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Hemispheric specialization for spatial frequency processing in the analysis of natural scenes

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Abstract

Experimental data coming from visual cognitive sciences suggest that visual analysis starts with a parallel extraction of different visual attributes at different scales/frequencies. Neuropsychological and functional imagery data have suggested that each hemisphere (at the level of temporo–parietal junctions—TPJ) could play a key role in spatial frequency processing: The right TPJ should predominantly be involved in low spatial frequency (LFs) analysis and the left TPJ in high spatial frequency (HFs) analysis. Nevertheless, this functional hypothesis had been inferred from data obtained when using the hierarchical form paradigm, without any explicit spatial frequency manipulation per se. The aims of this research are (i) to investigate, in healthy subjects, the hemispheric asymmetry hypothesis with an explicit manipulation of spatial frequencies of natural scenes and (ii) to examine whether the 'precedence effect' (the relative rapidity of LFs and HFs processing) depends on the visual field of scene presentation or not. For this purpose, participants were to identify either non-filtered or LFs and HFs filtered target scene displayed either in the left, central, or right visual field. Results showed a hemispheric specialization for spatial frequency processing and different 'precedence effects' depending on the visual field of presentation.

1. Introduction

Experimental data from psychophysics (Ginsburg, 1986), functional neuro-anatomy of magnocellular and parvocellular pathways (Van Essen & DeYoe, 1995) and ultra-rapid categorizations in humans and monkeys (Fabre-Thorpe, Richard, & Thorpe, 1998) confirm the idea that visual analysis starts with a parallel extraction of different elementary visual attributes at different spatial scales or frequencies, with a coarse to fine processing design. According to this design, a rapid extraction of low spatial frequencies (LFs) should provide a global outlook of a stimulus structure, thus allowing an initial perceptual categorization. This perceptual categorization should be refined, confirmed, or infirmed by the information conveyed by high spatial frequencies (HFs) whose extraction takes place later (Ginsburg, 1986; Hughes, Nozawa, & Kitterle, 1996; Schyns & Oliva, 1994). Moreover, behavioural and functional imagery studies conducted on healthy subjects as well as neuropsychological experiments indicated that there could be a hemispheric asymmetry for low and high spatial frequency processing (Fink et al., 1996; Fink, Marshall, Halligan, & Dolan, 2000; Fink et al., 1997; Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Mangun, Heinze, Scholz, & Hinrichs, 2000; Martinez et al., 1999; Robertson, Lamb, & Knight, 1988; Sergent, 1982; Wilkinson, Halligan, Marshall, Büchel, & Dolan, 2001; Yamaguchi, Yamagata, & Kobayashi, 2000) with a left hemisphere (LH) advantage for HFs processing and a right hemisphere (RH) superiority for LFs processing. However this hemispheric asymmetry was more inferred than clearly demonstrated, none of theses studies (except Kitterle's psychophysical experiments; Kitterle, Christman, & Hellige, 1990; Kitterle, Hellige, & Christman, 1992) explicitly manipulating the spatial frequencies of stimuli. The main aim of this research was to investigate this functional hypothesis in healthy subjects by directly manipulating the spatial frequencies during a natural scene categorization task.

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1.1. Hierarchical forms and hemispheric asymmetry: The TPJ hypothesis

Indeed, most of the experimental data dealing with the hypothesis of a hemispheric specialization for spatial frequencies have used hierarchical forms as stimuli (Kinchla, 1974). Usually, these forms represent a large global letter form constructed by small local letters. The subject's task is to identify a target letter either at the global level, at the 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, inconsistent global information slows down local information identification, but local information identification has no effect on global identification; this asymmetrical effect is called 'global interference' effect. However, these effects decrease or even vanish when the hierarchical forms are high-pass filtered (i.e., LFs are cut-off) or are affected by a subject's adaptation to a given frequency band (low vs high) suggesting that LFs should carry global information whereas HFs should carry local information (Badcock, Whitworth, Badcock, & Lovegrove, 1990; Lamb & Yund, 1993; Schulman, Sulivan, Gisch, & Sadoka, 1986). According to the global/local and LFs/HFs relationship, many authors have used the hierarchical forms paradigm to study the pattern of hemispheric specialization for spatial frequencies. Along these lines, a hemispheric specialization observed in the global vs local processing of hierarchical forms is interpreted as a hemispheric specialization pattern for low vs high spatial frequency processing. Among behavioural studies using lateralized hierarchical forms, Sergent's experiments (Sergent, 1982) clearly demonstrated that the right visual field/left hemisphere (RVF/LH) is specialized in local/HFs processing, whereas the left visual field/right hemisphere (LVF/RH) is specialized in global/LFs processing. Subsequently, neuropsychological and functional imagery data (obtained with the same paradigm) have suggested that a critical cerebral area could play a key role in spatial frequency processing: The temporo–parietal junction (TPJ). Whereas the left TPJ should predominantly be involved in the analysis of HFs, the right TPJ seems mainly involved in the analysis of LFs. For instance, Robertson et al. (1988) showed that unilateral damage of this critical brain area could impair patients' performance in the hierarchical form paradigm. Patients with a left superior temporal gyrus lesion thus exhibited a slowing down in the local form identification whereas patients with a lesion centred in the right temporo–parietal region were impaired during the global form identification. These data suggest the involvement of two independent perceptual sub-systems, the right TPJ which emphasises global information and the left TPJ which emphasises local information. Moreover, this study revealed an attentional cortical mechanism which exerts control over the perceptual processes involved in global and local processing. This mechanism should operate on the attentional selection of information presented either at the global level, at the local level, or at both levels according to task constraints. This mechanism should be located in the left and right parietal lobule (Wilkinson et al., 2001). Several functional imagery data corroborate the existence of such attentional processes located in the TPJ (Fink et al., 1996, 1997, 2000; Heinze et al., 1998; Mangun et al., 2000; Martinez et al., 1999; Robertson et al., 1988; Wilkinson et al., 2001; Yamaguchi et al., 2000).

1.2. Natural scenes

However, as mentioned above, the hemispheric specialization hypothesis for spatial frequency processing has been widely inferred rather than empirically demonstrated. Moreover, the relationship between local and global information and spatial frequencies within hierarchical forms is far from univocal (Palmer, 1993): For example, global information could be conveyed by not only LFs but also by HFs. For this reason, it seems necessary to test the hypothesis of a hemispheric asymmetry of spatial frequency processing by an explicit change in the spatial frequency spectrum of stimuli. The hierarchical forms do not allow such manipulation because a low-pass filtering cancels the local form rendering the task impossible to be carried out. For this reason, in the present research, we have substituted hierarchical forms by natural scenes. The relevance of this kind of stimuli for such a study is multiple: Besides their ecological nature, scenes may not only be visually recognised in many frequency bands (i.e., whatever the type of filtering—low-pass, high pass, or pass-band) but, as shown by neuromimetic simulations (Hérault, Oliva, & Guérin-Dugué, 1997), scenes may also be perceptually categorized by using a Fourier transformation.

To sum up, the aims of the present research were (i) to test the hypothesis of a hemispheric specialization for spatial frequency processing by manipulating the spatial frequency components of natural scenes and (ii) to investigate if natural scenes could produce a similar 'precedence effect' as the one reported with hierarchical letters.

2. Method

2.1. Participants

Ten right-handed male undergraduate students of Psychology from the Université Pierre Mendès-France in Grenoble participated in the experiments for course credit. All participants had normal or corrected-

Fig. 1. Natural scenes with different spatial frequency components. From left to right a non-filtered city, a LFs filtered city, a HFs filtered city, a non-filtered highway, a LFs filtered highway, and a HFs filtered highway.

to-normal vision and they were not aware of the purpose of the experiments.

2.2. Stimuli

Stimuli displays consisted of two scenes belonging to different perceptual/semantic categories (either a city or a highway). These scenes had similar dominant orientations so that their identification could not made on the basis of this information. Scenes were black and white square pictures of 256 grey-scales sized 256 per 256 pixels. Their angular size was of 4° per visual angle. Scenes were either non-filtered, or filtered either in LFs (below 4 cycles per degree of visual angle), or in HFs (above 6 cycles per degree of visual angle). Since at an equal level of contrast, LFs are more visible than HFs, the HFs contrast was increased (Fig. 1). A mask was used in order to prevent retinal persistence of the scene. The mask was built by the random sum of several natural scenes belonging to eight different categories. Therefore, the mean frequency spectrum of the mask was similar to natural scenes'. In each experimental session (see below), scenes were displayed either in the central visual field (CVF), in the left visual field (LVF), or in the right visual field (RVF). Eccentricity of lateralized scenes was 1° of visual angle from their inner edge.

2.3. Procedure

Participants were tested individually. Each participant sat at 110 cm from the screen (17 in. TM Ultra Scan P790 monitor which a resolution screen of 1024 per 768 pixels) in a darkened room. For each trial, the stimulus display was preceded by a fixation point and followed by a mask, then by a 2 s blank interval after the response was made. The fixation point was presented for 500 ms (in order to control the gaze direction to the centre of the screen). The stimulus display was presented for 100 ms, immediately following the offset of the fixation point. Thereafter, the mask was presented for 40 ms. For each trial, participants were to decide by pressing a response button (located in the saggital plane) with their dominant hand whether the target was a city or a highway (Go/NoGo response). Half of the subjects were to press the button when identifying the city and the remaining half pressed the button when identifying the highway. The target scene was present in half of the trials. After each experimental trial, reaction time (RT) was recorded to the nearest millisecond (ms) following the response, as well as the response accuracy.

2.4. Design

The design of the experiment included two factors, which were manipulated within subjects: Visual field of presentation (LVF, CVF, and RVF) and spatial frequency components of scenes (LFs and HFs). The experiment was divided into an initial training session followed by three experimental sessions which were successively performed by all the subjects. The sessions differed from one another in the visual field of presentation and in the spatial frequency components of displays. In the training session, scenes were not filtered and were displayed in the central visual field (CVF) in order to accustom participants to the task. In the first experimental session, non-filtered scenes were randomly displayed either in the RVF/LH, or in the LVF/RH, in order to examine whether non-filtered scenes were asymmetrically processed in the hemispheres. In the second and third sessions, scenes filtered either in LFs or in HFs were displayed either in the CVF (session 2), or laterally in each hemifield (session 3). The third session allowed us to test the hemispheric specialization for spatial frequency processing according to the hypothesis that LFs target scenes should be identified faster in the LVF/RH than in the RVF/LH, whereas HFs target scenes should be identified faster in the RVF/LH. Moreover, sessions 2 and 3 were designed to study the 'precedence effect' with natural scenes, in other words the relative rapidity of information stemming from LFs and HFs.

3. Results

Mean reaction times (mRT) and errors for each condition in sessions 1, 2, and 3 are reported in Table 1. To reduce the effect of extreme values, RT for each subject's correct response in each condition was trimmed by removing responses inferior and superior to two standard deviations from the mean of each condition. Whatever the experimental condition, the mean error rate was low, varying from 0.31% to 1.88% with a mean

Table 1
Mean reaction times in milliseconds (mRT), standard deviations (*SD*), and mean error rate (mER) for each level of filtering (non-filtered; LFs, low spatial frequencies and HFs, high spatial frequencies target scene) and for each hemifield/hemisphere of presentation (LVF/RH, left visual field/right hemisphere; CVF, central visual field; and RVF/LH, right visual field/left hemisphere)

	Session 1		Sessions 2 and 3					
	Non-filtered target scenes		LFs target scenes			HFs target scenes		
	LVF/RH	RVF/LH	LVF/RH	CVF	RVF/LH	LVF/RH	CVF	RVF/LH
mRT	366	363	366	390	412	389	363	373
SD	42	49	63	84	92	72	60	56
mER	0.62%	1.88%	1.88%	1.88%	0.94%	1.56%	0.31%	1.25%

error rate of 1.29%. Therefore, an analysis of variance (ANOVA) was only performed on the main dependent variable: Correct mRT. Separate ANOVA were conducted for the first experimental session on one side, and for the second and third sessions on other side.

For the first experimental session, a one-way ANOVA was conducted with hemifields of presentation (LVF/RH and RVF/LH) as a within-subject factor. The hemifield of presentation did not significantly affect the performance for non-filtered target scenes, [$F(1;8) < 1$, ns]. For the second and third experimental sessions, a two-way ANOVA was performed with visual field of presentation and spatial frequency components as within-subject factors. Firstly, with regard to the hypothesis of a hemispheric specialization for spatial frequency processing, the ANOVA revealed a significant interaction between a lateralized presentation (LVF and RVF) and the spatial frequency components of target scenes [$F(1;8) = 10.57, p < .02$] (Fig. 2a). This interaction stemmed from the fact that the hemifield presentation significantly affected the performance for LFs [$F(1;8) = 11.25, p = .01$] (Fig. 2b) but not for HFs. For HFs, mRT were faster in RVF/LH (373 ms) than in LVF/RH (389 ms) but this difference did not reach significance [$F(1;8) = 2.19, p = .18$] (Fig. 2b). Secondly, regarding the ‘precedence effect’ hypothesis, the ANOVA revealed a significant two-way interaction between the visual field of presentation and spatial frequency components of target scenes, [$F(2;16) = 4.58, p < .03$]. More precisely, in LVF/RH, LFs target scenes (366 ms) were identified faster, but not significantly faster than HFs target scenes (389 ms), [$F(1;8) = 2.52, p = .15$], whereas, HFs target scenes were processed slightly faster than LFs in the CVF, and significantly faster than LFs in RVF/LH [$F(1;8) = 4.22, p = .07$ and $F(1;8) = 5.32$, $p = .05$, respectively] (Fig. 2c).

4. Discussion

The two main aims of these experiments were to investigate the hemispheric specialization for spatial frequency processing and the ‘precedence effects’ during the categorization of natural scenes. Firstly, when the whole spatial frequency spectrum was present in natural scenes (non-filtered target scenes), there was no hemispheric superiority in detecting a target scene. This finding confirms Goldberg’s model (Goldberg & Costa, 1981) suggesting that natural scenes may be equally processed in both hemispheres.

Secondly, results showed that the two hemispheres differed significantly in the way they processed spatial frequencies: There was a right hemisphere superiority in LFs processing, whereas a left hemisphere superiority was observed for HFs. Moreover, we found a ‘precedence effect’ similar to what had been reported with lateralized hierarchical forms. As a matter of fact, we found a LFs precedence when the scenes were displayed

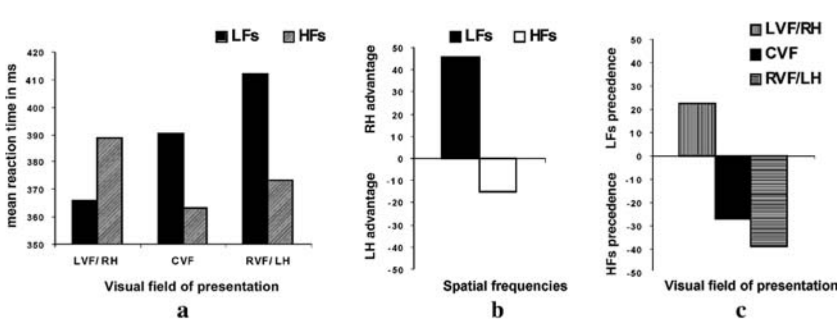

Fig. 2. Effect of interaction between the visual field of target scene presentations (LVF/RH, left visual field/right hemisphere; CVF, central visual field; and RVF/LH, right visual field/left hemisphere) and spatial frequency components (LFs, low spatial frequencies and HFs, high spatial frequencies) (a). Hemispheric specialization for spatial frequency processing (b). ‘Precedence effect’ depends on the visual field of target scene presentations (c).

in the LVF/RH and a HFs precedence when displayed in the RVF/LH. The HFs precedence in the CVF does not infirm neither Sergent's hypotheses (Sergent, 1982), nor the coarse to fine processing design. Sergent (1982) proposed that stimuli displayed in the CVF are also presented to the fovea, which is more powerful in conveyed HFs than LFs. So, in agreement with our results, the central presentation should induce a HFs advantage in natural scene processing. In addition, according to the coarse to fine processing design and Schyns and Oliva's (1994) findings, when the presentation of natural scenes in the CVF is long enough (around 150 ms), scene categorization is preferentially performed on the basis of HFs information. The time of exposure used in this study (100 ms) may thus explain why we obtained better identification performance with HFs target scenes.

In conclusion, our study provides the first empirical evidence of a hemispheric specialization for spatial frequency processing during a scene categorization task when using filtered stimuli. Henceforth, it would be interesting to disentangle perceptual from attentional mechanisms involved in this kind of task. If, as Robertson et al. (1988) proposed, there is a hemispheric asymmetry for the spatial frequency perceptual processing, attentional mechanisms could also be asymmetrically represented across the hemispheres (Yamaguchi et al., 2000). For this purpose, we are currently conducting an experiment using the same kind of paradigm in order to investigate the relative part of perceptual and attentional mechanisms, and in which way these mechanisms are controlled by the two hemispheres.

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