Optica Applicata, Vol. XLVIII, No. 3, 2018
10.5277/oa180311

Sensory processing related to vergence eye movements – an event-related potential study

Anna PRZEKORACKA-KRAWCZYK[1, 2*], Monika WOJTCZAK-KWAŚNIEWSKA[1, 2], Katarzyna PRZEKORACKA[1, 3], Fabrizio ZERI[3, 4], Ryszard NASKRĘCKI[1, 2]

[1]Laboratory of Vision Science and Optometry, Faculty of Physics, Adam Mickiewicz University, Umultowska 85, 61-614 Poznań, Poland

[2]Vision and Neuroscience Laboratory, NanoBioMedical Centre, Adam Mickiewicz University, Umultowska 85, 61-614 Poznań, Poland

[3]Degree Course in Optics and Optometry, Department of Sciences, Roma TRE University, Viale Guglielmo Marconi 446, 00146, Rome, Italy

[4]Ophthalmic Research Group, School of Life and Health Sciences, Aston University, Aston Triangle, Birmingham, B4 7ET, United Kingdom

[*]Corresponding author: ania_pk@amu.edu.pl

Vergence eye movements, movements executed in opposite directions, have a crucial role in depth perception and are necessary for maintaining proper binocular vision. Despite these facts, the neurophysiological studies of vergence eye movement on humans are rare and give ambiguous results. In the present study, the sensory event-related potentials (ERPs) related to the processing of stimuli called for convergence, divergence and saccade were explored. Sixteen healthy subjects (mean 23 years old) performed reflexive (visually-guided) eye movements and event-related potentials from 64 active electrodes were recorded. The significant preponderance of cortical activity for convergence among three conditions was revealed and it concerned both anterior (larger negativity) and posterior cortex (larger positivity). Here, we also reported the longest latency for convergence. These results may suggest larger cortical representation for stimuli presented in near visual space, thus the preponderance of near cells within cortex, which respond to cross retinal image disparity being a cue for convergence.

Keywords: eye movements, vergences, event-related potentials.

1. Introduction

Eye movements have a crucial role in exploring the world, since they maintain stable and clear images on the fovea of the right and left eyes, enabling a single and detailed perception of different objects and scenes. We shift our gaze in different directions,

performing rightward and leftward saccades, and in different depths through an inward rotation of the eyes (convergence) or an outward rotation of the eyes (divergence) [1]. In everyday activities, exploration of the visual space is performed using both saccades and vergences, however, majority of the studies on the eye movements on humans have been focused on pure saccades only. Neuroanatomy and neurophysiology of the vergences in humans were studied using functional magnetic resonance imaging (fMRI) [2–4] and positron emission tomography (PET) [5]. However, the poor temporal resolution of these investigative techniques does not allow to explore the dynamics of processes related to vergence's control.

According to our knowledge, there are only two studies on humans [6, 7], which used high temporal resolution event-related potentials (ERPs) method, for exploring differences in cortical activation between saccades and vergences.

In the first of these studies, Kapoula *et al*. [6] compared cortical activity preceded reflexive pure saccades, pure vergences and combined eye movements (saccades performed together with vergences). They found higher ERPs for divergence (eye movement executed from near into far space) compared to convergence (eye movement executed from far into near space) and explained this result by different far and near space segregation in the cortex.

In a second EEG study, performed by Tzelepi *et al*. [7], an opposite result was found: stimuli that called for convergence were related to greater negativity than stimuli called for divergence. The authors attributed this conflicting result to the differences between experimental paradigms used in the two studies and the type of the analyses performed. Kapoula *et al*. [6] investigated mechanism of motor preparation (saccade-locked activity) whereas Tzelepi *et al*. [7] examined sensory aspects of eye movement control (response-locked activity). Moreover, in the study by Tzelepi *et al*. [7] divergence eye movements were more predictable than convergence eye movements and this might have resulted in lower activity related to divergences [8].

Looking at the results of the two mentioned studies, the question whether the convergence or the divergence would induce a higher and wider cortical activity is still open. The aim of this study is to provide a further investigation on this topic using an experimental design able to avoid participants to predict the kind of eye movements requested during EEG recording and at the same time controlling the physical features of the stimuli presented in the near and far visual space (LEDs with controlled brightness). Thus, any differences in the ERPs occurred in our study could reflect differences in cortical representation of the stimuli calling for particular eye movement types, but could not be the effect of experimental paradigm used.

2. Materials and methods

2.1. Subjects

Sixteen healthy subjects (four males) participated in the study. The mean age was 23 years (range 21–26). Prior to the EEG examination, the subjects received an optometric assessment. All subjects had a best-corrected visual acuity not higher than 0.0 logMAR,

normal binocular vision, which was defined by the proper ocular alignment, the lack of interocular suppression, vergence ranges in normal values, according to the Morgan norms [9], and a stereoscopic acuity at least 50 sec of arc.

The study was approved by the local Ethics Committee of the Adam Mickiewicz University and was performed in accordance with the Declaration of Helsinki.

2.2. Stimuli and task

In Figure 1, a sketch of the display used in the experiment is presented. Six LEDs were placed on two isovergent circles at far (100 cm from the center of rotation of the eyes, that is 97.5 cm from the bridge of the nose) and near (20 cm from the center of rotation of the eyes, that is 17.5 cm from the bridge of the nose) distance. Lateral LEDs in each isovergent circle were shifted to the right and left by 6 degrees. The brightness of LEDs was controlled using lux meter L-100 (SONOPAN, Białystok, Poland) and was the same for each LED (0.35 lux). The subject' forehead and chin were stabilized to eliminate head movements.

The experiment was performed in a dark room. Each trial started with the central LED (fixation-LED) positioned in the far or near isovergent circle (number 2 or 5 in Fig. 1). The fixation-LED was presented between 2000 to 3000 ms, varied in duration randomly by a step of 50 ms. Eye movements were called when a lateral LED (target-LED) turned on. The target-LED was switched on for 2000 ms. In the experiment, ten types of eye movements were elicited:

1) pure convergences (from LED 2 to LED 5),
2) pure divergences (from LED 5 to LED 2),

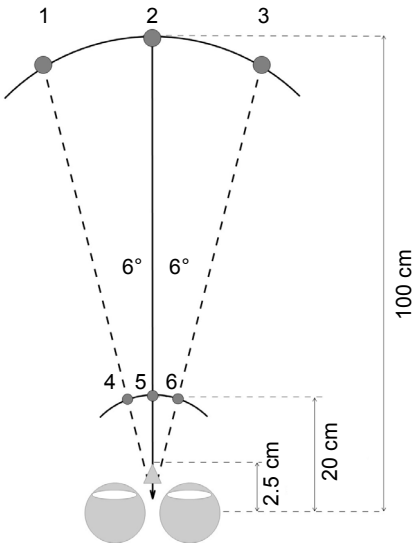

Fig. 1. The sketch of the LEDs display. Each trial started from middle fixation-LED positioned at the far (2) or near (5), then the target-LED, which called for pure divergence (from 5 to 2), pure convergence (from 2 to 5), pure saccade (from 2 to 1 or 3 and from 5 to 4 or 6) was switched on.

3) saccades to the left at far distance (from LED 2 to LED 1),
4) saccades to the right at far distance (from LED 2 to LED 3),
5) saccades to the left at near distance (from LED 5 to LED 4),
6) saccades to the right at near distance (from LED 5 to LED 6),
7) combined convergences to the left (from LED 2 to LED 4),
8) combined convergences to the right (from LED 2 to LED 6),
9) combined divergences to the left (from LED 5 to LED 1), and
10) combined divergences to the right (from LED 5 to LED 3).

The experiment consisted of five experimental blocks. In each block, each type of eye movements (pure convergences, pure divergences, saccades at far distance, saccades at near distance, combined convergences and combined divergences) was required 24 times, for a total of 120 repetitions per each type of eye movements. However, since we were interested in differences between pure saccades and pure vergences, only pure eye movement conditions (pure convergence, pure divergence, pure saccade at far and near distance) were used for statistical analyses. It gave 120 repetitions for convergence and divergence and 120 trials for pure saccades at near and far distance, which were averaged.

Before experiment, each subject was instructed to change the fixation from the fixation-LED to the target-LED as quickly and accurately as possible. Before experiment started, a demo trial block was presented and each type of eye movements was displayed three times.

2.3. Eye movements' recordings and analyses

Eye movements and blinks were registered by three pairs of bipolar electrodes (electrooculogram, EOG). One pair of EOG was mounted on the lower lid and above the eyebrow of the right eye to control blinks and vertical eye movements (vEOG). The remaining two pairs were applied on the inner and outer canthi of the left and right eye to monitor horizontal eye movements (right_hEOG and left_hEOG). EOG signal was amplified by QuickAmp128 amplifier (Brain Products GmbH, Munich, Germany) and recorded with 500 Hz sampling resolution by Brain Vision Recorder (Brain Products GmbH, Munich, Germany). Online high-pass filter at 0.25 Hz and low-pass filter at 30 Hz were used on the EOG channels to control eye movements visually during the experiment.

Next, EOG signal was analyzed offline with Brain Vision Analyzer 2.0.3 (Brain Products GmbH, Munich, Germany). The onset of the eye movements was determined based on data from hEOG channels using macro-application, which was combined with the Brain Vision Analyzer software. First, the amplitude of hEOG value for each eye movement was measured. Then the onset of eye movement was determined as the time where hEOG reached 10% of the amplitude level. The same procedure was performed separately for the right and left hEOG and the values obtained for the monocular hEOG were averaged. The latency of the eye movement was defined as the time measured between the appearance of the target-LED in the marker position and the onset of the eye movement. All improper trials: eye movements in wrong direction and

those characterized by a latency less than 100 ms or greater than 400 ms were excluded from the further analyses. Incorrect eye movements were about 10–15% of all trials.

2.4. EEG recordings and data analyses

EEG was measured from 64 active Ag/AgCl electrodes: FP1, FP2; AF7, AF3, AF4, AF8; F7, F5, F3, F1, Fz, F2, F4, F6, F8; FT9, FT7, FC5, FC3, FC1, FC2, FC4, FC6, FT8, FT10; T7, C5, C3, C1, Cz, C2, C4, C6, T8; TP9, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, TP10; P7, P5, P3, P1, Pz, P2, P4, P6, P8; PO7, PO3, POz, PO4, PO8; PO9, O1, Oz, O2, PO10, positioned according to the extended International 10/20 system [10]. Averaged reference was used and ground electrode was located at AFz. Electrode impedance was kept below 5 kΩ.

The EEG signal has been amplified by the QuickAmp128 (Brain Products GmbH, Munich, Germany), recorded simultaneously with EOG with 500 Hz sampling resolution and stored with Brain Vision Recorder (Brain Products, version 2.0.3). Online low-pass filter at 100 Hz was used, which is implemented in QuickAmp128 (filter value is determined by sampling resolution: 0.2 × sampling resolution). Additionally, high-pass filter at 0.015 Hz was used to exclude slow drifts.

Next offline analyses were carried out with Brain Vision Analyzer (Brain Products, version 2.0.4) software. First, the data was low-pass filtered at 30 Hz and segmented from 500 ms before to 800 ms after the stimulus onset. Segments with incorrect eye movements were removed. Ocular correction was carried out with the semiautomatic independent component analyses (ICA) implemented in Brain Vision Analyzer. Trials with major artifacts (maximum allowed voltage step: 50 μV/ms; minimum/maximum allowed amplitude: ±150 μV; maximum difference: 200 μV; lowest allowed activity within 50 ms intervals: 0.1 μV) were excluded from further analyses. Finally, averages were computed for each eye movement type to get ERPs. Based on visual inspection, signal from 24 electrodes was consider for further statistical analyses: AF7, AF3, AF4, AF8, F5, F1, F2, F6, TP7, C1, C2, TP8, P7, P3, P4, P8, PO7, PO3, PO4, PO8, PO9, O1, O2, PO10.

Since in this study we were interested in the sensory stimulus-locked activity, the signal in time window from 70 to 130 ms relative to the stimulus calling for saccades, and in time window from 70 to 150 ms relative to the stimulus calling for convergence and divergence, were selected for further statistical analyses. The difference in selected time windows between saccades and vergences conditions resulted from difference in eye movement latencies, since saccades were characterized by the shortest latencies and the activation observed for saccade in the last time interval might reflect spike potential related to the eye movement execution [11].

2.5. Statistical analyses

Statistical analyses were performed with STATISTICA 12 software.

The latencies of correctly performed eye movements were averaged and analyzed by ANOVAs with repeated measures with the *eye movement type* factor at three levels: saccades (Sacc), convergence (Conv) and divergence (Div).

Statistical analyses of the ERPs were carried out using ANOVA with repeated measures with the following factors:

1) *time* (four levels: 70–90 ms, 90–110 ms, 110–130 ms, 130–150 ms);

2) *stimulus type* (three levels: Sacc-stimulus, Conv-stimulus and Div-stimulus);

3) *electrode group* (six levels: AF – anterior-frontal, F – frontal, C – central, P – parietal, PO – parieto-occipital, O – occipital);

4) *hemisphere* (two levels: left, right);

5) *electrode position* (with respect to the midline of the head, two levels: far, near).

The significant effects were assigned at the $p \leq 0.05$ level. Post-hoc Tukey test was performed after ANOVA test and Huynh–Feldt correction was applied when necessary.

3. Results

3.1. Latencies of the eye movements

The latencies of the eye movements are shown in Fig. 2. As can be seen, saccades had shorter latency (178 ± 19 ms) than divergence (221 ± 46 ms) and convergence (230 ± 46 ms). The differences between latencies were confirmed by a significant main effect of the *eye movement type* ($F_{2, 62} = 13.51$, $p < 0.001$, $\eta^2 = 0.30$). Post-hoc test revealed that indeed saccades were characterized by the shortest latencies compared to both convergences ($p < 0.001$) and divergences ($p < 0.001$). However, no difference in the mean latencies between convergences and divergences was found ($p = 0.569$).

3.2. Event-related potentials

Stimulus-onset ERPs observed for three examined conditions are displayed in Fig. 3. For better visualization, topographic map of ERPs (Fig. 4) and ERPs difference between vergence and saccade stimuli (Fig. 5) are presented.

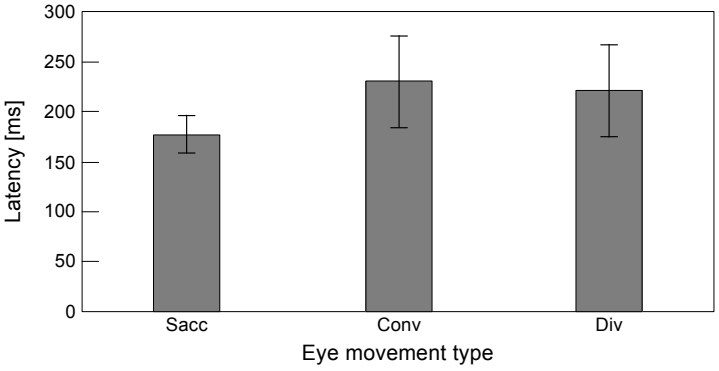

Fig. 2. Eye movement latencies for the three types of eye movements (pure saccades, pure convergences and pure divergences). Vertical bars denote standard deviation (SD). The latency was determined as the time from the appearance of the stimulus to the onset of the eye movement. First, the averaged value for each participant and for each type of eye movement was calculated and then averaged across all the subjects.

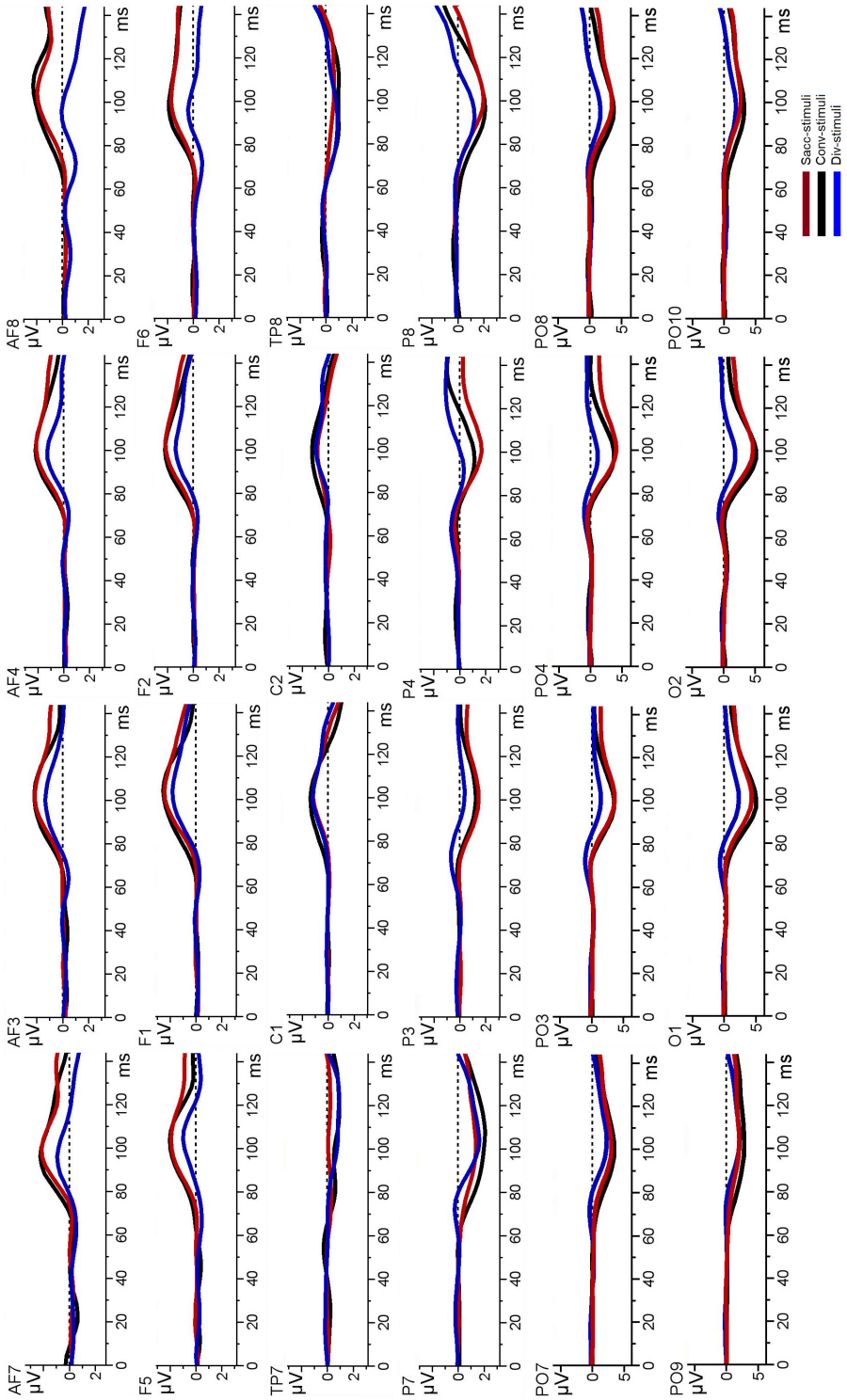

Fig. 3. Grand averages of ERPs in time interval 0–160 ms after the stimulus onset. Each row of graphs corresponds to one electrode groups: AF, F, C, P, PO and O.

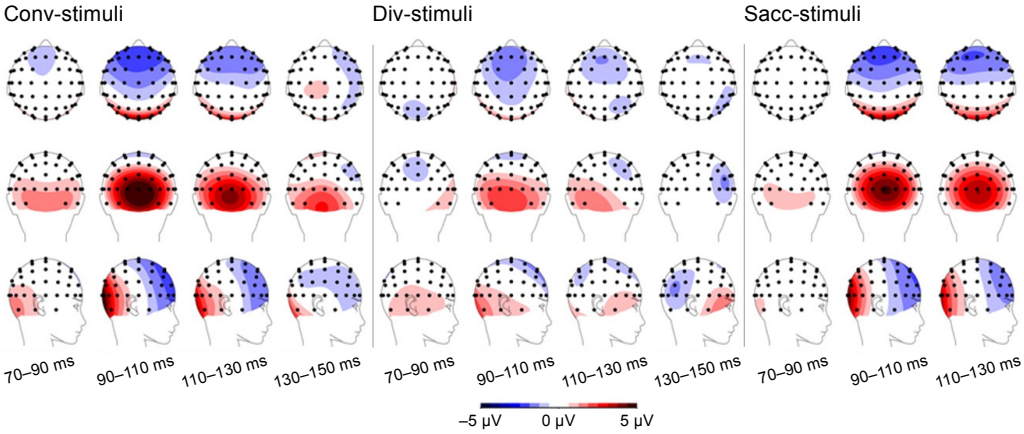

Fig. 4. Topographical maps of ERPs for Conv-stimuli and Div-stimuli in the time window 70–150 ms after the stimulus onset and for Sacc-stimulus in time window 70–130 ms after the stimulus onset.

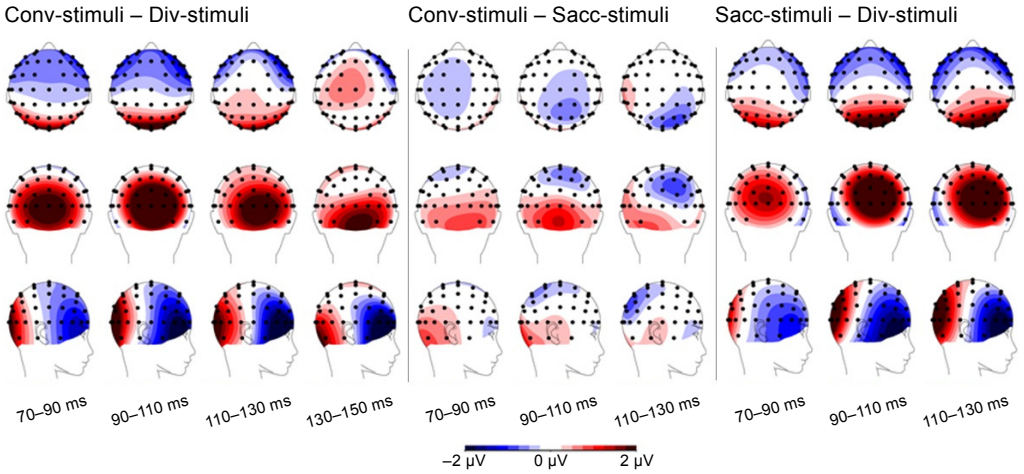

Fig. 5. Differential ERPs for three stimulus types. Potentials of convergences minus potential of divergences, potentials of convergences minus potentials of saccades, and potentials of saccades minus potentials of divergences.

As can be seen, about 70 ms after the stimulus onset, negative ERPs started in the anterior cortex and positive ERPs in posterior region, becoming stronger till the eye movement onset (about 130 ms after the stimulus). ANOVA showed that ERPs was dependent on the *stimulus type*, *electrode group*, *hemisphere*, *electrode position* and *time* (*stimulus type* × *electrode position* × *time* interaction, $F_{6,\,90} = 3.50$, $p = 0.008$, $\eta^2 = 0.19$; *stimulus type* × *electrode group* × *time* interaction, $F_{30,\,450} = 3.66$, $p = 0.004$, $\eta^2 = 0.20$; *stimulus type* × *electrode group* × *electrode position* × *time* interaction,

$F_{30, 450} = 6.24, p < 0.001, \eta^2 = 0.24$; *stimulus type* × *electrode group* × *electrode position* × *hemisphere* × *time* interaction, $F_{30, 450} = 2.25, p = 0.007, \eta^2 = 0.13$). To explain these interactions, separate ANOVAs in each 20-ms time window, were performed.

In the first time window (70–90 ms after the onset of the stimulus), Conv-stimulus evoked small negative ERP on the anterior channels (AF, F groups) and positive ERPs on the posterior electrodes (PO, O groups). Positive ERP was found also for Sacc-stimulus on the posterior channels, but this effect was not observed for Div-stimulus. The differences between conditions were confirmed by significant interaction between *stimulus type* and *electrode group* ($F_{10, 150} = 16.88, p < 0.001, \eta^2 = 0.53$). Post-hoc test showed that ERPs for Conv-stimulus were larger than for Div-stimulus on each electrode group ($p < 0.002$) and larger than for Sacc-stimulus on the O group ($p = 0.021$). Additionally, interaction between *stimulus type*, *electrode group* and *electrode position* ($F_{10, 150} = 5.59$, $p < 0.001$, $\eta^2 = 0.27$) indicated that ERPs evoked by Conv-stimulus were larger than for Div-stimulus on both near and far electrodes, but for Sacc-stimulus significant difference was found only in the whole O group (post-hoc test, $p = 0.002$) and on the far channels from P and PO groups (P7/8, PO7/8, post-hoc test, $p < 0.001$).

In the second time window (90–110 ms after the stimulus onset) ERPs had the largest values. Significant negative ERPs on the anterior channels and positive ERPs over posterior region were found for each type of the stimulus, but again, the strongest ERP value was found for Conv-stimulus and the weakest for Div-stimulus (*stimulus type* × *electrode group* interaction, $F_{10, 150} = 26.66, p < 0.001, \eta^2 = 0.64$). This effect was dependent also on the electrode position (*stimulus type* × *electrode group* × *electrode position* interaction, $F_{10, 150} = 4.60, p < 0.001, \eta^2 = 0.34$), showing that ERPs evoked by Conv-stimulus were larger than ERPs evoked by Div-stimulus, on each channel from all electrode groups (post-hoc, $p < 0.001$), besides C group, and larger than ERPs evoked by Sacc-stimulus on the channels from the whole O group (post-hoc, $p = 0.004$). Post-hoc test also revealed that ERPs evoked by Sacc-stimulus were larger than by Div-stimulus on each channel from anterior (AF and F, $p < 0.001$) and parieto-occipital group ($p < 0.001$) and on the near electrodes from the parietal and occipital groups (P3/4, O1/2, $p < 0.001$).

In the next time window (100–130 ms after stimulus onset) ERPs were dependent on the *stimulus type*, *electrode group* and *electrode position*, as well as on the *hemisphere* (interaction, $F_{10, 150} = 5.60, p < 0.001, \eta^2 = 0.27$). On the anterior channels (AF and F groups), similar pattern of results as in previous time windows was found: negative ERPs of similar value evoked by Conv- and Sacc-stimuli (post-hoc, $p > 0.050$) and significantly lower ERPs for Div-stimulus ($p < 0.001$). On the posterior channels, positive ERPs for Conv-stimulus were larger than for the Div one on all electrode groups (post-hoc, $p < 0.001$). Comparing Conv condition with Sacc one, larger ERPs evoked by the Conv-stimulus were found on the lateral channels of the left hemisphere (TP7, P7, PO9, post-hoc, $p < 0.001$) and on the middle channels from the right hemisphere (P4, PO4, post-hoc, $p < 0.001$). Div-stimuli evoked weaker ERPs than Sacc-stimuli

on the anterior (AF, F groups, post-hoc, $p < 0.001$) and posterior channels (PO, O groups, post-hoc, $p < 0.001$) and on the parietal electrodes from the right hemisphere (P4, P8, post-hoc, $p < 0.001$).

In the last analysed time window (130–150 ms after stimulus onset) ANOVA was performed only for Conv and Div conditions, since in Sacc condition spike potentials related to beginning of the eyes movement could interact with the ERPs (latency of saccades was shorter than latency of the vergences). Here, the ERPs were dependent on the *stimulus type*, *electrode group*, *electrode position* and *hemisphere* (interaction, $F_{5,\,75} = 5.28$, $p < 0.001$, $\eta^2 = 0.26$). The difference between conditions occurred mainly on the lateral channels where over the anterior region negative ERPs for Conv-stimulus and positive ERPs for Div-stimulus were found on the AF7/8 and F6 channels (post-hoc, $p < 0.001$), but on the posterior area significant positive ERPs for Conv-stimulus occurred on the O1/2 channels and on the PO8/9/10 channels, with no significant cortical activity for Div-stimulus (Conv *vs*. Div, post-hoc, $p < 0.001$).

4. Discussion

In the present study, the stimulus-locked cortical activity that is related to the processing of the stimuli called for convergence, divergence and saccades was investigated. The question whether stimuli called for convergence elicit a stronger brain cortex activation compare to divergences, as was found by Tzelepi *et al*. [7], was explored. However, in the present experimental setting, the participant prediction of the required eye movement, that could affect the cortical activation, was controlled by a random presentation of stimuli. Moreover, the study required more participants, more trials and more channels in respect to Tzelepi *et al*. [7] study. This allowed to explore more effectively the topography related to stimulus types calling for different eye movements.

A first outcome of the present study is that the latency of saccades was the shortest among all eye movement types. This is in agreement with other studies showing that vergences take more time to be executed than pure saccades [6, 7], since that kind of eye movements need to combine information from the accommodative and vergence system [12]. Although the latency resulted longer in convergence than divergence, the difference did not reach statistical significance. Interestingly, previous studies on the latencies showed inconsistent results: some researchers revealed longer latency in case of convergence than divergence [6, 7, 13], while other studies showed opposed results [14, 15].

The second outcome of the current study appears particularly interesting. First of all we found significant ERPs mainly over the frontal and occipital cortical regions. Our recent research based on the source analyses on ERPs showed that the neural generators related to the preparation of the vergence eye movements, are located in the frontal eye field and occipital cortex [16]. This could explain why ERPs found in the current study got the highest value on the frontal and occipital channels.

What is crucial for the current paper is that convergence stimuli evoked the greatest ERPs among all examined conditions. This was observed for each electrode groups. Initially, it was seen only within parietal and occipital brain areas, then the differences occurred also between hemispheres, showing larger ERPs on lateral electrodes of the left hemisphere and on the near electrodes of the right hemisphere. The significant preponderance of the activity for Conv-stimuli which evoked crossed retinal image disparity, compared to Div-stimuli, which evoked uncrossed retinal image disparity, or stimuli which stimulated corresponding retinal points (Sacc-stimuli), may reflect larger cortical representation for stimuli presented in near visual space. Binocular retinal disparity is a crucial factor, which triggers vergence eye movements. In the visual system, neurons which respond to crossed (near cells) or uncrossed (far cells) disparities were found in areas of visual cortex [1]. Studies on monkeys and cats revealed that disparity-tuned cells are located in the visual cortices [17–19], frontal eye field (FEF) [20] and also within subcortical areas (superior colliculus) [21]. Moreover, the studies revealed that the number of near cells within cortical areas exceeds the number of far cells. Thus, our results confirm the hypothesis of larger cortical representation of crossed disparity, which also calls for the convergence.

However, it cannot be excluded that the significantly higher activity observed during processing of Conv-stimuli may also be the result of the attention processes. Mangun and Hillyard found out that both attention and concentration processes can enhance the ERPs [22]. Therefore, changes in ERPs might reflect the effect of shifting attention. Valdés-Conroy *et al*. investigated the influence of distance on the ERPs amplitudes (N1 component) and showed that stimuli which appeared within near space elicited more negative amplitude, compared to the stimuli in far space [23]. Although in this study the N1 amplitude between conditions was not compared, because larger time windows were analyzed, the concept that stimuli in near space would enhance cortical activity is in line with the present results.

Tzelepi *et al*. [7] wondered if differences in cortical activity between convergence and divergence stimuli could be the effect of stimulus preponderance. In the current study, prediction of all eye movement types was not possible because the proportion of convergence, saccades and divergence was the same and the type of stimulus was randomly selected. So, higher ERPs for convergence cannot be the result of anticipation of the movement but instead reflect real higher cortical representation of the near stimulus, which call for convergence.

Furthermore, it should be noted that Kapoula *et al*. [6] study showed opposite results: divergent eye movements evoked stronger cortical activity than convergence. Their result could be explained by the differences in the way of data analyses, since they investigated response-locked cortical activity (with respect to the eye movement onset). In the present study, it was chosen an analysis focused on the stimulus-locked activity, similarly to the study by Tzelepi *et al*. [7]. Since response-locked and stimulus-locked activity reflects different aspects of signal processing, differences between

those studies may occur. Future researches comparing sensory and motor-related activity based on the same data sets are necessary to explore differences between stimulus processing and motor preparation related to the vergence eye movements.

Finally, in the current study, larger ERPs within right parietal cortex for Sacc-stimuli compared to Div-stimuli, shortly before the eye movement onset (110–130 ms), were observed. This may be associated with spatial attention and redirecting attention to the left or right. In the study of Shulman *et al*. such asymmetry, associated with right hemisphere dominance in spatial attention and target detection, was found [24]. A further confirmation of this result comes from the study of patients who have lesions in the right hemisphere and were diagnosed with visuo-spatial inattention [25].

5. Conclusions

The aim of the present study was to answer the question whether stimuli called for convergence are associated with the largest cortical activity as was observed by Tzelepi *et al*. [7] or whether the preponderance of activity for convergence stimuli was the effect of experimental design. In the present study, a more robust experimental design enabled us to control potential factors affecting cortical activity, such as the participants' awareness of required eye movement. Also with this new experimental setting, a higher cortical activity was evoked when stimuli appeared in near visual space and thus have crossed retinal disparity that evokes convergence compared to stimuli that evoke divergence. This may reflect the larger cortical representation for Conv-stimuli and/or greater engagement of attention.

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Received August 16, 2017
in revised form December 17, 2017