



Directional tuning of human motion adaptation as reflected by the motion VEP

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Abstract

Motion onset evoked visual potentials are dominated by a negativity (N2) at occipital electrodes and a positivity (P2) at the vertex. The degree of true motion processing reflected by N2 and P2 was estimated from the direction specificity of motion adaptation. Adapting stimuli moved to the right and test stimuli (random dot patterns of 26° diameter; 10% contrast; 10.5°/s velocity) moved in one of eight directions, which differed by 45°. VEPs were recorded from occipito/temporal and central sites in eight subjects. Two adaptation effects were observed for N2 ($P < 0.01$): a global amplitude reduction by 47% and a direction-specific reduction by a further 28%. For P2, only the global effect (54%; $P < 0.01$) was observed. The global adaptation effect could also be induced by pattern reversal and pattern-onset adaptation, i.e. stimuli containing ambiguous or very little motion energy, respectively. We conclude that at least 28% of the N2 amplitude reflects the activity of direction-specific elements, whereas P2 does not at all. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

A prerequisite for the investigation of visual motion processing is the identification of true motion detectors. A key element in this regard is the direction specificity of the response of motion detectors (e.g. Borst & Egelhaaf, 1989). This criterion has been successfully employed in single cell studies and showed that in macaque monkeys, a substantial degree of motion processing resides in cortical areas such as V1 (layer 4B), V2, V3, and V5 (MT) (reviewed by DeYoe & Van Essen, 1988). Measuring mass responses, such as visual evoked potentials (VEPs) and fMRI signals, the simple criterion of direction specificity cannot be applied directly. Here, responses of cells with different preferred directions are pooled, masking the direction specificity of the single detector's response. This problem can be overcome by exploiting the direction-specific adaptation of motion detectors (e.g. psychophysics: Levinson & Sekuler, 1980; Raymond, 1993; Wade, 1994; single cell

recordings: Barlow & Hill, 1963 (rabbit); Hammond, Mouat, & Smith, 1985, 1986 (cat); Petersen, Baker, & Allman, 1985 (owl monkey); fMRI in humans: Tootell, Reppas, Dale, & Look, 1995; He, Cohen, & Hu, 1998; Culham, Dukelow, Vilis, Hassard, Gati, Menon, & Goodale, 1999; Huk & Heeger, 2000). In the case of a true motion-detector signal, responses to the adapted stimulus direction should be more reduced than responses to other directions, especially the opposite direction. Thus, the direction specificity of motion adaptation should enable us to infer the proportion of true motion detection reflected by the signal.

In man, the neural basis of motion perception has been studied electrophysiologically with the motion-onset VEP (e.g. MacKay & Rietveld, 1968; Clarke, 1972, 1973a,b; Andreassi & Juszczak, 1982; Göpfert, Müller, Markwardt, & Schlykova, 1983; Kubová, Kuba, Hubáček, & Vit, 1990; Bach & Ullrich, 1994; Snowden, Ullrich, & Bach, 1995). Visual motion-onset evokes VEP components at two major sites, the occipital/occipito-temporal sites (O_v , O_t , and $O_{t'}$), visual motion onset evokes a potential that is dominated by a positiv-

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ity (P1, around 100–130 ms) and a negativity (N2, around 150–200 ms). These components have been studied thoroughly, as reviewed by Niedeggen and Wist (1998). N2 was identified as a motion related component by its velocity and contrast dependence, whereas P1 is more likely to be associated with pattern processing (Müller & Göpfert, 1988; Markwardt, Göpfert, & Müller, 1988; Schlykova, van Dijk, & Ehrenstein, 1993; Kubová, Kuba, Spekreijse, & Blackmore, 1995; Bach & Ullrich, 1997). N2 is very susceptible to motion adaptation (Göpfert et al., 1983; Göpfert, Müller, & Hartwig, 1984; Müller, Göpfert, & Hartwig, 1985; Schlykova et al., 1993; Bach & Ullrich, 1994; Wist, Gross, & Niedeggen, 1994) and its time course of motion adaptation and recovery matches psychophysical performance (Hoffmann, Dorn, & Bach, 1999). Source analysis showed that N2 originates in or around area MT (Probst, Plendel, Paulus, Wist, & Scherg, 1993), providing further evidence that N2 is related to motion detection. At the vertex electrode (C_z), P2 is evoked by visual motion onset with a latency of about 230 ms. This component is susceptible to motion adaptation, and its amplitude depends on stimulus velocity (Hoffmann & Bach, 1997), which suggests a possible relation of P2 to motion detection. In summary, there is broad evidence that N2 can be used to study human motion processing, whereas for P2 at C_z the evidence is less compelling.

Here, we test N2 and P2 for direction specificity of motion adaptation to determine if these components reflect true motion detector responses. Previous reports on the direction-specific adaptation of the steady-state VEP (Clarke, 1974; Tyler & Kaitz, 1977) indicate some degree of motion specific activity in the motion VEP. However, these reports do not allow interpretation of the components of the transient motion-onset VEP with respect to their content of true motion detector responses. Preliminary accounts of this work have been presented previously (Unsöld, Bach, Auw-Hädrich, & Hoffmann, 1998; Bach, Hoffmann, & Unsöld, 1999).

2. Methods

2.1. Subjects

VEPs and electrooculograms (EOGs) were recorded binocularly from eight (experiment 1) and seven (experiment 2) human observers with normal or corrected to normal visual acuity (≥ 1.0). They gave their informed written consent to participate in the experiment.

2.2. Stimuli

Stimuli were generated by a Power Macintosh 8500 with a program based on the Apple Game sprockets

(Bach, 1999) and presented on a CRT with a frame rate of 67 Hz at a viewing distance of 85 cm. The stimulus pattern consisted of random square dots (dot size $0.3^\circ \times 0.3^\circ$) moving within a circular mask of 26° diameter. The total number of light and dark dots was identical. The space-averaged mean luminance of the pattern was 24.5 cd/m^2 and the contrast was set at 10% to preferentially stimulate the magnocellular system (Kaplan & Shapley, 1986; Bach & Ullrich, 1997). A relatively large fixation target of 2° diameter to reduce optokinetic nystagmus was centered on the pattern. The stimulus patterns could move in one of eight directions, differing by 45° . The stimulus velocity was based on a dot displacement of three pixels for horizontal or vertical, and two pixels for the oblique directions, resulting in closely matching velocities of $10.7^\circ/\text{s}$ and $10.1^\circ/\text{s}$, respectively.

Stimulus trials were presented in a cyclic design. A stimulus trial of a total duration of 3000 ms comprised three epochs: 2200 ms adaptation; 500 ms stationary pattern; 300 ms of motion in one of eight randomly selected directions. During the 300 ms epoch, the motion onset potentials were recorded. The effect of motion adaptation on the eight different stimulus directions was assessed by comparing VEPs at baseline with VEPs after adaptation. For baseline measurements, the pattern remained stationary during the 2200 ms adaptation epoch. For the adaptation measurements, the pattern moved rightwards (0° in the polar graphs) at $10.7^\circ/\text{s}$. In experiment 2, the same stimuli were used, but only rightwards and leftwards motion were applied as test stimuli. In this experiment, more adaptation conditions were compared to baseline, so the adaptation epoch could consist of (1) rightwards motion (as in the first experiment), (2) pattern reversal with 22 rev/s, and (3) pattern onset on a gray background (same mean luminance as the random dot pattern: 24.5 cd/m^2) with 22 onsets/s and 50% duty cycle. Reversal and onset rates of 22 rev/s matched the estimated mean local luminance changes of a random dot pattern moving at $14.3^\circ/\text{s}$.

2.3. VEP recording

Potentials were recorded from four scalp electrodes referenced to linked ears: O_z (occipital zero) and C_z (central zero), according to the international 10–20 System (Jasper, 1958), and O_t and O_r (occipito-temporal left and right, at 5 cm left and right from O_z). The ground electrode was attached to the right wrist. VEPs were averaged from at least 50 trials for each motion direction. Signals were amplified, filtered (first-order bandpass, 0.3–70 Hz, Toennies 'Physiologic Amplifier'), and digitized to a resolution of 12 bits at a sampling frequency of 500 Hz with a Macintosh 7200 computer. Using LabView (National Instruments), sig-

nals were ‘streamed to disk’ and also averaged on-line (across all stimuli) to monitor the recording.

2.4. Eye movement recording

Eye movements were measured with the EOG. Horizontal movements were recorded with bitemporal electrodes, vertical eye movements and blinks with supra- and infraorbital electrodes. Trials with poor fixation were discarded off-line (see Section 2.6 for criteria).

2.5. Procedure

The EOG was recalibrated every 40 min. Motion recordings were taken in a counter-balanced blocked design (‘ABBA scheme’). Each block consisted of at least 144 trials. Twelve blocks were presented in the following order: three blocks of baseline, six blocks of motion adaptation (an adapted motion test with continuous re-adaptation, see Section 2.2), and a final three blocks of unadapted motion test (baseline). Between blocks, there was at least a 2 min break and at the adaptation/baseline transition, a 5 min break. In experiment 2, the procedure was similar. The different adaptation conditions (see Section 2.2) and baseline were tested in separate blocks. To have closely similar histories for the different blocks, the following interval was interleaved with the blocks: 2 min of motion adaptation and 2 min of recovery — or longer (until the subjects were certain that the motion aftereffect had ceased) — from this adaptation. Thus, adaptation overspill was minimised.

2.6. Data analysis

Trials were analysed off-line over an interval which began 100 ms prior to motion onset and ended 500 ms after motion onset. Trials with blinks, detected with a threshold criterion of 100 μV , were discarded, as were trials with poor fixation: in the interval from 0 to 300 ms after motion onset, the EOG was fitted with a linear regression. Eye velocity was estimated from the slope of the regression line. Trials with eye velocities $> 3^\circ/\text{s}$ or with eye positions deviating by $> 2^\circ$ from the regression line were excluded from further analysis. Averaged sweeps were digitally filtered (0–40 Hz). Baseline was defined as the mean value of the averaged trace from 100 ms before to 30 ms after stimulus onset and used as zero reference for peak measurements.

Motion-onset potentials are often strongly lateralized to the Ot_r or Ot_l derivation (Andreassi & Juszcak, 1982). In order to maximize the signal-to-noise ratio for N2 amplitudes, we selected the Ot derivation of each subject with the greater N2-amplitude (based on the mean of normalized N2 peaks of the responses to the baseline stimuli tested) for the grand mean and labeled it Ot^* . The direction specificity of P2 at C_z was evaluated

only for subjects with a pronounced P2 (mean of baseline response $> 2 \mu\text{V}$).

The high variability between subjects is largely due to a multiplicative factor common to all conditions. To minimize the resulting scatter in the parametric plots, we normalized the VEP data with respect to each subject’s mean baseline amplitude of N2 or P2.

In experiment 2, no differences in response to leftward and rightward motion onset were expected for baseline and adaptation with pattern reversal or pattern onset. Therefore, left/right motion-onset VEPs were averaged for these conditions to increase the signal-to-noise ratio.

2.7. Statistics

The statistical significance of experimental effects was assessed with an ANOVA and degrees of freedom (DF), and F -values are given for significant effects. For experiment 2, the data were normalized and tested post-hoc with Fisher’s protected LSD (least significant difference) test. Significance levels are indicated in the figures ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$).

3. Results

3.1. Experiment 1: direction specificity of the adaptation of motion-onset VEPs

Grand mean motion-onset VEP traces to all stimulus directions ‘around the clock’ are depicted in Fig. 1. For the baseline condition, we obtained the typical motion-onset VEP with the characteristic P1–N2–P2 complex. N2 was dominant at the lateral derivation (Ot^*). Only six out of eight subjects had a pronounced P2 at C_z . N2- and P2 amplitudes are given in the polar graphs of Fig. 2. There were no significant response differences between directions in the baseline condition (N2: O_z : $P = 0.83$; Ot^* : $P = 0.77$; P2 at C_z : $P = 0.77$); for the Ot^* derivation, the amplitudes were identical within $\pm 5\%$ in all eight directions. Adaptation reduced N2 at Ot^* and P2 at C_z irrespective of stimulus direction by 47 and 59% (‘global effect’; means of responses to 90–270° directions; $P < 0.001$ (DF = 1,7; F -value = 32.5) and $P < 0.01$, respectively (DF = 1,5; F -value = 25.4)). There was an additional 28% direction-specific reduction of N2 amplitudes at Ot^* when the test and adaptation direction were the same (interaction adaptation \times direction: $P < 0.01$; DF = 7,49; F -value = 3.4). At O_z , the results were similar. Here, N2 could even change polarity after adaptation. No direction-specific adaptation was observed for P2 ($P = 0.53$), so there was a global effect in all directions, which results in an overall reduction of amplitude after adaptation by 54%.

The stimulus onset induced only small eye movements (amplitudes: horizontal $< 0.06^\circ$, vertical $< 0.18^\circ$).

Vertical recordings for adaptation and baseline differ, but these differences do not depend on stimulus direction. The vertical derivation is of poorer quality than the horizontal and reflects not only eye movements but also blinks. Hence, the effects at the vertical EOG might be attributed to stimulus-induced small lid movements. Consequently, we regard the effects of eye movements on the motion-onset VEP as negligible.

3.2. Experiment 2: global adaptation to pattern-reversal and pattern-onset adaptation

In this experiment, we tested whether the global adaptation effect can also be elicited by adaptation to (1) pattern reversal, which contains ambiguous motion,

or (2) pattern onset, with little, if any, motion energy. Adaptability of N2 by a non-motion stimulus would imply that the global effect is due to the adaptation of detectors of local luminance changes rather than motion detectors.

VEPs (grand mean) and corresponding N2- and P2-amplitudes (normalized) are depicted in Fig. 3a and b. N2- and P2-amplitudes at O_z and C_z , respectively, were markedly reduced after all adaptation stimuli, i.e. after motion in the same and opposite direction, pattern reversal, and pattern onset (for significance levels, see Fig. 3b). There was less reduction of N2 amplitude after pattern-onset adaptation than after pattern-reversal adaptation (N2 reduction at O_t^* : 25 vs. 52%, $P = 0.014$).

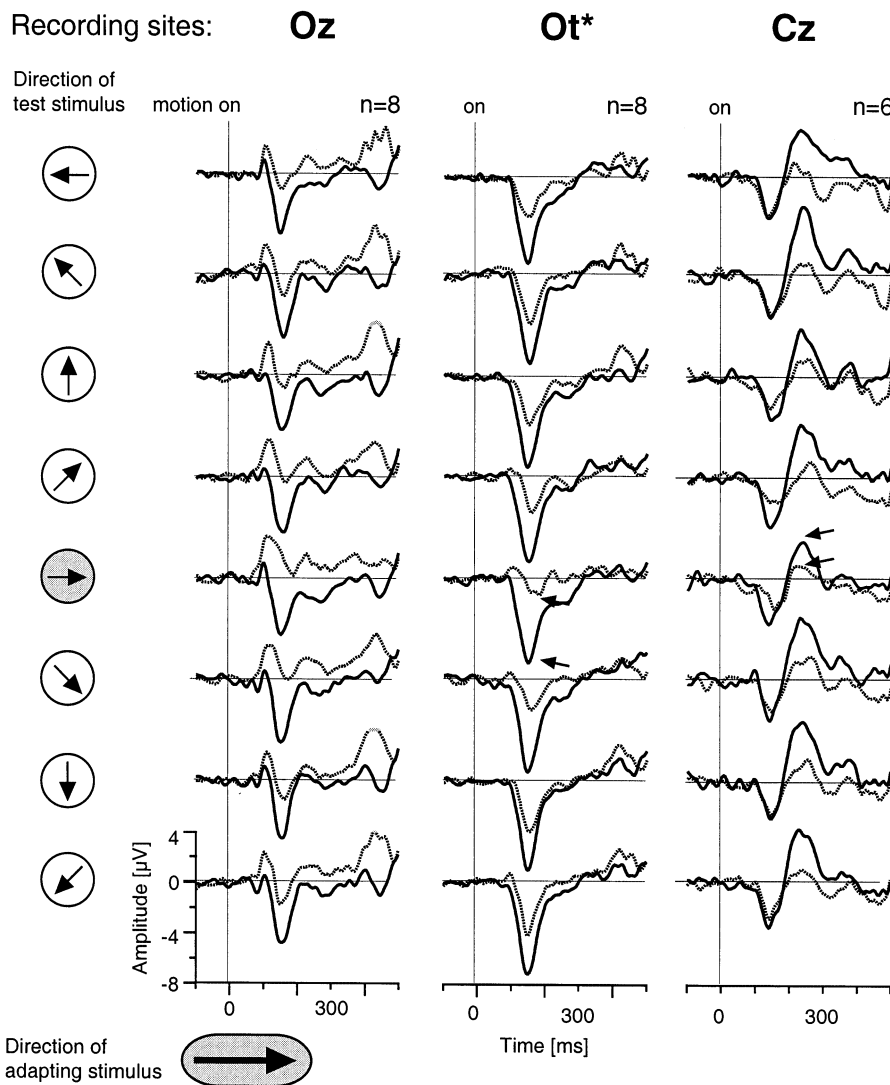


Fig. 1. Grand-mean VEP traces for the eight different stimulus directions at three recording sites (O_z — occipital zero, O_t^* — larger occipito-temporal, C_z — central zero) without adaptation (baseline, solid trace) and after adaptation to rightwards motion (dotted trace). The direction of the test stimuli is given on the left; recording sites are indicated at the top. The motion-onset VEP is dominated by N2 at the recording sites O_z and O_t^* and P2 at C_z (small arrows); both N2 and P2 are reduced after motion adaptation for all test directions (global effect) and reduction of N2-amplitude is maximal for identical adaptation and test direction (direction-specific effect).

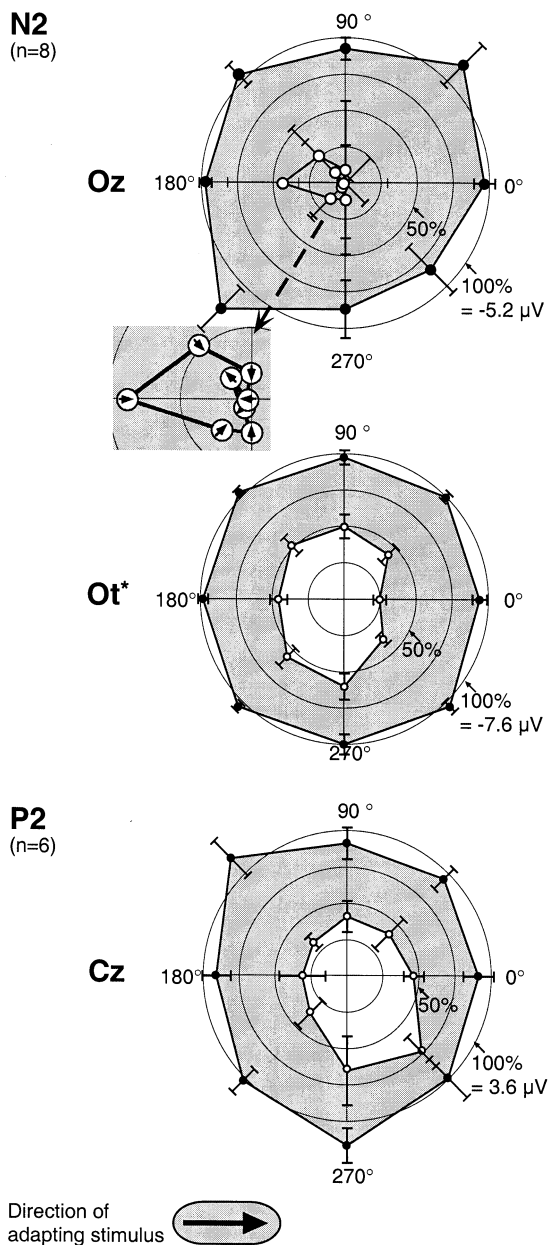


Fig. 2. Polar graph of the mean N2- and P2-amplitudes \pm S.E.M. Same data as for Fig. 1, but data are normalized with respect to the individual baseline response (mean of all eight test directions; the mean amplitude over all subjects is indicated). For the baseline condition (closed symbols, shaded area), there is no indication of an oblique effect. Adaptation with rightwards motion (open symbols, white area) induces a global effect on N2- and P2-amplitudes; for identical adaptation and test direction, there is an additional direction-specific amplitude reduction for N2 at O_z and O_t^* , but not for P2 at C_z . After adaptation, N2 amplitudes at O_z can reverse signs, resulting in negative percentages; this is indicated by omitting the white area; respective stimulus directions are given in the inset.

4. Discussion

It is well known that the N2 amplitude is susceptible to motion adaptation (e.g. Göpfert et al., 1983; Bach & Ullrich, 1994). Furthermore, by testing with two direc-

tions (adapting and opposite), it has been shown previously that motion adaptation of N2 is, to a large degree, 'global' (Bach, Ullrich, & Hoffmann, 1996), i.e. that it affects not only the adapting direction. In agreement, here, we report that the reduction of N2 amplitude after motion adaptation is specific for direction only partially (28%) and conclude that adaptation of more than one mechanism is responsible for the N2-amplitude reduction: (1) adaptation of motion mechanisms causes the direction-specific effect; (2) adaptation of temporal channels, i.e. any phasic mechanism that is driven by the local luminance modulation inherent in any motion stimulus, causes the global effect. Consequently, about half (47%) of the N2 is not a true motion response, whereas at least a quarter (28%) is. Amplitude reduction of P2 at C_z was not specific for direction, suggesting that P2 does not reflect any motion-specific processing. These conclusions for N2 and P2 may, to some degree, be specific for the experimental parameters used: for example, Wist et al. (1994), in investigations of the dynamics of motion adaptation in the VEP, report no direction specificity of the adaptation of the motion-onset VEP. However, they used the P1–N2 difference as an amplitude measure, which can hide adaptation effects (Hoffmann et al., 1999). Furthermore, focusing on adaptation dynamics, they applied an experimental paradigm optimized to determine the time course of motion adaptation and not the direction specificity of motion adaptation.

The effect of motion adaptation on responses to moving stimuli is well established in single-cell and psychophysical studies. Interestingly, direction selective adaptation is usually more pronounced when stimuli and paradigm directly address motion specific responses and bypass adaptation of pattern detecting systems (single cell: Hammond et al., 1985, 1986; Petersen et al., 1985; psychophysics: Levinson & Sekuler, 1980; Raymond, 1993; Raymond & Braddick, 1996). However, if that is not the case, a global effect is also observed (single cell: Saul & Cynader, 1989; psychophysics: Sekuler & Pantle, 1967; Levinson & Sekuler, 1980). This indicates that the global effect is not a by-product of the adaptation of motion detectors but is due to the adaptation of other non-direction selective mechanisms that respond to phasic stimuli (e.g. temporal luminance changes). This conclusion is supported by our finding that adaptation with pattern reversal — an ambiguous motion stimulus — or pattern-onset — a stimulus with little if any motion energy — also reduced N2- and P2-amplitudes. The respective mechanisms might already reside in the retina as motion adaptation not specific for direction already occurs at this level (Bach & Hoffmann, 2000).

Estimates of the bandwidth of motion adaptation on the basis of our study can only be tentative, due to the low direction resolution of 45° . The data suggest a

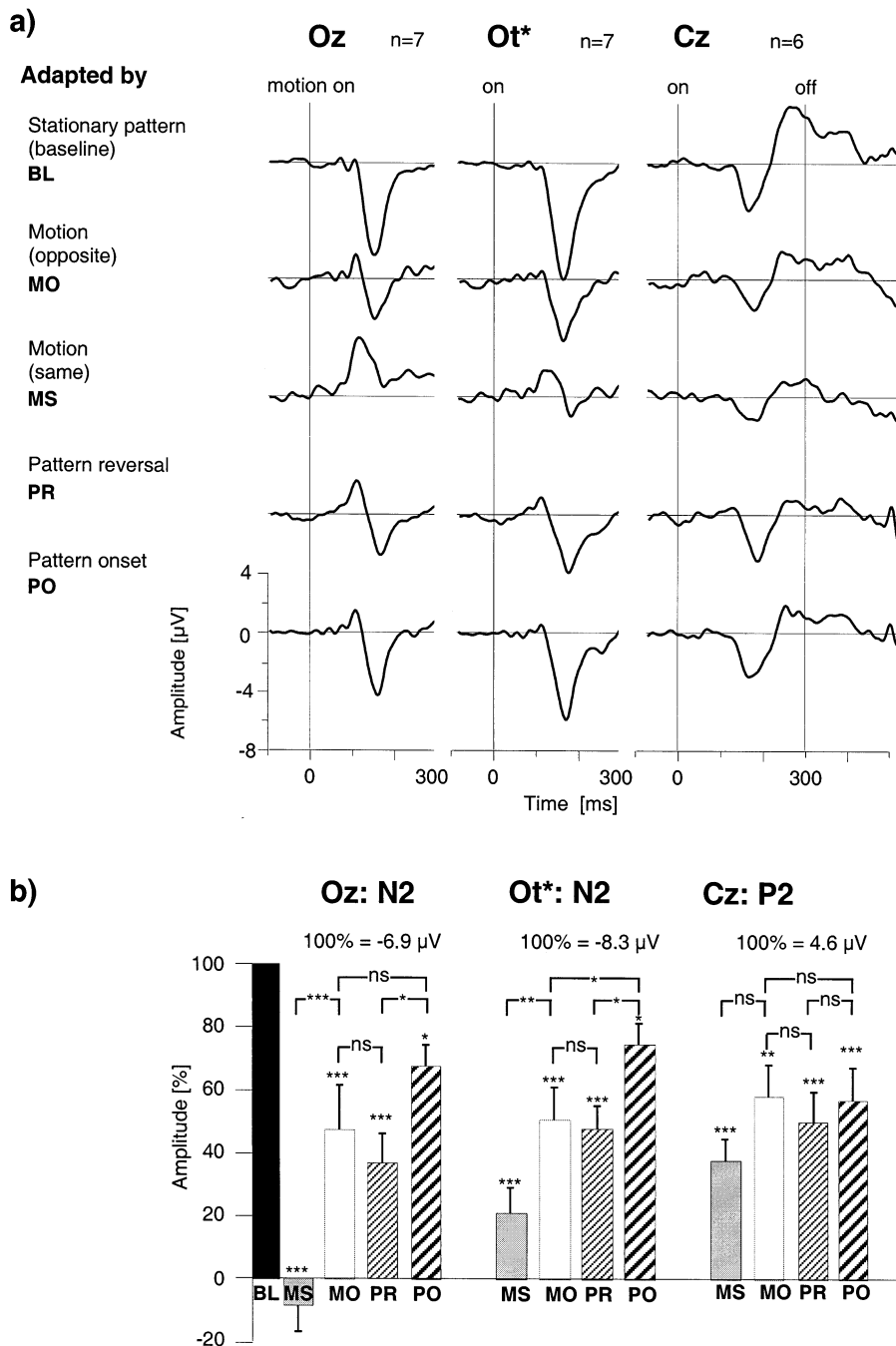


Fig. 3. Motion-onset VEPs for baseline and four adaptation conditions, to motion (same and opposite), pattern reversal, and pattern onset. (a) On the left, the adapting stimuli are indicated for each row; on the right, the grand mean traces for each recording site are depicted. (b) Mean N2- and P2 amplitudes \pm S.E.M. normalized for each subject with respect to baseline (100%; mean baseline amplitude is indicated). Significance levels from ANOVA (O_z , O_t^* : $DF = 4,24$; F -values = 17.3 and 21.5, respectively; C_z : $DF = 4,20$; F -values = 8.9) and post-hoc tests are given for differences from baseline (on top of the bars) and differences between conditions (brackets). All four adaptation stimuli reduce N2- and P2 amplitudes. However, caution should be exercised in interpreting the quantitative aspects of this effect: the adaptation effect was stronger for adaptation with pattern reversal than with pattern onset. This might be attributed to the luminance characteristics of the latter stimulus and not to its smaller influence on N2 adaptation per se: during pattern onset, the local luminance steps (gray to black or white) are smaller than during pattern reversal (black to white), which could well explain the smaller influence of pattern-onset adaptation on N2 amplitude. For abbreviations, see (a).

bandwidth at half height narrower than $\pm 45^\circ$ (reduction at 0° vs. a mean reduction of $+45^\circ$ and -45° vs. a mean reduction of 90° to 270° : 75% vs. 59% vs. 47%). In stimulus directions neighboring the adapting direction, the specific adaptation is about half its full value. This is in the range of bandwidths at half height reported previously (e.g. psychophysics: Ball & Sekuler, 1979: ± 45 – 50° ; Raymond, 1993: ± 35 – 40° ; electrophysiology (macaque-MT): Dubner & Zeki, 1971; Albright, 1984; Felleman & Kaas, 1984: ± 35 – 45°). Experiments with a higher direction resolution are needed to determine more accurately the bandwidth of motion adaptation in the motion-onset VEP.

VEPs to horizontal or vertical motion directions did not differ from those to oblique motion directions, i.e. there is no indication of an oblique effect in the motion-onset VEP. This is consistent with psychophysical reports on the lack of an oblique effect for pure motion detection. Motion-direction discrimination, however, has been shown to be anisotropic (Ball & Sekuler, 1982; Gros, Blake, & Hiris, 1998). This opens the possibility of an oblique effect for VEPs that would test mechanisms of motion-direction discrimination specifically, e.g. motion-direction change VEPs.

The motion-onset VEP is heavily affected by motion adaptation. We established two adaptation effects for the N2, a global effect and a direction-specific effect. For the vertex P2, only the global effect was observed. In conclusion, neural bases of visual motion perception in humans are accessible with the N2 component of the motion-onset VEP.

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