Effect of temporal parameters on visual evoked potentials elicited with tritan, red/green and achromatic stimuli

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Visual evoked potentials (VEPs) have been successfully employed in monitoring parvocellular and magnocellular activity in primates and humans. The aim of this study was to compare the temporal characteristics of red/green (R/G) and S-cone-system processing by examining integration times of VEPs elicited by the onset-offset of selective chromatic stimuli.

VEPs from three subjects were recorded using coarse 2c/deg gratings generated on a colour monitor. Chromatic square-wave gratings were modulated along R/G or Tritan axes and had a Michelson contrast of 0.3. Isoluminance of chromatic stimuli was set for every subject, using heterochromatic flicker photometry. The period of onset and offset duration was varied within duty cycles of either 520 (from 40 to 260 ms) or 1040 ms (from 80 to 400 ms). VEPs were recorded using an occipital scalp electrodes (position Oz) referred to linked ears. Waveforms of achromatic/chromatic contrast reversal and onset VEPs were compared in order to verify chromatic specificity of the response.

Conclusion: processing in S-cone-specific pathway requires longer integration time than in R/G and achromatic systems.

Key words: visual evoked potentials, colour-opponency, isoluminance, S-cone responses

INTRODUCTION

The segregation of primate retino-geniculate-striate projection containing two major parallel pathways projecting to and from the magnocellular or parvocellular layers of the dLGN is widely accepted [1–10]. The magno (M)-system derives input from the large phasic ganglion cells responding in a transient manner. The parvo (P)-system derives input from the tonic ganglion cells, which respond in a predominantly sustained fashion and are responsible for the coding of colour-opponent information. The P-system contains morphologically and functionally distinct red-green (R/G) and blue-yellow (B/Y, short-wavelength cone driven or S-cone-specific) subdivisions [11, 12], although recent evidence indicates that the S-cone driven pathway may form a distinct koniocellular (interlaminar) projection [13–16].

Visual evoked potentials (VEPs) have been successfully employed in monitoring parvocellular and magnocellular activity in primates and humans [17–28]. It is very important in this kind of experiments that stimulus should be selective for colour-processing system and minimally activate other mechanisms [12, 29, 30]. In this case VEPs can reflect the activity of separate colour-opponent channels [12, 31]. In particular, certain VEP components can reflect pre-cortical processing of tritanopic (Tritan) stimuli [10, 32, 33]. Such S-cone-pathway-specific VEPs tend to be smaller and of longer latency than equivalent VEPs from R/G system [31]. This study compares the temporal characteristics of R/G and S-cone-system processing by examining integration times of VEPs elicited by the onset-offset of selective chromatic stimuli.

METHODS

Grating stimuli were generated on a colour monitor using a computer-controlled, purpose-built interface.

Chromatic stimuli were calibrated using a Photoresearch PR1500-01 Spotmeter (Micron Techniques Ltd., England). The relative luminance of adjacent chromatic grating components could be adjusted to produce stimuli of varying luminance ratios. This allowed subjective specification of isoluminance using a minimum flicker paradigm [17, 18].

Ag/AgCl recording electrodes were attached to the occipital scalp according to the International 10/20 system (position Oz). Electrodes were referred to a linked ear reference. VEPs were amplified and averaged using a Medelec "Sensor" signal processor (256 or 512 sweeps).

Chromatic square-wave gratings were modulated along R/G or Tritan axes (Fig. 1).

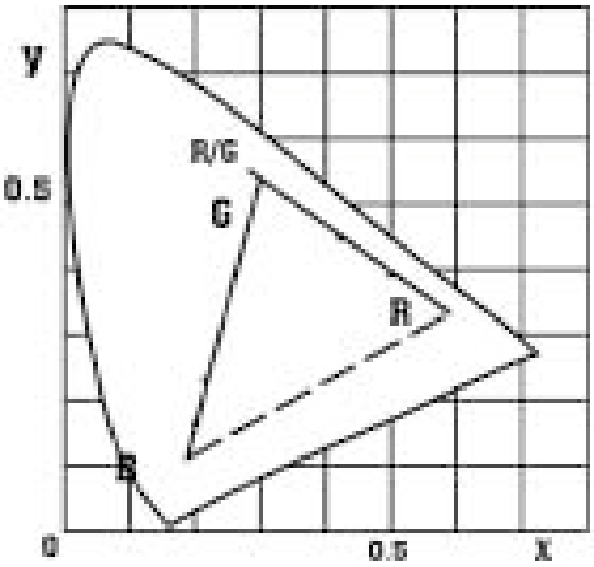

Fig. 1. CIE chromaticity diagram showing R/G and the purple/green chromatic axis of modulation. Filled circles show co-ordinates of the two components of the R/G and the purple/green gratings

Chromatic VEPs were recorded from two subjects using coarse grating stimuli which were restricted to a field size of 3° in order to minimize possible luminance-contrast intrusions due to chromatic aberration [32, 34–37] and macular pigmentation [38–40]. Spatial frequency was 2 c/deg as onset and reversal VEPs are maximally different at this spatial frequency [41]. Mean luminance was 30 cd/m^2; contrast was 0.3, defined as the equivalent Michelson contrast of each chromatic component [18]. The period of onset and offset duration was varied within duty cycles of either 520 (from 40 to 260 ms) or 1040 ms (from 80 to 400 ms).

In order to verify the chromatic specificity of the response, waveforms of VEPs elicited by achromatic/chromatic contrast reversal and onset stimuli were compared [17, 18, 42, 43].

RESULTS

1. Comparison of onset-offset and contrast reversal VEPs

Onset-offset, contrast reversal and contrast increment-decrement of coarse, low contrast achromatic gratings produce indistinguishable percepts of motion, consistent with selective activation of transiently responding motion detectors [44–46] of the magnocellular stream [30]. VEPs elicited using these methods of stimulation are almost identical in terms of amplitude and positive polarity [46–51]. Conversely, the onset-offset of isoluminant R/G or Tritan gratings produces no such effect and VEPs to onset are of opposite polarity to those elicited by offset and contrast reversal (Fig. 2 a, b). This difference is consistent with selective activation of sustained, chromatic-specific mechanisms as recognized in many earlier studies [17, 18].

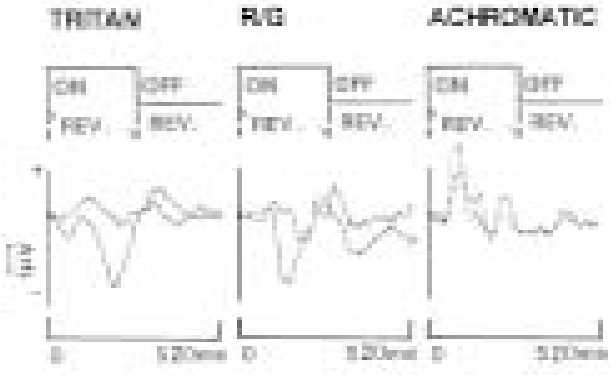

Fig. 2. Comparison of onset-offset (solid lines) and phase reversal (broken lines) responses with onset period stimulation within 520 ms duty cycle: (similar responses were recorded with onset period stimulation within 1040 ms duty cycle)

Achromatic onset VEPs are dominated by a positive component with a time to peak of approx. 85 ms (Fig. 2c). R/G and Tritan VEPs have long-latency negative components at approx. 155 ms and 200 ms, respectively. The R/G VEP also has an earlier negative component at 125 ms. These differences between bifid R/G onset VEP components and largely monophasic Tritan onset VEPs are consistent with previous studies [31] and further verify the high degree of stimulus selectivity attained in these experiments.

2. Temporal characteristics on Tritan VEPs

The optimum integration time for S-cone-specific VEPs was established by varying the onset period over a broad range (40 ms to 400 ms) within fixed duty cycles of either 520 ms or 1040 ms. The lon-

gest latency to the main negative peak was obtained when the stimulus onset period was 240 ms within both the 520 ms duty cycle (Fig. 3a) and the 1040 ms duty cycle (Fig. 3b). Maximum amplitude of S-cone-specific VEPs were obtained when the duration of stimulus onset was 160 ms (520 ms duty cycle) or 200 ms (1040 ms duty cycle). Optimal activation of the S-cone-system therefore requires onset periods between 160 ms and 200 ms.

The effect of stimulus offset duration on S-cone-specific VEPs has been studied by comparing latencies and amplitudes of VEPs elicited using identical onset periods but one of two stimulus duty cycles (520 ms and 1040 ms). The duration of the offset period had no affect on the latency of the S-cone VEP peak negativity. The amplitude of S-cone-pat-

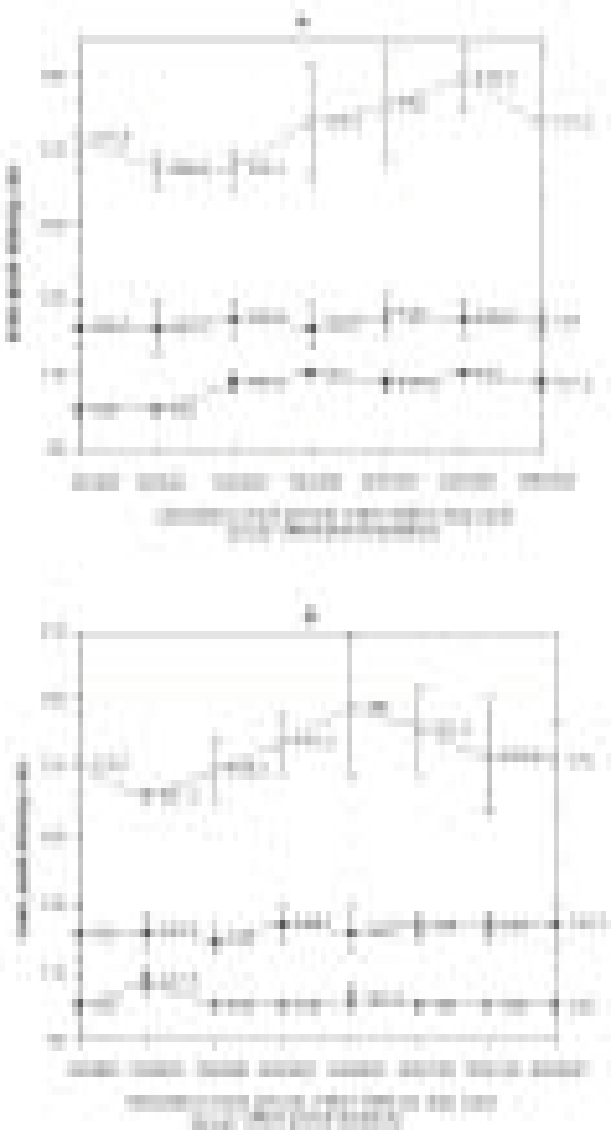

Fig. 3. Effect of stimulus onset duration on the main peak latency of tritan (o), R/G (■), and achromatic (▲) (mean from 2 subjects) VEPs: a – within 520ms duty cycle; b – within 1040 ms

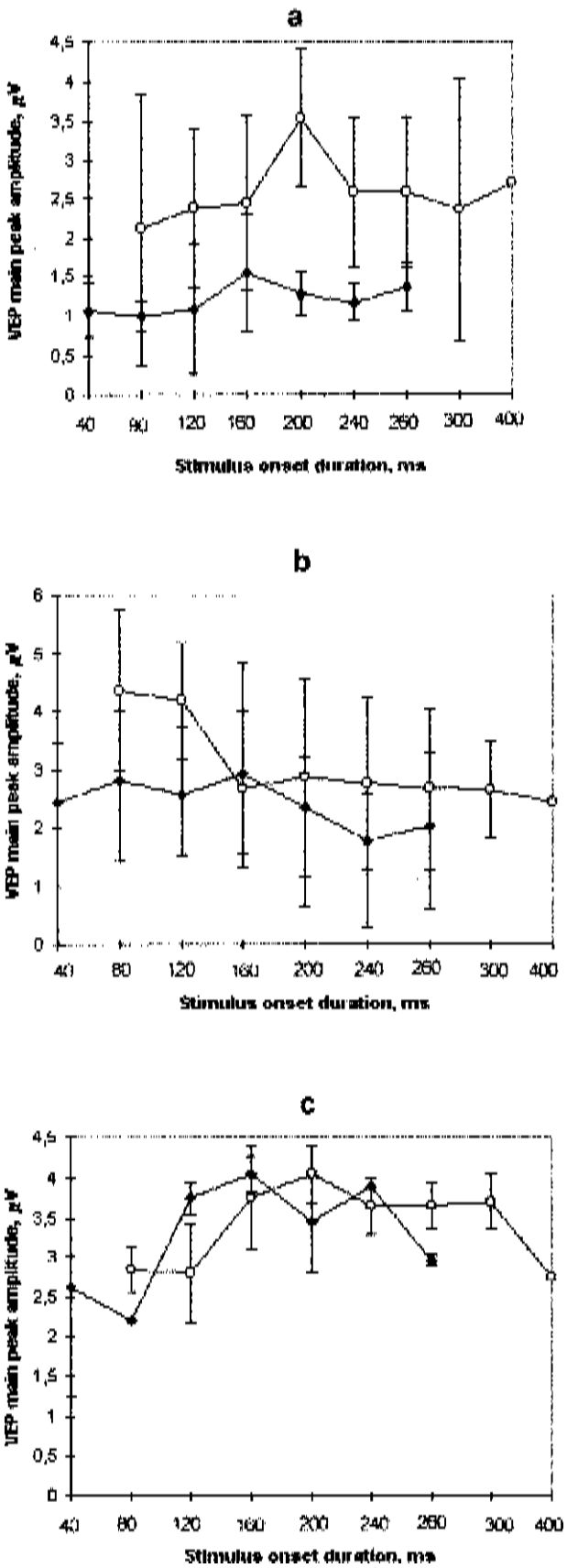

Fig. 4. Effect of stimulus onset duration on VEP amplitude (◆ – within 520ms duty cycle; o – within 1040ms duty cycle) during: a – tritanopic stimulation, b – R/G stimulation, c – achromatic stimulation (mean from 2 subjects)

hway VEPs does depend on the offset period (Fig. 4a) and this is statistically significant (T-test, p = 1.05E–06). It can be concluded that a longer stimulus offset period facilitates the generation of larger S-cone-pathway VEPs.

3. Temporal characteristics of R/G VEPs

The longest time to main negative peak for R/G VEPs was obtained when the duration of onset stimulus onset period was 200 ms irrespective of the length of stimulus cycle (Fig. 3 a, b), although there was a relatively little variability across the range.

The amplitudes were greatest when the stimulus onset period was 80 ms (Fig. 4b). The influence of stimulus offset on the amplitude of VEPs is illustrated in Fig. 4b. This difference between amplitudes obtained using different offset periods was found to be statistically significant according to the T-test (p = 1E–05).

4. Temporal characteristics of achromatic VEPs

There was a relatively little variability in the latency of achromatic onset VEPs (100–110 ms) across the range of onset periods (Fig. 3 a, b). Amplitudes of achromatic VEPs (Fig. 4c) also remained reasonably stable over a broad range of onset periods (between 120–260 ms). Changing the offset period had no significant effect (T-test, p = 0.76) on the latency or amplitude of achromatic VEPs.

DISCUSSION

The aim of the study was to compare the effects of temporal stimulus parameters on VEPs generated by selectively activated post-receptoral pathways. Low contrast gratings modulated along a subject-specific, isoluminant, tritanopic confusion line and restricted in size to 3-degrees elicited chromatic onset VEPs of opposite polarity to chromatic reversal VEPs.

The S-cone-pathway VEPs had a distinct monophasic shape and long latency (see also [31]) and were largest when generated by onset periods of 160–240 ms. The latency of S-cone-pathway VEPs was also longest when relatively long onset periods were employed (maximum time to the peak of the negative VEP was obtained when the onset period was extended to 240 ms). This can be interpreted as optimal stimulation of chromatic mechanisms which is traditionally considered to be slow [52–54], although recent evidence has questioned the apparent imbalance between the temporal properties of R/G parvocellular and S-cone koniocellular pathways [55].

R/G stimulation elicited responses with earlier negative components, possibly reflecting contributions from additional response mechanisms [31] such as a magno response to isoluminant R/G borders [15, 56, 57] or activation of chromatic texture mechanism [58–60]. R/G VEPs had shorter integration times and responses were largest when the onset period was between 80 and 120 ms. The latency of R/G VEPs was largely independent of onset period, suggesting that the response develops early or that more than one mechanism is operating across the range.

The latency of achromatic VEPs was shorter than for R/G VEPs, but also relatively stable across the range of onset periods used. This suggests faster achromatic (transient-type magnocellular) processing than for chromatic (sustained parvocellular) mechanisms. This difference in temporal processing has been reported in many psychophysiological [30, 35, 54, 59, 61–63] and electrophysiological [2, 30–32, 43, 64–66] studies.

Optimum integration times for achromatic VEPs also appear to be relatively stable over the range of onset periods used. Previous studies [67] have shown that early components of achromatic VEPs have a complete summation time of less than 50 ms (7.5 c/deg, contrast 0.016 to 0.7, sinusoidal grating). The relatively coarse gratings employed in the current study (2 c/deg) favor activation of more transient mechanisms, and it is possible that the minimum onset periods used in the study may have already exceeded the optimum integration time.

Our data clearly demonstrate that stimulus offset duration does not have any influence on the latency of VEPs elicited by the onset of Tritan, R/G or achromatic gratings. Longer offset periods do facilitate the generation of larger Tritan and R/G VEPs, possibly because the effects of chromatic pattern adaptation on chromatic-specific, sustained-type mechanisms [46, 68, 69] are less. Pre-adaptation to fine achromatic gratings also attenuates achromatic VEPs [70], but, at low spatial frequencies, even a high contrast mask fails to attenuate achromatic increment-decrement VEPs [31, 46]. It is therefore not surprising that offset duration has little effect on VEPs generated by the relatively coarse gratings employed in the current study. A short offset duration may also result in overlap of onset and offset response components, resulting in partial cancellation of responses [71].

CONCLUSIONS

Selective VEPs associated with S-cone-pathway, R/G and transient-type achromatic processing can be elicited by careful selection of chromatic, spatial and

temporal parameters of visual stimulus. The experiments described above additionally show how maximum differentiation between VEPs, associated with a particular pathway, depends on their varying temporal response properties, and this could be explained by different integration times. The experiments described above reveal that the period of chromatic stimulus offset is also an important factor and must be greater than 500 ms to avoid the confounding influence of component overlap and/or chromatic pattern adaptation. S-cone-specific processing requires longer integration times than for R/G or the fastest achromatic processing.

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TRITANOPINIO, RAUDONAI ŽALIO IR ACHROMATINIO STIMULŲ LAIKINIŲ PARAMETRŲ ĮTAKOS REGIMIESIEMS SUKELTINIAMS POTENCIALAMS TYRIMAS

S a n t r a u k a

Regimieji sukeltiniai potencialai (RSP) sėkmingai taikomi parvo- ir magnosistemų aktyvumui tirti.

Šio darbo tikslas buvo palyginti raudonai žalio (R/Ž) ir S-kolbelių specifinio kelio stimulo apdorojimo laikines savybes tiriant RSP, gautus naudojant selektyvius chromatinius stimulus su „onset-offset“ stimuliacija, sumacijos laikus.

Eksperimento metu buvo ištirti trys žmonės. Jiems buvo pateikiamos stačiakampės gardelės (2 cikl/laips) ir registruojami RSP. Chromatinės stačiakampės gardelės buvo moduliojamos pagal R/Ž arba Tritanopinę ašį; jų Michelsono kontrastas buvo lygus 0,3. Gardelių sudedamosios dalys turėjo vienodą skaistį, kuris buvo nustatomas taikant minimalaus blyksnio (angl. flicker) metodą kiekvienam tiriamajam atskirai prieš pradedant eksperimentą. „Onset“ ir „offset“ stimuliacijos trukmės svyravo 520 (nuo 40 iki 260 ms), arba 1040 (nuo 80 iki 400 ms) stimuliacijos laikotarpio ribose. RSP buvo registruojami naudojant aktyvų elektrodą pozicijoje Oz ir prie ausų spenelių pritvirtintus palyginamuosius elektrodus. Gauti atsakai buvo vidurkinami. Kaip kontrolė gautų potencialų grynumui nustatyti buvo naudojamos gardelės su tais pačiais parametrais, bet skirtingu pateikimo būdu – vadinamąją „reversal“ stimuliacija.

Pagrindinė darbo išvada: S-kolbelių specifinis kelias reikalauja ilgesnio informacijos sumavimo laiko negu R/Ž arba achromatinis keliai.