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Similarities and dissimilarities between pattern VEPs and motion VEPs

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Abstract. The contrast response functions (CRF) of pattern-appearance and motion-onset VEPs for periodic stimuli (gratings) were compared. The CRF for pattern-appearance is accelerative for the P100 component and compressive for the N200 component. Contrary to these results, the CRF for motion-onset shows an almost negligible slope for both components within the contrast range tested (0.5–64%). To better isolate the neural contributions to these different VEP components, we studied the effects of prior adaptation to stationary and moving gratings. Adaptation to stationary gratings has no effect on both VEP components for motion-onset and the P100 component for pattern-appearance, but did reduce the amplitude of the N200 for pattern-appearance. Adaptation to slow (1 deg/s) and fast (4 deg/s) gratings left the P100 amplitudes unaltered, while it significantly reduced the N200 amplitudes for both pattern-appearance and motion-onset. These results suggest that the N200 component of the motion-onset VEP is generated by motion-dependent neurons, whereas the same component for pattern-appearance arises from contrast-dependent neurons. The observed differences between P100 and N200 components appear to reflect the activity of both transient and sustained neural mechanisms.

Key words: adaptation, contrast dependence, motion VEP, N200 wave, pattern VEP, P100 wave

Introduction

Microelectrode investigations and cytoarchitectonic studies suggest the existence of separate pathways underlying the processing of pattern and motion in the mammalian visual cortex. In analogy, parallel visual pathways have been assumed in human visual cortex. The results of PET studies [1] and fMRI studies [2, 3] support this view. However, there is also recent indication for mutual functional interactions between these afferent pathways. Using single-unit recordings, Nealey and Maunsell [4] found superficial cortical neurons in V1 which were activated by both parvocellular and magnocellular geniculate pathways. Although normally thought to receive solely magnocellular affer-

ents, a possible parvocellular input to V5/MT could not be ruled out [5]. If such cross afferentation also exists in the human visual system, then pattern-appearance (i.e., when a stationary stimulus is presented) and motion-onset (i.e., when a stationary stimulus is set into motion) could generate VEPs over occipito-temporal derivations that arise from both parvo- and magnocellular pathways.

To delineate parvo- and magnocellular contributions in the pattern-appearance and motion-onset VEP we compared amplitudes of both VEP types in response to gratings of different contrast before and after pattern and motion adaptation.

Methods

Square-wave luminance gratings of vertical orientation were presented on a high resolution display (Joyce Electronics, Cambridge) having a green phosphor, a frame rate of 100 Hz, and a mean luminance of 50 cd/m^2 which was kept constant throughout. Pattern and motion VEP were evoked by a grating with a spatial frequency of 2 cpd, a contrast varied from 0.5 to 64% (eight equi-logarithmic steps) and an eccentricity extending 0.5 to 3 deg along the horizontal meridian in one visual hemifield. The stripes had a height of +/–5.5 deg. The stimulus was stationary or it moved at a velocity varied from 0.25 to 13.5 deg/s. The stationary stimulus was presented for 1 s and thereafter it was set into motion for another second. A trial lasted 12 s. Thus, in pre-adaptation sessions, the ISI had a duration of 10 s. In adaptation sessions, prior to stimulus-appearance, an adaptation grating was presented for 5 s (only at the beginning of a run for 30 s). The ISI between adaptation offset and the stimulus onset was 1 s, the inter-trial interval (ITI) between the stimulus and the beginning of the next adaptation period was 4 s. During ISI and ITI, a blank field with the fixation mark was displayed. The adaptation grating having the same spatial frequency and position as the stimulus and a contrast of 4% was either stationary or it moved at a speed of 1 or 4 deg/s in the same direction.

Seven observers participated following informed consent. Six had normal visual acuity and one hyperope wore his refractive corrections during the measurements. The observers viewed binocularly the display at a distance of 85.5 cm and fixated a small point in the center of the screen. The stimulus was presented in the hemifield that yielded the greater motion VEPs. This was the right visual hemifield in five subjects and the left visual hemifield in two subjects. Two sessions were performed in each subject for each adaptation condition. Each session consisted of four runs, and in each run four logarithmically equidistant contrast levels were used (0.5, 2, 8, 32 or 1, 4, 16,

64%) and presented in randomly interleaved staircases. Each run consisted of 80 trials with 20 presentations per contrast level.

The EEG electrodes were situated 10, 20, and 30% of the lateral O_z-Fp_z distance left and right of O_z. Linked earlobe electrodes served as reference, an electrode at the right mastoid served as ground. The EOG of one eye was recorded for control. Trials with eye movements or blinks during stimulation were excluded from averaging. The potential differences were measured by amplifiers (Jaeger-Toennies, Höchberg) with a bandwidth between 1 and 70 Hz. The VEPs elicited by pattern-appearance and motion-onset, respectively, were obtained by averaging of 40 EEG responses.

Results

Figure 1 presents an original registration of pattern-appearance VEPs and motion-onset VEPs under pre-adaptation conditions for right hemifield stimulation from the six derivations used. The shape of pattern-appearance VEP and motion-onset VEP is similar as also found by Mackie et al. [6].

The pattern VEP amplitudes of the contralateral hemifield (derivations 1, 2, 3) exceed the amplitudes of the ipsilateral hemifield (derivations 5, 6, 7). There are also differences between the derivations in one hemifield. As a rule, the occipital amplitudes exceed the lateral (see Figure 1b: decrease from 3 to 1 and from 5 to 7).

The motion VEP amplitudes are also greater in one hemifield than in the other, but these lateral differences are less pronounced than for pattern VEPs. The hemisphere showing greater amplitudes varies from subject to subject. In Figure 1 the amplitudes of the contralateral hemifield (derivations 1, 2, 3) exceed the ipsilateral amplitudes (derivations 5, 6, 7). The amplitude differences between derivations of one hemifield are small. There is a tendency for greater lateral amplitudes.

An increase in contrast by a factor of 4 (compare Figure 1a and b) gives rise to a clear enhancement of the pattern VEP amplitudes whereas the motion VEP remains unchanged.

Figure 2 shows the amplitudes of the motion VEP components as a function of the temporal frequency in the contralateral hemisphere. The N200 amplitude is clearly greater than the P100 amplitude and increases in dependence on temporal frequency at least until a temporal frequency of 11.3 Hz which corresponds to a speed of 5.7 deg/s. The ipsilateral amplitudes show a similar trend, but they are somewhat smaller. The mean ratio between ipsilateral and contralateral N200 amplitudes (Figure 2) is 0.86. The result is in line with a hemisphere activation ratio of 0.9 found by Tootell et al. [2] for area MT in fMRI experiments.

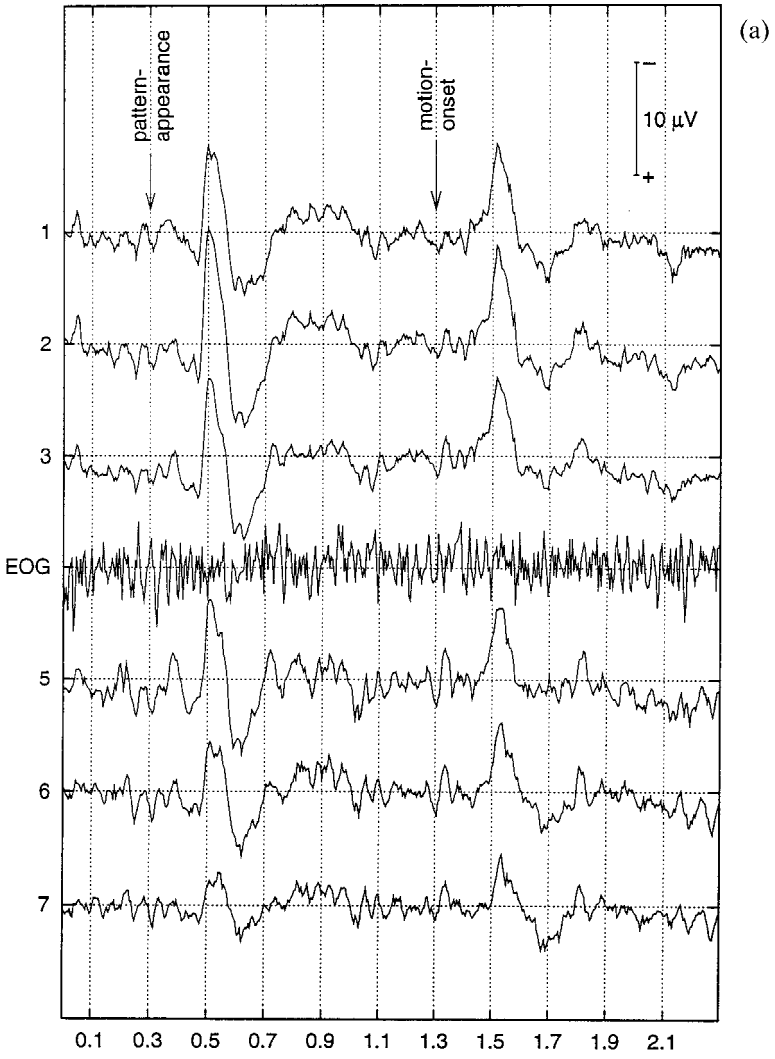


Figure 1. Original registration of averaged potentials (n = 40) for one subject evoked by pattern-appearance at 0.3 s and motion-onset at 1.3 s. The vertical distance between two horizontal lines corresponds to 10 μV with negative potential differences upward. Numbers at the left designate the electrode positions from left to right on the scalp. The stimulus in the right hemifield had a speed of 2 deg/s and a contrast of 2% (a) and 8% (b), respectively.

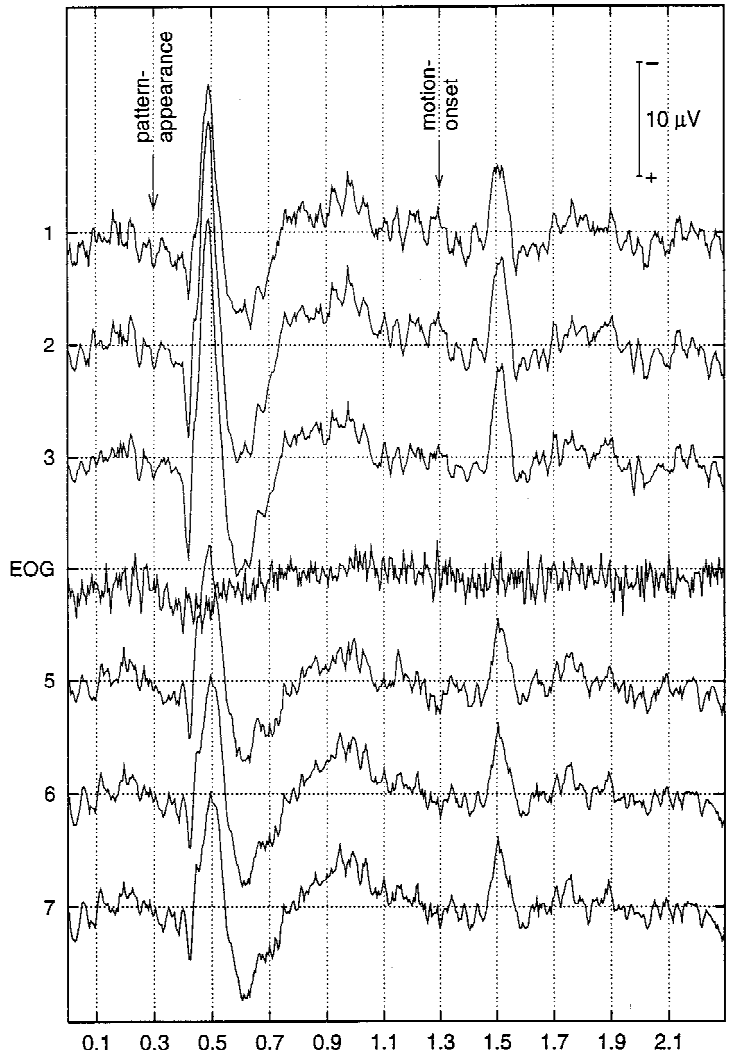


Figure 1. Continued.

Figure 3 presents the P100 and the N200 amplitude of the pattern VEP as a function of contrast. The mean amplitudes of the contralateral hemisphere are shown. The ipsilateral amplitudes exhibit a comparable trend, but they are clearly smaller in magnitude. The ratio between ipsi- and contralateral N200 amplitudes was, on average, 0.50. The following results are evident in Figure 3:

1. The N200 and P100 amplitudes increase with increasing contrast.

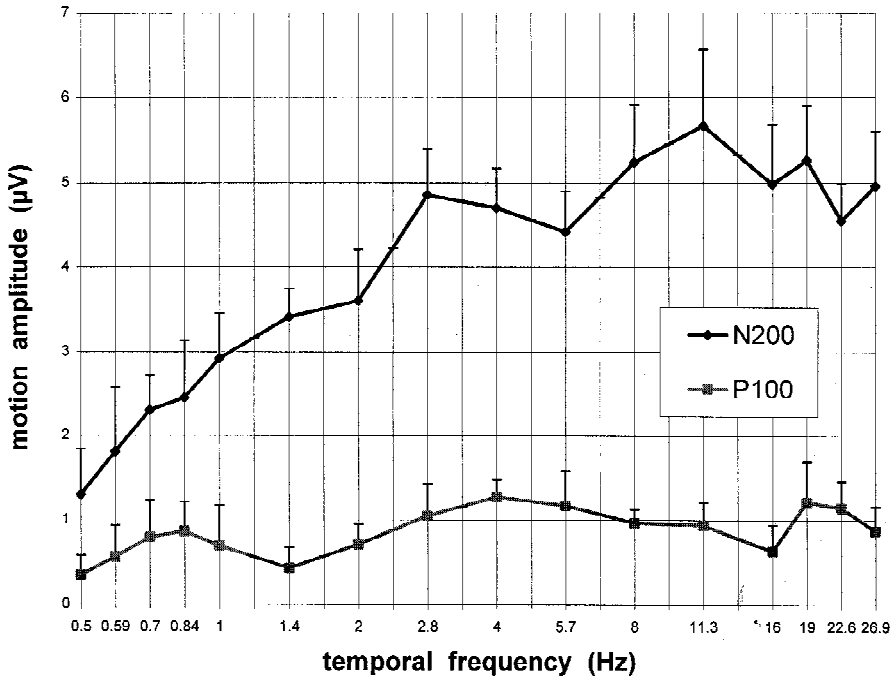


Figure 2. P100 and N200 motion VEP amplitude as a function of temporal frequency. A grating with a spatial frequency of 2 cpd and a contrast of 4% moved rightward (within an otherwise stationary window with an eccentricity of 0.5 to 3 deg) in one visual hemifield. Each point is the grand mean over the averaged VEPs (n = 40) of seven subjects and three electrode positions of the contralateral hemisphere. Vertical bars indicate standard errors.

2. The contrast response function of the N200 amplitude is compressive as a function of log contrast, whereas the contrast response function of the P100 amplitude is accelerative.
3. The N200 amplitude is significantly reduced after 0, 2, and 8 Hz adaptation, respectively (Wilcoxon test, one-tailed, p = 0.01), whereas the P100 amplitude remains unchanged after each of the three adaptation conditions.

Figure 4 shows the P100 and N200 amplitude of the motion VEP elicited by setting an already present grating into motion with a stimulus speed of 2 deg/s. The mean amplitudes of the contralateral hemisphere are shown. The amplitude difference between the two hemispheres is smaller than that of the pattern VEP, already evident in the speed varying experiment (Figure 2). The N200 amplitude interhemispheric ratio has a value of 0.72. The main results of Figure 4 are:

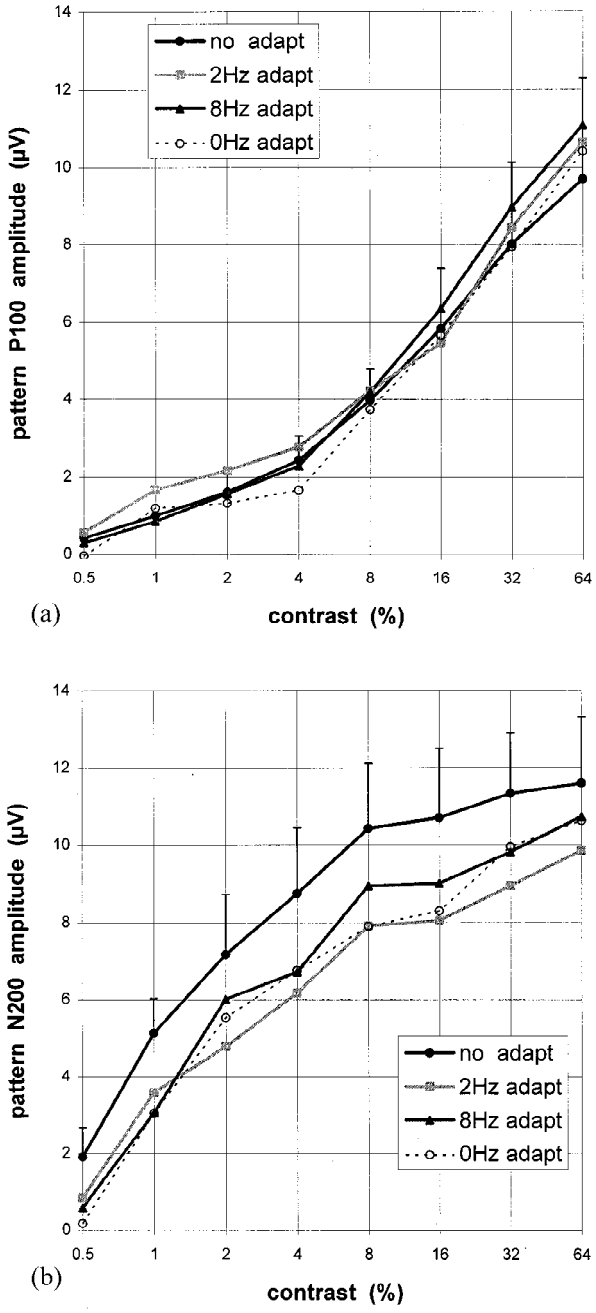
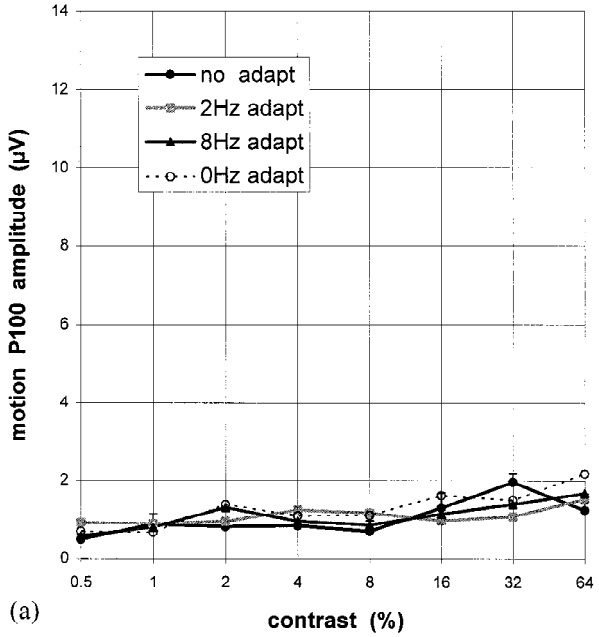
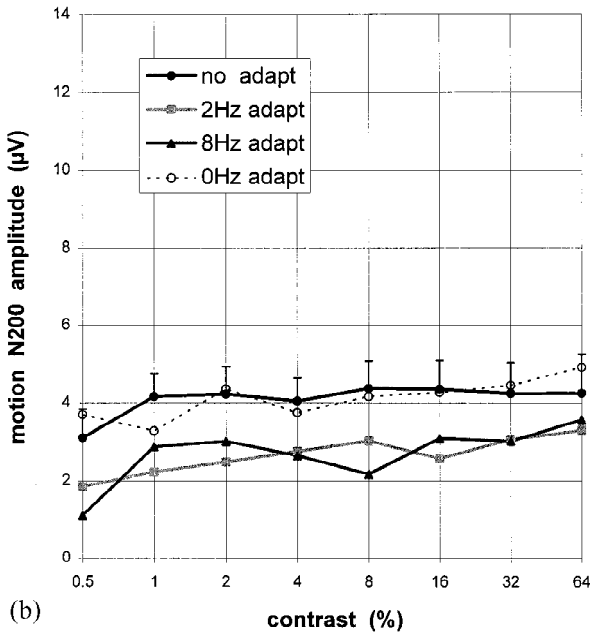


Figure 3. P100 amplitude (a) and N200 amplitude (b) of the pattern VEP as a function of contrast. The symbols show the results without adaptation and for three adaptation conditions (see inset). Each point is the grand mean over seven subjects (same as in Figure 2), based on two replications, from each of the three contralateral electrode positions. Vertical bars indicate standard errors for the pre-adaptation data. The standard errors of the other points are comparable in size and have been omitted for sake of clarity.



(a)



(b)

Figure 4. P100 amplitude (a) and N200 amplitude (b) of the motion VEP as a function of contrast. Otherwise as in Figure 3. The results are based on the same recordings used in Figure 3.

1. The N200 amplitude is significantly reduced after 2 Hz and 8 Hz adaptation (Wilcoxon test, one-tailed, $p = 0.01$) and unchanged after adaptation to a stationary (0 Hz) stimulus.
2. The P100 amplitudes are smaller than the N200 amplitudes and remain unchanged after each of the three adaptation conditions.
3. The dependence of N200 and P100 amplitude on contrast is less pronounced.

Discussion

Our results suggest that the pattern and motion VEPs have different characteristics. In the following, we discuss various aspects of these differences.

Components

The most obvious VEP component is the N200 which exceeds the P100 component in its amplitude for pattern-appearance as well as motion-onset VEPs. The N200/P100 amplitude ratio of motion-onset VEPs is about 4.0 (Figure 4). This same ratio is equally great for pattern-appearance VEP for low contrast levels (0.5–4%), whereas it approaches 1.0 at the highest contrast value of 64% (Figure 3). In other words, the P100 component exhibits relatively greater amplitudes in the pattern-appearance VEP at contrast values above 4%.

Comparing the N200 amplitudes of pattern and motion VEPs (generated in each case under optimal conditions), the VEP amplitude of motion-onset is clearly smaller than that of pattern-appearance. Figure 2 shows less than 6 μV as the optimal amplitude of the motion N200 component at a temporal frequency of 11.3 Hz (mean of seven subjects). In comparison, the optimal amplitude of the pattern N200 component at a contrast of 64% is nearly 12 μV and thus twice as great (Figure 3b, mean of the same seven subjects). The ratios were even greater after we selected that of the three derivations optimally situated over the site of generation (a near-midline derivation for pattern-appearance, a lateral derivation for motion-onset) because the pattern VEP is more strongly focussed than the motion VEP (see Figure 1 for an example).

Contrast dependence

The pattern VEP shows, as expected, a strong dependence on contrast both for the P100 and for the N200 amplitude (Figure 3). Contrary to this finding, motion VEP amplitudes hardly increase with increasing contrast (Figure 4).

The N200 amplitudes decline only for contrast values below 1%. This is in line with the result of Bach and Ullrich [7], who reported on a ‘fairly sharp drop for the motion response below 1.5%, and Kubova et al. [8], who found no significant N200 motion VEP variations above a contrast of 1.3%.

The two pattern-appearance VEP amplitudes show a clear difference in their slopes as a function of log contrast. N200 amplitudes increase most in the low contrast range (0.5 to 8%), whereas the P100 amplitude is more sensitive to variations in the upper contrast range (4 to 64%). Both empirical curves can well be approximated by hyperbolic ratios. This type of function has been found suitable to describe quantitatively the neuron contrast response behavior [9] and the relationship between contrast and perceived speed [10]. The P100 contrast response function could be generated by neurons with an average semisaturation contrast near 16%, whereas the N200 contrast response function appears to be generated by neurons with an average semisaturation contrast of 1 to 2%. Therefore, the neuron population underlying the N200 component appears to be more sensitive to stimulus contrast and saturates at lower contrast levels compared to the neuron population underlying the P100 component.

The relatively high N200 amplitude of the pattern VEP for low contrast values around 1%, which is unusual for contrast-sensitive processes [9], could have, in addition to origin in the activation of contrast-dependent neurons, an additional source. Tootell et al. [2] found activation of area MT with flickering stationary stimuli with the help of fMRI, and Anderson et al. [11] in MEG experiments reported that human V5 responds not only to moving patterns but also to the onset of stationary patterns. The N200 component could thus be a mixture of sustained activation of contrast-dependent neurons and transient activation of motion-dependent neurons.

Adaptation

The present results also suggest that stimulus-specific adaptation is a suitable method to reveal VEP features.

Motion VEP

N200 component. Significant amplitude reduction was found after motion adaptation to a 2 Hz and an 8 Hz drifting grating, respectively (Figure 4b). This is in agreement with earlier findings of Göpfert et al. [12] and shows that the motion-onset N200 component is, indeed, motion-dependent.

To avoid, or at least to reduce, additional luminance contrast-dependent and pattern-dependent activities in the N200 component Probst and Wist [13] used random-dot motion-contrast stimuli. Göpfert et al. [14] and Schlykowa et al. [15] stimulated with moving gratings after stationary presentation of the

gratings during the entire ISI. A rather long ISI of about 5 s was chosen in order to maximize the pattern adaptation and to minimize the motion adaptation. Bach and Ullrich [16] varied the ratio between time of motion and the total time of presentation of a grating to alter the motion-dependent activity of the N200 component to a varying extent.

In the present experiments one trial lasted 12 s. The stationary grating was presented for 1 s and then without any interruption the moving grating followed for another second. In the baseline state a uniform field of equal mean luminance was shown in the remaining 10 s. If the N200 component of the motion VEP should include contrast- and pattern-dependent activities, the presentation of stationary stimuli during the 10 s ISI should reduce the N200 amplitude. However, our stationary (0 Hz) adaptation grating lasting 5 s showed no effect (Figure 4b). We conclude that the state of adaptation of the contrast-dependent neurons has no significant effect on the N200 component of the motion VEP. Contrast-dependent neurons do not appear to significantly participate in the generation of this component. We also conclude that a stationary adapting pattern does not evoke a significant sustained activation of motion-dependent neurons.

P100 component. This minor component shows no post-adaptation amplitude reduction (Figure 4a). This finding might reflect that fact that this population of neurons responds only transiently, i.e. merely to velocity changes, but not to uniform velocity. Accordingly, a desensitizing effect on post-adaptation processes would not be expected.

In summary, we can consider the N200 component of the motion-onset VEP to be generated by motion-dependent neurons without any other significant contribution. Our results are in good agreement with the findings of Bach and Ullrich [16], who showed the differential effect of adaptation on the P100 and N200 components for motion onset. Our findings are also in line with those of Nealey and Maunsell [4], who reported that selective inactivation of parvocellular LGN neurons had only a negligible effect on the responses to motion in area MT in macaques.

Pattern VEP

N200 component. The N200 amplitude is significantly reduced by adaptation (Figure 3b). The amplitude reduction was comparable in size for both stationary and moving gratings. This effect could be related to the activity of contrast-dependent neurons that are activated by pattern-appearance independent of whether the grating moves. This assumption is further supported by the observation that motion-onset of a stationary pattern activates only motion-dependent neurons (see Figure 4b and below). In addition, stationary

pattern adaptation has no significant effect on the motion N200 amplitude, i.e. the activity of contrast-dependent neurons is unchanged during the transition of a grating from stationarity to motion.

P100 component. The P100 amplitude is unaffected by prior adaptation: it remains unaltered after stationary or moving adaptation (Figure 3a). In analogy to the P100 wave of the motion VEP we assume that this wave is generated by neurons that respond to variations in contrast, but do not show a sustained response to a constant stimulus contrast. If adaptation does occur at all in the P100 response, then our paradigm would be insensitive to this form of fast adaptation.

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