



Adaptation dynamics in pattern-reversal visual evoked potentials

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Abstract. Recording a VEP usually involves prolonged repetitions of the stimulus, but the influence of adaptation is rarely discussed in this context. Two experiments were performed. In Experiment 1 the time course of the response amplitude during steady-state stimulation was assessed. During the first seconds of stimulation we found an increase in amplitude, followed by a continuous exponential decline. This confirmed earlier results. There is considerable inter-subject variability concerning all aspects of the time course in our 19 subjects. Experiment 2 used two types of transient pattern reversal stimuli: one regular stimulus as used in standard clinical applications and one with a pause in between each reversal. N1 and P1 amplitudes did not show significant differential effects. N2 amplitude was reduced by 73% in the standard condition whereas P1 peak time increased slightly but significantly (3.2 ms).

Key words: evoked potentials, VEP, adaptation, steady-state, transient, pattern reversal

Abbreviations: ISI – inter-stimulus interval; MOP – motion onset potential; SNR – signal-to-noise ratio; ssVEP – steady-state VEP

Introduction

The recording of pattern reversal visual evoked potentials is a frequent technique in both clinical assessment of visual function and in basic research. Usually, the stimulus is presented to the subject throughout several minutes. Although adaptational effects are thus likely, this issue receives little attention in most applications of visual evoked potentials.

There is extensive psychophysical evidence for adaptation to many kinds of visual stimuli [35]. The adaptation of the transient VEP is well known for motion stimuli [9, 15, 16, 34].

The pattern-onset VEP is affected to some degree by both stationary [10, 28, 20] and drifting patterns [14]. Frequent long pauses result in slightly

decreased P1 peak time*[28], while no significant peak time changes were found during prolonged continuous stimulation [25, 36]. For normal subjects, pattern reversal N1–P1 and P1–N2 amplitudes tend to decrease over long stimulation periods, while migraine patients show a partially opposite effect [1].

The influence of adaptation on pattern reversal steady-state VEPs (ss-VEPs) has been demonstrated with sinusoidal gratings [17, 30, 41]. The results indicate an initial increase and subsequent decline of amplitude with a time constant in the order of 10 s, possibly depending on the spatial frequency of the stimuli. Abrupt changes in the pattern contrast of checkerboard reversal ssVEP result in much shorter time constants around 1 s [40]. Cross-adaptation with different spatial frequencies revealed complex interactions [39]. Adaptation might potentially affect ssVEP-based acuity measurements, but the actual influence was found to be insignificant [33]. Steady-state amplitudes can be enhanced during the recovery period 6–30 min after adaptation [32].

In the present study, we investigate the issue of inter-subject variability in more detail and extend the question of adaptation towards transient pattern reversal VEP recordings as used in many clinical and research settings.

Methods

Two experiments were performed, one with a steady-state stimulus (19 subjects, 19–35 years old) and one with a transient stimulus (nine subjects, 19–31 years old). All subjects had normal or corrected-to-normal visual acuity (acuity > 1.0, [3]) and gave their informed written consent to participate in the experiment.

VEP recordings

Visual evoked potentials (VEPs) were recorded at the occipital pole (position Oz according to standard nomenclature [2]) referenced to linked earlobes. Ground was attached to the right wrist. The vertical electrooculogram (EOG) was measured to detect eye blinks with a threshold criterion of 100 μ V. Signals were bandpass filtered (Experiment 1, 1–100 Hz; Experiment 2, 0.3–70 Hz), amplified, digitized (500 Hz sampling rate) and written to disk for off-line analysis. Preliminary averages of VEP and EOG were also displayed on-line to assess the recording quality.

* Apparently, there is no consensus regarding the proper use of the terms ‘latency’ and ‘implicit time’ to describe the timing of a VEP peak. We therefore use ‘peak time’ throughout this paper to avoid any ambiguity.

Stimuli

Checkerboard reversal stimuli were generated by a Macintosh G4 computer with a program based on the Apple GameSprockets [4] and displayed on a CRT screen with a frame rate of 67 Hz. Pattern contrast was 96%. The checkerboard was confined to a circular area (diameter 25°), the rest of the screen was dark. The checksize was 1.3° . Spatially homogenous gray stimuli displayed in pauses and in between the pattern stimuli had the same average luminance as the checkerboard patterns (13 cd/m^2). A fixation mark was provided in the center of the stimulus area.

Experiment 1: Steady-state VEP

The timing scheme is shown in Figure 1. Brief steady-state checkerboard reversal sweeps (2 s, $4.2 \text{ Hz} \hat{=} 8.3 \text{ rev/s}$) were alternated with homogenous gray stimuli of three different durations ('inter-stimulus intervals', ISIs) to generate three adaptational states: Continuous stimulation (0-s-ISI), intermediate (2-s-ISI) and low-adaptation (12-s-ISI) condition. All three conditions were embedded into the following stimulation procedure:

First, a homogenous gray area was displayed for 1 min to ensure that the subjects were in a well-defined non-adapted state. Ten seconds before the end a brief auditory signal allowed the subjects to prepare for the 1-min stimulation period. This was the sequence of steady-state epochs, each lasting for 2 s and alternating with ISIs in which a homogenous gray area was displayed. The ISIs lasted either 0.0, 2.0, or 12 s, but were constant within a 1-min sequence. One 2s epoch was recorded near the end of the pause prior to each stimulus sequence. For one stimulation block, this timing scheme (1-min pause and 1 min stimulus sequence) was repeated three times, each with a different length of the inter-stimulus intervals in random order. A total of six such blocks were presented to each subject.

Experiment 2: Transient VEP

Transient checkerboard reversal VEPs were recorded with two different stimulus sequences:

- (A) Standard checkerboard reversal stimulus: The stimulus pattern reversed every 500 ms. In between the reversals, the pattern was stationary.
- (B) Intermittent checkerboard reversal stimulus (Figure 2): After reversal, the stimulus remained stationary for 250 ms. Then it faded smoothly out over an interval of 667 ms and a homogenous gray area remained for 3333 ms. The same checkerboard pattern faded in again over an interval of 667 ms and remained stationary for 250 ms before the next reversal took place. This paradigm largely avoids adaptation to temporal and spatial stimulus properties.

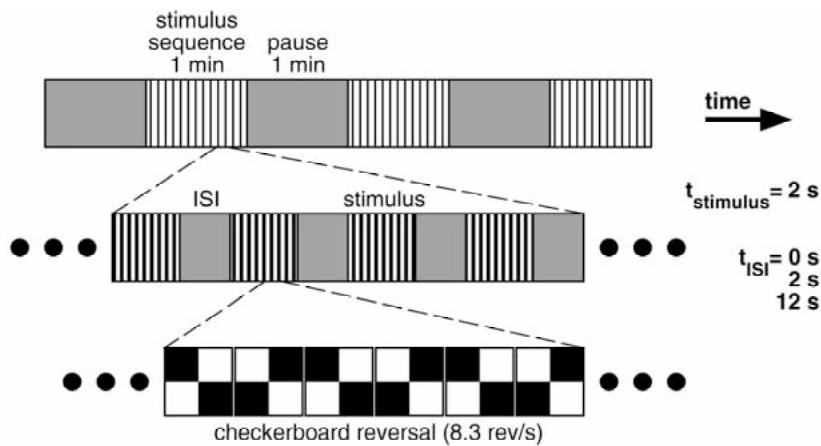


Figure 1. Timing scheme of the steady-state experiment. The center row shows the core stimulation sequence: Brief steady-state epochs (2 s) were interleaved with inter-stimulus intervals. This stimulus sequence was repeated three times with different ISI durations and a pause of one minute as shown in the top row.

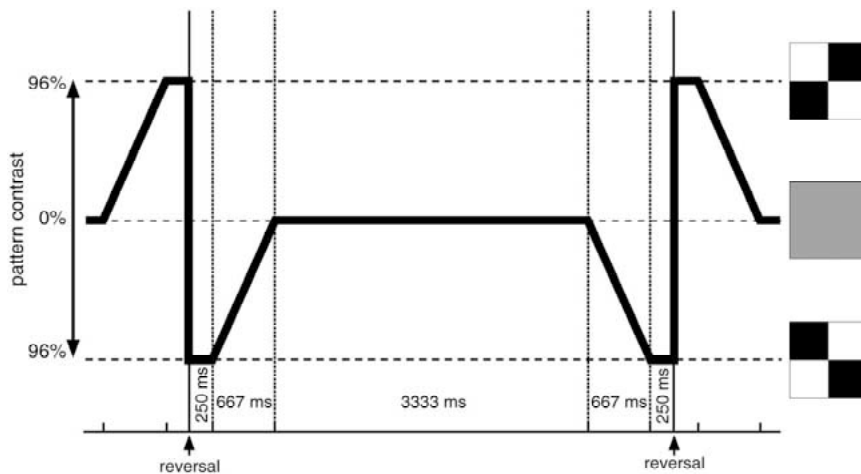


Figure 2. Timing scheme of the transient stimulus. After each reversal, the pattern remains stationary for 250 ms. In between the reversals, the pattern is faded out. A gray area stays on the screen for 3333 ms until the checkerboard fades in again. A 250-ms stationary pattern precedes the next reversal.

Two blocks of sequence A and B were recorded yielding a total of at least 200 artifact-free trials for each condition. The block order was counterbalanced in either an ABBA or a BAAB scheme.

Data processing

All analysis procedures were implemented with Igor Pro (Wavemetrics Inc.).

Experiment 1: Steady-state VEP

For each subject eye blink rejection typically left three to six steady-state epochs corresponding to the same ISI and to the same interval within a stimulation sequence. These were averaged to improve the signal-to-noise ratio for further processing.

The following procedure was then applied to each epoch:

- (1) Pattern-onset effects were eliminated by discarding the first 120 ms (i.e., the time between pattern onset and first reversal). This is necessary for epochs following an ISI or pause with a gray display, but was done for all epochs.
- (2) Any superimposed linear trend was removed to avoid contamination of the Fourier spectrum due to end effects [7].
- (3) The signal amplitude at 8.3 Hz, which is the second harmonic of the stimulus frequency (and thus corresponds to the reversal rate of the stimulus), was obtained via a discrete Fourier transform.
- (4) The amplitude value was corrected for noise [27, 7]. Noise levels were estimated by averaging the amplitudes at the neighboring spectral values. We here will refer to this corrected amplitude simply as ‘amplitude’. Noise correction was usually less than 5%.

Completing these steps for each 2-s epoch reveals how the amplitude evolves over a 1-min stimulation sequence. The pre-stimulus epoch was processed in the same way as the other epochs.

Inter-individual normalization was attained by dividing the amplitude estimates by the average computed from all amplitude values (except pre-sequence epochs) of all conditions, but separately for each subject.

Amplitude values cannot be expected to follow a gaussian distribution. Additionally, noise correction may occasionally lead to a zero amplitude estimate in case of small signal-to-noise ratios resulting in an artifactual distribution of values in the bottom range. To account for this, the median rather than the mean was chosen to combine the results of different subjects. Three subjects with an average signal-to-noise ratio (SNR) below 3.0 in the 0-s-ISI condition (cf. Figure 3) were excluded from the median. We defined SNR as

$$\text{SNR} = \frac{\text{corrected amplitude}}{\text{noise estimate}}.$$

Again, the average of the adjacent spectral values was taken as noise estimate.

Experiment 2: Transient VEP

Trials containing eye blink artifacts were excluded from further processing. Each trial was digitally filtered (40 Hz low pass). Standard VEP averaging techniques were applied. The interval from 100 ms before to 50 ms after stimulus reversal was used as a baseline estimate for peak measurements. The peak time and the amplitude of the positive deflection at around 100 ms (P1) as well as the amplitude of the preceding (N1) and following (N2) negativity were evaluated. The values obtained from all subjects were submitted to paired *t*-tests to compare both stimulus conditions. Significance levels were Bonferroni-adjusted to account for multiple testing.

Results*Experiment 1: Steady-state VEP*

Individual results for each subject are depicted in Figure 3 for the 0-s-ISI. Subjects are sorted by the signal-to-noise ratio of the 8.3 Hz ssVEP amplitude. The degree of variability is similar in the other conditions. The front trace in each pane shows the pre-stimulus recording.

For most subjects, strong 8.3 Hz responses can be seen, which represent the reversal rate of the stimulus (i.e., the second harmonic of the stimulus frequency). Additionally, many subjects also exhibit clear responses at 16.7 Hz (fourth harmonic of the stimulus frequency), e.g., 3-IH, 4-EJ, and 16-PM. Subsequently, we will only refer to the 8.3 Hz response, since higher harmonics are rarely used in ssVEP applications and interpretation is unclear.

There are considerable inter-individual differences in the time course. However, no quantitative measure of variability was computed since a single number will not give an appropriate account on the problem in this particular case. The most prominent adaptation is seen for subject 7-JK. Some adaptation can be found for subjects 2-AS and 9-JU. Several other subjects lack adaptation or show a continuous increase in amplitude (e.g., 6-KI, 8-CS, 10-BS). A number of subjects exhibit an initial increase before a stable level is reached or a decrease starts.

The median time course of the ssVEP amplitude is displayed in Figure 4. The very first point represents the pre-stimulus recording which is non-zero in spite of noise correction. This is due to the fact that amplitudes are positive, per definition. Hence, noise-induced values above zero are not counterbalanced by negative values.

Two properties can be recognized for the 0-s- and 2-s-ISIs: An initial increase in amplitude during the first few seconds before the maximum is reached. This is most prominent for the 0-s-ISI. The remainder of the curve

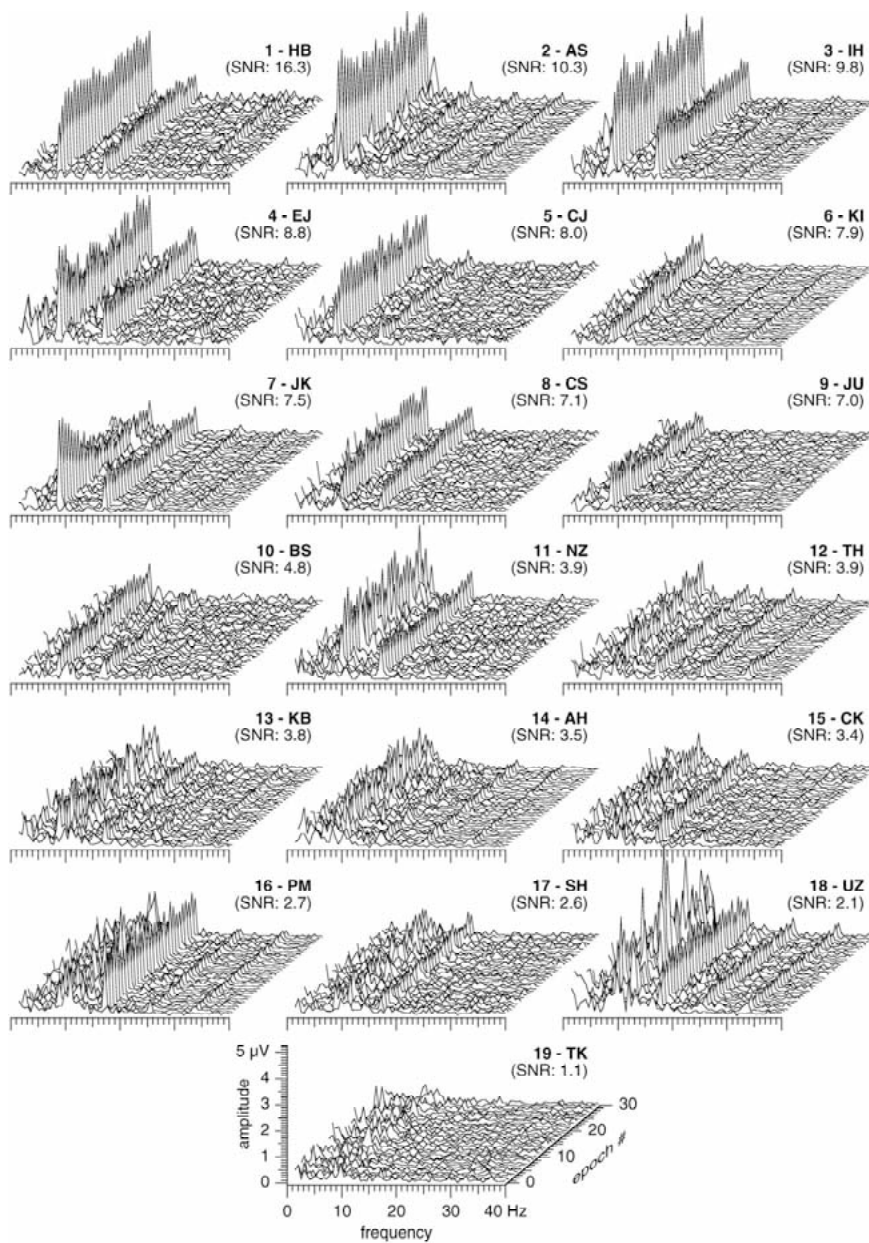


Figure 3. Fourier transform of steady-state epochs (0-s-ISI). Each pane shows the data of one subject sorted by the average signal-to-noise ratio (SNR) computed for the response at 8.3 Hz (= stimulus reversal rate). Bottom axes indicate the frequency, left axes the amplitude. Each trace represents one epoch: the front trace (0) is the pre-stimulus recording, the others from front to back show the 30 epochs recorded during the 1-min stimulus sequence. Most subjects produced distinct responses at 8.3 and 16.7 Hz. Some subjects, such as 18-UZ, show high alpha (≈ 10 Hz) activity.

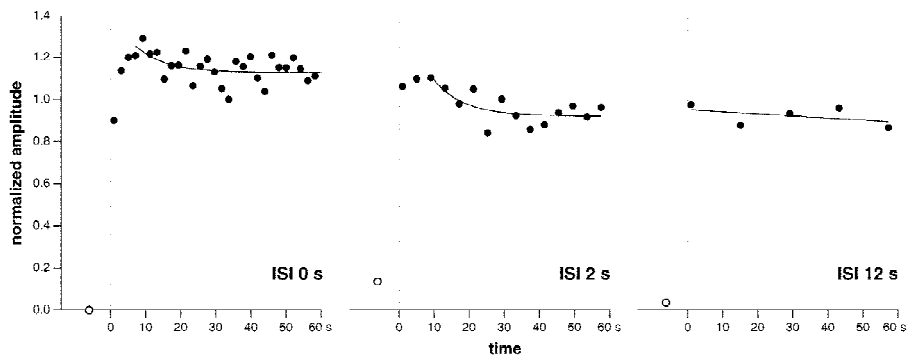


Figure 4. Time course of the median (16 subjects) for all three ISI durations. Each point represents the amplitude measured during one 2-s epoch. The very first point (open circle) shows the pre-stimulus recording. Exponentials were fitted to the data of the 0-s-ISI and 2-s-ISI condition. The time constants obtained were $8.2 \text{ s} \pm 6.3 \text{ s}$ (0-s-ISI) and $8.6 \text{ s} \pm 5.8 \text{ s}$ (2-s-ISI). A straight line was fitted in case of the 12-s-ISI, which was horizontal within the error range.

shows a continuous decline which can be described by an exponential. In order to find the section where the time course is dominated by the decrease rather than the increase, first a superposition of two exponentials, which account for both sections, was fitted to the 0-s-ISI data (least-squares fit). The point corresponding to twice the time constant of the rising exponential was taken as starting point for fitting a separate declining exponential. The same point, which was 6 s after the start of the stimulus sequence, was taken for the 2-s-ISI condition.

The time constants obtained for the exponential decline are $8.2 \text{ s} \pm 6.3 \text{ s}$ for the 0-s-ISI and $8.6 \text{ s} \pm 5.8 \text{ s}$ for the 2-s-ISI. The asymptotic level computed for the 2-s-ISI is reduced by 18% as compared to the 0-s-ISI (0.92 ± 0.03 vs. 1.13 ± 0.02). The 12-s-ISI condition produced a shallow curve, to which a straight line was fitted (slope: $-0.0010/\text{s} \pm 0.0011/\text{s}$, i.e., horizontal within the error range).

Experiment 2: Transient VEP

Figure 5 presents the results for both stimulation types as scatter diagrams. The peak values of the intermittent condition are plotted against those of the continuous condition. Significance levels were Bonferroni-adjusted (significant: $P < 0.0125$, highly significant: $P < 0.0025$).

The mean N1 amplitude was not significantly affected by the two experimental conditions (intermittent, $-1.2 \pm 0.4 \mu\text{V}$; continuous, $-2.3 \pm 0.3 \mu\text{V}$, $P = 0.038$), but there is some inter-subject variability. The mean P1 amplitude did not show any substantial difference between standard and

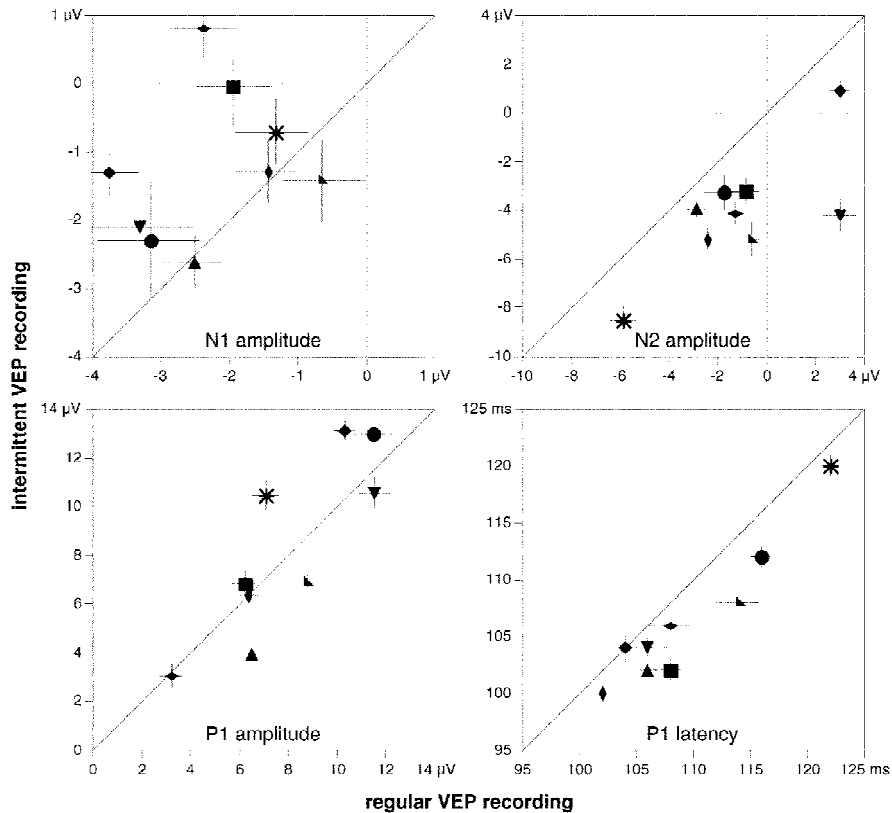


Figure 5. Comparison of peak measures between experimental conditions for all subjects. The abscissae represent the values for the regular continuous stimulus, the ordinates those for the intermittent stimulus. The two top panes show the amplitude of N1 and N2. In the bottom panes, amplitude and peak time of P1 are displayed. Amplitude error bars indicate the standard error. Peak time error bars represent half the difference between the results of the two recording blocks. Each marker shape represents one specific subject across panels.

intermittent stimulus (intermittent, $8.2 \pm 1.2 \mu\text{V}$, continuous, $8.0 \pm 0.9 \mu\text{V}$, $P = 0.69$). The P1 peak time is slightly but significantly reduced for the intermittent condition (106.4 ± 2.1 vs. 109.6 ± 2.2 ms, $P = 0.0017$). The mean N2 Amplitude was clearly enhanced for the intermittent condition (-4.0 ± 0.8 vs. $-1.1 \pm 0.9 \mu\text{V}$, $p = 0.0012$). The differences in P1 peak time and N2 amplitude were consistent for all subjects.

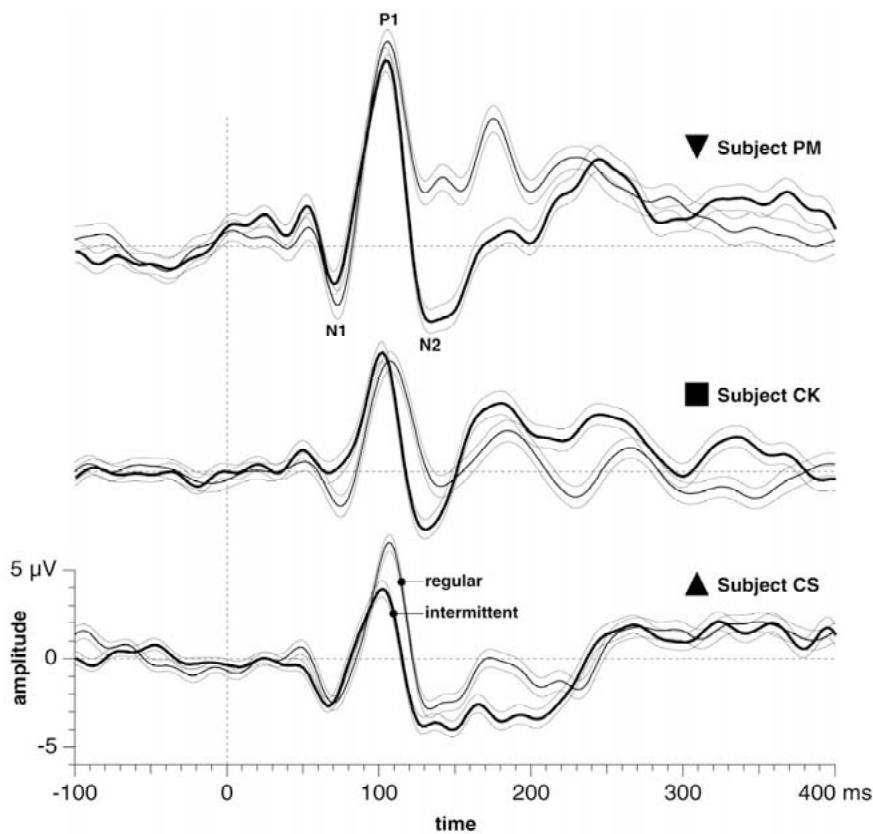


Figure 6. Selection of VEP traces representing different adaptational phenomena. Each pane shows the traces of one subject from the continuous (medium line) and intermittent (bold line) recording. Thin lines indicate the standard error. Symbols adjacent to the subject's initials are the same as used in Fig. 5 for the respective subjects. Top: Large difference in N2 amplitude but only small differences at other peaks. In the intermittent condition, the N2 clearly remains positive. Middle: Both N1 and N2 are affected, but P1 amplitude remains almost unchanged. P1 peak time is slightly reduced. Bottom: While N1 and N2 amplitudes are not affected, P1 amplitude is clearly reduced in the intermittent condition. There is a small influence on P1 peak time.

Discussion

Steady-state VEP

In the median time course of the steady-state VEP amplitude two features were found: an initial increase and a continuous decline. There is sizable quantitative and qualitative variability between subjects. In the 2-s-ISI condition, the asymptotic level is lower than in the 0-s-ISI. The 12-s-ISI produced

an almost constant amplitude which was the same as for the asymptotic level of the 2-s-ISI sequence.

The first 120 ms of each steady-state epoch were discarded to eliminate pattern-onset effects after pauses or ISIs. It might be argued that this was insufficient, thus causing the first values in the 0-s-ISI condition as well as the amplitude in the 2 and 12-s-ISI conditions to be reduced. However, the amount of amplitude reduction makes this very unlikely. Furthermore, a modified analysis with an additional 120 ms discarded was performed for some subjects. This did not markedly affect the result.

The general shape of the median time course resembles those described earlier for responses to sinusoidal gratings [17, 30]. The time constants are in good agreement with those found previously [17] following a stimulation and analysis procedure roughly similar to the one used in the present study (but based on the sum of the second and fourth harmonic).

Differences might be attributed to dissimilarity in spatial and temporal stimulus properties and stimulation sequence but might also be due to the choice of subjects [39]. This is supported by the large variation in time courses as can be seen in Figure 3.

The series of consistently low values obtained for the 12-s-ISI can be interpreted as a sequence of 'first' points each resembling the very first low value seen with the other ISIs. The shape of the 2-s-ISI time course probably reflects an interaction between two phenomena, a reduced amplitude after each ISI (similar to the 12-s-ISI) and an adaptation process as in the 0-s-ISI condition.

As can be seen from Figure 3, several subjects produced strong responses corresponding to the fourth harmonic of the stimulus frequency (16.7 Hz). For one subject (16-PM), these were more pronounced than the expected 8.3 Hz responses. In ssVEP studies, the fourth harmonic is hardly ever examined. Nevertheless, it seems worth noting that the time course of the fourth harmonic does not always mimic that of the second harmonic (e.g., subject 7-JK). This indicates that different processes are involved in the generation of the ssVEP. If one assumes that a steady-state response should, in principle, contain all components found in transient VEPs, this is not surprising.

The initial increase of steady-state amplitude parallels observations in single-cell recordings [41]. It has been speculated that this delay in reaching the maximum is caused by tonic inhibition between neighboring spatial frequency channels [17].

The decrease in amplitude found in the median time course is probably in part due to contrast adaptation [26, 13, 11]. It seems likely, though, that time-domain adaptation (flicker and motion which can be seen in a pattern reversal) [19] and spatial frequency adaptation [39, 5, 24, 37] supplement

this effect. The time constant for motion adaptation in the VEP is somewhat shorter (occipito-temporal, 2.5 ± 0.2 s; Oz, 5.2 ± 0.7 s [18]). However, it appears likely that different types of adaptation have different time constants such that the assumption of a simple exponential decline approximates only roughly the resultant of different effects.

The considerable inter-individual variability affects both initial increase and subsequent decline of the ssVEP amplitude. This cannot be solely attributed to noise. While some of the subjects which produced reliable low-noise VEPs also show very clear adaptation, others completely lack adaptation in spite of a high signal-to-noise ratio. Explanations for these large discrepancies can only be speculative but could include attention and arousal. Due to anatomical differences signals picked up by the electrodes might be dominated by different neural populations with different adaptational characteristics.

Transient VEP

The N2 amplitude of the transient VEP was found to be significantly enhanced for the intermittent stimulus condition. There is some inter-subject variability regarding N1 and P1 amplitude and P1 peak time. As depicted in Figure 6, subject CK, P1 amplitude itself may not change much for some subjects while the N1 amplitude may be reduced for the intermittent condition. Thus, the N1–P1 amplitude difference as assessed in some studies [1], would have been affected for this subject.

Commonly, the P1 peak time is considered to be very reproducible. We found a small peak time reduction for the intermittent condition, which was highly significant and consistent for all subjects, confirming previous findings [28]. In clinical practice, though, this small effect of 3 ms will usually be negligible. The lack of peak time effects in two earlier studies [25, 36] might be explained by different adaptation/recovery procedures: If VEPs are obtained from continuous stimulation, most adaptation already takes place during the first few pattern reversals. Consequently, subsequent VEPs will not show much additional adaptation.

It does not seem likely that the differences in amplitude are due to late components related to the end of the fade-in phase of the intermittent condition. An inspection of the time interval following the fading prior to the reversal revealed little or no VEP activity for all subjects. A possible late component would have to be in the P300 range to influence the N2 amplitude. The stimulus sequence used does not constitute a typical P300 paradigm [31]. Furthermore, if there was a superimposed P300, it should have reduced the N2 in the intermittent condition. We found the opposite, an enhanced N2. The differential effect on P1 and N2 is also inconsistent with the assumption of an interfering broad component.

The adaptation of the transient VEP N2 probably shares some of the mechanisms discussed for the ssVEP. The peak time of the pattern reversal N2 component resembles that of the N2 of motion onset potentials (MOPs) [9]. The MOP N2 is known to be partially adaptable by flickering stimuli and stimuli moving in other than the tested direction [19]. Furthermore, the checkerboard reversal can be seen as checks moving to new locations instead of reversing [38]. This suggests that a common mechanism underlies both the checkerboard reversal N2 adaptation and the non-directional MOP adaptation. This is not in contradiction to reports that pattern-onset VEPs are comparably adapted by both stationary and moving patterns [14], since pattern-onset stimuli do not contain motion information. An earlier study [23] did find differences in the case of pattern-onset.

There is also some evidence that texture contrast can induce adaptation of the pattern onset N2 [22]. The experiments reported comprised only two subjects and some stimulus parameters remain unclear. However, the time range which was found to be affected by texture contrast adaptation corresponds to the time range covered by VEP components specific for texture segregation [8]. Opposite to pattern onset, the pattern reversal as used in the present study does not contain a change in absolute texture contrast. Still, adaptable texture processing mechanisms might be involved.

In addition to cortical mechanisms, some adaptation might already take place in earlier processing stages. It is known that the human retina exhibits adaptation (predominantly not direction-specific) to motion stimuli [6]. The issue of retinal contrast adaptation is controversial [29, 12].

It is known that higher contrast leads to shorter P1 latencies [21]. This is paralleled by the reduced peak time in the intermittent condition found for some subjects in the present study and supports the idea of retinal adaptation: Reduced retinal response might result in reduced neuronal signal strength which would lead to increased conduction times and thus delayed cortical response.

Implications

Irrespective of the actual retinal or cortical processes involved, our findings affirm that the issue of adaptation needs to be taken into account when stimulation schemes are designed. Basic research might well be affected when stimuli are continuously repeated. The effects have to be considered on a case-by-case basis to avoid misinterpretation of the recorded data. In steady-state examinations, care should be taken especially when different conditions are compared in order to avoid adaptational bias being introduced into individual recordings.

Luckily, adaptation has little impact on typical clinical settings since P100 effects are small (peak time shift ≈ 3 ms, amplitude unchanged) and steady-state amplitude is only reduced by 10%.

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