



Documenta Ophthalmologica **97**: 121–134, 1999.
© 1999 Kluwer Academic Publishers. Printed in the Netherlands.

Motion VEPs with simultaneous measurement of perceived velocity

ROLF MÜLLER¹, EDITH GÖPFERT¹, DAVID BREUER¹ & MARK W. GREENLEE²

¹*Carl Ludwig Institute of Physiology, Leipzig University, Leipzig, and* ²*Department of Neurology, Freiburg University, Freiburg, Germany*

Accepted 11 April 1999

Abstract. The dependency of the N200 amplitude of the motion-onset VEP evoked by a parafoveal grating of variable speed (0.25 – 13.5 deg/s, corresponding to 0.5 – 27 Hz) and constant contrast (4%) was studied. Additional measurements were made with parafoveally presented gratings of constant speed (2 deg/s, corresponding to 4 Hz) and a variable contrast (0.5 – 64%) before and after adaptation to a stationary or drifting grating. In this latter experiment, simultaneous psychophysical measurements were made of the perceived speed. The amplitude of the N200 wave increased with increasing stimulus speed within the slow speed range up to 1.5 deg/s (corresponding to 3 Hz). Adaptation to a stationary grating had no significant effect on the relationship between the N200 amplitude and stimulus contrast. Contrary to this, adaptation to a slowly drifting grating (1 deg/s, corresponding to 2 Hz) or to a rapidly drifting grating (4 deg/s, corresponding to 8 Hz) reduced the N200 amplitude significantly. Adaptation to a stationary grating slightly reduced the perceived speed of subsequently viewed gratings. Adaptation to a slowly drifting grating increased the perceived speed of the subsequently viewed gratings, whereas adaptation to a rapidly drifting grating decreased the perceived speed. The findings can be best explained by a two-channel model of speed perception. While the motion VEP reflects the sum of both channel activities, the psychophysical measures point to the antagonistic encoding of low and high velocities.

Key words: adaptation, channels, motion-onset VEP, N200 wave, perceived velocity, speed dependence

Introduction

The N200 amplitude of motion VEPs under foveal binocular viewing increases when the speed of an otherwise constant grating is increased. An early study [1] showed a clear positive slope for speeds between 0.1 and 0.9 deg/s (0.3 and 2.3 Hz) and a shallower slope beyond 0.9 up to 3.1 deg/s (2.3 to 8 Hz). Such a relationship can be generated by motion-sensitive neurons in several ways.

Hypothesis 1. There is a single population of neurons whose integral activation increases monotonically, but not necessarily linearly, from zero (corresponding to stationarity, or the lower threshold of perceived speed) up to a maximum (corresponding to the highest perceived speed). In other words, there is a unique relationship between the extent of integral activation of the motion-sensitive neuronal population and the perceived speed.

Hypothesis 2. There are two temporal frequency channels, a ‘slow’ and a ‘fast’ channel, and the relative activity within these channels mediates our sense of stimulus speed. Accordingly, activity in the ‘slow’ channel neurons would correlate with the perception of low speeds and activity in the ‘fast’ channel neurons with the perception of high speeds. Assuming the anatomical locations of these channels are similar, the motion VEP would necessarily be ambiguous and reflect the activity of both channels. This argument holds even if human motion perception is based on more than two channels.

Prior exposure to a high-contrast drifting grating increases the contrast threshold for detecting a subsequently viewed grating [2], increases the lower threshold for motion [3], and alters the perceived speed of subsequently viewed gratings [3, 4]. Psychophysical experiments [5–9] applying adaptation and masking suggest the existence of at least two wide-band temporal frequency channels. Corresponding motion VEP recordings employing adaptation also indicate the existence of a second channel [10, 11].

According to the two-channel view, increments in temporal frequencies in the medium range evoke an increase in the activation of ‘fast’ neurons, which is accompanied by a decrease in activation in the ‘slow’ neurons. This range is limited at the lower end by the maximal activity of the slow channel (for a stimulus temporal frequency of 1 – 2 Hz) and at the upper end by the maximal activity of the fast channel (for a stimulus temporal frequency of 8 – 16 Hz). This speed opponency between the ‘slow’ and ‘fast’ channels could explain the shallow slope of the N200 amplitude as a function of temporal frequency observed within this range [1].

Further independent information about neural processes evoked by moving stimuli comes from recording of single cell activity. Studies of functional properties of macaque speed-dependent neurons in cortical areas V1 and V2 [12], area V3 [13], and area MT [14] revealed their lowpass and bandpass characteristics as a function of temporal frequency.

To better understand how temporal frequency and speed are encoded in the human cortex, we simultaneously measured motion-onset VEPs and perceived speed before and after adaptation to a drifting grating. Simultaneous measurement of motion-onset VEP and perceived speed of a stimulus, set into motion after a short stationary period, enables us to judge the goodness of cor-

respondence between the two measures. We asked to what extent the motion VEP, recorded over the occipito-temporal cortex, can reflect psychophysically determined speed perception. If the two-channel hypothesis is valid, an N200 amplitude evoked by moderate temporal frequencies (between 2 and 8 Hz) should be reduced following adaptation to either a 2 Hz or an 8 Hz stimulus. The effect of adaptation at 2 Hz or 8 Hz should have opposite effects on the simultaneously measured perceived speed.

Methods

Subjects

Six emmetropic subjects (three males, three females) participated in the experiments, five of whom were naive and one experienced. Only the latter subject was informed about the aims of the study. The observers viewed the pattern binocularly at a distance of 85.5 cm. During the runs they were asked to fixate a small point presented in the center of the display.

Stimuli

Square-wave luminance gratings of vertical orientation were created by a VSG 2/2 graphics board (Cambridge Research Ltd., Rochester, England) and presented on a high resolution display (Joyce Electronics, Cambridge, England) with a green phosphor, a frame rate of 100 Hz, and an average mean luminance of 50 cd/m².

Procedure

On each trial, three stimuli were successively presented: the adaptation stimulus for 5 s (at the beginning of a run for 30 s), the reference stimulus, and the test stimulus. An ISI of 1 s duration occurred prior to reference and test stimulus presentation. Both reference and test stimuli were presented for a total duration of 2 s. The stimulus presentation consisted of a 1 s period of stationary, followed by a 1 s period of drifting presentation of the grating. An additional 1 to 1.5 s response period followed (see Speed judgment). Thus, each trial had a duration of 12 to 12.5 s. An effect of adaptation on the appearance of the moving reference stimulus was expected under these temporal conditions [15, 16].

Adaptation and reference stimuli were presented eccentric of the fixation point (extending from 0.5 to 3 deg along the horizontal meridian) in one visual hemifield only. They had a height of 11 deg (5.5 deg above and below

the horizontal meridian) and a spatial frequency of 2 cpd. The test stimulus subtended 4.2 deg in width and was presented in the opposite hemifield at an eccentricity between 3 to 7.2 deg. The test stimulus had the same height as reference and adaptation stimulus, a contrast level of 4%, and a spatial frequency of 1.2 cpd, adjusted in spatial frequency to compensate for the additional eccentricity according to the cortical magnification factor [17]. All stimuli drifted rightward within a stationary window.

The reference stimulus was presented in that hemifield where it evoked the larger motion VEP. This was the right visual hemifield in five observers, and the left visual hemifield in the other observer.

Experiment 1. We repeated the temporal frequency experiment of Göpfert et al. [1]. Two sessions took place for each subject. Each session consisted of four runs and in each run four reference temporal frequencies were used (0.5, 1, 4, 16 Hz, or 0.59, 1.4, 5.7, 19 Hz, or 0.7, 2, 8, 22.6 Hz, or 0.84, 2.8, 11.3, 26.9 Hz). These different temporal frequencies were presented in randomly interleaved staircases. Each run consisted of 80 trials with 20 presentations of each reference temporal frequency. The reference contrast level was held constant at 4%.

Experiment 2. Two sessions were performed in each subject for each adaptation condition. Each session consisted of four runs and in each run four logarithmically equi-distant reference contrast levels were used (0.5, 2, 8, 32%, or 1, 4, 16, 64%). These different contrast levels were presented in randomly interleaved staircases. Each run consisted of 80 trials with 20 presentations of each reference contrast level. The reference stimulus drifted with a temporal frequency of 4 Hz. The adaptation contrast level remained constant at 4%. Three conditions of adaptation were conducted: no prior adaptation stimulus (pre-adaptation experiment), stationary adaptation, or unidirectional motion adaptation (temporal frequency of 2 or 8 Hz).

VEP recording

The EEG electrodes were situated left and right of O_z , at locations corresponding to 5, 10, and 15% of the O_z - Fp_z head circumference away from the midline. Linked earlobe electrodes served as reference, an electrode at the right mastoid as ground. The potential differences were measured by amplifiers (Jaeger-Toennies, Höchberg) with a bandwidth between 1 to 70 Hz, recorded on an 8-channel-recorder (Sony, Tokyo), and off-line averaged after 200 Hz sampling. The EEG was filtered with a digital narrow-band 50 Hz notch filter to eliminate noise from the mains. The reference VEPs elicited by motion-onset were obtained by averaging 40 EEG responses from runs 1 and

2, and additional 40 responses from runs 3 and 4, separately. In addition, the EOG over one eye was recorded. The EOG electrodes were situated on nasal and lateral brow, thus forming a diagonal derivation with respect to the eye. Trials with eye movements, blinks, or other artifacts during reference stimulus presentation were excluded from averaging. EOG and EEG signals were amplified and averaged in the same way. We found no temporal coincidence between the EOG and VEP amplitudes for the data from all included trials.

The N200 amplitude of the motion VEP varied in its size from derivation to derivation. The site with the maximal amplitude varied over subjects. In some observers, the amplitude of the most lateral derivations (15% left and right of the midline, see above) exceeded the value of the 10% ipsilateral derivation, whereas in other observers the amplitudes of the latter derivations exceeded those of the electrodes at the 15% location. In order to balance the individual variations we averaged the values of the three derivations of each hemisphere. Thus, a representative N200 value of each hemisphere was obtained which is a mean of the individual derivations over each cortical hemisphere.

Speed judgment

During each trial, the observer judged whether the reference or the test stimulus moved faster and signaled this judgment by pressing the corresponding button on a response box. The initial speed of the test stimulus was distinctly faster (in terms of temporal frequency, twice as fast) or slower (stationary) than the reference speed. The temporal frequency of the test stimulus was varied in dependence on the previously given response according to the ‘yes-no’ variant of the Best-PEST algorithm [18], which has been shown to be appropriate for perceptual matching tasks [3]. The test stimulus speed was decreased after a judgment ‘test stimulus faster’ and increased after a judgment ‘reference stimulus faster’. At the end of a run (after 20 decisions per reference stimulus) the perceived test stimulus speed corresponded to the perceived reference stimulus speed. The variable

$$\begin{aligned}
 v' &= v_{test}/v_{ref} \\
 &= (tf_{test}/tf_{ref}) * (sf_{ref}/sf_{test}) \\
 &= (tf_{test}/tf_{ref}) * 1.67
 \end{aligned}
 \tag{1}$$

sf_{test} : spatial frequency of the test stimulus,

tf_{test}, v_{test} : temporal frequency and speed of the test stimulus at the end of a run,

$sf_{ref}, tf_{ref}, v_{ref}$: spatial frequency, temporal frequency, and speed of the reference stimulus,

can then be considered a relative measure of the perceived speed of the reference stimulus. Values above unity indicate that the physical speed of the test stimulus has to be increased relative to the reference to match it perceptually, values below unity indicate that the test speed had to be decreased to match that of the reference [3].

In the same way

$$tf' = tf_{test}/tf_{ref} \quad (2)$$

can be considered a relative measure of the perceived temporal frequency of the reference stimulus.

The different eccentricities used for reference and test stimuli were chosen to minimize the effect of the adaptation and reference stimulus, presented in one visual hemifield, on the perception of the test stimulus, presented in the opposite hemifield. Such effects could occur via commissural connections or ipsilateral visual field representation in V5 [19]. Although the comparison of gratings of unequal spatial frequency could appear, at first glance, to be more difficult, Chen et al. [20] found no measurable deterioration of speed discrimination performance under similar conditions.

Results

Experiment 1: Temporal frequency variation

Figure 1 presents the N200 amplitude of the motion-onset VEP as a function of temporal frequency (log scale). The results of the contralateral and ipsilateral hemisphere derivations are plotted separately. The results obtained for parafoveal vision show the same trend as the foveal data acquired in an earlier study [1]. Two separate regression lines were fitted to the lower and to the upper half of temporal frequency range (see Figure 1). The best fitting bilinear functions for the contralateral hemisphere are:

$$a = 4.80 * \log tf + 2.51 \quad (0.5 \leq tf \leq 2.8 \text{ Hz}), \quad (3)$$

$$a = -0.55 * \log tf + 5.10 \quad (4.0 \leq tf \leq 26.9 \text{ Hz}). \quad (4)$$

a: N200 amplitude of the motion-onset VEP (μV),

tf: temporal frequency (Hz).

Two trends are noticeable in the data: first, the N200 amplitude increases with a clear positive slope as a function of log temporal frequency up to 2.8

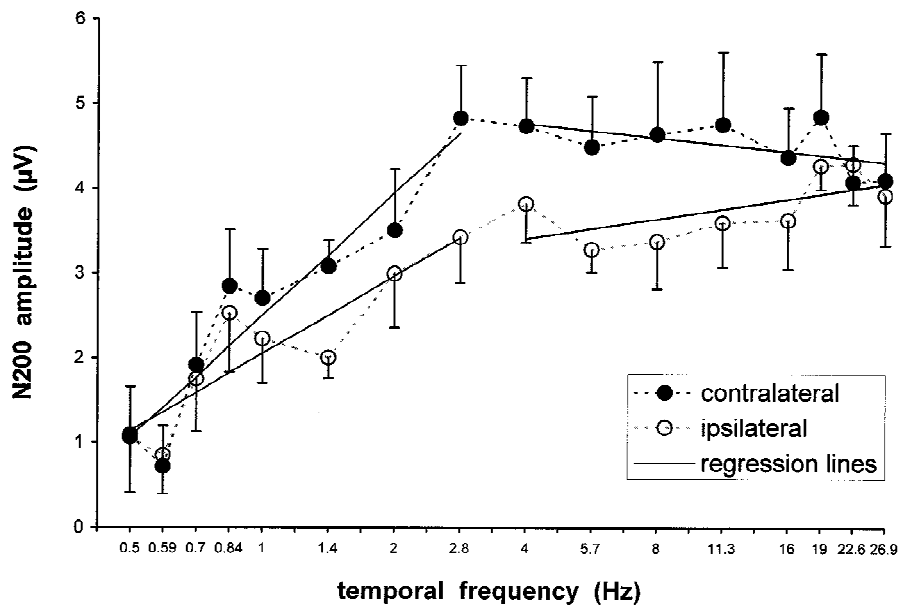


Figure 1. N200 amplitude of the motion-onset VEP as a function of temporal frequency of the reference stimulus (note log scale). A vertically oriented grating with a spatial frequency of 2 cpd and a contrast of 4% moved rightward within a stationary window (eccentricity between 0.5 to 3 deg) in one visual hemifield. Each data point is the grand mean over the averaged VEPs ($n = 40$) of six subjects and three derivations. The vertical bars show the standard errors. Upper dotted curve: contralateral hemisphere, lower dotted curve: ipsilateral hemisphere (see inset). The straight lines were fitted by linear regression for the lower and upper temporal frequency range.

Hz; second, the N200 amplitude vs. temporal frequency function exhibits a shallow slope for temporal frequencies above 2.8 Hz. Above 2.8 Hz the slope is slightly positive for the ipsilateral data and negative for the contralateral data.

Experiment 2: Adaptation

The effect of different adaptation conditions on the N200 motion-onset VEP amplitude is plotted in Figure 2 as a function of contrast. The following results are evident in the grand means over the six subjects:

1. The N200 amplitude evoked by the 4 Hz reference stimulus is significantly reduced in both hemispheres after adaptation to gratings with a temporal frequency of 2 Hz and 8 Hz, respectively (Wilcoxon test, $p < 0.01$).
2. Adaptation to slow (2 Hz) and fast (8 Hz) motion yields similar effects on the N200 amplitude.

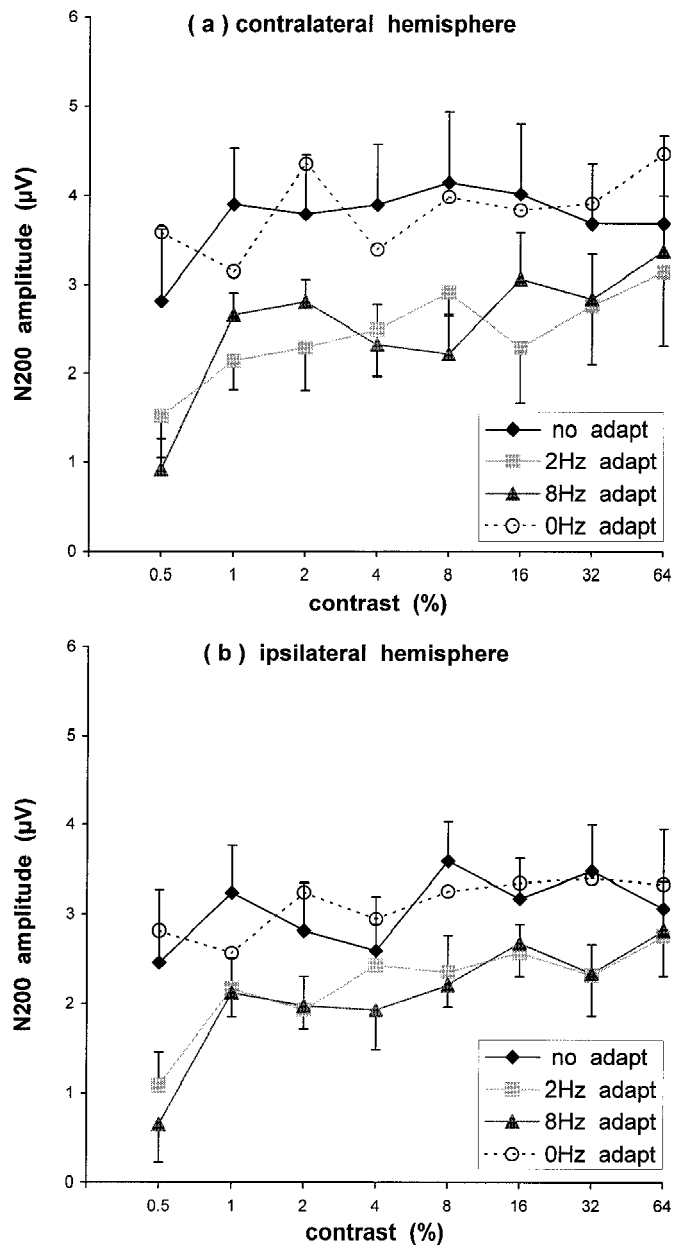


Figure 2. N200 amplitude of the motion-onset VEP as a function of reference contrast (logarithmic scale). (a) contralateral hemisphere; (b) ipsilateral hemisphere. The data points are grand means over the six observers and the three derivations (as in Figure 1) with two averaged VEPs ($n = 40$) each (vertical bars: standard errors). The adaptation stimulus was either stationary (0 Hz adapt) or it moved in the reference direction (rightward) at a temporal frequency of 2 Hz or 8 Hz (see inset). In the no-adapt condition, the time scheme remained unchanged but no adaptation stimulus was presented (blank screen).

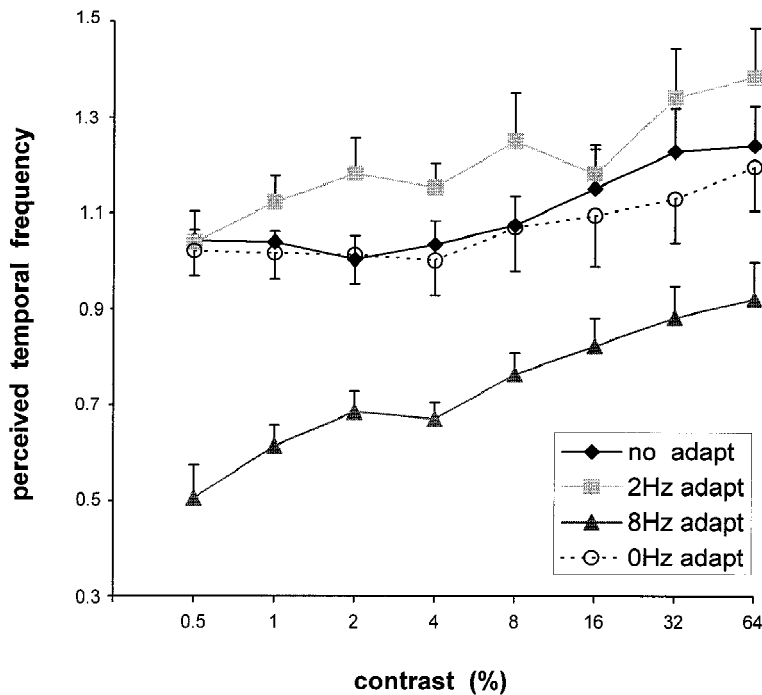


Figure 3. Perceived temporal frequency of the reference stimulus as a function of reference contrast (log scale). The data points are grand means over the six observers of Figure 1 (vertical bars: standard errors). The perceived temporal frequency is equal to the ratio of test temporal frequency estimated by the Best-PEST (i.e., the perceptual match) and reference temporal frequency (held constant at 4 Hz). The perceived speed matches (four runs per subject, contrast value, and adaptation state) were simultaneously acquired together with the motion VEPs of Figure 2.

3. Adaptation to a stationary stimulus has no significant effect on the N200 amplitude.

Figure 3 shows the perceived temporal frequency values of the reference stimulus, plotted as a function of contrast, which were recorded simultaneously with the motion-onset VEPs (cf., Figure 2). The perceived temporal frequency of a reference stimulus is defined as a ratio of the test temporal frequency (i.e., the Best-PEST defined match speed) and the reference temporal frequency (cf., Methods, Equation [2]). A value of 1 would then mean that a test stimulus of 4 Hz has the same perceived speed as the reference stimulus of 4 Hz (i.e., veridical match). The ascending curves in Figure 3 reflect the increasing test temporal frequency required to match the perceived speed of the reference stimulus. Thus, the curves reflect increasing perceived temporal frequency (and increasing perceived speed) of the reference stimu-

lus as a function of contrast (log scale), despite its constant physical temporal frequency of 4 Hz.

The main results are as follows:

1. The perceived speed of a 4 Hz reference stimulus is significantly reduced by a preceding isodirectional 8 Hz adapting stimulus with a contrast of 4% (Wilcoxon, $p < 0.01$).
2. The perceived speed of a 4 Hz reference stimulus is significantly increased by a preceding isodirectional 2 Hz adapting stimulus with a contrast of 4% (Wilcoxon, $p < 0.05$).
3. The perceived speed of a 4 Hz reference stimulus is significantly reduced by a preceding stationary adapting stimulus with a contrast of 4% (Wilcoxon, $p < 0.05$).

Discussion

The result of Experiment 1 (temporal frequency variation in parafoveal vision, Figure 1) confirms the data found in foveal vision in an earlier study [1]. The empirical values of the N200 motion-VEP amplitude suggest that the function can be well described by two linear segments, consisting of a range with significant positive slope for low temporal frequencies (0.5 to 2.8 Hz, corresponding to 0.25 and 1.4 deg/s; cf., Equation [3]), and a range with little or no slope for higher temporal frequencies (above 2.8 Hz; cf., Equation [4]). The observation over the ipsilateral hemisphere is in line with predictions from both the single-channel and two-channel model. The results over the contralateral hemisphere for temporal frequencies above 2.8 Hz could only be explained by the two-channel hypothesis (if the negative slope would prove to be significant). Further experiments are thus required to obtain data that could support the one or the other model. Can the results of the adaptation experiment be explained by the one- or the two-channel hypothesis?

The N200 amplitude of a 4 Hz reference stimulus (speed of 2 deg/s) is not significantly affected by adaptation to a stationary grating (Figure 2). This observation is in agreement with a study of Dorn et al. [16]. They found a considerable adaptation effect on the N200 amplitude of the motion-onset VEP by repeated presentation of a random dot pattern, which was stationary for 1 s and then moved for 2.333 s. The presentation mode is unable to provide information, whether or not the stationary pattern contributes to the adaptation of the N200 motion-VEP amplitude. In that study, the adaptation period (23 s duration) was followed by a recovery period (23 s duration), in which the pattern was presented repeatedly, but first stationary for 3.1 s and then moving for 0.233 s. A significant contribution from the stationary pattern to the adaptation of the N200 motion-VEP amplitude can be excluded in this

second presentation mode since a complete recovery would have occurred after 23 s.

Under the condition of stationary grating adaptation in our Experiment 2, the stimulus was shown as stationary only for 50% of the trial duration. A significant stationary grating effect on the N200 motion-VEP amplitude would not be expected, since a presentation of the stimulus as stationary in even 93% of the trial period, as used in [16], had no noticeable effect. In addition, we can conclude, that the 1 s presentation of the reference stimulus as stationary in our pre-adaptation condition (corresponding to 8.3% of the trial duration) has no appreciable effect on the N200 motion-VEP amplitude.

The absence of a significant adaptation effect by the stationary grating on the N200 amplitude confirms that our mode of motion stimulation (sudden motion-onset of a previously stationary reference grating) primarily affects the activity of motion-sensitive neurons. Accordingly, the activity of contrast-dependent neurons would remain constant and thus would not contribute to the motion-onset VEP.

As can be seen in Figure 2, adaptation to 2 and 8 Hz (speed of 1 and 4 deg/s) has an equivalent effect on the amplitudes of the N200 wave. This result is surprising from the view of the one-channel model of temporal frequency coding. An 8 Hz stimulus should have a greater intensity than a 2 Hz stimulus and should evoke a greater integral activity of the speed-dependent neurons. This argument is partly supported by the results of Experiment 1 (cf., Figure 1), which show an increase of the N200 amplitude between a temporal frequency of 2 and 8 Hz. The 8 Hz adaptation stimulus should therefore evoke a greater reduction in the N200 amplitude elicited by the 4 Hz reference stimulus, which is clearly not the case.

The result can, however, be explained by the two-channel hypothesis. A pre-adaptation 4 Hz reference stimulus would elicit a motion-onset VEP generated by activity in both the 'slow' and 'fast' channel neurons. The 2 Hz adaptation stimulus lowers the integral activity in the 'slow' channel neurons by an amount comparable to that caused by the 8 Hz adaptation stimulus in the activity of the 'fast' channel neurons. Assuming that this is the case, the post-adaptation response to the 4 Hz reference stimulus will be reduced to a similar extent by both 2 Hz and 8 Hz adaptation. In other words, the sum of both channel activities does not noticeably differ after 2 Hz or 8 Hz adaptation but the distribution of activity over the channels is different.

If the two-channel interpretation is viable the different activity distributions over the channels should be accompanied by different perceived temporal frequencies. The dominant 'fast' channel activity after 2 Hz adaptation should enhance the perceived temporal frequency over the pre-adaptation value, whereas the dominant 'slow' channel activity after 8 Hz adaptation

should reduce the perceived temporal frequency below the pre-adaptation value. The predicted result is in agreement with the experimental data of Figure 3. If the one-channel interpretation were valid the perceived temporal frequency after 2 Hz adaptation would reduce below the pre-adaptation value which is not the case. Thus, both electrophysiological and psychophysical results are in clear conflict with a one-channel hypothesis.

Single cell studies of speed dependent neurons in the macaque visual cortex support the two-channel hypothesis of speed encoding. Foster et al. [12] recorded optimal temporal frequencies of neurons in area V1 and V2 for parafoveal viewing. The distribution of either cell population across temporal frequencies exhibits a double-peaked function, with a 'slow' peak at 1 Hz (V1) and 2 Hz (V2), respectively, and a 'fast' peak at 4 Hz. A similar distribution, but with peaks shifted to higher temporal frequencies (5 and 16 Hz), was found in area V3 by Gegenfurtner et al. [13]. The classification of MT cells, performed with the help of their speed-dependent response characteristics, also suggests the existence of two or three speed channels [14].

Figure 2 shows a similar N200 amplitude decrease after 2 Hz and 8 Hz adaptation, respectively. The curves of Figure 3 indicate that the percentage of perceived temporal frequency increase after 2 Hz adaptation is significantly lower than the percentage of perceived temporal frequency decrease after 8 Hz adaptation (Wilcoxon test, $p < 0.01$). The curves could be accounted for by a model of temporal frequency perception that implies different coefficients for 'slow' channel and 'fast' channel activities. To fit the empirical data the weight assigned to the 'fast' channel activity would have to be larger than that assigned to the 'slow' channel activity. This is in line with the coefficients found by Smith & Edgar [8] in their perceived temporal frequency model applied to parafoveal viewing. This also corresponds with a weighted-average scheme for determining perceived temporal frequency, as proposed by Yo & Wilson [21] for peripheral viewing.

The pre-adaptation curve of Figure 2 shows a clear positive slope only for contrast values between 0.5 and 1%. Above that range the N200 motion VEP amplitude can be considered as 'saturated'. This agrees with results of Kubova et al. [22] and Bach & Ullrich [23] who found a clear reduction of the N200 amplitude for contrast values below 1.3 and 1.5%, respectively. The finding also agrees with fMRI results [24].

The pre-adaptation curve of the perceived temporal frequency (Figure 3) shows a shallow positive slope as a function of contrast. This is in agreement with findings of earlier papers that perceived speed increases with increasing contrast [3, 25, 26]. This dependency can also be observed after adaptation to stationary or moving gratings (see Figure 3). The corresponding tendency of the N200 motion-VEP amplitude as a function of contrast can be seen in Fig-

ure 2. The curves, at first glance appear constant for contrast values between 1% to 64%, do have a shallow positive slope in dependence on contrast.

The perceived temporal frequency values after adaptation to a stationary pattern (dotted curve in Figure 3) show a small, but significant, decrease in comparison to the values of the no-adapt condition. The effect can be explained by the contrast dependency of perceived speed. The adaptation to a stationary stimulus reduces the perceived contrast of a subsequently presented reference stimulus which again causes a decrease of perceived speed (see also [3]). Since it is a minor effect, a corresponding significant N200 amplitude reduction does not occur.

In summary, the present results based on simultaneous recordings of motion VEP and perceived speed can be parsimoniously explained by the two-channel hypothesis of speed encoding in the human visual system.

Acknowledgements

We thank Bengt Bartsch for his support in software development and Eva-Maria Albert for her assistance in performing the experiments and evaluating the data. Author MWG was supported by the Schilling Foundation.

References

1. Göpfert E, Müller R, Markwardt F, Schlykowa L. Visuell evozierte Potentiale bei Musterbewegung. *Z EEG-EMG* 1983; 14: 47–51.
2. Blakemore C, Campbell FW. On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images. *J Physiol (London)* 1969; 203: 237–260.
3. Müller R, Greenlee MW. Effect of contrast and adaptation on the perception of the direction and speed of drifting gratings. *Vision Res* 1994; 34: 2071–2092.
4. Thompson P. Velocity after-effects: The effects of adaptation to moving stimuli on the perception of subsequently seen moving stimuli. *Vision Res* 1981; 21: 337–345.
5. Thompson P. The coding of velocity of movement in the human visual system. *Vision Res* 1984; 24: 41–45.
6. Anderson SJ, Burr DC. Spatial and temporal selectivity of the human motion detection system. *Vision Res* 1985; 25: 1147–1154.
7. Hess RF, Snowden RJ. Temporal properties of human visual filters: number, shapes and spatial covariation. *Vision Res* 1992; 32: 47–59.
8. Smith AT, Edgar GK. Antagonistic comparison of temporal frequency filter outputs as a basis for speed perception. *Vision Res* 1994; 34: 253–265.
9. Hess RF, Bex PJ, Fredericksen ER, Brady N. Is human motion detection subserved by a single or multiple channel mechanism? *Vision Res* 1998; 38: 259–266.
10. Müller R, Göpfert E, Hartwig M. VEP-Untersuchungen zur Kodierung der Geschwindigkeit bewegter Streifenmuster im Kortex des Menschen. *Z EEG-EMG* 1985; 16: 75–80.

11. Müller R, Göpfert E, Hartwig M. The effect of movement adaptation on human cortical potentials evoked by pattern movement. *Acta Neurobiol Exp* 1986; 46: 293–301.
12. Foster KH, Gaska JP, Nagler M, Pollen DA. Spatial and temporal frequency selectivity of neurons in visual cortical areas V1 and V2 of the macaque monkey. *J Physiol (London)* 1985; 365: 331–363.
13. Gegenfurtner KR, Kiper DC, Levitt JB. Functional properties of neurons in macaque area V3. *J Neurophysiol* 1997; 77: 1906–1923.
14. Lagae L, Raiguel S, Orban GA. Speed and direction selectivity of macaque middle temporal neurons. *J Neurophysiol* 1993; 69: 19–39.
15. Bach M, Ullrich D. Motion adaptation governs the shape of motion-evoked cortical potentials. *Vision Res* 1994; 34: 1541–1547.
16. Dorn TJ, Hoffmann M, Bach M. Motion adaptation time constants of the motion-onset VEP. *Invest Ophthal and Visual Science* 1997; 38: S992.
17. Rovamo J, Virsu V. An estimation and application of the human cortical magnification factor. *Exp Brain Res* 1979; 37: 495–510.
18. Lieberman H, Pentland AP. Microcomputer-based estimation of psychophysical thresholds: the best PEST. *Behavior Research Methods Instruments and Computers* 1982; 14: 21–25.
19. Tootell RBH, Mendola JD, Hadjikhani NK, Liu AK, Dale AM. The representation of the ipsilateral visual field in human cerebral cortex. *Proc Natl Acad Sci USA* 1998; 95: 818–824.
20. Chen Y, Bedell HE, Frishman LJ. Velocity discrimination between stimuli of different spatial frequencies. *Invest Ophthal and Visual Science* 1995; 36: S54.
21. Yo C, Wilson HR. Peripheral temporal frequency channels code frequency and speed inaccurately but allow accurate discrimination. *Vision Res* 1993; 33: 33–45.
22. Kubova Z, Kuba M, Spekreijse H, Blakemore C. Contrast dependence of motion-onset and pattern-reversal evoked potentials. *Vision Res* 1995; 35: 197–205.
23. Bach M, Ullrich D. Contrast dependency of motion-onset and pattern-reversal VEPs: Interaction of stimulus type, recording site and response component. *Vision Res* 1997; 37: 1845–1849.
24. Tootell RBH, Reppas JB, Kwong KK, Malach R, Born RT, Brady TJ, Rosen BR, Belliveau JW. Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J Neurosci* 1995; 15: 3215–30.
25. Thompson P. Perceived rate of movement depends on contrast. *Vision Res* 1982; 22: 377–380.
26. Stone LS, Thompson P. Human speed perception is contrast dependent. *Vision Res*; 32: 1535–1549.

Address for correspondence: R. Mueller, Carl Ludwig Institute of Physiology, School of Medicine, Leipzig University, Liebigstr. 27, D-04103 Leipzig, Germany
Phone: 01149-341-9715564; Fax: 01149-341-9715509