Asymmetry in visual evoked potentials to gratings registered in the two hemispheres of the human brain

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Abstract. The study aimed at testing, by a visual evoked potential method, the hypothesis of the hemispheric specialization in processing of high and low spatial frequencies. Twenty four right-handed subjects (12 males and 12 females) were presented with square-wave vertical gratings of various spatial frequencies (0.67, 0.86, 1.20, 2.00, 2.40, 3.00, 3.30, 6.00 and 7.50 c/deg). Gratings were presented in nine separate blocks each containing 64 exposures. Time of exposure was 30 ms and the interstimulus interval varied from 2 to 3.5 s. VEPs were recorded with electrodes located at O1 and O2 and referred to Cz according to the 10/20 system. Amplitudes and latencies of two VEP components (N130-150 and P200-240) were analyzed. The results showed larger amplitudes of VEPs registered in the right hemisphere of both males and females. This difference, however, was apparent in the earlier component of VEPs in females and in the later component in males. The observed hemispheric asymmetry did not depend on the spatial frequency of grating. Females demonstrated longer latencies than males for both N and P components. Our data suggest that the right hemisphere predominates in processing grating stimuli, but the dynamics of this process differ in the two sexes. The results do not support Sergent’s hypothesis which postulate the right hemisphere specialization for low spatial frequencies and the left hemisphere specialization for high spatial frequencies.

Key words: hemispheric asymmetry, evoked potentials, gratings, spatial frequency
INTRODUCTION

For the time of Sperry’s pioneer investigations on comissurotomized patients a considerable amount of data has been collected indicating that the two hemispheres of the human brain specialize in various functions. That growing interest in the lateralization of brain functions resulted also in formulation of several theoretical concepts which intended to explain the variety of experimental findings (Zaidel 1978, Bradshaw and Nettleton 1981, Hellige 1983). According to one of the most popular theory the left hemisphere is superior in dealing with various kinds of verbal material and the right hemisphere dominates in processing of nonverbal stimuli. Another hypothesis, which become a basis for interpretation of many researches, proposed that the left hemisphere processes the incoming information in an analytical and sequential manner, whereas the right hemisphere does it in a global, holistic way. Unfortunately, none of these theories was able to account for the existing data.

In early eighties there appeared a quite new theoretical approach to the problem of hemispheric specialization. J. Sergent postulated that the two hemispheres differ in their ability to process high and low spatial frequency information (Sergent 1982, 1983, 1985). Basing on the analysis of several earlier papers Sergent assumed that the left hemisphere is biased toward efficient use of high spatial frequencies, whereas the right hemisphere shows an advantage in handling low spatial frequencies.

That new hypothesis attracted much attention of the researchers investigating the problem of brain lateralization. Many experiments have been carried out to verify it. Most of them used the traditional tachistoscopic, lateral presentation method, using both simple stimuli of the type of grating controlled with respect of their spatial frequency content (Rose 1983, Fiorentini and Berardi 1984, Kitterle and Kaye 1985, Peterzell et al. 1989, Kitterle et al. 1990, Nevskaya et al. 1990, Kitterle and Selig 1991), and more complex pictures of natural objects which were filtered or blurred to remove high frequency components (Sergent 1985, Johnson and Hellige 1986, Michimata and Hellige 1987, Nevskaja and Leushina 1987, Petrzell et al. 1989, Christman 1990). Those researches were accompanied by few clinical studies on patients with unilateral brain damage (Grabowska et al. 1989, Fendrich and Gazzaniga 1990, Spinelli et al. 1990).

The results of these researches appeared to be very inconsistent. Although, some of the data directly corroborated the Sergent’s predictions, i.e. they suggested the right hemisphere specialization for low and the left hemisphere specialization for high spatial frequencies (Sergent 1985, Kitterle et al. 1990 exp. 4, Kitterle and Selig 1991), there was also quite a number of studies which showed the right hemisphere superiority in processing a wide spectrum of spatial frequencies (Rovamo and Virsu 1979, Beaton and Blakemore 1981, Grabowska et al. 1989, Kitterle et al. 1990 exp. 2, Nevskaya et al. 1990). Moreover, some researchers did not find any hemispheric differences (Peterzell et al. 1989, Spinelli et al. 1990).

As the behavioural studies did not resolve the question of the possible asymmetrical involvement of the two hemispheres in the spatial frequency processing, during the last few years there have appeared a few electrophysiological studies which have addressed the same issue.

Meccacci and Spinelli (1987) recorded, in the left and right temporal lobes, visual evoked potentials (VEPs) to checkerboard patterns which were phase-reversed (i.e. white checks were reversed with black ones) at a rate of either 1 or 8 Hz. The size of check which might be considered to be equivalent to spatial frequency, was varied from 2.8 min of arc to 16 min. The results of this study showed that time frequency of the reversals was a critical factor influencing VEPs: 8 Hz frequency produced larger visual evoked potentials amplitudes in the left hemisphere, whereas 1 Hz frequency condition yielded the right hemisphere predominance or no clear effect. The size of check did not interact with the hemispheres; although, the smaller the check, the smaller the amplitude of evoked potentials was
observed. The slope of the curve representing that function seemed to be more pronounced for the left hemisphere, though the authors did not mention this. VEPs to black and white reversing checks were also recorded by Cohn et al. (1985). In this study, the temporal frequency and check size were kept constant (2/s and 70 min of arc respectively). Under such a condition, amplitudes registered in the RH were larger.

Another VEPs study by Rebai et al. (1989) is even more relevant to the problem of hemispheric specialization in spatial frequency processing because it utilized gratings of various spatial frequency (0.5-16 c/deg). They were phase reversed at a rate of 4 and 12 Hz. As in the previous investigations, the temporal frequency appeared to be the major factor influencing the pattern of lateralization: the evoked activities were greater in the RH at 4 Hz and in the LH at 12 Hz. This effect was present for the spatial frequencies ranging from 3 to 12 c/deg. Neither lower nor higher spatial frequencies yielded pronounced differences.

The electrophysiological data presented above suggest that the temporal rather than the spatial frequency determines the pattern of hemispheric asymmetry. The results show that high temporal frequencies activate the left hemisphere more, whereas low temporal frequencies, the right hemisphere. If spatial frequency exerts an effect on hemispheric asymmetry, it is masked by a much more pronounced influence of the temporal frequency factor.

The Experiment we present in the this study is another attempt to test spatial frequency theory by an electrophysiological method. We tried to solve the problem of temporal frequency effect by using different method of VEPs measurement than that of pattern reversal. We used "pattern onset" type of stimulation, i.e. we registered VEPs to grating stimuli separated by a few seconds of interstimulus interval. Such a method not only avoids the temporal frequency problem, but it also makes it possible to study the dynamics of VEP, because its earlier and later components can be registered. This is not possible with the other method where patterns change several times per second. The onset stimulation method has proven to be useful in studies on hemispheric specialization. For example such VEPs studies have shown hemispheric asymmetry for words, faces or emotional stimuli (Rugg 1983, Small 1983, Sobóta et al. 1984, Sobótka and Grodzicka 1989, Sobótka et al. 1992) similar to the RT and accuracy studies.

In the present study we registered VEPs to gratings of various spatial frequency in a condition where no task was given to subject except to look at the stimuli and be attentive. We chose to do this for two reasons: first, we wished to relate our results to electrophysiological studies with pattern reversal, and second, we wanted to see whether sensory stimulation per se (with no task which would require higher cognitive function involvement), could produce asymmetrical response.

**METHODS**

**Subjects**

Twelve males and 12 females ranging from 20 to 40 years of age were tested. Only right-handed subjects (according to the Edinburgh Inventory - Oldfield, 1971), without familial left-handedness were selected, and all had normal or corrected-to-normal vision.

**Material and procedure**

The stimuli consisted of square wave gratings each subtending a circular area with a diameter of 5 deg. Nine different (0.67, 0.86, 1.20, 2.00, 2.40, 3.00, 3.30, 6.00 and 7.50 c/deg) spatial frequencies were presented in separate sessions, each containing 64 exposures. Time of exposure was 30 ms and interstimulus interval was varied randomly from 2 to 3.5 s. Stimuli were presented with a Kodak Carousel 140 slide projector equipped with a Lafayette shutter. The order of experimental sessions was randomly counterbalanced over subjects.

Subjects were comfortably seated in an electrically and acoustically shielded chamber. They were
Evoked potentials recording

The evoked potentials were recorded with silver disc electrodes located over the left and right occipital regions of the scalp (O1 and O2 according to the 10/20 system) and referred to Cz. The grounded electrode was placed on central forehead. Electrode impedances were below 5,000 Ω and particular care was taken to equalize impedances of the left and right side links. The electrical signals were amplified by differential amplifiers of bandwidth 0.23-30 Hz and gain 25x10^3. Signals from the EEG amplifiers were digitized on IBM AT compatible computer. Sampling rate was 3 ms. The registration began 250 m prior to and finished 800 ms after the stimulus onset. In each session 64 potentials were summed, averaged, and stored on a computer disk.

RESULTS

Figure 1 shows examples of VEPs registered in the left and right hemispheres of four subjects. They requested to fixate a dot in the centre of a screen placed 180 cm from their eyes. At the beginning of the experiment subjects were presented with several grating stimuli to make them familiar with the experimental situation and to reject orientation response. The subjects’ behaviour was observed on a TV monitor.
Amplitudes of N 130 males

![Diagram showing amplitudes of N130 in left and right hemispheres for male subjects](image)

Fig. 2. Mean amplitudes of N130 registered in the left and right hemispheres of male subjects. The amplitudes are plotted as a function of spatial frequency of the grating stimuli.

Indicate that although, in the majority of subjects two regularly appearing components could be distinguished (an earlier negative N and later positive P waves), the individual recordings differed to some extent in overall shape, amplitude and latency. That created some problems for identification of particular VEPs components in different subjects. In identifying them we considered both the regularities appearing in recordings of individual subjects (there were 18 recordings for each subject) and those which were evident in different subjects. That problem can be illustrated by analyzing VEPs presented in the upper right of Fig. 1 (subject D.H.). The N and P components in that recording have shorter latencies than those in other subjects. One may doubt, therefore, whether they represent similar brain processes. However, just at those latencies the VEPs registered in subjects D.H. contained regular positive and negative waves (other deflections were much smaller and appeared only occasionally). Moreover, they were similar in their shapes and latencies to some other recordings not shown in Fig. 1. The VEPs registered in our 24 subjects formed a continuum and thus we could not limit the criteria of identification of particular VEPs components to very narrow bands of latencies.

**VEPs latency**

A repeated measures analysis of variance with sex (male, female), hemisphere (left, right) and spatial frequency, as factors, performed separately on N and P latency data, revealed a significant main effect of sex \((F_{1,22}=6.18, P<0.02\) and \(F_{1,22}=12.83, P<0.002\) for N and P components respectively). Both for earlier and for later components VEPs of males had shorter latencies than those of females. The mean latencies of N component were 130 and 150 ms for male and female subjects respectively, and the mean latencies of P component were 200 and 240 ms. Neither the hemisphere nor the spatial frequency influenced the VEPs latency. Interactions were also statistically nonsignificant.
Amplitudes of N 150
females

Fig. 3. Mean amplitudes of N150 registered in the left and right hemispheres of female subjects. The amplitudes are plotted as a function of spatial frequency of the grating stimuli.

**VEPs amplitude**

Since the latencies of the two VEPs components significantly differed in male and female subjects, an analysis was performed separately for those two groups of subjects. The amplitudes of the two VEPs components were estimated in relation to zero line determined on the basis of EEG recording during the 250 msec period preceding the stimulus onset.

**THE EARLY N130-150 COMPONENT**

The amplitudes of N130 in males and N150 in females were analyzed with two-factor repeated measures ANOVAs with hemisphere and frequency as factors. Figure 2 shows mean amplitudes of N130 for male subjects plotted as a function of spatial frequency. The only significant main effect was that of spatial frequency \( (F_{8,88}=2.54, P<0.016) \). Neither the main factor of hemisphere \( (F_{1,11}=0.38, P<0.55) \) nor the interaction between the two factors \( (F_{8,88}=0.59, P<0.78) \) reached statistical significance. Although Fig. 2 might suggest larger amplitudes in the LH, that effect was incidental and resulted from the fact that in five subjects the difference in favour of the LH recordings was very large.

Figure 3 shows amplitudes of the early N150 component averaged over all female subjects. An analysis by a two-factor repeated measures ANOVA revealed significant effects of both hemisphere \( (F_{1,11}=6.39, P<0.03) \) and frequency \( (F_{8,88}=3.64, P<0.03) \) factors, whereas the interaction was not statistically significant \( (F_{8,88}=0.23, P<0.98) \). Potentials registered in the RH were larger than those registered in the LH. This effect was present in all spatial frequency registrations.

**THE LATER P200-240 COMPONENT**

Similar to the earlier N component, two analyses of variance were performed for the later components of P200 in males and P240 in females. ANOVA conducted on P amplitude values in males
Hemispheric asymmetry in VEPs to gratings

Amplitudes of P 200
males

Fig. 4. Mean amplitudes of P200 registered in the left and right hemispheres of male subjects. The amplitudes are plotted as a function of spatial frequency of the grating stimuli.

Amplitudes of P 240
females

Fig. 5. Mean amplitudes of P240 registered in the left and right hemispheres of female subjects. The amplitudes are plotted as a function of spatial frequency of the grating stimuli.
revealed the statistical significance of hemisphere 
\((F_{1,11}=5.16, \ P<0.04)\), the right hemisphere ampli-

tudes being larger than those of the left hemisphere. 
Neither the frequency factor \((F_{8,88}=1.79, \ P<0.09)\) 
or the interaction \((F_{8,88}=1.09, \ P<0.37)\) were sig-

ificant.

ANOVA performed on P240 amplitude values 
in females (Fig. 5) did not show statistically signi-
cificant main effects \((F_{1,11}=0.24, \ P<0.63 \text{ and } F_{8,88}=1.12, \ P<0.36 \text{ for hemisphere and frequency, respectively})\). The interaction was also insignificant \((F_{8,88}=0.37, \ P<0.94)\).

**DISCUSSION**

The results of the present study show that the 
electrical activity of the two hemispheres, elicited 
by grating stimuli, differ: the right hemisphere was 
activated more than the left one. Interestingly these 
differences were apparent either in an earlier (N) or 
in a later (P) component of VEPs, depending on the 
subjects’ gender. In female subjects whose response 
latencies were longer, the hemispheric asymmetry 
emerged readily in the earlier N150 component, 
whereas in male subjects who demonstrated shorter 
latencies, the difference was apparent in the later 
P200 component.

The most important finding, for the purpose this 
study, was that we did not observe any interaction 
between hemisphere and frequency. The differences, 
indicating stronger RH involvement, existed essentially within the whole range of the tested spatial 
frequencies, and they were evident despite the 
lack of any task given to subjects. Our data, there-
fore, do not corroborate the Sergent’s model of 
hemispheric asymmetry either in respect to the 
specific pattern of the brain lateralization or in re-
spect to the level of processing at which the asym-
metry arises. According to Sergent’s view, the two 
hemispheres are equipotential in the efficiency of 
spatial frequency information processing at a lower, 
sensory level; whereas they are biased toward effi-
cient use of higher or lower spatial frequency at 
higher level of processing which involves cognitive 
functions. One problem in resolving the issue of the 
level of processing at which asymmetries arise is 
that the meanings of such terms as "level of process-
ing" or "sensory or cognitive functions", are not pre-
cisely defined. If one restricts testing of the so called 
"early processing" to contrast sensitivity measure-
ment then, indeed, hemispheric asymmetry could 
be rather attributed to processes that occur at a 
"higher cognitive level". Even the contrast sensitiv-
ity studies, however, provide sometimes evidence 
on hemispheric asymmetry. It is important to men-
tion that if such an asymmetry exists, it always 
points to the right hemisphere prevalence (Rovamo 
and Virsu 1979, Beaton and Blakemore 1981, Rao 

Some data indicate that even detection tasks can 
yield asymmetrical results under a condition of 
suprathreshold stimulation (Fiorentini and Berardi 
1984, Kitterle 1990). Moreover, several electrophys-
iological studies provide additional evidence of the 
asymmetrical response of the brain to gratings or 
check-type stimuli, controlled as to their spatial fre-
quency content (Vella et al. 1972, Dustman and 
Snyder 1981, Cohn et al. 1985). Those differences 
were observed despite lack of any "cognitive" en-
gagement of subject. Interestingly, much of these 
data suggested the right hemisphere predominance 
for those stimuli, independent of the spatial fre-
quency components they contained. On the other 
hand there are researches which essentially do par-
allel Sergent’s predictions; when tasks involve rela-
tively complicated decision making processes then 
the interaction between the hemisphere and spatial 
frequency becomes more evident (Kitterle et al. 

Considering these apparently discrepant find-
ings, it is reasonable to assume that hemispheric 
asymmetry emerge both at the "earlier" and "later" 
level of processing and that the specific pattern of 
that asymmetry differ in the two stages. The early 
stage of processing may result in the right hemis-
phere superiority for the whole range of spatial fre-
quencies whereas the later stage of processing in the 
left hemisphere advantage for high spatial frequen-
cies and the right hemisphere advantage for low. 
There is much data which show the right hemis-
Hemispheric asymmetry in the perception of several basic features of visual stimuli. It has been proved that the right hemisphere is superior in depth detection (Grabowska 1983), in colour and brightness sensitivity (Davidoff 1975, Davidoff 1976), in dot detection (Davidoff 1977) and localization (Kimura 1969), in orientation matching (Longden et al. 1976), or in adaptation to orientation (Grabowska 1987, Hegarty et al. 1991). The right-hemisphere superiority for such elementary visuospatial functions may change into a different pattern of hemispheric asymmetry when later cognitive processes are involved. According to the logic of such approach, the brain lateralization should not be considered as a stable feature which determines the left or right hemisphere predominance in a given function, but rather as a dynamic process that depends both on stimuli characteristics and task demands, and that may change in the course of information processing.

Further electrophysiological studies with various task demands would be very useful for learning more about the information processing locus of cerebral lateralization.

Another finding of our study was that the evoked potentials to grating stimuli varied as a function of spatial frequency. That was true only for the earlier components (i.e. N130 in males and N150 in females). The highest amplitudes of VEPs were observed within the region of 2 c/deg, which suggests the highest sensitivity of the visual system for that range of frequencies. This function resemble those of psychophysical threshold contrast sensitivity (Blakemore and Campbell 1969). A direct relationship between thresholds of grating visibility determined by psychophysical and visual evoked potential methods was earlier demonstrated by Campbell and Maffei (1970) and Cannon (1983).

Finally, we wish to note the sex related differences in evoked potentials. Unfortunately, there are very few studies which concern that problem and they do not provide clear data (e.g. Allison et al. 1983, Buchsbaum et al. 1974, Cohn et al. 1985). Our results suggest that the dynamics of the hemispheric asymmetry in male and female subjects differ. In female subjects, who show longer VEPs latencies, hemispheric asymmetry emerges already in the earlier N150 component, whereas in male subjects whose VEPs latencies are shorter, it emerges in the later P200 component. Further studies of electrophysiological hemispheric asymmetries with respect to sex differences might contribute to our understanding of hemispheric asymmetry that seems to be a dynamic process rather than a stable feature.

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REFERENCES


