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Effect of extending grating length and width on human visually evoked potentials

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Visually evoked potentials (VEPs) were elicited by Gabor gratings with different lengths and widths at three spatial frequencies (SFs): low, 1.45 c/deg, medium, 2.9 c/deg and high, 5.8 c/deg and at a contrast 3 times above the detection threshold at each SF. An increase of grating length enhanced N1 amplitude at occipital and parietal positions stronger than the increase of grating width at aspect ratios (length : width) above 4:1. The stronger effect of stimulus length than width was reflected also in the amplitude of the later P1 component at central and parietal positions. The larger effect of stimulus length than width on the VEP amplitude was SF specific: it was stronger at 5.8 c/deg, smaller at 2.9 c/deg and vanished at 1.45 c/deg. The results obtained suggest anisotropy in the physiological mechanisms that underlie grating perception and involve bottom-up processes initiated in the occipital cortex.

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

INTRODUCTION

An important question in contemporary visual neuroscience is an assessment of characteristics of the mechanisms underlying the different aspects of grating detection. Gabor patterns have been widely used in vision research. Precise assessment of the effects of their size and form on visual information processing would help to improve our understanding of the mechanisms underlying changes in psychophysical measurements such as contrast thresholds or reaction time.

Many studies, using psychophysical and electrophysiological techniques, have examined the effect of grating size and form (for a review see Korth and Nguyen 1997, Foley et al. 2007, Meese and Hess 2007). Contrast sensitivity was measured for centrally (e.g. Polat and Norcia 1998, Polat and Tyler 1999, Foley et al. 2007, Meese and Hess 2007) and peripherally (Manahilov et al. 2001, Meese and Hess 2007) presented patterns. Foley and colleagues (2007) proposed a model in which gratings stimulate an array of visual cortical neurons with slightly elongated receptive fields. This model predicts a different effect of grating length (the spatial constant of the Gaussian window along the grating orientation) and width (the spatial constant of the Gaussian window perpendicularly the grating orientation).

Earlier studies on spatial summation of rectangular stimuli revealed that the length increase produced visibility enhancement up to 40 min of arc while width effect was limited up to 0–5 min of arc (Vassilev and Penchev 1976). The authors suggested that summation and detection of line stimuli is a function of orientation selective cortical receptive fields. It was later assumed that orientation- and SF-selective units are substrate responsible for the different width and length effects (Thomas 1978).

A more recent psychophysical study showed that the threshold contrast for grating detection was affected more by stimulus length than by stimulus width (Foley et al. 2007). These results were confirmed and further extended by another psychophysical study (Mitov and Totev 2007) where an interaction between this effect and grating spatial frequency (SF) was found. The stronger length effect was greater at higher SFs: 5.9 and 10.8 c/deg, smaller at lower SF, 2.9 c/deg and neg-

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ligible at the lowest SF, 1.45 c/deg (Mitov and Totev 2007). Similarly, electrophysiological work has shown that increasing stimulus area results in configuration-specific improvement in contrast threshold (Polat and Norcia 1998). Larger response amplitudes and higher contrast sensitivity was found when patterns were elongated along the axis defined by the grating orientation (collinear configurations).

Further psychophysical work has found higher contrast sensitivity thresholds for collinear than orthogonal configurations using vertical and circular Gabor patches, implying extensive spatial summation along the length of the receptive field (Polat and Tyler 1999). The authors interpreted data as consistent with preferential physiological summation along the collinear direction and suggested that the human cortex exhibits a preferential orientation pooling along the orientation axis over considerable distances in cortical space.

A more recent study (Meese and Hess 2007) failed to replicate Polat and Tyler's results relating to configuration specific summation. Detection thresholds were measured for "skunk-tails" (the envelope is elongated along the grating stripes) and "tiger-tails" (the envelope is elongated at right angles to the grating stripes) stimuli that were vertical or horizontal gratings. The results for foveal viewing showed that contrast sensitivity increased for skunk-tails over tiger-tails for horizontal gratings only, while the sensitivity was similar for vertical gratings. Moreover, the authors reviewed a number of studies that showed very similar thresholds for Gabors elongated either along or orthogonal to the orientation of the carrier (for a review see Meese and Hess 2007).

It should be noted that in the studies cited above stimulus SF was limited to only one value (3 c/deg Polat and Norcia 1998; 4 c/deg Polat and Tyler 1999, Foley et al. 2007) or two values (1 and 4 c/deg Meese and Hess 2007). It is therefore uncertain if any potential difference in the effect of grating length and width would be SF dependent (Mitov and Totev 2007). Additionally, Polat and Norcia's experiments compared activity only from the occipital cortex and could not reveal the spatio-temporal relationships of these effects over higher cortical areas.

The aim of the present study was to evaluate the effects of Gabor grating width and length at low, medium and high SFs and over occipital, parietal and central cortex. The results obtained would reveal properties of the mechanisms underlying stimulus width and length perception as well as the spreading of the effect over different cortical areas.

METHODS

Stimuli

Vertical sinusoidal carrier gratings of 3 different SFs – 1.45, 2.9 and 5.8 c/deg modulated by a 2-D Gaussian window with independently varied horizontal and vertical spatial constants (σ_x and σ_y) were used as stimuli (Fig. 1).

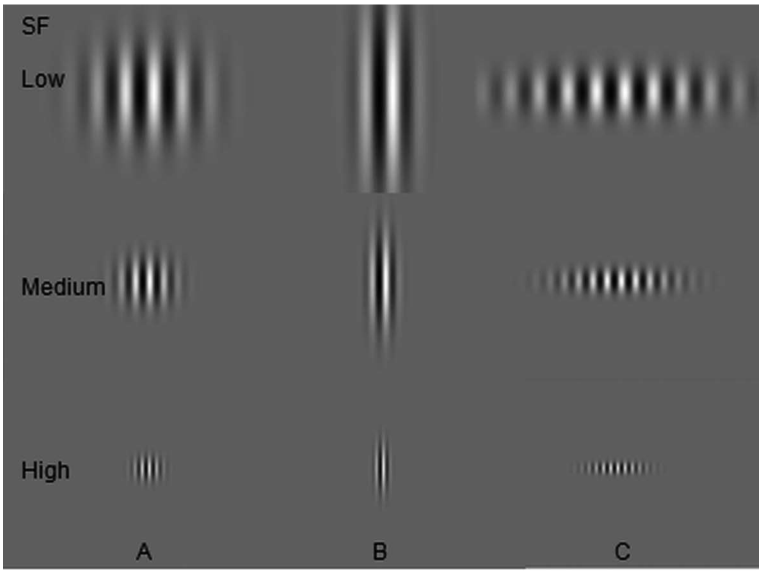

Fig. 1. Illustration of high contrast Gabor gratings with different lengths and widths at low, medium and high SF. (A): Circular Gabor gratings. (B): Elongated Gabor gratings with maximal σ_y. (C): Elongated Gabor gratings with maximal σ_x.

Table I

Aspect ratios (length : width) at each SF and stimulus size

	STIMULUS SIZE (deg)				
SF (c/deg)	0.15	0.29	0.58	1.17	2.33
1.45	1:4	1:2	1:1	2:1	4:1
2.9	1:2	1:1	2:1	4:1	8:1
5.8	1:1	2:1	4:1	8:1	16:1

In the text we will refer to SF of 1.45 c/deg as low, SF of 2.9 c/deg – as medium and SF of 5.8 c/deg – as high. At each SF a fixed value of one of the stimulus dimensions (σ_x or σ_y) 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 that produced equal number of periods at each SF) and the other stimulus dimension (σ_y or σ_x, respectively) varied within the range of 0.146÷2.33 deg.

The aspect ratios (length : width) generated in such a way are presented in Table I. Stimulus contrast was 3 times above the individual detection threshold, measured for each observer at each SF at the smallest values of the grating width and length. The stimulus duration was 100 ms.

Apparatus

Stimuli were presented on a black & white monitor (phosphor P4) by electronics designed in our laboratory. The spatial resolution was 640×480 pixels, the frame rate – 60 Hz, 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. The stimuli always appeared in the center of the screen and small fixation lines were located along the central horizontal line at the distance of 3σ from the center.

Procedure and VEP recording

VEPs were recorded from 9 scalp positions (10/20 system) using Ag/AgCl Nihon-Kohden electrodes. The reference electrodes were positioned on both mastoids and the ground electrode was on Fp. An oculogram (EOG) was also recorded from electrodes placed above and bellow the lateral cantus of left eye for a detection of eye movements and blink artifacts. EEG and EOG signals were amplified and band-pass filtered (0.3–70 Hz) using Nihon Kohden EEG-4314F electroencephalograph connected to a computer, which recorded the signals at a sampling interval of 2 ms. The length of the VEP segment was chosen to cover 500 ms pre-stimulus and 1000 ms post-stimulus interval. Only artifact-free VEP records were processed after they were digitally filtered at 50 Hz. The amplitudes of the VEP components were measured from the baseline to the corresponding peak. The baseline was defined as the mean value of the traces for 200 ms pre-stimulus interval (−300ms to −100ms).

Stimuli of each combination of SF, width and length 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. Observers were instructed to fixate at the screen center. 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 for each subject.

Contrast threshold measurement

Contrast thresholds were measured by a two-interval forced-choice method combined with a staircase procedure.

Observers

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

RESULTS

Examples of VEPs recorded at three SFs, 1.45, 2.9 and 5.8 c/deg for circular stimuli, illustrated in Fig. 1 A ($\sigma_x=\sigma_y$, gratings with aspect ratio 1:1 in Table I) are shown in Fig. 2. Although the stimuli were presented at a relatively low contrast levels, 3 times above the detection threshold at each SF, the recorded VEPs were well defined and their form and latency of the main components were consistent among the participants. The negative–positive wave complex, well described in the literature (Jones and Keck 1978, Vassilev and Strashimirov 1979, Musselwhite and Jeffreys 1985, Vassilev et al. 1994) as well as in our previous studies (Mihaylova et al. 1999, Vassilev et al. 2002), was characteristic for the VEPs obtained in the present experiment. In agreement with the above-cited studies Fig. 2 demonstrates VEP latency delay on increasing grating SF. This was also observed in more recent studies (e.g. Jemel et al. 2010).

Further analysis traced the effects of stimulus length and width on amplitude and on latency of the first negative wave (N1) as well as the next positive component (P1). Figure 3 illustrates N1 amplitude as a function of σ_x and σ_y increase at the 3 SFs used in the present study. Separate graphs were grouped in 3 rows according to the scalp recording position. The lower row represents N1 amplitude at occipital positions, while the medium and upper rows illustrate parietal and central sites respectively. Factorial ANOVA analysis (stimulus length and width, SF, size, position and subject as a random factor), with alpha level set at 0.05, revealed a significant main effect of stimulus length and width ($F_{1,5}=11.3$, $P<0.05$) and position ($F_{8,40}=4.49$, $P<0.01$) on N1 amplitude. When stimulus length increased N1 amplitude increased more than when stimulus width increased in the same range. As shown in Fig. 3 the effects of length and width differ mainly at greater stimulus sizes (0.58°–2.33°) and aspect ratios (length : width) above 4:1 (see Table I) while the curves overlap at smaller grating sizes (0.15°–0.29°). This observation was confirmed by the significant interaction between effects of factors length and width, and size ($F_{4,20}=5.03$, $P<0.01$).

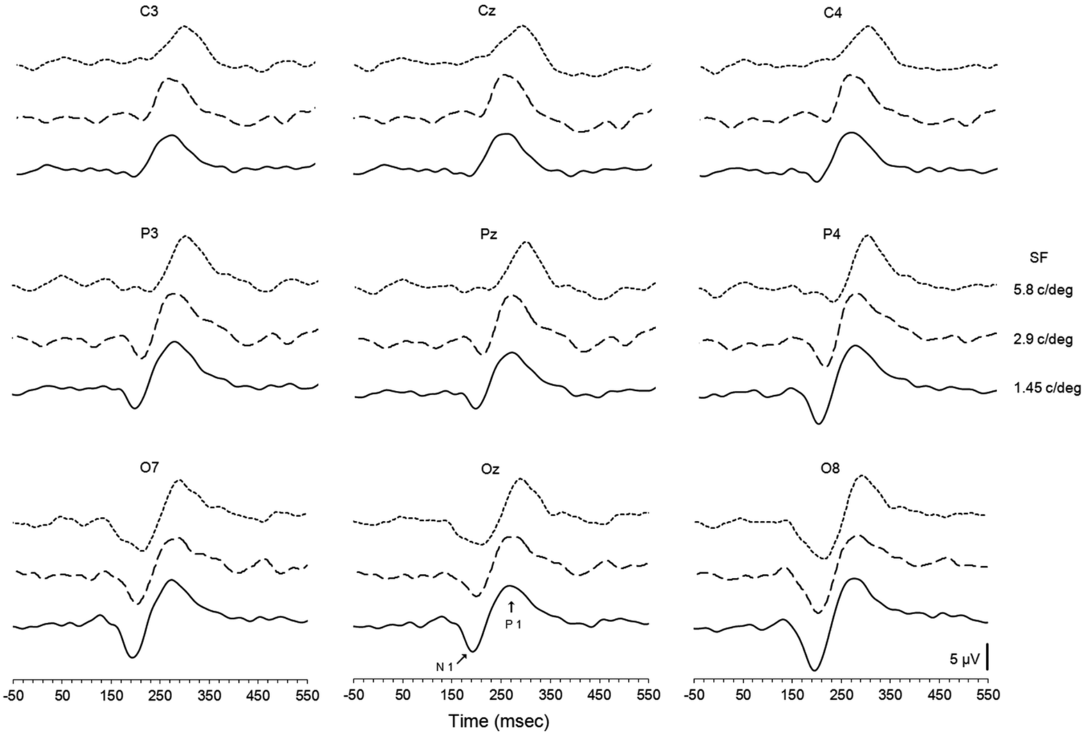

Fig. 2. Examples of onset VEPs, recorded from 9 positions shown on the top of each group of records. Within each group VEPs to the three SFs (given on the right) are presented: 1.45 c/deg (solid line), 2.9 c/deg (dashed line) and 5.8 c/deg (dotted line). Stimuli were circular ($\sigma_x=\sigma_y$) and their size was 0.58 deg at 1.45 c/deg, 0.29 at 2.9 c/deg and 0.146 at 5.8 c/deg. N1 and P1 peaks are indicated by arrows. VEPs were averaged among six observers.

Figure 3 also shows that grating length influenced N1 amplitude stronger than grating width at SFs of 2.9 and 5.8 c/deg, while at 1.45 c/deg the effect of σ_x and σ_y was similar. This finding was reflected in the significant interaction between the factors length and width and SF ($F_{2,10}$=11.9, P<0.01).

The significant main effect of position is not surprising because the response of lower-level visual areas located under occipital electrodes is much more dependent on the characteristics of visual stimuli. It is important however to note that greater effect of grating length than width on the early wave amplitude appeared only at occipital and parietal positions as illustrated in Fig. 3. At central positions width and length curves at all SFs lie together. Indeed, the interaction between factors length and width, size and position was significant ($F_{23,949}$=1.8, P<0.01).

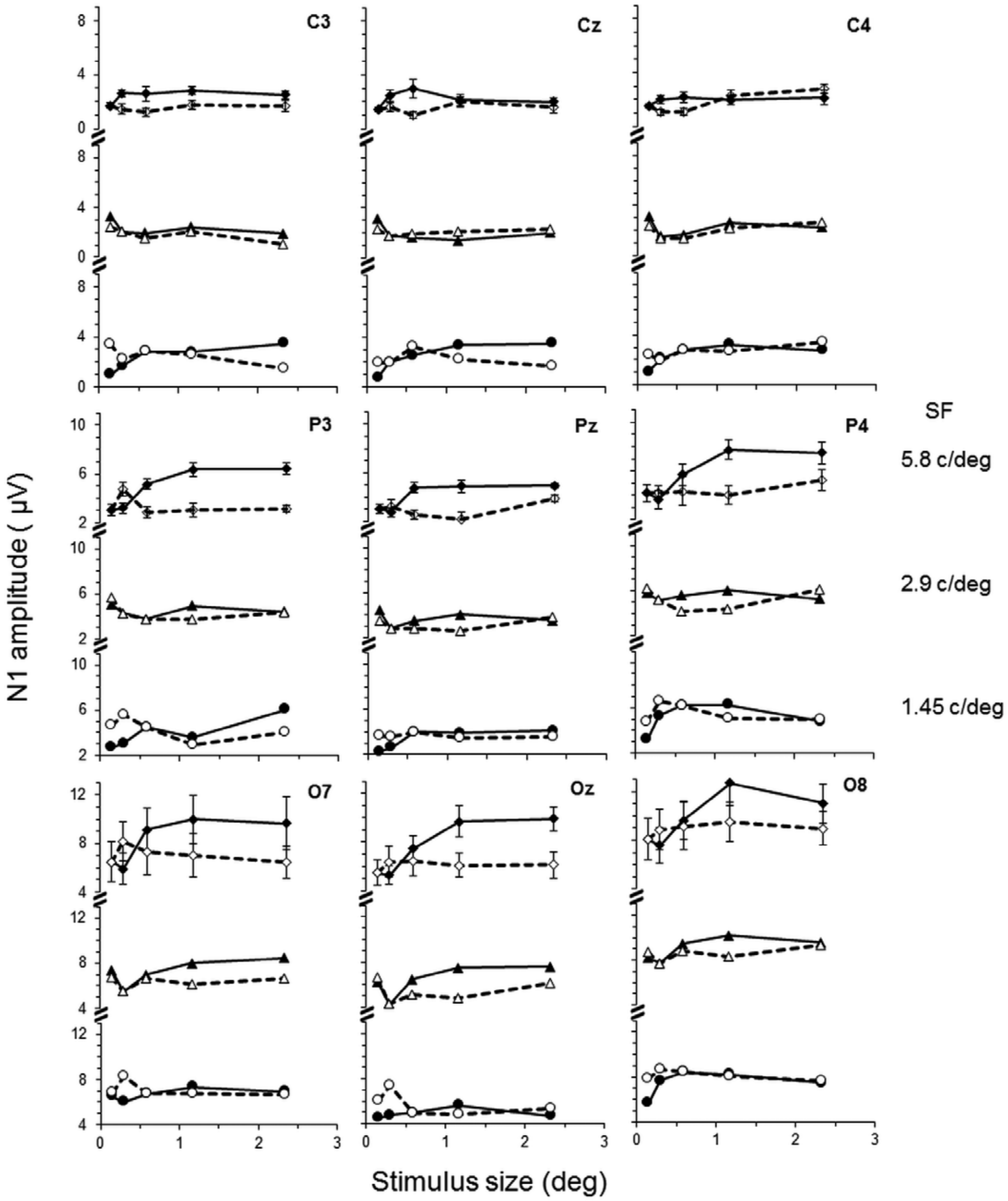

Fig. 3. N1 amplitudes as functions of stimulus length, σ_y (solid lines and symbols) and stimulus width, σ_x (dashed lines and open symbols) at three SFs: 1.45 (circles), 2.9 (triangles) and 5.8 (diamonds) c/deg. Stimulus SF is pointed to the right. Each graph represents data at the separate recording position shown on the top: occipital (lower row), parietal (middle row) and central (upper row). Here and in all next figures, vertical bars represent the 95% confidence intervals of the means. For the sake of visibility they are presented with the data of 5.8 c/deg only. Data averaged of six observers.

Figure 4 represents the early negative VEP wave latency dependency on grating length and width. Similar to Fig. 3 the graphs were grouped according to the scalp recording position: occipital (lower row), parietal (middle row) and central positions (upper row).

ANOVA results showed significant main effects of size ($F_{4,20}$=13.3, P<0.0001) and length and width ($F_{1,5}$=9.3, P<0.05) on N1 latency. The effect of σ_x and σ_y on the N1 latency was similar at most recording positions and for all SFs. However, at central recording sites, C3, Cz and C4 at the highest SF certain difference between grating width and length effect on N1 latency could be observed, a finding supported by significant interaction of factors width and length and position ($F_{8,40}$=5.6, P<0.001). ANOVA results showed

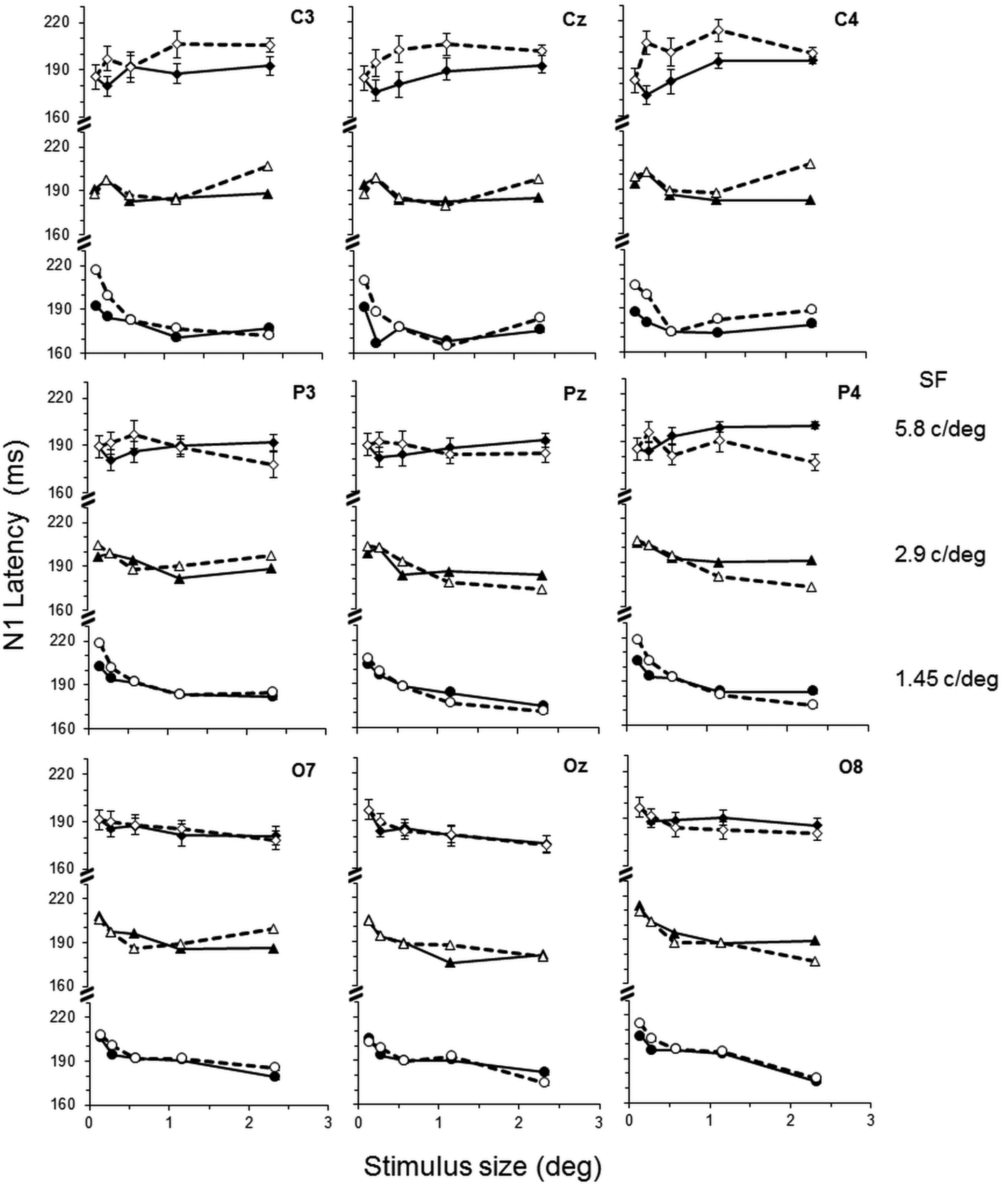

Fig. 4. N1 latencies as functions of stimulus length, σ_y (solid lines and symbols) and stimulus width, σ_x (dashed lines and open symbols) at three SFs: 1.45 (circles), 2.9 (triangles) and 5.8 (diamonds) c/deg. Stimulus SF is pointed to the right. Each graph represents data at the separate recording position shown on the top: occipital (lower row), parietal (middle row) and central (upper row). Data averaged of six observers.

that size effect on N1 latency depends on grating SF: interaction between factors size and SF was significant ($F_{8,40}$=3.6, P<0.01). Significant interaction ($F_{8,948}$=3.81, P<0.001) between factors length and width, size and SF reflected difference in width and length effect at greater stimulus sizes and medium and high SFs.

The behavior of the second VEP component, which is of positive polarity, P1, differs in some aspects from N1 behavior. Figure 5 represents the dependency of the P1 amplitude on the stimulus size. The graphs were grouped according to the scalp recording position.

At most recording sites and SFs the amplitude of P1 initially increased with increasing stimulus size and decreased at the largest grating size. Factorial ANOVA (width and length, SF, size, position, subject as a random factor) revealed a significant main effect of size ($F_{4,20}$= 4.18, P<0.05) on P1 amplitude. The main effect of width and length was also statistically significant ($F_{1,5}$=6.61, P<0.05). The interaction between the two factors was significant ($F_{4,20}$=3.16, P<0.05) reflecting result that is illustrated in Fig. 5 that the curves of σ_x and σ_y diverge predominantly at grating sizes above

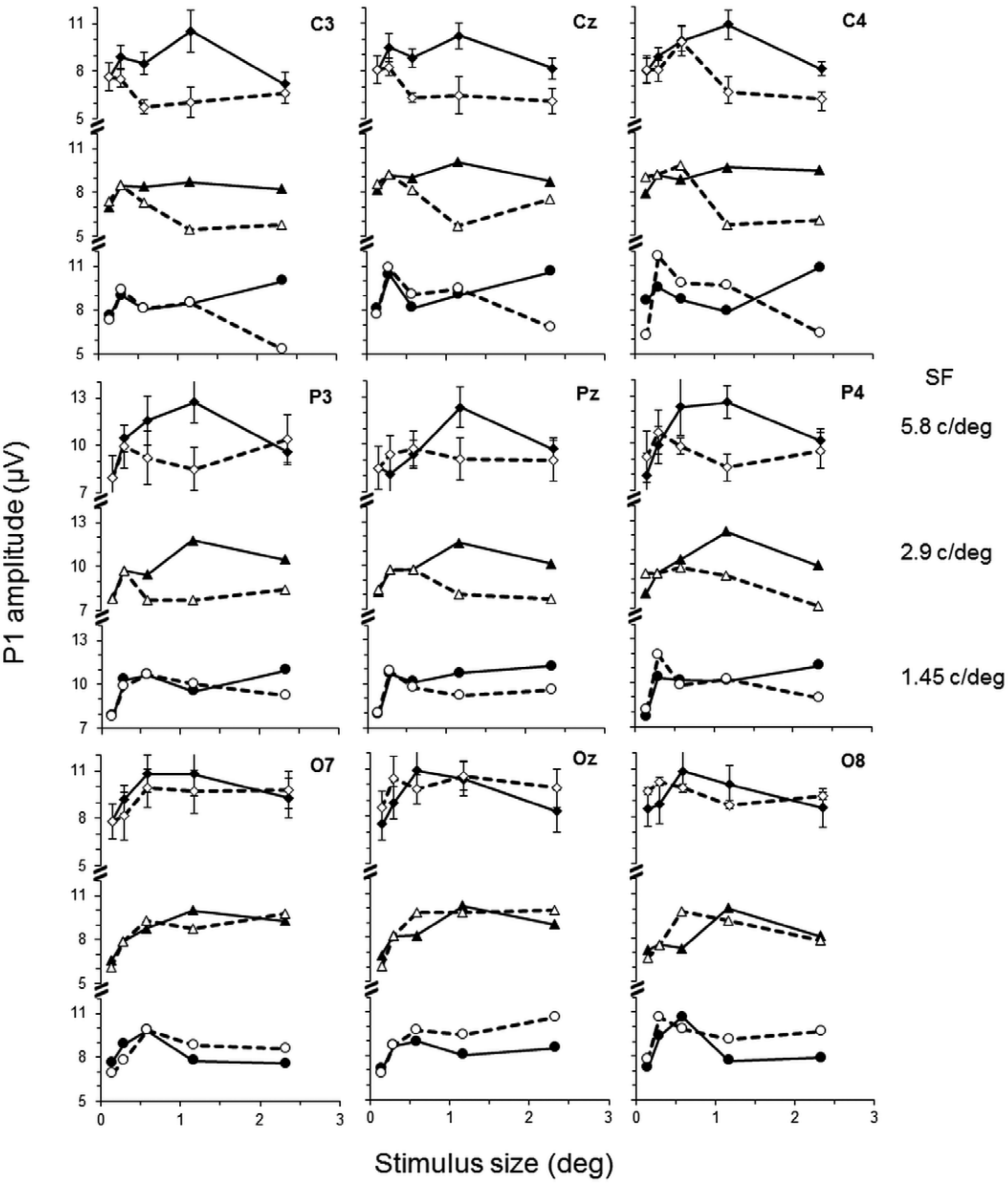

Fig. 5. P1 amplitudes as functions of stimulus length, σ_y, and stimulus width, σ_x, at three SFs. All designations are the same as in the Fig. 3. Data averaged of six observers.

0.58 deg, i.e. at aspect ratios (σ_y:$\sigma_{x)}$ above 4:1. Additionally, the significant interaction of factors width and length and position ($F_{8,41}$=7.65, P<0.0001) reflects the difference between the separate positions: while at occipital recording sites curves of increasing stimulus width and length lied close and overlapped, at parietal and central positions they dissociated for grating sizes 0.58 – 2.33 deg. The interaction between factors length and width, size and position was also significant ($F_{32,928}$=2.31, P<0.0001).

Interaction between factors length and width, size and SF was significant too ($F_{8,928}$=11.4, P<0.0001): Fig. 5 shows that P1 amplitude measured at the lowest SF, did not differ for σ_x and σ_y curves in contrast to the curves at medium and high SFs and stimulus sizes between 0.58–2.33 deg.

Figure 6 illustrates P1 latency as a function of grating size. The latency of the second positive wave, similarly to the latency of the first negative component, decreased significantly with increasing stimulus size ($F_{4,20}$=8.07, P<0.001). Main effects of SF ($F_{2,10}$=6.36, P<0.05) and position ($F_{8,40}$=4.28, P<0.0001) were also significant while the effect of grating width and length was not significant ($F_{1,5}$=3.38, P=0.125). The size effect

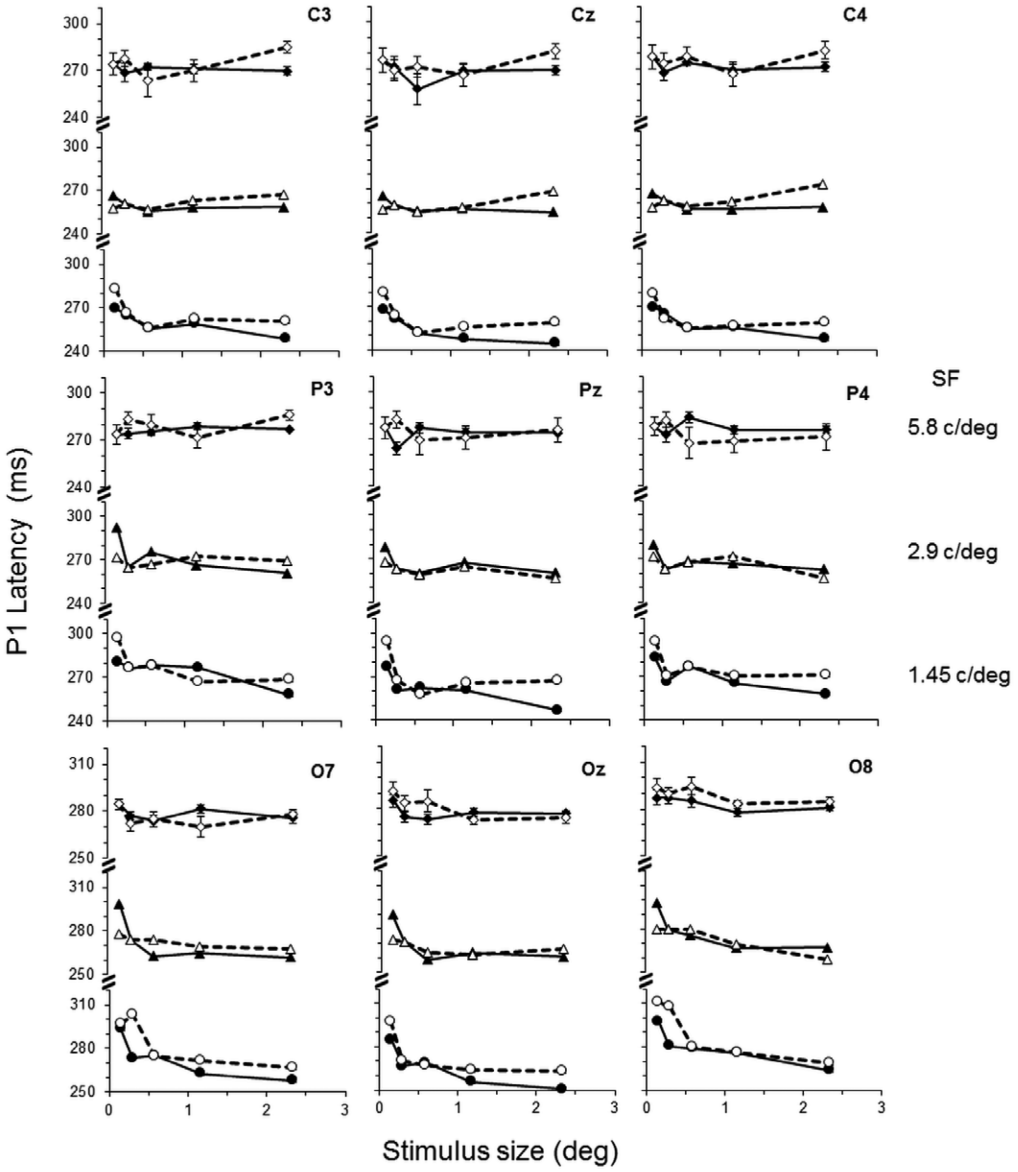

Fig. 6. P1 latencies as functions of stimulus length, σ_y, and stimulus width, σ_x, at three SFs. All designations are the same as in the Fig. 4. Data averaged of six observers.

on N1 latency did not depend on grating SF: interaction between factors size and SF was not significant.

Interaction between factors size and position was significant ($F_{32,163}$=1.89, $P<0.01$), indicating stronger decrease on increasing grating size at occipital positions, a result illustrated in Fig. 6.

DISCUSSION

We found that an increase in grating length produced greater amplification of VEP amplitude than the increase of grating width at aspect ratios (length : width) above 4:1. This effect depended on stimulus SF; being more pronounced at high SF, 5.8 c/deg. The difference in grating length and width effect appeared in both the early VEP component N1 in the early occipital visual areas and in the later component P1 in the hierarchically higher parietal and central cortical areas.

The stronger effect of grating length on VEP amplitudes compared to that of grating width agrees with psychophysical (Polat and Tyler 1999, Foley et al. 2007, Mitov and Totev 2007) and electrophysiological (Polat and Norcia 1998) findings. The present study explored stimulus length and width effects over three SFs, 1.45, 2.9 and 5.8 c/deg, thus extending the results of previous electrophysiological studies in which the size effects have been investigated predominately at a single SF only – 0.88 c/deg (Korth and Nguyen 1997) or 3 c/deg (Polat and Norcia 1998). In the first study circular stimuli were used and length and width relationship were not examined (Korth and Nguyen 1997), while in the second study (Polat and Norcia 1998) elongated gratings were used. However, in these experiments the aspect ratio between stimulus width and length varied within the range of 1:6 to 6:1. In the present study the aspect ratio between length and width varied within the range of 16:1 to 1:16 at the highest SF, 5.8 c/deg. Due to limitations in the monitor size it was not possible to reach similar aspect ratios with medium 2.9 c/deg (8:1 and 1:8) and low 1.45 c/deg (4:1 and 1:4) SFs (see Table I). Nevertheless, the results in Figs 3 and 5 suggest that the differences in the effect of stimulus width and length for gratings of 2.9 c/deg and 1.45 c/deg will not increase further. Figures 3 and 5 show that the size effect reached a plateau at lower dimensions: up to 1.17 deg for both VEP components, N1 and P1, at all scalp positions.

A similar effect of grating length and width at smaller grating sizes (0.15–0.29 degrees) and aspect ratios up to 4:1 was found for both N1 amplitude (Fig. 3) as well as P1 amplitude (Fig. 5); confirming the finding of similar sensitivity for collinearly and orthogonally orientated elongated envelopes of vertical gratings (Meese and Hess 2007). In general, our present result about VEP amplitude dependency on grating size are in line with results of both groups of studies – supporting (e.g. Polat and Norcia 1998, Polat and Tyler 1999) or not supporting (Meese and Hess 2007) stronger effect of grating length and width. As can be seen on both Figs 3 and 5 when the aspect ratios (length:width) is up to 4 : 1 the effect of length and width is similar. However, at aspect ratios of 8:1 and 16:1 the stimulus length exhibits a stronger effect on VEP N1 and P1 amplitude. Indeed, at higher aspect ratios increasing grating length produced a stronger increase in the amplitude of early and late VEP components. As suggested by (Polat and Norcia 1998) elongation of a grating along the orientation axis produced more physiological summation than elongation along an orthogonal axis. However, the authors noted that no clear saturation point was reached in their experiments. In the present study we used higher aspect ratios and sizes and reached saturation levels for both N1 and P1 amplitudes at all SFs used (Figs 3 and 5).

In accordance with previous psychophysical reports (Mitov and Totev 2007) the difference in effect of grating length and width was largest at high SF, smaller – at medium SF, and vanished at low SF. This finding holds for all scalp positions explored in the study and for both N1 and P1 VEP waves. SF-specific differences could be due at least partly to V1 morphology. Similar to previous studies (Plant et al. 1983) Figs 3 and 5 show that when grating SF was low the increase in stimulus size produced less amplitude enhancement than for medium and high SF gratings. This difference between SFs is most pronounced at occipital positions and for early negative wave N1. Although amplitude increased initially with the increase in stimulus length, Figs 3 and 5 show a reduction in the N1 and P1 amplitudes at larger sizes. This might be partially explained by striate cortex retinotopic organization. The central foveal retina contributes much more to the occipital VEP in comparison with the peripheral retinal areas (Korth and Nguyen 1997). Central foveal retinal parts are represented in the posterior area of the primary visual cortex whereas the peripheral retina is represented in more anterior regions deep in the calcarine sulcus. Higher SFs would require receptive fields with higher spatial resolution and would preferably stimulate the central foveal retina. Low SFs would stimulate effectively more peripheral regions of the retina where the receptive fields have lower spatial resolution. More effective stimulation of 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 (Parker et al. 1982, Di Russo et al. 2002).

Although the stimulus effect on the VEP latency has been studied less intensively, a clear tendency for shortening peak times with increasing stimulus size has been documented (for a review see Korth and Nguyen 1997). Our data show a size effect on N1 but not on P1 latency that is dependent on grating SF. In contrast to the different stimulus width and length effect on VEP amplitude, the effect of grating σ_x and σ_y was similar on both N1 and P1 latencies. At most scalp positions and SFs tested grating width and length showed similar effects on N1 and P1 latency. The only exception is a stronger N1 latency delay with width increase in comparison to the length increase at central scalp positions and high SF conditions. It is possible that this result might be explained by some inhibitory process.

Our study also found a greater effect of stimulus length in comparison to stimulus width over more scalp locations in earlier and later VEP components. The width – length interrelations were traced from the stimulus onset to about 350 ms and across nine scalp positions over occipital, parietal and central cortical areas. The larger effect of grating length was observed for the amplitudes of both the earliest negative wave and the following positive component of the VEPs. It was found that the grating width and length effect varied with time across different scalp positions. The earliest significantly different effect of stimulus width and length on N1 amplitude was registered over occipital scalp positions and to a smaller extent over parietal positions in the 170–220 ms range. At the same time, the early VEP wave recorded from central positions did not show any difference in stimulus width and length effects. At 250–330 ms the difference in length and width effects on P1 amplitude was shifted towards parietal and central positions. This spatio-temporal pattern is consistent with an interpretation of a bottom-up process that initiates in early occipital visual areas and spreads over higher parietal and central cortical areas.

The present data agree with the suggested anisotropy in the underlying physiology (Meese and Hess 2007). However, the authors found clear advantage for collinearly over orthogonally elongated horizontal gratings while vertical carriers summation was similar. In our experiments we did not use horizontal gratings but vertical gratings showed strong advantage for gratings elongated collinearly (increasing their length) over gratings elongated orthogonally (increasing their width). It should be noted that this effect was observed mostly at aspect ratios 8:1 and 16:1. The greatest aspect ratio in the above cited study (Meese and Hess 2007) was about 6.8:1.

It was assumed (Foley et al. 2007) that the mechanisms involved in processing grating characteristics should be arrays of slightly elongated receptive fields. Based on their psychophysical contrast thresholds experiments the authors proposed a model in which patterns excite an array of neurons with slightly elongated receptive fields. They suggested that the detection of all except the smallest patterns were mediated by the summation of responses from multiple receptive fields.

Evidence was also presented (Polat and Tyler 1999) for the involvement of mechanisms with elongated receptive fields along the stripes in grating detection. Similar to their results the different effect of grating width and length found in our experiments holds up to the highest aspect ratio used: 16:1 at 5.8 c/deg. The effect was observed for the early VEP activity (N1 amplitude) in the occipital cortex as well as for the later activity (P1 amplitude) in the central cortex.

Elongated receptive fields have been described in different cortical areas. Moving along ventral stream up to area V4, a large number of cells are well tuned for main stimulus characteristics such as length (Desimone et al. 1985, Desimone and Schein 1987, Cheng et al. 1994, Hinkle and Connor 2001, Watanabe et al. 2002). Temporal visual areas beyond V4 show a progressive loss of retinotopy and high sensitivity to complex shapes and patterns. This suggests their role in encoding grating length and width is less significant than the role of lower temporal visual areas. The question of whether the stronger effect of stimulus length than width on VEP amplitudes can be fully explained by the elongated receptive fields or whether additional factors contribute to the effect is beyond the scope of the present study. It is difficult to discriminate between separate receptive field models (reviewed in Martinez and Alonso 2003) on a basis of our data, because effects were observed beyond the primary visual cortex. Probably, our results could partly be explained by small-scale or large-scale (Serre 2014) hierarchical models. Similar pictures of grating length and width effects were observed for early N1 wave amplitude over occipital cortex and later P1 amplitude over central cortex. It could be suggested that these effects were formed at some earlier state and further moved to the higher cortical areas. However, a stronger N1 latency delay with width increase in comparison to the length increase was measured at central scalp positions and high SF (Fig. 4). This could be a sign of a recurrent feedback from higher levels that influence the gain control of the feature detectors as it was supposed in an extensive review (Martinez and Alonso 2003). Most probably, a combination of different models could account for our results as suggested by a small-scale consensus model (Martinez and Alonso 2003).

Polat and Norcia (1998) discussed that the average values of simple cell receptive field length-to-width elongation combined across studies available in the literature are about 1.5:1. These values are substantially less elongated than the summation areas (6:1) found in Polat and Norcia's experiments. Results of the present study showed even more elongated areas of summation. Our results could probably be modelled by recently proposed theory (Lindeberg 2013) that can explain various receptive fields that are tuned to different sizes and orientations.

Alternately, as suggested earlier (Foley et al. 2007) a spatial array of receptive fields instead of a single receptive field could mediate stimulus detection and receptive field responses could be combined nonlinearly. To evaluate the receptive field properties from psychophysical or even VEP measurements is a difficult task. For most stimulus patterns, many neurons with different receptive fields are likely to contribute to pattern detection. These fields may vary with the size of the pattern. Narrow patterns contain a wide range of SFs and may stimulate neurons with receptive fields tuned to very different SFs. On the other hand, larger patterns stimulate many neurons with receptive fields at different retinal sites that differ in spatial sensitivity. Although results from VEP experiments cannot distinguish between separate summation models, the stronger effect of grating length than width on early VEP components in occipital and on later VEP components in parietal and central recording cites suggests that the underlying processes are bottom-up and are initiated in early visual areas.

CONCLUSION

The results of the present study improve our understanding of the mechanisms underlying the stronger grating length than width effect on VEP. The significantly larger effect of stimulus length than width on the VEP amplitude observed at higher SFs and aspect ratios above 4:1 suggests a certain anisotropy in the underlying physiological mechanisms. Moreover, this effect is observed consequently from lower to higher cortical areas. While the effect occurs in the early VEP activity at 170–220 ms over occipital areas, it disappeared from these sites at about 250–330 ms and moved to higher parietal and central sites. This spatio-temporal organization probably implies the involvement of bottom-up processes initiated in early visual areas before moving to higher parietal and central cortical areas.

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