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EARLY VEP WAVES TO STIMULI-GRATINGS WITH DIFFERENT LENGTH AND WIDTH

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Abstract

Visually evoked potentials (VEPs) to stimuli-gratings with varying length and width were recorded at 3 spatial frequencies (SFs), 1.45, 2.9 and 5.8 c/deg and contrast three times above the detection threshold for each SF. The amplitude of the first negative VEP wave, N1, increased to a greater extent with increase of stimulus length than with increase of stimulus width at higher and medium SFs, 5.8 and 2.9 c/deg. However, at low SF, 1.45 c/deg, the effects of the grating length and the width on N1 amplitude were similar. Moreover, the difference between the effects of stimulus length and width on the amplitude of the second VEP component, P1, was not observed at all three SFs studied. The results obtained, along with the psychophysical data showing stronger effect of stimulus length in comparison with width on the detection threshold [1,2], might be interpreted as neurophysiological evidence that the underlying mechanisms are arrays of elongated receptive fields.

Key words: VEP, spatial summation, receptive fields, spatial frequency

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Introduction. Spatial properties of human grating detecting mechanisms have been intensively studied in both psychophysical [1,2] and electrophysiological [3] experiments. In these studies the length and the width of stimuli-gratings were varied independently, as to this aim the gratings were presented in a 2D Gaussian window with different spatial constants along and perpendicular to the grating orientation. In the psychophysical studies [1,2], threshold contrast for grating detection was measured as a function of grating length and width. It was found that stimulus length (the spatial constant of the Gaussian window along the grating orientation) changed to a higher extent the threshold contrast than stimulus width (the spatial constant of the Gaussian window perpendicular to the grating orientation). FOLEY et al. [1] explained this result by a model in which the stimuli excite an array of slightly elongated receptive fields. The results of the other psychophysical study [2] also demonstrated greater effect of stimulus length than the width on the detection threshold. In addition, it has been found that the difference between length and width effects on the detection threshold is greater at higher SFs – 5.9 and 10.8 c/deg, being smaller at lower SF – 2.9 c/deg or even negligible at the lowest SF – 1.45 c/deg studied. Similarly, the data obtained in the electrophysiological experiments showed stronger effect of stimulus length than width on the visually evoked potentials (VEPs) response [3]. It was found that response amplitudes were larger and consequently the contrast sensitivity was higher for patterns that were elongated along the axis defined by the grating orientation. However, in this study the SF was fixed to one value only, 3 c/deg, and it is not clear whether the difference between the length and width effects on the contrast sensitivity would exist at different SFs as it was observed psychophysically [2]. It is known that the visibility of stimuli might improve with increasing their area because of "probability summation between the outputs of linear independent spatial filters, although non-linear spatial summation can have similar effect" [3]. Thus studying the difference between the length and width effects on contrast sensitivity not only psychophysically, but also by means of VEPs within a wide range of SFs could help to distinguish between probabilistic and physiological summation models.

Methods. ***Stimuli.*** Stimuli were vertical sinusoidal gratings of three different SFs – 1.45, 2.9 and 5.8 c/deg. They were presented in a 2D Gaussian window with independently varied horizontal and vertical spatial constants (σ_x and σ_y). At each SF one fixed value of σ_x or σ_y, respectively was employed (0.58 deg at 1.45 c/deg, 0.29 at 2.9 c/deg and 0.146 at 5.8 c/deg) and the other spatial constant varied within the range of 0.146–2.33 deg. Stimulus contrast was three times above the individual detection threshold, measured at each SF at the smallest values of the grating length and width (for each observer). Stimulus duration was 100 ms.

Apparatus. Stimuli were generated on a black and white monitor (phosphor P4) by electronics designed in our laboratory. The frame rate was 60 Hz, the spatial resolution was 640 × 480 pixels, and the mean luminance – 100 cd/m^2, which was not changed by stimulus onset and offset. Viewing was binocular, with natural pupils, from a distance of 114 cm, at which the screen subtended 11.6/8.7 deg of visual angle at the eyes. The stimuli always appeared in the centre of the screen and small fixation lines were located along the central horizontal line at the distance of $3 \times \sigma$ from the centre.

Procedure and VEP recording. Stimuli of each combination of SF, length and width were presented in separate blocks. The interstimulus interval was varied randomly within the range of 1900–2700 ms. Each daily session consisted of 9–12 blocks, presented in a random order. VEPs were recorded from Oz position (10/20 system) using Ag/AgCl Nihon-Kohden electrodes with a reference to both processi mastoidei and a ground electrode placed on the forehead. An oculogram (EOG) was also recorded from electrodes placed above and below the lateral cantus of the left eye for a detection of eye movements and blink artifacts. EEG and EOG data were recorded using a Nihon-Kohden EEG-4314F (cut-off frequencies of 0.3–70 Hz) together with markers of the stimulus onset. The signals were digitized at a rate of 500 Hz and written to hard disk for off-line analysis. The data records were synchronized to the marker of stimulus onset. The length of VEP segment was chosen to cover 500 ms pre-stimulus and 1000 ms post-stimulus interval. Only artifact-free VEP records were processed. The amplitudes of the VEP components were measured from the baseline to the corresponding peak, as the baseline was defined as a mean value of the traces for 200 ms pre-stimulus interval (−300 ms to −100 ms). Data were averaged over all observers after amplitude normalizing. Observers were instructed to fixate at the screen centre. Depending on signal-to-noise level at each combination of SF, σ_x and σ_y 100–200 sweeps were recorded in 3–4 daily sessions with each subject.

Contrast threshold measurement. Contrast thresholds were measured by the two-interval forced-choice method combined by the staircase procedure (three – correct/one – wrong response).

Observers. Six emmetropic right-handed observers (3 females and 3 males, aged 27–46 years), with a normal (6/6) visual acuity participated in the experiments. The subjects were naive to the aim of the experiments and their informed written consent was obtained according to the declaration of Helsinki.

Results. Early VEPs to grating stimuli at Oz scalp position consisted of negative-positive complex, which is in accordance with the findings of many authors [4–6]. The behaviour of the first negative wave – N1, as a function of stimulus sizes (the length or the width) at different SFs, and averaged over all observers, is illustrated in Fig. 1.

The upper row of panels in this figure corresponds to the N1 amplitude changes and the lower row of panels corresponds to the N1 latency changes caused by grating length and width variations. It might be seen that stimulus enlargement first increased the N1 amplitude and then either did not influence it or even

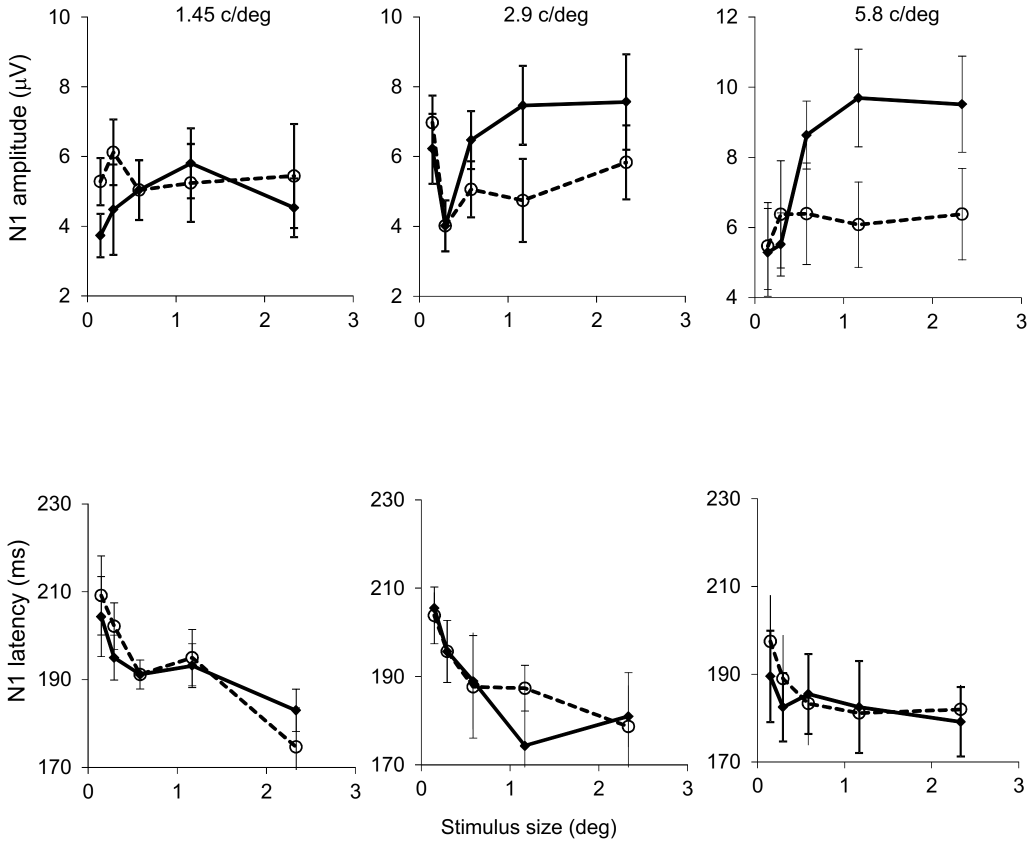

Fig. 1. Amplitudes (upper row) and latencies (lower row) of early VEP N1 wave recorded at Oz scalp position, as functions of stimulus length, σ_y (solid lines and symbols) and stimulus width, σ_x (dashed lines and open symbols), at three SFs: 1.45 c/deg (left panel), 2.9 c/deg (middle panel) and 5.8 c/deg (right panel). Averaged data of six observers

decreased it slightly at the highest size values. Moreover, for test SF of 2.9 c/deg (the middle upper panel) and for SF of 5.8 c/deg (the right upper panel) increasing stimulus length (σ_y) increases substantially the N1 amplitude (the solid lines) whereas increasing stimulus width (σ_x) increases slightly the N1 amplitude (the dashed lines). The difference between the effects of grating length and width on N1 amplitude was statistically significant when the stimulus length and width were higher than 0.58 deg ($F = 7.27$, $p = 0.01$ for SF of 2.9 c/deg and $F = 7.99$, $p < 0.01$ for SF of 5.8 c/deg). At the lowest SF studied (1.45 c/deg) variation of the stimulus sizes caused smaller effect on the N1 amplitude and no statistically significant difference between the effects of grating length and width on the N1 amplitude was observed ($F = 2.35$, $p = 0.13$). Enlargement of the stimulus size influences also N1 latency making it shorter (Fig. 1, lower row). ANOVA analysis

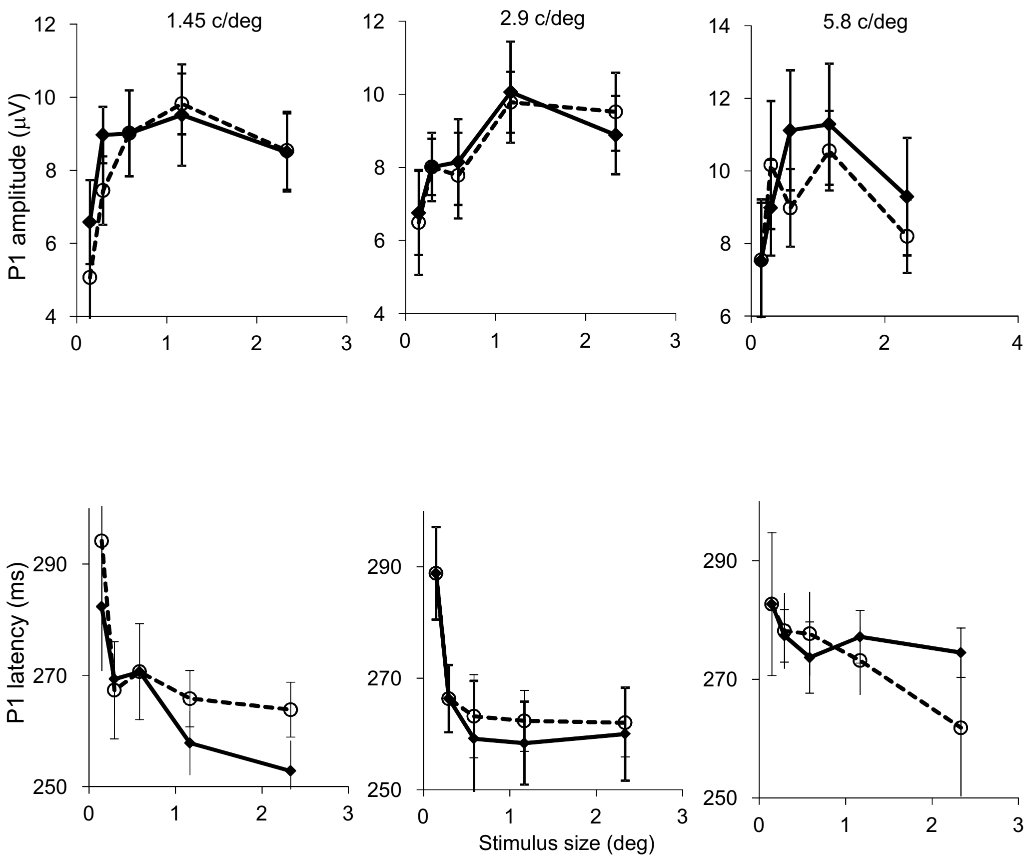

Fig. 2. Amplitudes (upper row) and latencies (lower row) of early VEP P1 wave recorded at Oz scalp position, as functions of stimulus length, σ_y (solid lines and symbols) and stimulus width, σ_x (dashed lines and open symbols), at three SFs: 1.45 c/deg (left panel), 2.9 c/deg (middle panel) and 5.8 c/deg (right panel). Averaged data of six observers

showed significant effect of grating length (solid lines) and width (dashed lines) on N1 latency at SF of 1.45 c/deg – $F = 16.2$, $p < 0.0001$ (the left lower panel) as well as at SF of 2.9 c/deg – $F = 12.9$, $p < 0.0001$ (the middle lower panel). However, the N1 latency decrease at SF of 5.8 c/deg was not statistically significant ($F = 0.81$, $p = 0.5$).

The behaviour of the second VEP wave, P1, as a function of the stimulus length and width and recorded at different SFs is illustrated in Fig. 2. Data are averaged over all observers.

The upper panels correspond to the amplitude values of P1 and the lower panels correspond to the latency values of P1. Similarly to the wave N1, stimulus enlargement first increased P1 amplitude and then either did not influence it or even decreased it slightly at the highest size values. However, contrary to the wave N1, length and width variations influenced P1 amplitude to a similar extent. The difference between the effects of grating length and width on P1 amplitude was not statistically significant at all SFs used in the present experiment: 1.45 c/deg ($F = 0.33$, $p = 0.6$), 2.9 c/deg ($F = 0.01$, $p = 0.9$) and 5.8 c/deg ($F = 0.09$, $p = 0.8$). Similarly to wave N1, enlargement of the stimulus sizes reduced the P1 latency (Fig. 2, lower row). Statistical analysis showed that P1 latency shortened more substantially (about 30 ms) with size enlargement (from 0.146 to 2.33 degrees) for stimuli of the lowest and the middle SF employed – 1.45 c/deg ($F = 4.58$, $p < 0.05$) and 2.9 c/deg ($F = 14.8$, $p < 0.0001$). At the highest SF employed, 5.8 c/deg, the effect of stimulus enlargement on P1 latency was smaller – about 10 ms. However, this effect was not statistically significant ($F = 0.81$, $p = 0.5$). No difference between the effects of stimulus length and width on P1 latency was found.

Discussion. The effects of grating size on the early VEP waves were studied in the present experiments. This is not the first attempt to evaluate how the stimulus size influences the VEP parameters (for a review see [7]). However, the size effects were mostly investigated at a single SF only – 0.88 c/deg [7] or 3 c/deg [3] as greater effect of the grating length than the effect of the width on the sensitivity was observed in the latter study. Moreover, the aspect ratio between stimulus length and width was relatively limited and varied within the range of 1:6 to 6:1. In the psychophysical studies either single SF (4 c/deg) was employed [1] or four different SFs within a wide range of SFs were used [2]. Similarly to VEP data, greater effect of grating length than the effect of width on the threshold contrast was observed, as the difference between the length and the width effects was more substantial at higher SFs in comparison with the lower SFs [2].

In the present work, three different stimulus SFs were employed as the aspect ratio between length and width varied within the range of 1:16 to 16:1. We also found greater effect of grating length in comparison with the effect of width on the N1 amplitude. However, this was observed at higher SFs – 2.9 c/deg and 5.8 deg, as no difference between the length and the width effects was found at lower SF – 1.45 c/deg. The stronger effect of stimulus length than the effect of width on the N1 amplitude at higher SFs obtained in the present experiment supports the assumption that the underlying mechanisms should be arrays of slightly elongated receptive fields [1], i.e. non-linear spatial summation should be effectuated at that level. The behaviour of N1 amplitude at the lowest SF – 1.45 c/deg, similarly to the psychophysical data, does not support this assumption.

It is reasonable to assume that higher SFs require receptive fields with higher spatial resolution and preferably stimulate the central retina, while low SFs stimulate effectively more peripheral retina where the receptive fields are with lower spatial resolution respectively. Moreover, the central retinal parts are represented in the posterior area of the primary visual cortex, whereas more peripheral retina is represented in more anterior regions deep into calcarine sulcus. Thus the central retina contributes much more to the occipital VEP in comparison with the peripheral retinal areas [7]. In addition, more effective stimulation of the peripheral retina at low SFs leads to certain cancellation among more distant and deeper generators with opposite orientations in both hemispheres and thus to lower VEP amplitudes [8, 9]. This assumption might explain the small reduction of the N1 amplitude, following its initial increase of this amplitude caused by length increase, observed both in our data (Fig. 1, the left upper panel) as well as in the literature [10]. In VEP experiments, a source of variability might also be introduced as a consequence of the substantial inter-subject differences of the representation of the central visual field on the convexity of the cortical occipital pole. Thus different response components might be summated and cancelled depending on the individual cortical representations and topographic potential distributions [7]. The other reason to observe different behaviour of the N1 component at low and high SFs comes from the finding of Jones and Keck [4] who report that the earliest VEP components at low SF (below 3 c/deg) are with properties different from those generated at higher SFs.

Contrary to N1 wave, the effects of stimulus length and width on the amplitude of the second VEP wave – P1, were the same at all SFs studied. This finding implies that the mechanisms responsible for the non-linear spatial summation and having elongated receptive fields influence the initial part of the VEP response only.

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