one hemisphere irrespective of the visual field of presentation. For example, in an fMRI study using hierarchical shapes as stimuli, Lux et al. (2004) showed stronger activation of the right occipital cortex when global information was projected to the opposite left hemisphere (in the RVF) and in the left occipital cortex when local information was projected to the right hemisphere (in the LVF). Similarly, in a recent ERPs study using LAURA for

distributed linear source estimation of cerebral activations (see Michel et al., 2004), Ortigue et al. (2004) showed a selective right occipital cortex activation at early latencies when emotional words were projected to the opposite left hemisphere (in the RVF). Taken together, these data suggest that visual information may be rapidly transferred across hemispheres for preferential processing in specialized cortical areas. Some electrophysiological data have already provided evidence for such fast transfer of information to the specialized hemisphere when initially projected to the non-specialized hemisphere (Nowicka et al., 1996). In keeping with these data, our new findings suggest that SF information might be rapidly transferred from the non-specialized to the specialized hemisphere when the temporal sequence of visual analysis begins with an SF-band initially presented to the non-specialized hemisphere (i.e., from the left to the right hemisphere when LSF information is presented in the RVF first, and from the right to the left when HSF information is presented in the LVF).

In conclusion, our study provides new insights into previous controversies concerning which information in the visual field is processed first—the whole (e.g., LSF information) or its parts (e.g., HSF information). Our novel findings of hemispheric specialization within the ventral extrastriate areas suggest that, during a visual classification task, either type of SF information might be processed prior to the other in different regions of the human brain. We therefore conclude that both types of sequence processing may coexist in the visual system, but each predominate in different hemispheres. The “whole” (i.e., LSF) seems preferentially processed before the “parts” (i.e., HSF) in the right hemisphere, whereas the parts seem preferentially processed before the whole in the left hemisphere. It remains to be determined whether these different sequences of visual analysis can be performed in parallel, and how they may vary as a function of the type of stimuli and for different task purposes. Finally, this study has important implications for models of visual recognition. Our findings indicate that the visual system might be equipped with two cortical apparatus that can differentially and flexibly support visual recognition according to task demands or input sequence, one in the right occipito-temporal cortex prioritizing low SF analysis and the other in the left occipito-temporal junction prioritizing high SF analysis.

Acknowledgments

This research was funded by a fellowship from the Fondation Fyssen awarded to CP, by the National Centre for Scientific Research in France, by research grants from the Swiss National Science Foundation to PV (632-65935) and to SS (3100-AO-102133), and by donations from the Fondation De Reuter in Geneva for eye-tracking equipments.

References

- Aguirre, G.K., Zarahn, E., D'Esposito, M., 1998. An area within human ventral cortex sensitive to “building” stimuli: evidence and implications. *Neuron* 21, 373–383.
- Baciu, M., Juphard, A., Cousin, E., Le Bas, J.F., in press. Evaluating fMRI methods for assessing hemispheric language dominance in healthy subjects. *Eur. J. Radiol.*
- Badcock, J.C., Whitworth, F.A., Badcock, D.R., Lovegrove, W.J., 1990. Low frequency filtering and the processing of local–global stimuli. *Perception* 19, 617–629.
- Bar, M., 2003. A cortical mechanism for triggering top–down facilitation in visual object recognition. *J. Cogn. Neurosci.* 15, 600–609.
- Blanca, M.J., Zalabardo, C., Gari-Criado, F., Siles, R., 1994. Hemispheric differences in global and local processing dependant on exposure duration. *Neuropsychologia* 32, 1343–1351.
- Bullier, J., 2001. Integrated model of visual processing. *Brain Res. Brain Res. Rev.* 36, 96–107.
- Chokron, S., Brickman, A.M., Wei, T., Buchsbaum, M.S., 2000. Hemispheric asymmetry for selective attention. *Brain Res. Cogn. Brain Res.* 9, 85–90.
- Christman, S., 1989. Perceptual characteristics in visual laterality research. *Brain Cogn.* 11, 238–257.
- Christman, S., Kitterle, F.L., Hellige, J., 1991. Hemispheric asymmetry in the processing of absolute versus relative spatial frequency. *Brain Cogn.* 16, 62–73.
- Delis, D.C., Robertson, L.C., Efron, R., 1986. Hemispheric specialization of memory for visual hierarchical stimuli. *Neuropsychologia* 24, 205–214.
- Doyon, J., Milner, B., 1991. Right temporal-lobe contribution to global visual processing. *Neuropsychologia* 29, 343–360.
- Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. *Nature* 392, 598–601.
- Evans, M.A., Shedden, J.M., Hevenor, S.J., Hahn, M.C., 2000. The effect of variability of unattended information on global and local processing: evidence for lateralization at early stages of processing. *Neuropsychologia* 38, 225–239.
- Fink, G.R., Halligan, P.W., Marshall, J.C., Frith, C.D., Frackowiak, R.S., Dolan, R.J., 1996. Where in the brain does visual attention select the forest and the trees? *Nature* 382, 626–628.
- Fink, G.R., Halligan, P.W., Marshall, J.C., Frith, C.D., Frackowiak, R.S., Dolan, R.J., 1997. Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. *Brain* 120, 1779–1791.
- Fink, G.R., Marshall, J.C., Halligan, P.W., Dolan, R.J., 1999. Hemispheric asymmetries in global/local processing are modulated by perceptual salience. *Neuropsychologia* 37, 31–40.
- Fize, D., Boulanouar, K., Chatel, Y., Ranjeva, J.P., Fabre-Thorpe, M., Thorpe, S., 2000. Brain areas involved in rapid categorization of natural images: an event-related fMRI study. *NeuroImage* 11, 634–643.
- Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.P., Frith, C.D., Frackowiack, R.S., 1995. Statistical parametric maps in functional imaging: a general linear approach. *Hum. Brain Mapp.* 2, 189–210.
- Friston, K.J., Zarahn, E., Josephs, O., Henson, R.N., Dale, A.M., 1999. Stochastic designs in event-related fMRI. *NeuroImage* 10, 607–619.
- Ginsburg, A.P., 1986. Spatial filtering and visual form perception. In: Boff, K., Kaumann, L., Thomas, J. (Eds.), *Handbook of Perception and Human Performance*. Wiley, New York, pp. 1–41.
- Grusser, O., Landis, T., 1991. *Visual Agnosia and Other Disturbances of Visual Perception and Cognition*. MacMillan Press, London.
- Habib, M., Sirigu, A., 1987. Pure topographical disorientation: a definition and anatomical basis. *Cortex* 23, 73–85.
- Han, S., Weaver, J.A., Murray, S.O., Kang, X., Yund, E.W., Woods, D.L., 2002. Hemispheric asymmetry in global/local processing: effects of stimulus position and spatial frequency. *NeuroImage* 17, 1290–1299.
- Heilman, K.M., Watson, R.T., Valenstein, E., 1993. Neglect and related disorders. In: Heilman, K.M., Valenstein, E. (Eds.), *Clinical Neuropsychology*, 3rd ed. Oxford Univ. Press, New York, pp. 279–336.
- Heinze, H.J., Hinrichs, H., Scholz, M., Burchert, W., Mangun, G.R., 1998. Neural mechanisms of global and local processing. A combined PET and ERP study. *J. Cogn. Neurosci.* 10, 485–498.

- Hughes, H.C., Nozawa, G., Kitterle, F.L., 1996. Global precedence, spatial frequency channels, and the statistic of the natural image. *J. Cogn. Neurosci.* 8, 197–230.
- Iidaka, T., Yamashita, K., Kashikura, K., Yonekura, Y., 2004. Spatial frequency of visual image modulates neural responses in the temporoparietal lobe. An investigation with event-related fMRI. *Brain Res. Cogn. Brain Res.* 18, 196–204.
- Josephs, O., Henson, R.N., 1999. Event-related functional magnetic resonance imaging: modelling, inference and optimization. *Philos. Trans. R. Soc. Lond., Ser. B Biol. Sci.* 354, 1215–1228.
- Kinchla, R.A., Wolfe, J.M., 1979. The order of visual processing: “top-down,” “bottom-up”, or “middle-out”. *Percept. Psychophys.* 25, 225–231.
- Kitterle, F.L., Selig, L.M., 1991. Visual field effects in the discrimination of sine-wave gratings. *Percept. Psychophys.* 50, 15–18.
- Kitterle, F.L., Christman, S., Hellige, J.B., 1990. Hemispheric differences are found in the identification, but not the detection, of low versus high spatial frequencies. *Percept. Psychophys.* 48, 297–306.
- Kitterle, F.L., Hellige, J.B., Christman, S., 1992. Visual hemispheric asymmetries depend on which spatial frequencies are task relevant. *Brain Cogn.* 20, 308–314.
- Lamb, M.R., Robertson, L.C., 1990. The effect of visual angle on global and local reaction times depends on the set of visual angles presented. *Percept. Psychophys.* 47, 489–496.
- Lamb, M.R., Yund, E.W., 1993. The role of spatial frequency in the processing of hierarchically organized stimuli. *Percept. Psychophys.* 54, 773–784.
- Lamb, M.R., Robertson, L.C., Knight, R.T., 1990. Component mechanisms underlying the processing of hierarchically organized patterns: inferences from patients with unilateral cortical lesions. *J. Exp. Psychol. Hum. Percept. Perform.* 16, 471–483.
- Landis, T., Cummings, J.L., Benson, D.F., Palmer, E.P., 1986. Loss of topographic familiarity. An environmental agnosia. *Arch. Neurol.* 43, 132–136.
- Livingstone, M., Hubel, D., 1988. Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science* 240, 740–749.
- Lux, S., Marshall, J.C., Ritzl, A., Weiss, P.H., Pietrzyk, U., Shah, N.J., Zilles, K., Fink, G.R., 2004. A functional magnetic resonance imaging study of local/global processing with stimulus presentation in the peripheral visual hemifields. *Neuroscience* 124, 113–120.
- Maguire, E.A., Burgess, N., Donnett, J.G., Frackowiak, R.S., Frith, C.D., O’Keefe, J., 1998. Knowing where and getting there: a human navigation network. *Science* 280, 921–924.
- Martin, M., 1979. Hemispheric specialization for local and global processing. *Neuropsychologia* 17, 33–40.
- Martinez, A., Moses, P., Frank, L., Buxton, R., Wong, E., Stiles, J., 1997. Hemispheric asymmetries in global and local processing: evidence from fMRI. *NeuroReport* 8, 1685–1689.
- Mesulam, M.M., 1985. Attention, confusional states and neglect. In: Mesulam, M.M. (Ed.), *Principles of Behavior Neurology*. F.A. Davis, Philadelphia, pp. 125–168.
- Michel, C.M., Murray, M.M., Lantz, G., Gonzales, S., Spinelli, L., Grave de Peralta, R., 2004. EEG source imaging. *Clin. Neurophysiol.* 115, 2195–2222.
- Mishkin, M., Ungerleider, L.G., Macko, K.A., 1983. Object vision and spatial vision: two cortical pathways. *Trends Neurosci.* 6, 414–417.
- Munk, M.H., Nowak, L.G., Girard, P., Chouinamountri, N., Bullier, J., 1995. Visual latencies in cytochrome oxidase bands of macaque area V2. *Proc. Natl. Acad. Sci. U. S. A.* 92, 988–992.
- Nakamura, K., Kawashima, R., Sato, N., Nakamura, A., Sugiura, M., Kato, T., et al., 2000. Functional delineation of the human occipitotemporal areas to face and scene processing. A pet study. *Brain* 123, 1903–1912.
- Navon, D., 1977. Forest before trees: the precedence of global features in visual perception. *Cogn. Psychol.* 9, 353–383.
- Nowak, L.G., Munk, M.H., Girard, P., Bullier, J., 1995. Visual latencies in areas V1 and V2 of the macaque monkey. *Vis. Neurosci.* 12, 371–384.
- Nowicka, A., Grabowska, A., Fersten, E., 1996. Interhemispheric transmission of information and functional asymmetry of the human brain. *Neuropsychologia* 34, 147–151.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Oliva, A., Schyns, P.G., 1997. Coarse blobs or fine edges? Evidence that information diagnosticity changes the perception of complex visual stimuli. *Cogn. Psychol.* 34, 72–107.
- Ortigue, S., Michel, C.M., Murray, M.M., Mohr, C., Carbonnel, S., Landis, T., 2004. Electrical neuroimaging reveals early generator modulation to emotional words. *NeuroImage* 21, 1242–1251.
- Parker, D.M., Lishman, J.R., Hughes, J.C., 1992. Temporal integration of spatial filtered visual images. *Perception* 21, 147–160.
- Peyrin, C., Chauvin, A., Chokron, S., Marendaz, C., 2003. Hemispheric specialization for spatial frequency processing in the analysis of natural scenes. *Brain Cogn.* 53, 278–282.
- Peyrin, C., Baciuc, M., Segebarth, C., Marendaz, C., 2004. Cerebral regions and hemispheric specialization for processing spatial frequencies during natural scene recognition. An event-related fMRI study. *NeuroImage* 23, 697–706.
- Peyrin, C., Michel, C., Schwartz, S., Thut, G., Seghier, M., Ortigue, S., Landis, T., Vuilleumier, P., 2005. Effects of low-spatial frequency components during visual natural scene processing: a combined fMRI and ERP study. Annual Meeting of the Cognitive Neuroscience Society, New York, USA.
- Proverbio, A.M., Minniti, A., Zani, A., 1998. Electrophysiological evidence of a perceptual precedence of global vs. local visual information. *Brain Res. Cogn. Brain Res.* 6, 321–334.
- Rafal, R.T., Robertson, L., 1995. The neurology of visual attention. In: Gazzaniga, M.S. (Ed.), *The Cognitive Neurosciences*. MIT Press, Cambridge, MA, pp. 625–648.
- Robertson, L.C., Lamb, M.R., 1991. Neuropsychological contributions to theories of part/whole organization. *Cogn. Psychol.* 23, 299–330.
- Robertson, L.C., Lamb, M.R., Knight, R.T., 1988. Effects of lesions of temporal-parietal junction on perceptual and attentional processing in humans. *J. Cogn. Neurosci.* 8, 3757–3769.
- Sato, N., Nakamura, K., Nakamura, A., Sugiura, M., Ito, K., Fukuda, H., et al., 1999. Different time course between scene processing and face processing: a MEG study. *NeuroReport* 10, 3633–3637.
- Schulman, G., Sullivan, M., Gisch, K., Sadoka, W., 1986. The role of spatial frequency channels in the perception of local and global structure. *Perception* 15, 259–273.
- Schyns, P.G., Oliva, A., 1994. From blobs to boundary edges: evidence for time- and spatial-scale-dependant scene recognition. *Psychol. Sci.* 5, 195–200.
- Schyns, P.G., Oliva, A., 1997. Flexible, diagnosticity-driven, rather than fixed, perceptually determined scale selection in scene and face recognition. *Perception* 26, 1027–1038.
- Schyns, P.G., Oliva, A., 1999. Dr. Angry and Mr. Smile: when categorization flexibly modifies the perception of faces in rapid visual presentations. *Cognition* 69, 243–265.
- Sergent, J., 1982. The cerebral balance of power: confrontation or cooperation? *J. Exp. Psychol. Hum. Percept. Perform.* 8, 253–272.
- Sugase, Y., Yamane, S., Ueno, S., Kawano, K., 1999. Global and fine information coded by single neurons in the temporal visual cortex. *Nature* 400, 869–873.
- Talairach, J., Tournoux, P., 1988. *Co-Planar Stereotaxic Atlas of the Human Brain. 3-Dimensional Proportional System: An Approach to Cerebral Imaging*. Thieme, New York.
- Tanaka, K., 1996. Inferotemporal cortex and object vision. *Annu. Rev. Neurosci.* 19, 109–139.
- Van Essen, D.C., DeYoe, E.A., 1995. Concurrent processing in the primate visual cortex. In: Gazzaniga, M.S. (Ed.), *The Cognitive Neurosciences*. MIT Press, Cambridge, MA, pp. 383–400.

- Van Kleeck, M.H., 1989. Hemispheric differences in global versus local processing of hierarchical visual stimuli by normal subjects: new data and a meta-analysis of previous studies. *Neuropsychologia* 27, 1165–1178.
- Voyer, D., 1996. On the magnitude of laterality effects and sex differences in functional lateralities. *Laterality* 1, 51–83.
- Yamaguchi, S., Yamagata, S., Kobayashi, S., 2000. Cerebral asymmetry of the “top–down” allocation of attention to global and local features. *J. Neurosci.* 20, RC72.
- Yovel, G., Yovel, I., Levy, J., 2001. Hemispheric asymmetries for global and local visual perception: effects of stimulus and task factors. *J. Exp. Psychol. Hum. Percept. Perform.* 27, 1369–1385.