Temporal resolution of orientation-defined texture segregation: a VEP study

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Abstract

Orientation is one of the visual dimensions that subserve figure-ground discrimination. A spatial gradient in orientation leads to “texture segregation”, which is thought to be concurrent parallel processing across the visual field, without scanning. In the visual-evoked potential (VEP) a component can be isolated which is related to texture segregation (“tsVEP”). Our objective was to evaluate the temporal frequency dependence of the tsVEP to compare processing speed of low-level features (e.g., orientation, using the VEP, here denoted llVEP) with texture segregation because of a recent literature controversy in that regard. Visual-evoked potentials (VEPs) were recorded in seven normal adults. Oriented line segments of $0.1^\circ \times 0.8^\circ$ at 100% contrast were presented in four different arrangements: either oriented in parallel for two homogeneous stimuli (from which were obtained the low-level VEP (llVEP)) or with a 90° orientation gradient for two textured ones (from which were obtained the texture VEP). The orientation texture condition was presented at eight different temporal frequencies ranging from 7.5 to 45 Hz. Fourier analysis was used to isolate low-level components at the pattern-change frequency and texture-segregation components at half that frequency. For all subjects, there was lower high-cutoff frequency for tsVEP than for llVEPs, on average 12 Hz vs. 17 Hz ($P = 0.017$). The results suggest that the processing of feature gradients to extract texture segregation requires additional processing time, resulting in a lower fusion frequency.

Keywords

Orientation; Texture segregation; Temporal resolution; Visual-evoked potentials

Introduction

The visual system segregates a figure from its background when the border is defined by a gradient in one of the following basic features (motion, stereo, color, luminance, or spatial frequency) [1, 2]. This capability of the visual system, referred to as texture segregation, is closely related to the pop-out phenomenon [3]. Orientation was shown to be a key feature of the visual pop-out phenomenon where lines with sufficient orientation contrast (e.g., orthogonal) to their neighbors become more salient and thus “pop out” [4]. When defined by the orientation of the components, texture segregation is currently modeled in two main steps, namely: (1) coding of local orientations within the stimulus [5] and (2) coding of orientation contrast, that is, the detection of (generalized) contrast differences between adjacent regions [6, 7]. This additional step presumably adds additional processing time. Although the exact loci where this supplementary processing takes place awaits to be confirmed, visual area V1 is that which has received most attention with feedback information from associative visual areas V2 and V3 [8]. A recent fMRI study, however, found activation of areas V4, TEO, and also V3A [9].

Recent studies on pop-out in humans are somewhat controversial with respect to the speed of perceptual processing: which of the two, texture segregation or low-level processing, requires more time? Comparing detection of pop-out stimuli to that of single lines, Nothdurft [10] found that subjects required longer presentation times to detect pop-out, suggesting a prolonged processing time compared to single line detection (or low-level processing). In contrast, Motoyoshi & Nishida [11] found with texture stimuli made of arrangement of lines that the time needed to segregate the texture stimulus was just as long as that required to code a single (local) stimulus. Both studies used a temporal resolution paradigm to test their hypothesis, where opposite stimuli were alternated with a gradually increasing temporal frequencies until fusion occurred, at which point the two stimuli were no longer perceived. In humans, the visual-evoked potentials (VEPs) represent a tool to assess the neuronal activity involved in the processing of visual information. Comparing the VEPs evoked to an alternation of low-level and texture stimuli could help us to determine whether the processing of these two stimuli requires the same amount of time or not. Previous studies have shown that in protocols using steady-state VEPs, Fourier analysis of the resulting signals could be used to this end [12].

Using evoked potentials as a tool, we pursued two aims: (1) to compare the temporal frequency tuning curves of the texture segregation (tsVEP) and low-level (llVEPs) VEPs with the aim of demonstrating that the tsVEPs peak response occurred at a lower temporal frequency compared to llVEPs and (2) to estimate from the latter the additional neuronal time required to process the more complex texture stimuli.

Methods

Subjects

Visual-evoked potentials associated with texture segregation (tsVEPs) were recorded in seven subjects (three female and four male) with best-corrected visual acuities of 20/20 or

better and ranging in age from 24 to 51 years (mean: 31 years). The research followed the Tenets of the declaration of Helsinki and was approved by the ethical committee of the Centre de réadaptation Lucie-Bruneau. An informed consent was obtained from all subjects after the nature and possible consequences of the study had been fully explained to them. All subjects were paid for their participation.

Electrophysiology

Signals were recorded from a single active electrode installed at Oz in keeping with the 10/20 electrode placement system [13, 14]. An electrode placed on the forehead served as reference and the ground was attached to one earlobe. Signals were digitally low pass filtered at 40 Hz. The stimuli were presented using a Macintosh G4 computer with a resolution of 800×600 pixels at a frame rate of 90 Hz. They were generated by the EP-2000 Freiburg-evoked potentials system [15], and viewed at a distance of 1.14 m from the subject. The screen covered 19° horizontally and 18° vertically.

Stimuli

Oriented line segments of 0.8° in length and 0.1° in width at 100% contrast were presented in four different arrangements, where the lines were either all oriented in parallel for two homogeneous stimuli (Fig. 1a, c) or locally rotated by 90° to form a global orientation-defined checkerboard for two textured ones (Fig. 1b, d). A two-dimensional random positional jitter was added to the stimuli in order to avoid luminance cues. Thus between any pair of frames each line element was slightly repositioned, and half of them would change their orientation by 90° .

The four different stimuli arrangements (Fig. 1a, b, c, d) were presented in sequence at the following temporal frequencies: 7.5, 9, 11.0, 15.0, 18.0, 22.5, 30, and 45 Hz. From the response, two frequencies (F0 and F1) were isolated (Fig. 2) using a discrete Fourier transform. F1, which identified the response at the pattern renewal frequency, served as an indicator for low-level processing ("lIVEP") while the response obtained at half of that frequency (F0) was taken to represent the tsVEP. For example, when the stimuli were presented at 9 Hz, the signal recorded was dominated by a 9 Hz low-level response and a 4.5 Hz texture response.

Data analysis

For each subject, lIVEP and tsVEP temporal frequency tuning curves were obtained (Fig. 4) where the amplitude of the VEP response was plotted against the temporal frequency of the stimulus. The upper frequency limit was derived from these curves to compare lIVEPs and tsVEPs recorded from each subjects. The latter characterize the (highest) temporal frequency of the stimulus where the amplitude of the response reaches half of the maximal amplitude (Fig. 4). Data analysis involved in-house programs based on Igor Pro (WaveMetrics), statistical analysis was done using R [16].

Results

Figure 2 illustrates a representative waveform and its corresponding magnitude spectrum from one subject in response to a stimulation frequency of 15 Hz. The response is dominated by two main components, a fast 15 Hz (F1) and a slow 7.5 Hz (F0) one. The faster response is evoked by the low-level aspects of the stimulus (local pattern change between every frame), while the slower response represents the difference between global structure (orientation-defined checkerboard versus homogenous). These two components are obvious as discrete lines in the magnitude spectrum (Fig. 2, bottom) and can also be discerned in the time series (Fig. 2, top).

Figure 3 displays tsVEP waveforms obtained from another subject covering all presentation rates as indicated at the left of each tracing. Depending on the stimulus frequencies used, F1 (low-level response, llVEP, full arrows) or F0 (tsVEP, dashed arrows) dominate the response and the spectrum. In the case of a stimulus presented at 11 Hz for example, the most prominent peak was found at 11 Hz (low-level response) while the secondary one was observed at 5.5 Hz (texture response). From the magnitude spectra we derived the temporal frequency tuning curves as illustrated in Fig. 4. It can be seen that the tuning curves have a wide interindividual variability, but all follow an inverted-U shape, thus are of band-pass type. We characterized the upper end of the band-pass by the frequency where the response drops to half maximal value, here called the upper frequency limit. Excepting subject #14, the upper frequency limit of the low-level response was markedly higher than the tsVEP. Averaging across all subjects yielded an upper frequency limit of 11.9 ± 1.3 Hz for tsVEPs, significantly lower than that for llVEPs (17.3 ± 3.6 , $P = 0.017$). When calculating an estimate of the corresponding time constants, thereby tentatively modeling the neural response as a linear low-pass above the peak frequency, a value of $\tau_{ll} = 13.4$ ms for the llVEP obtains, and $\tau_{ts} = 9.2$ for the tsVEP. Thus there is a difference in time constant of 4.2 ms between the two types of response.

When the data from Fig. 4 are averaged across all subjects, the grand mean llVEP and tsVEP temporal frequency tuning curves result as depicted in Fig. 5. Its major features were statistically tested as follows: An ANOVA with the factors TYPE (llVEP = F1 and tsVEP = F0) and FREQUENCY (comprising only the four levels where responses for both the llVEP and tsVEP are available, 7.5, 11.0, 15.0, and 22.5 Hz) found significant effects for TYPE ($P = 0.013$), FREQUENCY ($P < 0.001$) and the interaction of the two ($P = 0.025$). The significant effect for TYPE just means that the tsVEPs are, on average, a little smaller. The significant effect for FREQUENCY describes the amplitude fall-off with increasing frequency, and the significant interaction means that this fall-off differs between llVEP and tsVEP.

From the response phase obtained via Fourier analysis the response latency can be derived. In general this is not a unique solution because latency can be higher than one cycle. When results to a range of temporal frequencies are available, as here, one can arrive at a unique solution by assuming that latency varies only slowly with stimulus frequency [17]. We calculated the peak-time t from the response phase ϕ at frequency f with the following formula:

$$t = (\varphi + n \cdot 360^\circ) / 360^\circ / f,$$

where n is an integer multiplier with the values 1, 2, or 3, selected to yield the closest peak time compared with the next lower frequency. For the lowest frequency, $n = 1$ was chosen, since this lead to values in the range of normal peak times (around 100 ms for the VEP, around 180 ms for the tsVEP). Any other choice for the multiplier n would have lead to extraneous peak time excursions, very different from the relatively smooth values seen in Fig. 6. The mean difference in peak time across the five frequencies (the ones which are paired across lIVEP and tsVEP) is 51 ± 18 ms.

Discussion

With appropriate stimulus sequences and time-domain analysis we extracted both a low-level response component (the lIVEP, in response to local pattern change) and a higher-level one, here associated with the appearance–disappearance of global structure (tsVEP). The main question was how these two components behave over a range of stimulus frequencies from 3 to 45 Hz.

The main findings were a band-pass shape of the temporal tuning curves for both components. At the upper frequency end there was a significantly higher half-amplitude cut-off frequency of 17.3 Hz for the lIVEP as compared to 11.9 Hz for the tsVEP. In other words, texture segregation cannot follow the stimulus as rapidly as low-level features. Indeed, when informally observing our stimulus display at frequencies above 10 Hz, the global structure appears to be continuously present. Our results thus support Nothdurft's [10] conclusions that texture segregation is a time-consuming process that does not follow rapid variations in orientation. It thus relies on a slower mechanism than low-level VEPs.

Since pattern perception and texture segregation also occurs with static patterns, why would there be a cut-off for the lower frequency end too? This is, effectively, an artifact of the Fourier analysis. At relatively high frequencies the response is sinusoidal. However, for slower, so-called transient stimulation the response shape becomes more complicated and is spread out over a band of frequencies, this it cannot adequately be described—and is always underestimated—by a single frequency. Thus anything below about 8 Hz in the present context needs to be interpreted with this caveat in mind.

Returning to the difference in the upper frequency limit between lIVEPs and tsVEPs, our findings are in line with previous electrophysiological studies which have shown that normal texture segregation produced a negative component peaking at around 150–200 ms in responses evoked to orientation textured stimuli [18, 19]. The longer time required to process texture might be due, as previously advanced, to the fact that the excitation of the neuron by an oriented line segment would be inhibited by a line segment placed outside the receptive field, such as center-surround inhibition of receptive fields of visual cells in primary visual pathways. This inhibition would be maximal when the center-surround line segments are placed orthogonally to each other [20–24].

What remains unsatisfactory to us is a quantitative estimate of the additional time required for texture-segregation processing based on the present data. Nothdurft [10] estimated 10–20 ms. Animal studies have also reported delays around 20 ms [21, 23, 24] and even longer delays for others; 80–100 ms [22, 25], separating the earliest response in V1 with that of other visual areas. The present work would either suggest around 50 ms when based on the peak time difference (Fig. 6), or around 4 ms when modeling the upper frequency end as a linear first order low-pass. While the upper measure seems too high, the other a little low and both are not consistent with existing data. We are unable to resolve this issue at this time.

All-in-all, the tsVEP represents a measure of intermediate visual processing that is situated between the simple processing of basic stimulus attributes represented with the early lIVEP peaking at around 100 ms and the more complex event-related cognitive potentials (which occur around 300 ms) that requires the longest time to be processed. Given that tsVEPs require more neuronal time to be processed compared to lIVEPs, we believe that their use would add valuable knowledge to the evaluation of the integrity of the global information processing of the brain, particularly in the presence of developmental or acquired injuries which are diffuse by nature and which often affect the processing of visual information due to the localization and organization of the visual pathways in the brain (i.e., perinatal brain hemorrhages due to prematurity, traumatic brain injury, etc.) [26].

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Fig. 1.
TsVEP orientation stimulus made up of four different stimuli: two homogeneous (**a** & **c**) and two textured (**b** & **d**)

Fig. 2.

Top: Representative waveform dominated by two main components: F1 in response to low-level stimulation (pattern change for every frame) and F0 evoked by texture on vs. texture off. Bottom: Corresponding magnitude spectrum

Fig. 3. On the left tsVEP waveforms are illustrated, obtained from one subject to temporal frequencies from 7.5 Hz (bottom) to 45 Hz (top). On the right is the corresponding magnitude spectrum; dashed arrows indicate F0 (tsVEP), full arrows F1 (low-level VEP)

Fig. 4. Temporal frequency tuning curves for each subjects including the frequency cut-off of the texture segregation VEP and the low-level VEP

Fig. 5.
Grand mean liveVEP and tsVEP temporal frequency tuning curves

Fig. 6.

Peak time for the five frequencies where both low-level VEP and texture-segregation associated VEP are available. Peak time was estimated from phase taking wrap-around into account (see text). At all frequencies the peak time for the tsVEP is above that of the llVEP, 51 ms on average