THE EFFECT OF MOVEMENT ADAPTATION ON HUMAN CORTICAL
POTENTIALS EVOKED BY PATTERN MOVEMENT

R. MÜLLER, E. GÖPFERT and M. HARTWIG
Carl Ludwig Institute for Physiology, Karl Marx University
Liebigstrasse 27, Leipzig 7010, GDR

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Abstract. Human visually evoked cortical potentials (VEPs) were elicited by the onset of movement of grating patterns (test stimuli). The most prominent VEP waves N2 and P2 increased with accelerating test stimulus velocity (within a range of 0.2-4 deg/s). Two kinds of runs were presented. Reference runs involved only test stimuli and stationary pattern periods between them. In test runs moving gratings were additionally presented between the test stimuli effecting a stable level of movement adaptation. The additional movement stimulation reduced the VEP amplitudes throughout. The relative amplitude reduction was nearly constant for all test stimulus velocities if a fixed velocity of the adaptation stimulus was used. When the adaptation stimulus velocity was raised (within a range of 0.1-4 deg/s), the relative VEP amplitude became smaller. The results support the additive model of velocity coding in human occipital cortex rather than the substitutive model.

INTRODUCTION

The coding of several values of any perceived variable in the human cortex can be imagined in two ways. Increasing magnitudes could produce increasing activity of one and the same detector sensitive to that variable (additive model). On the other hand, each detector could be activated by a relatively narrow range of magnitudes. The activity could be greatest at an intermediate magnitude and lesser at both smaller and greater magnitudes. Furthermore, each detector had to be optimally
activated by a different magnitude (substitutive model, see (7)). In that case it is usual to speak of the existence of "channels".

In this paper we shall deal with the coding of the variable "pattern velocity". Some authors have obtained information with the help of psychophysical methods. But their results are not uniform (see Discussion). Therefore it is advisable to obtain further data with other experimental procedures. Electrophysiological methods are available. Visually evoked potentials (VEPs) measurable at the human occipital scalp could be a useful tool. They would supply suitable information if they could be generated in the main by activity changes of movement-sensitive detectors. Properties of VEPs elicited by pattern movement (movement VEPs) have been investigated in more detail by several authors (2, 3, 6). In our own experiments (4) we could detect the conditions of stimulation that would produce movement VEPs which met the above requirement. The aim of this paper is to extend the knowledge about the coding of pattern velocity in human cortex using this "instrument". In analogy to psychophysical procedures, we shall perform adaptation experiments. In our special case adaptation means movement adaptation.

METHODS

Subjects. Experiments were carried out three emmetropic 20-, 40- and 47-year-old females (Experiment I and II with subject E.G., Experiment III with subjects C.Z. and E.Z.).

Apparatus. The EEG was measured with silver cup electrodes in the midline 2.5, 5, 7.5 and 10 cm above the inion and 5 cm bilaterally from the lowest midline point. It was recorded on electroencephalograph EEG-8.111 (Messgerätewerk Zwönitz, time constant 0.3 s, upper frequency limit 30 Hz) and tape recorder EMM 141 (Tesla Bratislava, frequency range 0-312 Hz). Averaging was performed on a multichannel analyzer NTA 1024 in combination with an averaging converter NE-243.2 (Mettrimpex Budapest, sampling frequency 250 Hz).

The experiments were carried out in a semi-dark, electrically and acoustically shielded chamber. Patterns were presented by a projection of stationary or horizontally moving film strips onto a translucent glass screen. The projection area, with a mean luminance of 17 cd/m², was 18 × 18 cm, viewed from a distance of 2.6 m (4 × 4 deg of arc). We used in all cases vertical square-wave gratings with a spatial frequency of 2.6 c/deg. The area ratio between light and dark pattern elements was 1 : 1. The subjects were seated comfortably in a dentist's armchair. They fixated binocularly a small spot in the center of the screen. The surround of the screen was a uniform matblack field.
Procedure. The stimulus consisted in a movement of the projected pattern. Two different types of stimuli can be distinguished. Test stimuli were presented for ≈ 1.5 s to obtain movement VEPs. We considered VEPs evoked by the onset of movement (movement-on VEPs). Adaptation stimuli were presented for ≈ 10 s in order to maintain movement adaptation (see below).

About 250 test stimuli were given in each session. The interval between two test stimuli lasted ≈ 13 s in Experiments I, III and ≈ 8 s in Experiment II. Short breaks were made after each run consisting of 40-50 test stimuli (Experiments I, III) and 20-25 test stimuli, respectively (Experiment II). The kind of stimulation was only changed between runs. The sequence of runs was varied from session to session in order to reduce sequential effects. Each session lasted 60-90 minutes.

In Experiments I and III one run with movement adaptation (test run) was followed by a corresponding run without movement adaptation (reference run) or vice versa. The direct temporal juxtaposition of test and reference run was preferred, to minimize changes in the subjects' state during this period. In order to ensure movement adaptation in the test runs, a moving grating was presented during a period of 60 s before the first test stimulus. The presentation of the moving pattern was continued during the test run according to the time scheme of Fig. 1 to maintain a stable level of movement adaptation throughout the entire run. The contrast and direction of movement of an adaptation and its corresponding test stimulus were always equal. Three different contrasts (C = 0.8, 0.2 and 0.05) were used. Movement adaptation was produced by different velocities of the adaptation stimulus.

![Figure 1](image.png)

**Fig. 1.** Time lapse of stimulation in experiments without (reference run) and with movement adaptation (test run).

In Experiment II only test stimuli were presented. Movement-on VEPs were elicited by contrasts between 0.036 and 0.83. The test stimulus velocity was varied in four steps.

In all the experiments the grating was stationarily presented between stimulations (Fig. 1). This was necessary to keep constant the sum-
marized activity of pattern-sensitive detectors in the cortex and to avoid as far as possible their participation in the generation of movement VEPs.

Averaged potentials were obtained from \( n = 40 \) single potentials. The VEP waves were designated with N (negative) or P (positive against the reference line) indexed by whole numbers. Amplitudes of the waves were determined, both peak to peak and against the reference line. As reference line the mean amplitude of the initial and final part of the averaged curve was taken (as a rule, the first 50 and the last 500 ms had no VEP-conditioned deviations).

The EOG was simultaneously recorded enabling us to control eye movements and blinking. We excepted from averaging those stimuli which coincided with EOG deflections, distinct \( \alpha \)-waves, muscle potentials or other artifacts within the EEG. No stimulus-correlated waves could be detected in the EOG simultaneously averaged with the VEPs.

RESULTS

Typical examples of movement-on VEPs obtained from the subjects used in the experiments are shown in Fig. 2. All three VEPs are similar in their shape. Waves N2 and P2 have the most distinct amplitudes (in the case of subject E.G. only N2). The peak latencies are 160...350 and 250...450 ms depending on the subject and the speed of the moving patterns.

![Fig. 2. Typical examples of averaged VEPs from three subjects evoked by movement-onset of a grating (spatial frequency = 2.6 c/deg, velocity = 2.1 deg/s, electrode 7.5 cm above the inion, \( n = 40 \)). A principal similarity can be seen between potentials. Waves N2 and P2 are most prominent.](image-url)
Fig. 3. Left column: amplitude $A$ of VEP-wave N2 depending on test stimulus velocity $v$. The four adaptation stimulus velocities used are indicated by symbols with arrow under the abscissa. Weak lines: Amplitudes $A_{test}$ obtained in test runs. $A_{test}$ is the mean of the amplitudes from six different occipital scalp positions (see Methods) and two sessions (with $n = 40$ in each session). Vertical bars indicate standard error. Each curve is attached to a special adaptation velocity (according to symbol). Strong line: Means of the four amplitudes $A_{ref}$ obtained in analogy to $A_{test}$ in the corresponding reference runs. Right column: quotient $A_{test}/A_{ref}$ depending on test stimulus velocity $v$ (parameter: adaptation stimulus velocity). The quotient has been calculated with values $A_{test}$ and corresponding $A_{ref}$ (see Methods), thus magnitude $A_{ref}$ is not identical to the mean value plotted in the left column. The diagrams in each row are attached to a special contrast $C$ (Fig. A, B: $C = 0.8$; Fig. C, D: $C = 0.2$; Fig. E, F: $C = 0.05$). Spatial frequency $= 2.6$ c/deg. Subject E.G.
Experiment I. We examined the effect of movement adaptation on movement-on VEPs for gratings with a contrast of $C = 0.8$. The result is illustrated in Fig. 3A for amplitude $N2$ of subject E.G. The amplitude increases with the accelerated test stimulus velocity, for both reference and test runs. A distinct adaptation-conditioned decrease of $N2$ can be seen for any velocity of the adaptation stimulus. The faster the adaptation stimulus velocity, the greater is the amplitude reduction. The size of this effect can be represented more distinctly by the quotient of the amplitudes obtained in the test and corresponding reference run (because this term abstracts from the different size of wave amplitudes for several test stimulus velocities). The quotient curves concerning Fig. 3A are plotted in Fig. 3B.

It may be possible that the obtained results are only valid for strong contrasts. For instance, it is conceivable that the presentation of an adaptation stimulus with high contrast reduces the perceived contrast of the test stimulus (1). The consequence could be a VEP-reduction by contrast adaptation disturbing our analysis of movement adaptation. The experiments were therefore repeated with a moderate contrast $C = 0.2$ and a low contrast $C = 0.05$ (Fig. 3C and E). The results are not substantially different from those found with $C = 0.8$. The quotients in Fig. 3D and F support this statement.

Experiment II. The weak dependence of movement adaptation effects on pattern contrast suggested the testing of the relationship between contrast and movement-on VEP directly, in a separate experiment. Movement-on VEPs were evaluated for different contrasts varying the test stimulus velocity additionally (Fig. 4). The amplitudes are — as expected from Experiment I — first of all velocity-dependent. There is hardly any variation of amplitude dependent on contrast. A slight decrease is only visible for the lowest velocity and weak contrasts. The analysis of peak latencies shows a corresponding trend (increase with
decreasing velocities, but in the main independence of contrast vari-
ations).

The results of this experiment are consistent with the data illustrated
in Fig. 3. Proceeding from the curves in Fig. 4, it becomes clear that
adaptation-conditioned diminutions of the perceived contrast — if exi-

tent — will not noticeably reduce our movement-on VEPs.

**Experiment III.** The adaptation effect on movement-on VEPs has
been tested on two further subjects. The sessions were carried out with
the contrast $C = 0.05$ in the same manner as in Experiment I. Some-
what higher test stimulus velocities were used (the VEPs of either sub-
ject were not detectable for slow test stimulus speeds and $n = 40$).
Furthermore it should be noted that a slight difference between VEPs
of our subjects can be seen in Fig. 2. The VEP of subject E.G. shows
only one prominent wave N2. In the case of C.Z. and E.Z. both N2 and
P2 are prominent and velocity-dependent. We therefore preferred the
peak-to-peak amplitude N2 — P2, assuming that it could better indicate
adaptation-conditioned changes than N2 or P2 per se. The experimental
results are shown in Fig. 5. Accelerated adaptation stimulus velocities
are accompanied by decreasing amplitudes N2 — P2 as in Fig. 3.

**DISCUSSION**

What can we learn about velocity coding in the human cortex with
the help of our results? The validity of the substitutive model would
include adaptation maxima (i.e. quotient minima) for test stimulus ve-
locities which are equal to the adaptation stimulus velocities actually
used. The additive model, on the other hand, would imply an adaptation-
conditioned diminution of the VEP-amplitude over the entire range of
test stimulus velocities, without preference to any special velocity. Fur-
thermore we had to expect increasing adaptation effects (decreasing
VEP-amplitudes) with accelerated velocities of the adaptation stimulus.
Of course these two models are extremes and the real coding could be
a combination of both.

The results represented above (Figs. 3 and 5) support the additive
model rather than the substitutive model. There are no reliable re-
ferences to minima in the quotient curves, but a decrease in the ampli-
tudes with accelerated adaptation stimulus velocity is clearly visible
(excepting the fastest adaptation velocity).

This result is in good agreement with psychophysical investigations
of Thompson (8). His data (Fig. 2, quotients of estimates of perceived
test grating velocities with and without previous presentation of adap-
tation stimuli) can be compared to our quotient values (Fig. 3 and 5).
Fig. 5. Amplitude $A = N2-P2$ of movement-on VEPs (plots above) and quotient $A_{\text{test}}/A_{\text{ref}}$ (plots below) depending on test stimulus velocity $v$. Parameter, adaptation stimulus velocity (the three magnitudes used are indicated by symbols with arrow under the abscissa). Contrast $= 0.05$. Top an third diagram, subject C.Z.; second and bottom diagram, subject E.Z. For further details see caption of Fig. 3.
One of his results shows that the perceived test grating velocity diminishes with increasing adaptation grating velocity (again excepting the fastest adaptation velocity). This fact is incompatible with the substitutive model. Surprisingly, Tolhurst et al. (9) have detected relatively narrow-tuned velocity channels. Green (5), however, advises to take the experimental evidence for their existence with some caution, because the experiments are not comprehensive enough to exclude other conclusions.

Considering altogether it is very probable that velocity is coded additively a wide part of the investigated range. Besides, there is some indication that a second channel exists for faster velocities (see exceptions mentioned above). But there are no reliable facts supporting the concept of a greater number of narrow-tuned velocity channels being implicated in the substitutive model of coding.

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REFERENCES


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