Article

Hemispheric asymmetry in visual processing: an ERP study on spatial frequency gratings

Alice Mado Proverbio [1], *, and Alberto Zani [2]

[1] Dept. of Psychology, University of Milano-Bicocca, mado.proverbio@unimib.it
[2] School of Psychology, Vita-Salute San Raffaele University, zani.alberto@hsr.it
* Correspondence: AMP mado.proverbio@unimib.it

Abstract: A hemispheric asymmetry is known for the processing of global vs. local visual information. In this study, we investigated the existence of a hemispheric asymmetry for visual processing of low vs. high spatial frequency gratings. Event-related potentials were recorded in a group of healthy right-handed volunteers from 30 scalp sites. Six types of stimuli (1.5, 3 and 6 c/deg gratings) were randomly flashed 180 times in the left and right upper hemi-fields. Stimulus duration was 80 ms and ISI ranged between 850-1000 ms. Participants had to pay attention and respond to targets based on their spatial frequency and location, or to passively look at the stimuli. C1 and P1 visual responses, as well as a later *Selection negativity* and a P300 components of ERPs were quantified and subjected to repeated-measure ANOVAs. Overall, performance was faster for the RVF, thus suggesting a left hemispheric advantage for attentional selection of local elements. Similarly, the analysis of mean area amplitude of C1 (60-110 ms) sensory response showed a stronger attentional effect (F+L+ vs. F-L+) at left occipital areas, thus suggesting the sensory nature of this hemispheric asymmetry.

Keywords: ERPs; selective attention; global/local; cerebral hemispheres; VEPs; spatial frequency; Attentional tuning; Left hemisphere

1. Introduction

The issue of a hemispheric asymmetry in perceptual processing of visual information has been largely debated [1,2,3,4,5,6,7,8,9,10]. The main lines of research and theoretical discussions have led to the conclusion that there might be a hemispheric asymmetry: i) in the way the left and right hemisphere process information in an analytic vs. holistic manner, or ii) in the way they select object features as opposed to pay sustained attention in space. Finally, iii) it was argued that, probably, the two hemispheres possess functional and neuroanatomical differences that render them more able to process information based on a low vs. high spectrum of spatial frequency (magno- vs. parvo-cellular content). These three approaches and the experimental evidence in their support are briefly discussed below.

1.1. A role of the right vs. left hemisphere in global/local processing

Robertson and coauthors [11] theorized that a hemispheric asymmetry existed for processing of global vs. local content of visual information, with a left hemispheric advantage for the local analysis and a right hemispheric advantage for the global analysis. In an interesting neuropsychological study, Robertson et al. [12] found that a left temporo/parietal lesion compromised the patients' ability to reproduce the local elements of both geometrical and linguistic hierarchical stimuli (so-called Navon configurations [13]), while a right-sided lesion compromised the patients' ability to reproduce their global form.

These findings are consistent with the existence of a left-lateralized brain network for local (vs. global) stimulus processing [14,15,16]. For example, using a task in which participants were instructed to recognize a target letter (within compound stimuli) at the hierarchical level (local or global), indicated by a pre-stimulus cue, Yamaguchi and colleagues [6] found that the local and global targets elicited an increased N2 response (250–350 ms) over the left and right hemispheres, respectively. In another event-related potential (ERP) study, a larger negativity (N2) was elicited by the perception of small illusory contours of a Kanizsa square over the left occipital regions [17], consistent with the idea of left-sided object-based feature selection and local (vs. global) stimulus processing [16,18].

1.2. *Object-based vs. space-based hemispheric asymmetry*

At the same time, evidence from several studies seems to suggest left-lateralized neural substrates underlying object-based (vs. space-based) focused selective attention [9,19,20,21]. In an ERP study by Proverbio et al. (2004) participants were presented with images of familiar objects and animals that were associated or not-associated with their prototypical color (e.g., a pink vs a blue piglet). They were instructed to pay heed either to the shape or to the color of the stimuli, ignoring the other trait. Target stimuli associated with the prototypical color/shape combination elicited a larger N2 component (or *selection negativity*, SN) over posterior scalp sites as compared with the not-associated combination, during the attention to color condition only. This effect was found over the left but not the right hemisphere, as also confirmed by the topographic mapping of voltage distribution computed on the difference wave (associated features minus not-associated features targets). These results seem to suggest a specific involvement of the left occipito-temporal cortex for a conjoined color/ shape processing of objects. Similarly, Orlandi and Proverbio [22] have shown a left-hemispheric selectivity in the ability to discriminate object-shapes, as indexed by the amplitude of SN response. Participants were presented with 3D images of shapes of wooden dummies, chairs, and Shepard cubes displayed in standard or rotated views, in many different orientations. They were instructed to pay attention to and select via a button-press one given target shape. The results showed a left hemispheric advantage for the attentional selection, resulting in an enhanced SN to targets, over left occipito/temporal sites. The swLORETA performed on EEG signals in the SN time range (240–280 ms) showed left lateralized neural sources, including the left superior/middle temporal (BA 22) and the left inferior frontal/precentral gyri. On the other side, many different studies support the view of a right hemispheric control and dominance for visuospatial orienting of attention [e.g., 23,24,25].

1.3. *The spatial frequency hypothesis*

According to some researchers [10,18,26,27] asymmetry in perceptual strategy would be grounded on a lower-level (sensory) hemispheric asymmetry for processing the spatial frequency content of visual information. There would be a right hemispheric advantage for processing the low-spatial frequency range, and a left hemispheric greater ability for processing finer details, such as the high-spatial frequency spectrum. Dos Santos et al. [28] investigated the hemispheric specialization for spatial frequency processing by measuring the contrast sensitivity curves of sinusoidal gratings in 30 patients with left or right brain damage. The results showed that patients with left brain damage were selectively impaired in high frequency processing, while patients with right brain damage were more impaired in low frequency processing. These findings can be interpreted in terms of a hemispheric asymmetry for spatial frequency discrimination.

Furthermore, the electrophysiological investigation by Martínez et al. [27] reported a larger SN component in response to target than non-target checkboard patterns. The attentional selection of high spatial frequencies (5 c/deg) elicited larger SN responses over the left hemisphere, while the attention selection of low spatial frequencies (0.8 c/deg) elicited larger SN responses over the right hemisphere, thus indicating a hemispheric asymmetry for spatial frequency processing. Similarly, Proverbio et al. [26] recorded visual evoked potentials to spatial

frequency gratings and found that the N80/P1 responses were differentially modulated by spatial frequency content. The N80 showed a negative focus (current sink), centered at mesial-occipital areas, while the P1 showed a positive focus (current source), centered at lateral-occipital regions of the scalp. The current source was much more prominent than the sink for lower spatial frequency, and vice versa. Moreover, the positive focus (P1) was larger over the right side of the scalp, whereas the current sink (N80) shifted from the right to the left side as spatial frequency increased. The authors concluded that visual sensory-evoked potentials elicited by low versus high spatial frequencies had different polarity and topographic localization, that might reflect the activation of functionally distinct, topographically segregated, neural generators differentially activated as a function of spatial frequency.

These results of a hemispheric asymmetry for sensory processing are also consistent with those reported by Zani and Proverbio [29] in their ERP study on selective attention to check-size. In that study, relevant checks elicited larger ERP components at both occipital (N165 and P3b) and frontal (LP, long latency positivity) scalp sites over the left but not the right hemisphere as compared to the irrelevant ones. Moreover, right-and left-sided hemispheric asymmetries were found being consistent with a P90 right-sided specialization for low spatial frequencies, and a N115 left-sided specialization for high spatial frequencies, respectively.

Notwithstanding the bulk of evidence of left sided attentional ERP components (such as *Selection Negativity* or N2 responses), the evidence of lateralized attention effects indexed by sensory VEPs are quite scarce. In the present study, visual ERPs were recorded in healthy participants during perception and attentional selection of non-square/wave spatial frequency gratings. Sensory responses C1 and P1 were measured to obtain data about a possible hemispheric asymmetry in attentional selection. Longer-latency *Selection Negativity* and P300 responses were also measured and an increase in their amplitude as result of attentional selection was expected based on previous investigations of Harter's research group [30,31,32].

There is multiple evidence in psychophysiological literature that the morphology of visual sensory components (C1 and P1) is strongly modulated by a series of stimulus physical characteristics, such as the orientation, the spatial frequency and the visual field of presentation of gratings and checkerboards [33,34,35,36]. On the basis of previous literature, we expected that C1 would be larger at ipsilateral sites, whereas P1 would be larger at contralateral sites. Moreover, C1 would have a mesial-occipital distribution and P1 a lateral-occipital distribution [26]. Finally, it was expected an early object-based attention modulation of both C1 and P1 responses [e.g., 37].

2. Materials and Methods

2.1. Participants

Eight healthy students (4 females and 4 males) with normal or lens-corrected vision took part in the study. Their mean age was 28.5 years, and their socio/economic and cultural levels were similar. All participants were psychically and neurologically healthy. Before the EEG registration, they were asked to fill in the informed consent to the research and the documentation regarding the minimum risk. They were then administered the Edinburgh Inventory to assess their right-handedness. Experiments were conducted with the understanding and written consent of each participant according to the Declaration of Helsinki (BMJ 1991; 302: 1194), and approval of the local ethical committee (University of Trieste). One subject was discarded in subsequent statistical analyses for excessive ocular artifacts.

2.2.Stimuli

Stimuli were three spatial frequency gratings whose contrast was degraded to obtain a quasi-sinusoidal luminance variation. Their spatial frequency was 1.5, 3 and 6 cycles degree (c/deg) at the viewing distance of 114 cm, respectively. Gratings were briefly flashed in the upper left or right visual hemifields, with respect to the center of the screen where a small cross acted as fixation point.

The background was gray and isoluminant with respect to gratings to avoid perceptual after effects or consecutive image phenomena. Within each quadrant, the stimulation started at 0 30' of visual angle above the fixation point and extended up to 4° 30' above it, while laterally the stimulus started from 2° and went up to 6° 03'. The stimulus duration was 80 ms. Interstimulus interval (ISI) ranged randomly between 850 and 1000 ms. Since participants had to keep their gaze on the fixation point, the decentralization of the stimuli allowed the stimulation of the extrafoveal retinal areas. The gratings presented to the left or to the right with respect to the fixation point were reversed by 180° in order to obtain specular stimuli that provided an identical cortical representation whether they were projected to the right or left of the hemi-retinas.

2.3.Procedure

Participants sat inside a silent cubicle with medium soundproofing and weak symmetrical lighting in front of a double-glazed window measuring 70x55 cm. Outside the cubicle was a 17" Macintosh monitor used for the presentation of visual stimuli that was connected to an IBM PC controlling stimulus presentation, located outside the cubicle. A 30 channels "Electro-Cap" cap was applied to each subject for recording his or her EEG waves. Two extra pairs of surface electrodes were applied to record vertical and horizontal ocular movements (EOG). Averaged-ears acted as reference electrodes. All the electrodes were connected to a panel interfaced with a 32-channel SynAmps amplifier. The amplification unit was in turn connected to another IBM PC in which "*NeuroScan 3.0*" software controlled the continuous recording of the EEG traces, and stimulus/response synchronization. The subjects responded through a "*StimPad*" push-button panel interfaced with "*NeuroScan 3.0*" software, so that the response signals, recorded on the rough traces, might later be analyzed through "*Respwin*" software in order to obtain the data relating to the behavioral performance of the subject.

Subjects were provided with written instructions describing the experimental task. A "training" phase preceded the experimental session, so that participants might familiarize with the different types of stimuli and experimental setting. This training phase ended when the subject showed an optimal ability to discriminate the various spatial sequences of gratings.

The six types of stimuli (3 frequencies for 2 locations) were projected in random order 180 times (30 repetitions for each type of stimulus). Participants were administered 30 different sequences (of 180 stimuli each), featuring a specific stimulus selection task requirement. At the beginning of each run, subjects were given the experimental instructions of paying attention to gratings of one specific frequency at one spatial location (e.g., "during this run, pay attention and respond to the high frequency grating to the right visual field, and ignore all other types of stimuli"). Participants were instructed to press a button with the index finger of one of the two hands as quickly and efficiently as possible, while ignoring non-target stimuli. In half of the trials subjects used the right hand and in the remaining half the left hand. The order of the hands was randomized between trials and between subjects. There were four attentional conditions: attention to 6/deg spatial frequency gratings on the right, to 6/deg spatial frequency gratings on the left, to 1.5 c/deg spatial frequency gratings on the right and to 1.5 c/deg spatial frequency gratings on the left. 3 c/deg spatial frequency gratings were included as distractor stimuli since they were

never a target. Stimuli might therefore be target in both spatial frequency and location (L+F+), target only in location (L+F-), target only in spatial frequency (L-F+) and non-targets (L-F-).

2.4. EEG recordings

EEG data were continuously recorded from 30 scalp sites according to the 10–20 International System at a sampling rate of 500 Hz. Two pairs of bipolar electrodes were applied to the subject for the detection of saccades and vertical eye movements. Two electrodes placed on the earlobes were used as reference electrodes, while the ground electrode was included in the recording cap in the center-frontal position. The EEG and electro-oculogram (EOG) were filtered with a half-amplitude band pass of 0.016–50 Hz. Electrode impedance was maintained below 5 kΩ. Computerized artifact rejection was performed prior to averaging in order to discard epochs in which ocular movements, blinks or other artifacts occurred. The artifact rejection criterion was a peak-to-peak amplitude exceeding 50 µV and resulted in a rejection rate of ~15%. Event-related potentials (ERPs) going from 100 ms before through 1000 ms after stimulus onset were averaged off-line. ERP components were measured when in time and where on scalp they reached their maximum amplitudes.

2.5. Statistical analysis

For each subject mean area amplitude values of C1 (60-110 ms), P1 (110-160 ms), *Selection Negativity* (N2, 165-330 ms) and P300 (330-600 ms) ERP responses were quantified and subjected to repeated-measures analyses of variance (ANOVA). ERP responses to target gratings (1.5 c/deg left, 1.5 c/deg right, 6 c/deg left, 6 c/deg right) gratings were compared to the responses to the same gratings in the other attention condition (when irrelevant, when shared one feature (i.e., either frequency or location) with target, or when target). Factors were Attentional condition, Hemisphere (for C1 and P1 component) and Electrode. Attention condition had 4 levels of variance: target (L+F+), location specific (L-F+), frequency specific (L+F-), irrelevant (L-F-). Hemisphere had 2 levels of variance (left and right). Electrode had 3 levels of variance: occipital (O1,O2), lateral-occipital (OL-OR), occipito/temporal (T5-T6) for sensory components C1 and P1, and 9 levels for later components *Selection Negativity* and P300 (O1, O2, OL, OR, T5, T6, Oz, Cz, Pz).

Response times (RTs) and the percentage of correct responses (hits) were recorded and quantified. RTs that exceeded the mean value ±2 standard deviations were discarded, which resulted in a rejection rate of approximately 5%. Both RTs and accuracy percentages were subjected to separate multifactorial repeated-measures ANOVAs with 3 within-subjects factors, whose factors of variability were: visual field of presentation (left or right), grating spatial frequency (1.5 or 6 c/deg), response hand (left or right).

3. Results

3.1. Behavioural data

The analysis of variance performed on the response times of the subjects did not result in any statistical significance, except for a very close to significance visual field factor for reaction times analyses ($F(1,6)=5.6$, $p=0.055$). Response times were faster when stimuli were presented in the right visual field (RVF, left hemisphere) compared to the left visual field (LVF, right hemisphere). False alarms responses incorrectly directed to non-targets (i.e., 3 c/deg gratings) were less than 2% of the total amount of emitted responses. Omissions (lack of response to 1.5 and 6 c/deg target gratings) was slightly superior to 3 % of emitted responses. Accuracy analyses did not yield any statistical significance.

3.2.Electrophysiological data

C1 component.

C1 response was much larger in the ipsilateral than contralateral field (see Fig. 1), as shown by hemisphere per visual field factors interaction (F (1,6)=14.3, p<0.009). Indeed, C1 responses were much larger over the left hemisphere for LVF gratings, and, vice versa, over the right hemisphere for RVF ones.
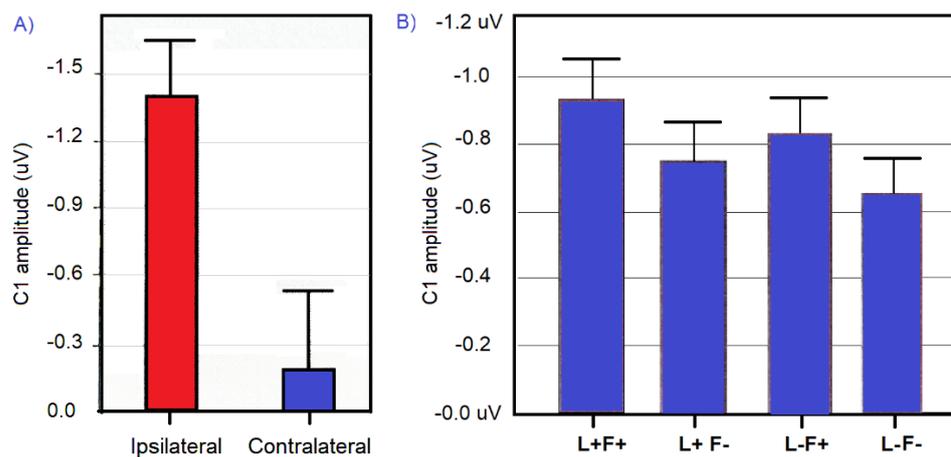

Figure 1. (A) Mean amplitude values of C1 response recorded at ipsilateral vs. contralateral stimuli regardless of attentional condition. **(B)** Mean amplitude values of C1 response recorded in the different attentional conditions regardless of spatial frequency of stimulation.

The significance of electrode x spatial frequency factors (F(2,12)=16.3, p=0.0004) showed a larger C1 response over striate (O1, O2) than extra-striate (OL, OR) and occipito/temporal sites (T5, T6), especially for the higher spatial frequency.
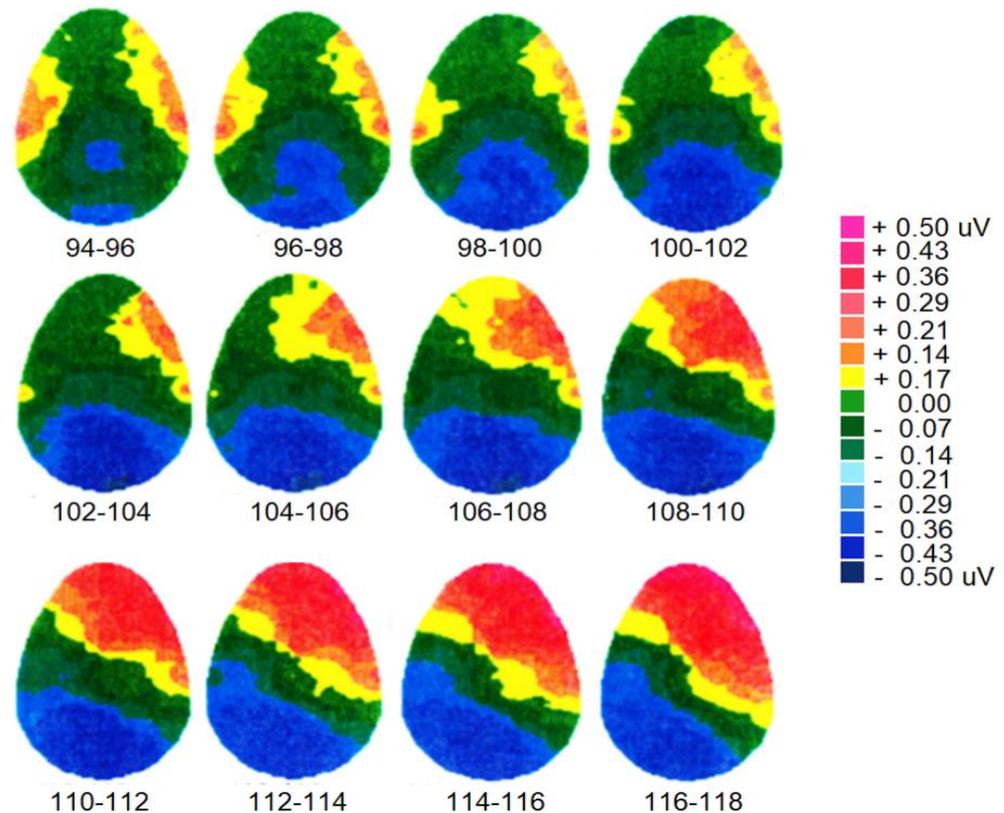
Figure 2. Effect of spatial frequency specific attentional selection (L+F+ minus L+F-), regardless of visual field of presentation. Temporal series of topographical distribution of surface voltage (top view) recorded between 94 and 118 ms of post-stimulus latency (every 2 ms) in the C1 latency range. The data indicate an early enhanced negativity (larger C1 response) to target frequencies focused over mesial-occipital scalp areas, which progressively spread over the scalp in time. It is also visible a hemispheric asymmetry in the topographical distribution of attentional selection. The asymmetry would indicate a greater ability of the left visual cortex in the discrimination of fine differences in spatial frequency.

C1 response was strongly modulated by attentional factors, in interaction with cerebral hemisphere ($F(4,24) = 3.8$, $p < 0.01$). Post-hoc comparisons showed that both for 6 c/deg gratings ($p = 0.0008$) and 1.5 c/deg gratings, the frequency-based attentional effect (L+F+ vs. L+F-) was much larger over the left hemisphere (irrespective of visual field of stimulation), as can be appreciated in Fig. 2. Also significant was the main effect of attentional task ($F(4,24) = 3.1$, $p < 0.03$), with larger C1 to target (L+F+) than location-specific (L-F+) or frequency-specific (L+F-) non-targets, which in turns were more negative than C1 to irrelevant stimuli (L-F-), as demonstrated by post-hoc comparisons among means ($p < 0.002$) and visible in Fig. 3.
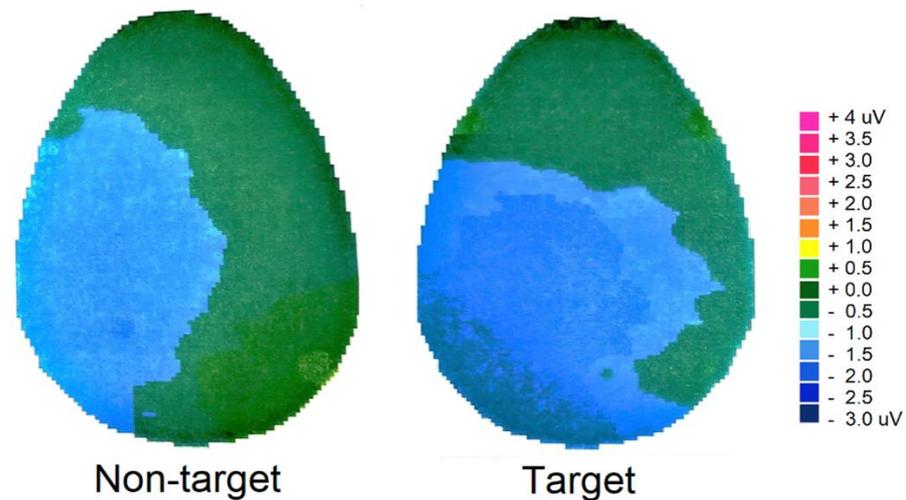
Figure 3. Topographical maps (top view) of scalp voltage of C1 component recorded in response to 1.5 c/deg gratings in the left visual field, when target and when non-target. As can be observed, the response was ipsilateral to the stimulated field, and was modulated by attention, being more negative to target- than non-target gratings.

P1 Component.

The significant electrode factor showed that P1 was more focused over occipital (O1, O2, OL, OR) than infero/temporal scalp areas (F $(2,12)$= 4.68, p <0.03) as also visible in topographical maps of Fig. 4.
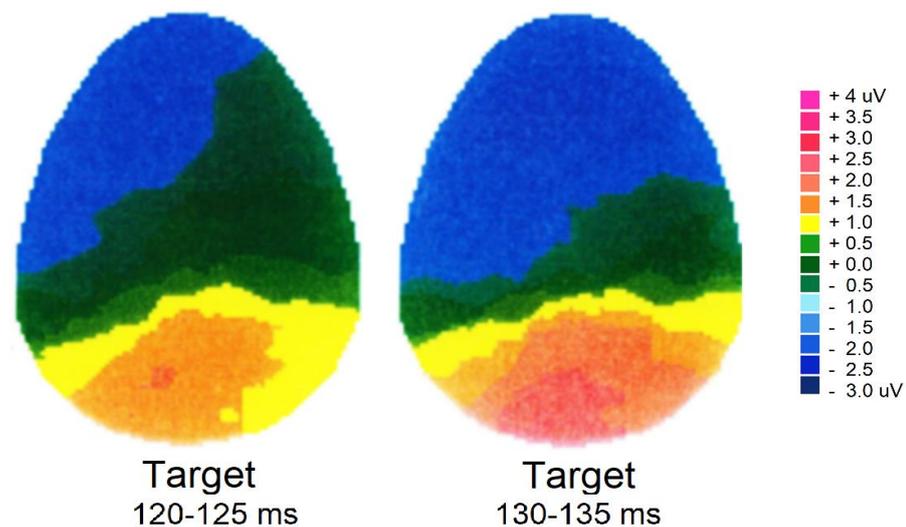

Figure 4. Topographical maps (top view) of scalp voltage of P1 component recorded in response to 1.5 c/deg gratings presented in the RVF. As can be seen, the elicited positive potential is first contralateral to the stimulated field (left hemisphere) and then as times goes by it propagates to the ipsilateral one.

The ANOVA yielded the significant effect of attention condition (F $(4,24)$=4.08, p<0.02) with larger P1 responses to target than location-specific stimuli (p=0.024, L-F+), and, in turn to location- and frequency-specific than irrelevant gratings (as shown by

post hoc comparisons, p=0.0001). The attentional effect was smaller for stimuli presented in the LVF (right hemisphere) as shown by the significant triple interaction of Attention x Electrode x Hemisphere (F(8,48)=2.2, p<0.04). Furthermore, frequency-specific effects (L+F+ vs. L+F-) were larger (p<0.01) at striate and extra-striate than infero/temporal scalp areas.

Selection Negativity (SN)

The ANOVA performed on SN mean area amplitude values showed a significant effect of attention condition (F(4,24)=8.3, p<0.0002). Post-hoc comparisons showed large statistical differences between SN to targets and all other stimulus types (see Fig. 5, left). The significance of electrode factor (F(2,12)=5.02; p<0.02) and relative post-hoc comparisons showed that SN was of maximal amplitude over occipital scalp sites.
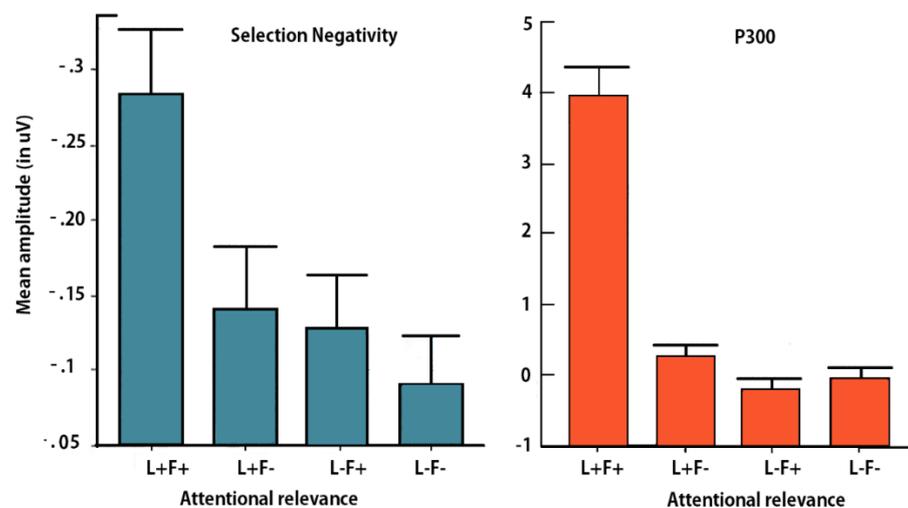

Figure 5. (Left) Mean amplitude values of Selection Negativity (165-330 ms) recorded in response to gratings when target, when sharing one feature with target or when irrelevant, independent of spatial frequency of stimulation. (Right) Mean amplitude values of P300 (330-600 ms) recorded in the same attention conditions as for the SN, no matter the spatial frequency considered.

P300 component

The ANOVA performed on P300 amplitude values gave rise to the significance of Attention factor (F(32,192)= 9.5, p<0.0001). Post-hoc comparisons showed that P300 was largely greater to targets than all other stimulus types (see Fig. 5, right). The further interaction of Attention x Electrode (F(4,240)= 24.8, p<0.0001) showed the P300 was of maximal amplitude at centro/parietal sites, as can be clearly appreciated by looking at amplitude data of Fig. 6.
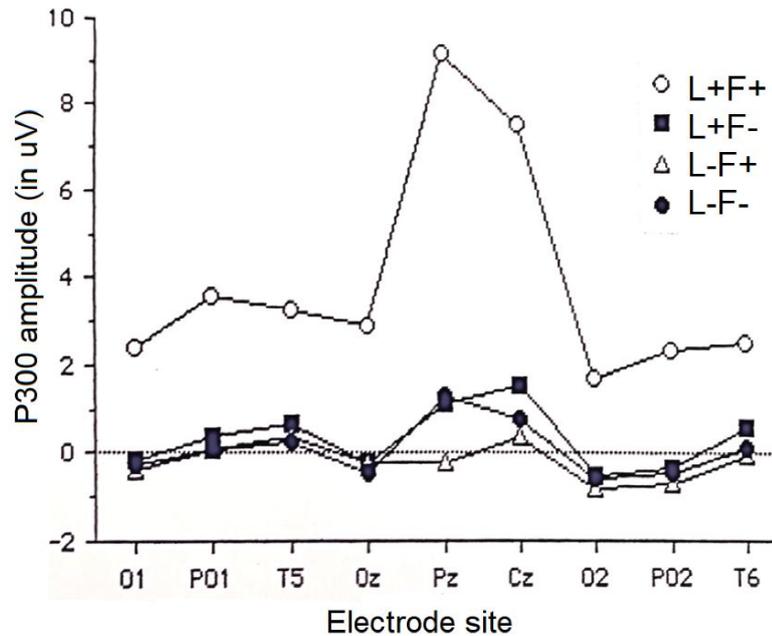
Figure 6. Mean area values recorded in response to spatial frequency gratings when target and when task-irrelevant, at various central, parietal and posterior scalp sites, regardless of spatial frequency of stimulation. A maximum distribution of this ERP component at midline centro/parietal scalp areas can be clearly observed.

4. Discussion

Aim of this study was to explore the existence of hemispheric asymmetries for attentional selection of spatial frequency gratings. Overall, RTs to target gratings presented in the RVF (left hemisphere) were faster than those to stimuli presented in the LVF (right hemisphere), regardless of gratings spatial frequency and response hand. This would support the hypothesis according to which the left hemisphere would have a greater selective capacity in subtle discrimination tasks [38], a more analytical attentional strategy [39], and would be dominant in object-based attentional selection [9].

Moreover, ERP data showed that selective attention modulated the earliest sensory responses. C1 was enhanced in negativity in response to targets (L+F+) than frequency-specific stimuli (L+F-). In turn, C1 elicited by the latter was more negative than that elicited by spatial frequency gratings irrelevant in both features. These results fit well with the more recent literature on ERP attentional modulation of striate cortex during selective attention to grating spatial frequency [37,40].

P1 was also modulated by attention, being more positive to targets than location-specific stimuli. In turn, irrelevant stimuli elicited a smaller P1 than gratings sharing only one feature with target. As predicted by the literature, C1 was larger to ipsilateral stimuli [41,42] and enhanced in negativity by attention [43], while P1, focused on lateral occipital sites and enhanced in positivity by attention [44,37], was larger to contralateral stimuli.

The attentional effects grew as post-stimulus processing latency increased and showed a more focused attentional gating for later latency components. Indeed, *Selec-*

tion negativity, and even more, P300 responses were strongly enhanced by spatial frequency targetness, and less responsive to the attentional relevance of one single feature (either location or spatial frequency of gratings). This evidence fits well with previous ERP literature on spatial frequency selection [45,30,31,32,27], demonstrating that the bandwidth of selective attention effect narrowed during the processing time course.

In the present investigation, the most interesting piece of data was the hemispheric asymmetry in attentional selection, evidenced by C1 and P1 sensory responses, also fitting with behavioral data trend. Indeed, C1 (60-100 ms) data showed that for both 6 c/deg gratings (p=0.0008) and 1.5 c/deg gratings the frequency-specific attentional effect (L+F+ vs. L+F-) was stronger over the left hemisphere, irrespective of visual field of stimulation. Consistently, at P1 level (110-16 ms) the attentional effect was larger for stimuli presented in the RVF (left hemisphere), as shown by the significance of the triple interaction of Attention x Electrode x Hemisphere.

This evidence of a left hemispheric advantage is consistent with previous ERP studies on object-based selective attention for shape [22], orientation [46], color [20], as well as local vs. global stimuli [4] and illusory contour detection [17]. More closely, these data recall the left-sided attentional effect for N1 response (100-200 ms) found in a task in which the orientation of spatial frequency gratings was the target feature [47]. A N165 attentional modulation was also left-sided in a task requiring the selection of the check size of checkerboards of different spatial frequencies [29].

Overall, these data (which, in our knowledge, are the earliest-latency attention effect of a hemispheric asymmetry in the selection of spatial frequency), fully support the theory advanced by Sergent [48] according to which the left hemisphere would be dominant in the processing of local elements of visual information, such as small check sizes, subtle bars or multiple luminance variations. Indeed, regardless of response hand, we also found in the present study that targets were more quickly detected when appeared in the observers' RVF (left hemisphere). From a broader perspective, this line of evidence might also account for the left hemispheric lateralization of the *visual word form area* (VWFA, namely the fusiform gyrus of the occipito/temporal cortex) devoted to orthographic processing [49,50], since letters are characterized by higher spatial frequencies. On the opposite side, the right hemispheric advantage for low spatial frequencies, global processing would explain the right-sided lateralization (at least in the male brain) of the *fusiform face area* (FFA) for the holistic recognition of faces [51,52].

Study limits. One limit of the present investigation might be the limited sample size, so that further investigation might be needed to corroborate the present findings that, however, appear solid from the statistical point of view.

Conflicts of Interest: The authors declare no conflict of interest.

5. References

1. Christian, S. *Cerebral Asymmetries in Sensory and Perceptual Processing*, 1st Ed, **Elsevier,** North Holland 1997. **ISBN:** 9780444825100.
2. Hellige, J.B.; Laeng, B.; Michimata, C. *Processing asymmetries in the visual system.* In K. Hugdahl & R. Westerhausen (Eds.), *The two halves of the brain: Information processing in the cerebral hemispheres* (p. 379–415). MIT Press, 2010.
3. Hugdahl, K. Hemispheric asymmetry: contributions from brain imaging. Wiley Interdiscip Rev Cogn Sci. **2011** Sep;2(5):461-478.

4. Gable, P.A.; Poole, B.D.; Cook, M.S. Asymmetrical hemisphere activation enhances global-local processing. Brain Cogn. 2013, 83, 337–341.

5. Van Kleeck, M.H. Hemispheric differences in global versus local processing of hierarchical visual stimuli by normal subjects: New data and a meta-analysis of previous studies. *Neuropsychol* **1989**, *27*, 1165–1178.

6.   Yamaguchi, S.; Yamagata, S.; Kobayashi, S. Cerebral asymmetry of the "top-down" allocation of attention to global and local features. *J. Neurosci.* **2000**, *20*, RC72

7. Yovel, G.; Levy, J.; Yovel, I. Hemispheric asymmetries for global and local visual perception: effects of stimulus and task factors. J Exp Psychol Hum Percept Perform. **2001** Dec;27(6):1369-85.

8. Johannes, S.; Wieringa, B.M.; Matzke, M.; Münte, T.F. Hierarchical visual stimuli: Electrophysiological evidence for separate left hemispheric global and local processing mechanisms in humans. *Neurosci. Lett.* **1996**, *210*, 111–114.

9. Proverbio, A.M. Left and Right Hemisphere Role for Selective and Sustained Attention: An Electrophysiological Approach. Ph.D. Thesis, University of Padua, Padua, 1993.

10. Proverbio, A.M.; Zani, A.; Avella, C. Hemispheric asymmetries for spatial frequency discrimination in a selective attention task. *Brain Cogn.* **1997**, *34*, 311–320.

11. Robertson, L.C.; Lamb, M.R. Neuropsychological contributions to theories of part/whole organization. *Cognit. Psychol.* **1991**, *23*, 299–330.

12. Robertson, L.C.; Lamb, M.R.; Knight, R.T. Effects of lesions of temporal-parietal junction on perceptual and attentional processing in humans. *J. Neurosci.* **1988**, *8*, 3757–3769.

13. Navon, D. Forest before trees: The precedence of global features in visual perception. *Cognit. Psychol.* **1977**, *9*, 353–383.

14. Christie, J.; Ginsberg, J.P.; Steedman, J.; Fridriksson, J.; Bonilha, L.; Rorden, C. Global versus local processing: seeing the left side of the forest and the right side of the trees. Front Hum Neurosci. **2012** Feb 22;6:28.

15. Proverbio, A.M.; Minniti, A.; Zani, A. Electrophysiological evidence of a perceptual precedence of global vs. local visual information. *Cognit. Brain Res.* **1998**, *6*, 321–334.

16. Fink, G.R.; Halligan, P.W.; Marshall, J.C.; Frith, C.D.; Frackowiak, R.S.; Dolan, R.J. Where in the brain does visual attention select the forest and the trees? Nature **1996** Aug 15;382(6592):626-8.

17.   Proverbio, A.M.; Zani, A. Electrophysiological indexes of illusory contours perception in humans. *Neuropsychol* **2002**, *40*, 479–491.

18. Baas, J.M.; Kenemans, J.L.; Mangun, G.R. Selective attention to spatial frequency: An ERP and source localization analysis. *Clin. Neurophysiol.* **2002**, *113*, 1840–1854.

19. Georgopoulos, A.P.; Whang, K.; Georgopoulos, M.A.; Tagaris, G.A.; Amirikian, B.; Richter, W.; Kim, S.; Uğurbil, K. Functional magnetic resonance imaging of visual object construction and shape discrimination: Relations among task, hemispheric lateralization, and gender. *J. Cognit. Neurosci.* **2001**, *13*, 72–89.

20. Proverbio, A.M.; Burco, F.; Del Zotto, M.; Zani, A. Blue piglets? Electrophysiological evidence for the primacy of shape over color in object recognition. *Cognit. Brain Res.* **2004**, *18*, 288–300.

21. Milham, M.P.; Banich, M.T.; Webb, A.; Barad, V.; Cohen, N.J.; Wszalek, T.; Kramer, A.F. The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Cognit. Brain Res.* **2001**, *12*, 467–473.

22. Orlandi, A.; Proverbio, A.M. Left-Hemispheric Asymmetry for Object-Based Attention: an ERP Study. Brain Sci. **2019**, 8;9(11), 315. doi: 10.3390/brainsci9110315.

23. Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. Ann Rev Neurosci, 34, 569–599.

24. Nobre, A.C.; Sebestyen, G.N.; Gitelman, D.R.; Mesulam, M.M.; Frackowiack, R.S.; Frith, C.D. Functional localization of the system for visuospatial attention using positron emission tomography. *Brain* **1997**;120:515–533.

25. Pardo, J.V.; Fox, P.T.; Raichle, M.E. Localization of a human system for sustained attention by positron emission tomography. Nature. **1991** Jan 3;349(6304): 61-4.

26. Proverbio, A.M.; Zani, A.; Avella, C. Differential activation of multiple current sources of foveal VEPs as a function of spatial frequency. *Brain Top* **1996**, *9*, 59–68.

27. Martınez, A.; Di Russo, F.; Anllo-Vento, L.; Hillyard, S.A. Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. *Clin. Neurophysiol.* **2001**, *112*, 1980–1998.

28. Dos Santos, N.A.; Andrade, S.M.; Fernandez Calvo, B. Detection of spatial frequency in brain-damaged patients: influence of hemispheric asymmetries and hemineglect. Front Hum Neurosci. **2013** Apr 3;7:92.

29. Zani, A.; Proverbio, A.M. ERP signs of early selective attention effects to check size. *Electroencephal. Clin. Neurophysiol.* **1995**, *95*, 277–292.

30. Harter, M.R.; Previc, F.H. (1978). Size-specific information channels and selective attention: visual evoked potentials and behavioural measures**.** Electroenceph. Clin. Neurophysiol. **1978**, 45, pp. 628-640.

31. Harter, M.R., White C.T. Evoked cortical response to checkerboard patterns: effect of check-size as a function of visual acuity**.** Electroenceph. Clin. Neurophysiol. **1970**, 28, pp. 48-54.

32. Harter, M.R., C.J. Aine, C. Schroeder (1982). Hemispheric differences in the neural processing of stimulus location and type: effects of selective attention on visual evoked potentials. Neuropsychol. **1982**, 20, pp. 421-438.

33. Mauguiere, F.; Giard, M.H.; Ibanez, V.; Pernier, J. Sequential spatial maps of visual potentials evoked by checkerboard-pattern reversal: effect of the retinal field stimulated on response topography. Rev Electroencephalogr Neurophysiol Clin **1985**, 15, pp. 129-137.

34. Hudnell, H.K.; Boyes, W.K.; Otto, D.A. Stationary pattern adaptation and the early components in human visual evoked potentials. Electroencephalogr Clin Neurophysiol. **1990**, 77, pp. 190-198.

35. Blumhardt, L.D.; Barret, G.; Halliday, A.M.; Kriss, A. The effect of field size on the pattern reversal visual evoked response. Clin Vision Sci **1989**, 4, pp. 27-40.

36. Bodis-Wollner, I.; Brannan, J.R.; Nicoll, J.; Frkovic, S.; Mylin, L.H. A short latency cortical component of the foveal VEP is revealed by hemifield stimulation. Electroencephal Clin Neurophysiol **1992**, 84, pp. 201-208.

37. Proverbio, A.M.; Del Zotto, M.; Zani, A. Electrical neuroimaging evidence that spatial frequency-based selective attention affects V1 activity as early as 40-60 ms in humans. BMC Neurosci. **2010**, May 6;11:59.

38. Reuter-Lorentz, P.A.; Kinsbourne, M.; Moscovitch, M. Hemispheric control of spatial attention. Brain Cogn. **1990**, 12: 240-266.

39. Palmer, T.; Tzeng, O.J. Cerebral asymmetry in visual attention. Brain Cogn. **1990**, 13: 46-58. 1.

40. Papera, M.; Richards, A. Attentional gain and processing capacity limits predict the propensity to neglect unexpected visual stimuli. Psychophysiol. **2016** May;53(5):634-49. doi: 10.1111/psyp.12614.

41. Jeffreys, D.A.; Axford, J.G. Source locations of pattern-specific components of human visual evoked potentials. I. Component of striate cortical origin. Exp Brain Res. **1972**, 16**,** 1–21.

42. Zani, A.; Proverbio, A.M. Selective attention to spatial frequency gratings affects visual processing as early as 60 msec. poststimulus. Percept Mot Skills. **2009** Aug;109(1):140-58.

43. Zani, A.; Proverbio, A.M. Is that a belt or a snake? Object attentional selection affects the early stages of visual sensory processing. Behav Brain Funct **2012**, 8, 6.

44. Zani, A.; Proverbio, A.M. Endogenous attention to object features modulates the ERP C1 component, *Cog Neurosci* **2018**, 9:1-2, 66-67.

45. Czigler, I.; Balázs, L.; Lénárt, A. Attention to features of separate objects: an ERP study of target-shooters and control participants. Int J Psychophysiol. 1998 Dec;31(1):77-87. doi: 10.1016/s0167-8760(98)00045-2.

46. Orlandi, A.; Proverbio, A.M. ERP indices of an orientation-dependent recognition of the human body schema. Neuropsychol. **2020**, Sep;146, 107535.

47. Proverbio, A.M.; Esposito, P., Zani, A. Early involvement of the temporal area in attentional selection of grating orientation: an ERP study. Brain Res Cogn Brain Res. **2002** Feb;13(1):139-51.

48. Sergent, J. The cerebral balance of power: Confrontation or cooperation? *J Exp Psychol: Hum Percept Perform* **1982**, 8(2), 253–272

49. Proverbio, A.M.; Zani, A.; Adorni, R. The left fusiform area is affected by written frequency of words. Neuropsychol. **2008**; 46(9):2292-9.

50. Fink, G.R.; Canário, N.; Jorge, L.; Castelo-Branco, M. Distinct mechanisms drive hemispheric lateralization of object recognition in the visual word form and fusiform face areas. Brain Lang. **2020** Nov;210:104860.

51. Halligan, P.W.; Marshall, J.C.; Frith, C.D.; Frackowiak, R.S.J.; Dolan, R.J. Where in the brain does visual attention select the forest and the trees? *Nature* **1996**, *382*, 626.

52. Hildesheim, F.E.; Debus, I.; Kessler, R.; Thome, I.; Zimmermann, K.M.; Steinsträter, O.; Sommer, J.; Kamp-Becker, I.; Stark, R.; Jansen, A. The Trajectory of Hemispheric Lateralization in the Core System of Face Processing: A Cross-Sectional Functional Magnetic Resonance Imaging Pilot Study. Front Psychol. **2020** Oct 2;11:507199.