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ScienceDirect
International Journal of Psychophysiology 64 (2007) 184–189
INTERNATIONAL JOURNAL OF PSYCHOPHYSIOLOGY
www.elsevier.com/locate/ijpsycho

Vertical asymmetries in pre-attentive detection of changes in motion direction

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Received 21 December 2006; received in revised form 30 January 2007; accepted 1 February 2007
Available online 8 February 2007

Abstract

Stimulus localization affects visual motion processing. Vertical asymmetries favouring lower visual field have been reported in event-related potentials (ERPs) and behavioural studies under different attention conditions. However, there are no studies examining such asymmetries to non-attended motion changes. The present study investigated whether the asymmetry in processing information from the upper and lower visual fields also affects the automatic detection of motion-direction changes as indexed by visual Mismatch Negativity (vMMN). We recorded vMMN to changes in sinusoidal gratings differing in motion direction presented in the periphery of visual field in three different locations: upper and lower (ULVF), upper (UVF) and lower (LVF) along the vertical meridian. The N2 component elicited to peripheral motion presented lower amplitudes when the UVF was stimulated. The vMMN elicited to infrequent motion-direction changes was present in all stimulation conditions. However, it was reduced to UVF stimulation. These results suggest that the visual system automatically detects motion-direction changes presented at both upper–lower visual fields; however they also indicate that the process is favoured when stimuli are presented in the LVF alone.

Keywords: Visual evoked potentials; Motion-direction changes; vMMN; Upper/lower hemifield stimulation

1. Introduction

Human visual processing depends on the location of information in the visual field. Behavioural studies have found vertical asymmetries favouring the lower visual field (LVF) in contrast-sensitivity (Cameron et al., 2002; Carrasco et al., 2002), spatial resolution (Carrasco et al., 2002; Rezec and Dobkins, 2004), orientation (Raymond, 1994) and hue (Levine and McAnany, 2005). Neurophysiological studies have also confirmed the higher sensitivity of the LVF to contrast patterns (Portin et al., 1999), high contrast checkerboards (Fioretto et al., 1995), and non-attended colour changes (Czigler et al., 2004).

Lower–upper visual field asymmetries have also been found in motion processing (see Christman and Niebauer, 1997 for a review). Employing behavioural measures, a LVF advantage has been found in sensitivity to motion in depth (Edwards and Badcock, 1993), sensitivity to chromatic motion (Bilodeau and Faubert, 1997), discrimination thresholds for motion (Rezec and Dobkins, 2004), lateral motion perception (Levine and McAnany, 2005), anisotropy in motion coherence thresholds for upwards and downwards movement (Raymond, 1994), and for moving targets embedded in static distracters demanding segmentation by motion (Lakha and Humphreys, 2005). Finally, in a motion-onset visual evoked potential (VEP) study, Kremláček et al. (2004) found greater amplitudes and shorter latencies when the LVF was stimulated.

Vertical asymmetries have been interpreted in terms of attentional mechanisms, suggesting a higher attentional resolution in the LVF, especially in crowding paradigms or when the attentional load is manipulated (He et al., 1996). However, visual sensory constraints may also contribute to these asymmetries and therefore the LVF advantage cannot be solely explained by attentional biases across the visual field (Levine and McAnany, 2005). Moreover, upper visual field (UVF) advantages have been shown in various visual tasks such as visual search (Previc and Blume, 1993), and object recognition (Chambers et al., 1999).

Most studies have examined visual field asymmetries employing experimental conditions that required different degrees of attention. In motion processing there are no studies

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doi:10.1016/j.ijpsycho.2007.02.001

having examined these upper–lower differences under non-attention conditions. Previous studies (Pazo-Alvarez et al., 2004a,b) have shown that it is possible to record an electrophysiological response to changes in motion direction, the visual Mismatch Negativity (vMMN), which indexes the ability of the human brain to pre-attentively detect those changes. Moreover, a vMMN to changes in motion direction has been recently obtained in an independent laboratory (Kremláček et al., 2006) confirming the existence of such automatic detection mechanism for motion stimulation. In this context, the present study aimed to investigate whether the asymmetry in processing information from UVF and LVF also affects the pre-attentive detection of motion-direction changes.

2. Materials and methods

Twelve healthy subjects (7 females, 5 males, 25.3±4.75 years, range 18–35) with normal or corrected-to-normal vision participated in the experiment. Subjects gave informed consent to participate in this study.

To assess the effects of upper and lower visual field stimulation on the automatic processing of infrequent changes in motion direction, we presented upper (UVF), lower (LVF), or simultaneous upper–lower (ULVF) visual field stimulation in separate conditions (one block per condition). Stimuli consisted in sinusoidal gratings differing in the direction of motion placed in the periphery (10.70° to the center of the grating) of the visual field (1 cd/m^2 mean luminance). The gratings (20% contrast, 0.70 c/degree of spatial frequency, 4.13° of visual angle, 17 cd/m^2 mean luminance) were presented in oddball sequences of repetitive upward (p=0.8) and infrequent downward-drifting gratings (p=0.2). Gratings drifted with a speed of 1.95°/s for 133 ms and were followed by a blank screen interstimulus interval of 665 ms (mean luminance 1 cd/m^2). Frequent and infrequent stimuli were presented randomly with the restriction that at least one standard motion direction would occur before each deviant motion direction.

Subjects were requested to ignore the peripheral gratings and to keep their eyes in a small fixation cross placed at the centre of the visual field. Over this point one of nine possible digits (i.e., 1 to 9; 1.03° height and 0.66° width of visual angle) was equiprobably presented in three different colours (red, green and blue) for 40 ms. Subjects were required to press the left button of a standard mouse with their left hand in response to odd numbers (except 9, that required no response), and the right button with their right hand in response to even numbers, as rapidly and accurately as possible. Assignment of response keys and the order of stimulation conditions were counterbalanced across subjects. Each experimental block consisted of 770 trials (500 trials corresponded to task-irrelevant gratings, 400 frequent and 100 deviant, and 270 to task-relevant digits). Digits and gratings alternated asynchronously. All stimuli were presented with a stimulus onset asynchrony (SOA) of 798 ms.

Reaction times (RTs) were on-line recorded for each trial, and hit rates were defined as the percentage of correct responses to target digits with RTs no longer than 798 ms. RTs were analyzed for hits only. Hit rates and mean RTs were compared across conditions using repeated-measures ANOVA with condition (UVF, LVF, ULVF) as the within-subject factor.

The electroencephalogram (EEG) was recorded with a NeuroScan system using scalp electrocaps (ECI, Inc.) with electrodes placed at FP1, FPz, FP2, F3, Fz, F4, F7, F8, FCz, C3, Cz, C4, CP3, CPz, CP4, P3, Pz, P4, T3, T4, T5, T6, PO3, POz, PO4, O1, Oz, and O2 (10/20 International System). Two extra electrodes were fixed to the scalp, located halfway between O1 and T5 (OL), and O2 and T6 (OR). The active electrodes were referred to the nose-tip and grounded with an electrode at the nasion. Electrical activity elicited to vertical and horizontal eye movements was monitored by EOG recorded bipolarly from above and below the left eye and from the outer canthi of both eyes. EEG was acquired as continuous signals digitized at 500 Hz and filtered on-line with a bandpass of 0.05–100 Hz. Trials with eye blinks, eye movements, or exceeding ±100 μV were excluded from analyses. EEG epochs (500 ms post-stimulus and 50 ms pre-stimulus) were obtained off-line and averaged separately for standard and deviant gratings in each subject and condition. Averages were off-line filtered between 0.1 and 30 Hz.

To sample possible differences between the event-related potentials (ERPs) elicited to standard and deviant gratings, we analyzed successive mean voltage values over separate regions of the scalp. Thus, mean amplitudes of the ERP waveforms were measured separately across consecutive 20 ms latency windows within a 105 and 225 ms latency range. Analyses were restricted to this latency range at occipital (OL, O1, Oz, O2, OR), parieto-occipital (PO3, POz, PO4) and temporal (T5, T6) locations. This decision was based on previous results (Pazo-Alvarez et al., 2004a) showing that the reliable difference between deviant and standard ERPs was located at these time ranges and scalp derivations. For each latency window mean amplitude values were entered into separate repeated-measures ANOVAs with factors of condition (UVF, LVF, ULVF), deviance (standard, deviant) and hemisphere (left, right) at the above detailed electrodes.

Difference waveforms (vMMN) were obtained for each subject and condition by subtracting the ERPs elicited to standard from those elicited to deviant stimuli. In the resulting waves, mean amplitude values were calculated separately across consecutive 20 ms latency windows within the above referred time range. One-sample t tests were used to determine whether the obtained mean amplitudes were significantly different from zero (alpha level 0.05). The hemispheric differences in scalp distribution of vMMN and among stimulation conditions were analyzed using repeated-measures ANOVAs with the within-subject factors of condition (UVF, LVF, ULVF) and hemisphere (left, right) at the same occipital, parieto-occipital and temporal electrodes. When appropriate, degrees of freedom were corrected using the Greenhouse–Geisser estimate. Post hoc comparisons were performed using the Bonferroni adjustment for multiple comparisons (alpha level 0.05).

Moreover, voltage maps were computed for both the ERPs elicited by standard and deviant gratings, and for vMMN. EEGLAB open source toolbox (Delorme and Makeig, 2004), which plots topographic maps of EEG fields as a 2D

circular view using cointerpolation on a fine cartesian grid, was employed to this end.

3. Results

Repeated-measures ANOVA revealed no significant differences in reaction time (UVF, 445.34±37.73 ms; LVF, 444.54± 39.99 ms; ULVF, 443.60±23.89 ms; $F(2,22)=0.055$, $p=0.946$) or hit rates (UVF, 91.52±5.54%; LVF, 91.01±4.95%; ULVF, 91.79±5.98%; $F(2,22)=0.163$, $p=0.851$) among conditions.

The grand-average ERPs elicited to standard and deviant stimuli under different conditions at the midline occipital electrode (Oz) are shown in Fig. 1. At occipital locations repeated-measures ANOVAs for mean amplitudes revealed a significant main effect of condition from 145 to 225 ms (145–165: $F(2, 22)=8.275$, $p=0.002$; 165–185: $F(2, 22)=8.897$, $p=0.001$; 185–205: $F(2, 22)=5.539$, $p=0.011$; 205–225: $F(2, 22)=4.103$, $p=0.031$). Post hoc Bonferroni corrected comparisons revealed that amplitudes were larger during LVF and ULVF stimulations than during UVF stimulation from 145 to 185 ms (lowest $p=0.044$, highest $p=0.006$). From 185 to 225 ms, only the LVF condition significantly differed from the UVF condition (lowest $p=0.048$, highest $p=0.017$). At parieto-occipital sites a significant effect of condition was found between 125 and 225 ms (125–145: $F(2, 22)=7.253$, $p=0.004$, $\epsilon=0.487$; 145–165: $F(2,22)=16.341$, $p=0.0001$; 165–185: $F(2,22)=16.116$, $p=0.0001$; 185–205: $F(2,22)=8.980$, $p=0.001$; 205–225: $F(2,22)=4.973$, $p=0.017$). Post hoc analyses indicated that from 145 to 185 ms the three conditions showed significantly different amplitudes. LVF stimulation elicited the largest amplitudes (lowest $p=0.003$, highest $p=0.001$). Again resembling the effects observed at the occipital locations, from 185 to 225 ms post hoc analyses revealed significant differences at parieto-occipital locations just between LVF and UVF stimulation (lowest $p=0.037$, highest $p=0.002$). At temporal sites a significant effect of condition was found between 145 and 205 ms (145–165: $F(2,22)=4.582$, $p=0.022$; 165–185: $F(2,22)=5.858$, $p=0.009$; 185–205: $F(2,22)=3.654$, $p=0.043$). Post hoc comparisons revealed that from 165 to 205 ms the main effects were again due to higher amplitudes for LVF than for UVF stimulation (lowest $p=0.017$, highest $p=0.013$).

The ERPs to deviant gratings were negatively displaced relative to the ERPs elicited to standard gratings (Fig. 1). ANOVAs revealed that this main effect of deviance was significant from 125 to 225 ms at occipital and parieto-occipital locations (smallest significance, $F(1,11)=5.372$, $p=0.041$), and from 145 to 205 ms at temporal locations (smallest significance, $F(1,11)=12.181$, $p=0.005$). At occipital locations, no significant interactions between deviance and condition were found from 105 to 225 ms, suggesting that this effect was similar for all stimulus conditions tested. At parieto-occipital locations, a significant 'deviance by condition' interaction was found from 185 to 225 ms (185–205: $F(2, 22)=3.938$, $p=0.035$; 205–225: $F(2, 22)=5.105$, $p=0.015$) indicating that deviant and standard waveforms did not differ significantly at the UVF stimulation condition (lowest $p=0.037$, highest $p=0.003$). At temporal locations analyses revealed a significant interaction 'deviance by condition' from 185 to 205 ms ($F(2, 22)=4.693$, $p=0.020$). Post hoc tests revealed that deviants and standards differed only when the LVF was stimulated ($p=0.019$).

The difference waveforms containing vMMN are shown in Fig. 2. One-tailed paired t tests assessing mean amplitudes obtained at different sites against zero-level, yielded significant results at posterior locations (occipital, parieto-occipital and temporal) from 145 to 225 ms during LVF stimulation. A similar finding was found during ULVF stimulation. UVF stimulation

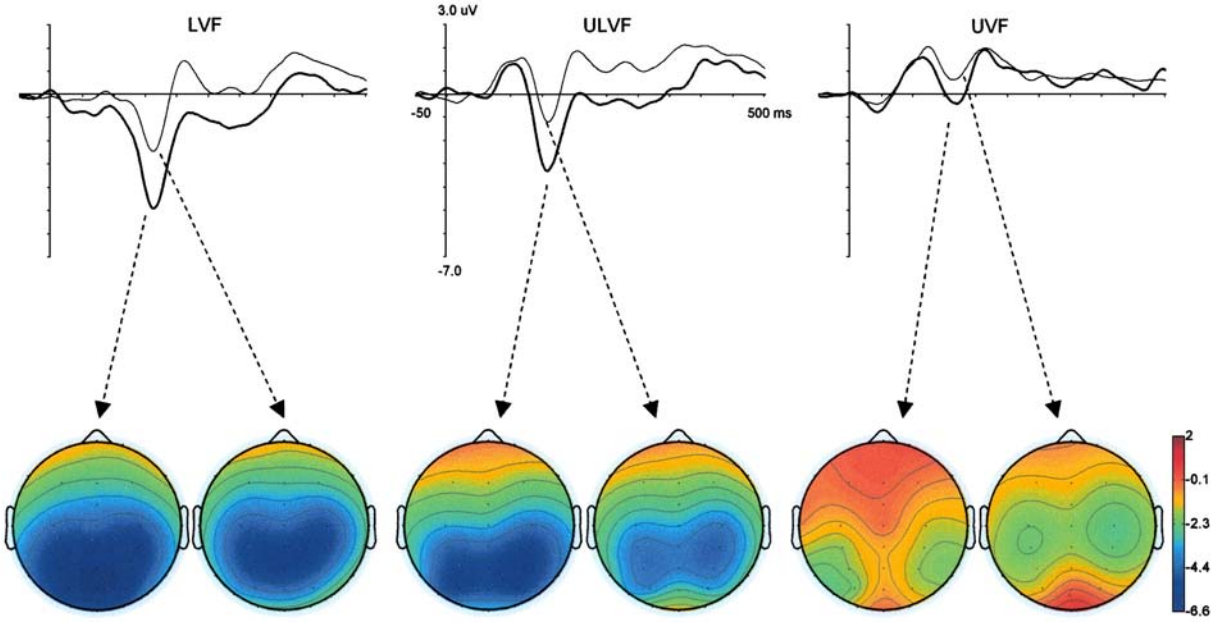

Fig. 1. Grand-average ERPs to deviant (thick line) and standard (thin line) motion direction across stimulation conditions at Oz sowing the N2 component. Below appear the scalp maps at the latencies of maximum N2 amplitudes to both deviant and standard stimuli (LVF: 162 ms; UVF: 168 ms; ULVF: 158 ms).

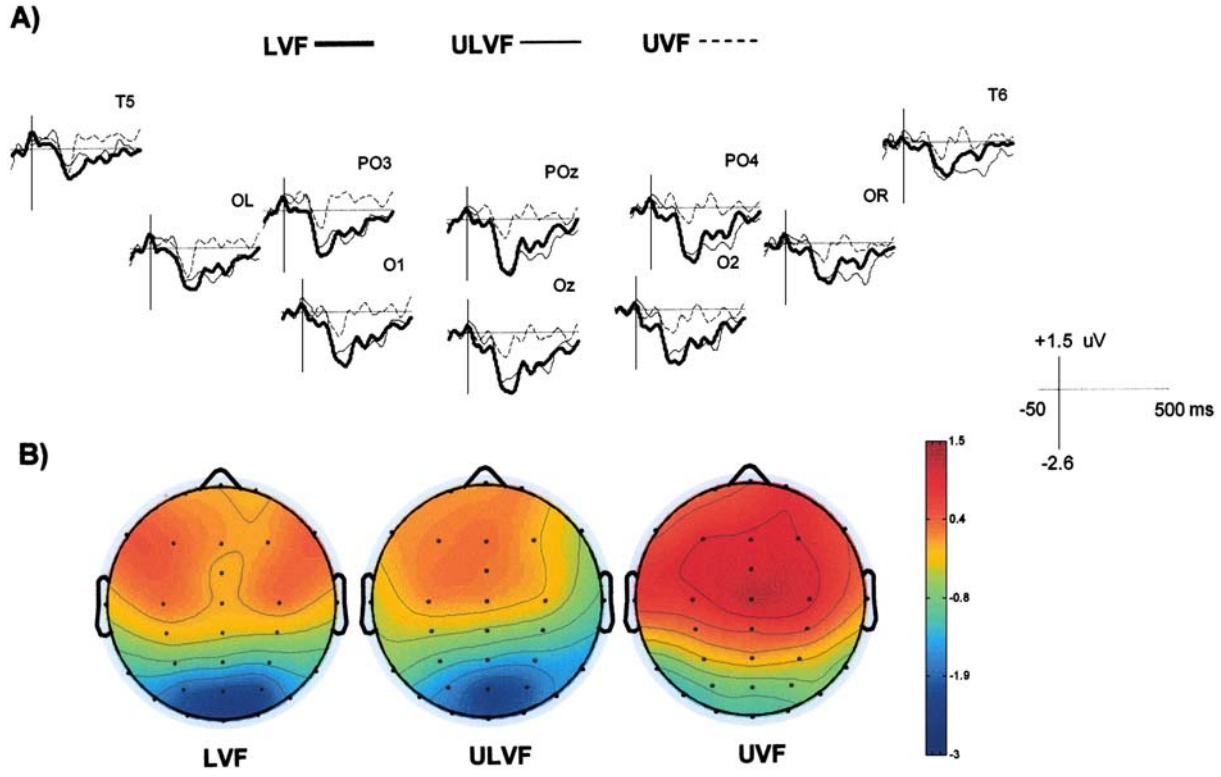

Fig. 2. A) Difference waveforms showing vMMN across stimulation conditions at posterior electrodes. B) Scalp maps at the latency of maximum vMMN amplitude in each condition (LVF: 198 ms; UVF: 172 ms; ULVF: 150 ms).

yielded significant different from zero results only at O1, O2, Oz and OL from 165 to 185 ms. O1, O2 and OL were also significant from 145 to 165 ms (Table 1).

The ANOVAs to test whether vMMN amplitudes differed across conditions at the locations and latency windows where all three conditions were significantly different from zero showed that between 145 and 165 ms the interaction 'electrode by condition' was significant ($F(4,44)=3.823$, $p=0.026$, $\varepsilon=0.637$). Post hoc comparisons revealed that at O2 electrode LVF stimulation elicited larger amplitudes than UVF stimulation ($p=0.045$).

4. Discussion

The N2 component evoked by non-attended peripheral motion revealed vertical asymmetries characterized by smaller

Table 1
Student *t*-test values (*p*) for mean amplitudes of vMMN against zero-level at each latency window, stimulation condition, and electrode site

		Electrode site									
Latency window (ms)	Visual field	O1	O2	OL	OR	Oz	PO3	PO4	POz	T5	T6
125–145	LVF	**2.82 (0.02)**	**2.71 (0.02)**	**2.08 (0.06)**	1.5 (0.15)	**2.94 (0.01)**	1.79 (0.10)	**2.02 (0.07)**	**2.02 (0.07)**	1.34 (0.21)	1.54 (0.15)
	ULVF	**3.87 (0.00)**	**3.5 (0.00)**	**2.18 (0.05)**	1.7 (0.11)	**3.63 (0.00)**	1.68 (0.12)	**2.5 (0.03)**	**2.32 (0.04)**	0.74 (0.47)	**2.38 (0.04)**
	UVF	1.81 (0.1)	**1.87 (0.09)**	1.45 (0.17)	0.91 (0.38)	1.81 (0.1)	0.53 (0.60)	0.95 (0.36)	1.10 (0.29)	0.76 (0.46)	0.96 (0.36)
145–165	LVF	**4.16 (0.00)**	**4.24 (0.00)**	**3.75 (0.00)**	**2.87 (0.02)**	**4.31 (0.00)**	**3.43 (0.01)**	**3.78 (0.00)**	**3.75 (0.00)**	**2.84 (0.02)**	**2.89 (0.01)**
	ULVF	**3.34 (0.01)**	**3.28 (0.01)**	**2.73 (0.02)**	**2.25 (0.05)**	**3.29 (0.01)**	**2.5 (0.03)**	**2.98 (0.01)**	**2.74 (0.02)**	1.51 (0.16)	**2.67 (0.02)**
	UVF	**2.36 (0.04)**	**2.33 (0.04)**	**2.6 (0.02)**	1.35 (0.20)	**2.19 (0.05)**	1.58 (0.14)	1.49 (0.16)	1.5 (0.16)	**1.91 (0.08)**	1.51 (0.16)
165–185	LVF	**3.3 (0.01)**	**3.64 (0.00)**	**3.01 (0.01)**	**2.35 (0.04)**	**3.56 (0.00)**	**2.98 (0.01)**	**3.22 (0.01)**	**3.21 (0.01)**	**2.65 (0.02)**	**2.46 (0.03)**
	ULVF	**3.08 (0.01)**	**2.85 (0.02)**	**2.99 (0.01)**	**2.21 (0.05)**	**3.06 (0.01)**	**2.92 (0.01)**	**3.11 (0.01)**	**2.97 (0.01)**	**2.26 (0.05)**	**2.98 (0.01)**
	UVF	**2.37 (0.04)**	**2.4 (0.04)**	**2.56 (0.03)**	1.77 (0.1)	**2.3 (0.04)**	1.55 (0.15)	1.70 (0.12)	1.56 (0.15)	**1.93 (0.08)**	**2.17 (0.05)**
185–205	LVF	**3.64 (0.00)**	**3.9 (0.00)**	**3.63 (0.00)**	**2.98 (0.01)**	**3.74 (0.00)**	**3.44 (0.01)**	**3.85 (0.00)**	**3.56 (0.00)**	**3.18 (0.01)**	**3.56 (0.00)**
	ULVF	**3.03 (0.01)**	**3.17 (0.01)**	**2.49 (0.03)**	**2.68 (0.02)**	**3.27 (0.01)**	**2.43 (0.03)**	**3.67 (0.00)**	**3.31 (0.01)**	1.85 (0.26)	**2.8 (0.02)**
	UVF	0.87 (0.40)	1.11 (0.29)	0.78 (0.45)	0.62 (0.55)	0.94 (0.37)	0.04 (0.96)	0.56 (0.59)	0.50 (0.63)	0.06 (0.95)	0.61 (0.55)
205–225	LVF	**3.42 (0.01)**	**3.53 (0.00)**	**3.03 (0.01)**	**2.67 (0.02)**	**3.45 (0.01)**	**2.7 (0.02)**	**3.24 (0.01)**	**2.98 (0.01)**	**2.64 (0.02)**	**2.75 (0.02)**
	ULVF	2.25 (0.05)	**2.84 (0.02)**	1.59 (0.14)	**2.38 (0.04)**	**2.68 (0.02)**	1.36 (0.20)	**2.97 (0.01)**	**2.6 (0.02)**	0.39 (0.70)	**2.27 (0.04)**
	UVF	0.04 (0.97)	0.67 (0.51)	0.54 (0.60)	0.07 (0.94)	0.40 (0.69)	1.07 (0.31)	0.12 (0.90)	0.23 (0.81)	1.41 (0.18)	0.34 (0.74)

Significant values appear in bold characters.

amplitudes to both deviant and standard stimuli when the UVF was stimulated. At occipital, parieto-occipital and temporal sites the ERPs elicited to deviants were negatively displaced in relation to ERPs elicited to standards independently of the hemifield stimulated. However, these differences were smaller for UVF stimulation. These results agree with those obtained by Kremláček et al. (2004) who found significantly greater amplitudes of motion-onset VEP components when they stimulated the LVF. Moreover, they complement them because in the present study motion VEPs were obtained under non-attended stimulation conditions, indicating that even in this case the visual system processes better the information coming from the LVF.

The N2 component of the motion-onset VEPs has been identified as a motion-related component which also matches motion perception in its susceptibility to adaptation (Bach and Ullrich, 1994). The adaptation effects are to a larger extent global, since the amplitude reduction of N2 is non-direction specific, however when a stimulus shares the same direction with the adapting stimulus the amplitude of N2 can be reduced up to 28% more (Hoffmann et al., 2001). These reductions are also present even with very low duty cycles (i.e., the relation of motion to total presentation time) such as those used in the present study (Hoffmann et al., 1999). Therefore, one could argue that the lower amplitude of N2 elicited to standards could be due to the direction-specific additional reduction of this component elicited by frequent directions of motion. However, in a previous study (Pazo-Alvarez et al., 2004a) we provided evidence precluding that the effects could be due to a differential sensory adaptation. In that study we presented an additional control block which consisted in the presentation of equiprobably gratings ($p=0.2$) drifting in five different directions. We found that the control stimuli that shared the same low probability and physical features with deviant stimuli elicited an N2 component with similar amplitude to that elicited by standard stimuli. That is, the responses elicited to oddball-motion deviants were significantly more negative than both oddball-standards and controls. This result suggests that the larger negative displacement observed in deviants was not related to a differential sensory adaptation between frequent and infrequent directions of motion but to a mechanism dependent on a deviance from the stimulus context. It could also be claimed that the enhanced negativity in response to deviants was due to an exogenous effect of the stimulus change. However, in that study (Pazo-Alvarez et al., 2004a) we also observed that reversing the stimuli that acted as infrequent and frequent directions of motion did not affect the vMMN. Therefore, this negative deviant-related response was not related to the direction of motion *per se*, but to a change in the direction of motion.

The automatic change detection mechanism indexed by vMMN was present to changes in motion direction during all stimulation conditions. However, during UVF stimulation the amplitude of vMMN was markedly reduced, its length was shortened and its distribution restricted to occipital electrodes. On the other hand, when the LVF was stimulated the vMMN showed the largest amplitudes, was significant through a larger latency range and presented a broader scalp distribution at posterior locations. This suggests that the human visual system pre-attentively detects motion-direction changes when they are presented in both the UVF and LVF; however the process seems to be favoured when stimuli are presented in the LVF alone.

Pazo-Alvarez et al. (2004b) observed an absence of asymmetries in vMMN when the changes in motion direction were presented along the horizontal meridian with the same stimulation parameters and procedure. Such divergence between the two studies may have several non-exclusive explanations. Firstly, hemispheric differences have been reported to be less pronounced for motion stimuli, since extrastriate motion areas in the dominant hemisphere receive motion stimulation inputs from both the ipsilateral and contralateral visual fields (Tootell et al., 1988, 1995). However, upper–lower differences have been frequently observed in motion perception studies. From an ecological perspective the existence of lateral biases between the left and right visual fields when automatically detecting changes in movement would not be adaptative. Any subject showing such bias would be at risk of losing important information in daily situations where moving stimuli can come from any side of the visual world. Alternatively, the vertical asymmetries seem to have a functional nature and may be modulated by environmental factors. Thus, it is tentative to suggest that the existence of vertical biases in pre-attentive motion detection may be important for survival and daily life activities under most viewing conditions, mainly in biped species, in whose surroundings most of the moving objects are below the centre of their visual fields (for similar interpretations see Ohtani and Ejima, 1997; Talgar and Carrasco, 2002; Tootell et al., 1988).

Vertical asymmetries in motion processing have been explained attending to both sensory and cognitive factors. Within the first kind of explanations, the larger amplitudes recorded to the lower half of the visual field can be explained by the recording positions employed to obtain visual ERPs, since the different orientation of neural generators makes the posterior locations more sensitive to lower visual field responses (see Kremláček et al., 2004). The amplitude of the vMMN response is maximal in posterior locations; therefore the lower amplitudes during UVF stimulation do not necessary reflect a weaker processing of changes in the upper visual field, but an unsuitable position of the vMMN generator with respect to recording electrodes.

Alternatively, the existence of higher densities of ganglion cells in upper retina of primate visual system has been interpreted as indicating an overrepresentation of the LVF (Perry et al., 1984). This overrepresentation has been found to extend to the lateral geniculate and striate and extrastriate cortical areas (Tootell et al., 1988; Van Essen et al., 1984). Attending to cognitive factors, it has been suggested that the observed asymmetries may be driven in part by an attentional bias that favours the LVF (Rezec and Dobkins, 2004). In the present study, the motion-related evoked responses (N2) and the detection of motion-direction changes (vMMN) showed a LVF advantage. These responses were elicited by peripheral stimuli presented outside the focus of attention. Although we did not manipulate the processing load of the central task to completely

preclude a possible attentional effect, the advantage of the LVF to motion processing seems to be difficult to interpret here in terms of mere attentional mechanisms. Moreover, an extended explanation of the predominance of LVF in motion perception has been linked to its role in locomotion and visuomotor coordination (Previc, 1990), although the existence of conflicting results on this subject precludes making any conclusion (Binsted and Heath, 2005; Brown et al., 2005).

To our knowledge, the only study having analyzed the existence of vertical asymmetries on vMMN (Czigler et al., 2004) found that colour changes elicited vMMN only in case of LVF stimulation. In contrast with this study, we found that vMMN was present to changes in the direction of motion during all stimulation conditions, although it was favoured during LVF stimulation. These results may suggest that, as observed in other sensory modalities (i.e. auditory MMN), different neural sources contribute to the generation of vMMN within specific visual dimensions. The vertical asymmetry found for colour changes has been interpreted as indirect evidence that vMMN originated in retinotopically organized areas of the visual system (Czigler et al., 2004). Thus, we could consider that this result adds support to results indicating that visual motion change detection sources are located in less retinotopically organized areas (i.e., motion-related cortical areas, see Pazo-Alvarez et al., 2004b; Tootell et al., 1995). In fact, receptive fields are broader and extend more into the periphery of the visual field in motion-related cortical areas (Tootell et al., 1995).

In summary, the present results suggest that under unattended stimulation conditions the human visual system pre-attentively processes motion information and detects changes in motion direction in both the lower and upper vertical meridians; however the detection is enhanced when the lower part of the visual field is stimulated.

Acknowledgements

Study supported by Spanish Ministerio de Ciencia y Tecnología (grant SEJ2004-01377) and by the Galician Secretaría Xeral de I+D (grant PGIDIT05PXIC21101PN).

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