Simultaneously recorded retinal and cerebral potentials to windmill stimulation

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Abstract. Visual evoked retinal and cerebral potentials were recorded to onset rotation of an isoluminant sectored disc. While the retinal potentials recorded to onset rotation closely resembled the electroretinogram to a checkerboard or stripe pattern of fixed element size, the visual evoked potential changed interindividually and intraindividually from a fast positive wave at high contrasts, velocities and number of windmill segments to a later negative component at low contrasts, velocities and windmill segments. With change in luminance, contrast, speed and extent of rotation field size and number of disc segments, the visual evoked potential was generally less affected than the electroretinogram.

Introduction

Recently, visual evoked cerebral potentials (VEPs) were recorded to rotation of plane-polarized blue light (which evokes Haidinger’s entoptic polarization brushes) and compared to those evoked by (extrinsic) windmill stimulation of the macula designed to stimulate Haidinger’s brushes [1]. Attempts to obtain retinal potentials (electroretinogram, [ERGs]) under related stimulus conditions were unsuccessful unless the field size, number of cycles and luminance contrast of the windmill were greatly increased. Since retinal windmill stimulation seems to be more closely related to the receptive field size at different eccentricities than the pattern of uniform element size [2], we investigated the ERG and VEP to windmill rotation at different stimulus parameters. These include field size and luminance, number of cycles (paired to white plus black windmill segment) and contrast of the disc segments as well as speed and extent of rotation.

With stepwise extension of windmill rotation, the ERG onset amplitude was first seen to increase, then to fall, which provides evidence of tuning, indicating an excitation-inhibitory center-surround mechanism of the receptive fields of the retina. Maximum response was obtained when rotation was equal to one segment (0.5 cycle) of the sectored disc. By comparison, the
Fig. 1. (A1) Setup and stimulus display to evoke cortical (VEP) and retinal (ERG) potentials to isoluminant pattern motion by windmill rotation. (A2) Sectored disc consisting of 16 dark and 16 light segments, projected on a transilluminated white screen, and viewed at the center of the windmill. The numbers denote the visual angle of the individual dark and light segments (right) at different eccentricities (left). (B1 and B2) VEP and ERG responses to a size step of contrast reversal of windmill rotation (500 ms, 16 cycles, velocity of 720°/s, field size of 33°, mean luminance of 240 cd/m², contrast of 0.87.

Simultaneously recorded VEP windmill response exhibited lower threshold to luminance, field size and number of cycles, contrast of the sectored disc and speed of rotation.

Materials and methods

The light source was a slide projector equipped with a frame holder for sectored discs so that the slide mount could be rotated. In combination with an additional projector, the assembly permitted isoluminant windmill stimulation of different contrasts between the light and the dark segments. Movement of the disc was provided by an electronically controlled step motor permitting rotation of different speeds and extents. Stimulus luminance was altered by neutral density filters. The image of the sectored disc was projected on a white screen and centrally viewed at a distance of 760 mm. Figure 1A illustrates the size of the individual light and dark segments of a windmill of 16 opaque and 16 transparent vanes (32 segments; see Fig: 1A) at different eccentricities ranging from about 0.5° (at 2.5° eccentricity) to 1° (at 5°), 2° (at 10°) and 3.3° (at 16.5°).
Binocular VEPs were recorded in three unipolar leads by a 0.3–70-Hz Schwarzer picket, the electrode placed at O2 and 5 cm to the right and left and in the bipolar O2-C3 lead. For simultaneous ERG recordings, Arden's gold foil electrodes were inserted without topical anesthesia into the lower fornix, the reference and ground electrodes being placed ipsilaterally at the outer canthus and centrally on the forehead to avoid contamination by brain potentials. A total of 32 or 64 individual responses to the onset of rotation (not in all recordings) were averaged and plotted. Altogether, 18 subjects aged 15 to 34 years and two subjects aged 67 and 68 years took part in the investigation. For evaluation, an average of interpeak amplitudes of the cerebral (\([P_1-N_1] + [N_1-P_2]/2\)) and retinal rotation-onset potentials \([p-q]+[q-r]/2\) were measured as well as their latencies (Fig. 1B). (The described variant of amplitude measurements was used to enable an evaluation of size of VEPs that have high interindividual variability of their shape.)

The standard stimulus mainly used was a sectored disc illuminating a retinal field of 33° with 16 light and 16 dark wings moving at a constant angular speed of 720°/s in steps of 11.5° of rotation. The rotation period was 16 ms (white to black or black to white) (not in all recordings), which
was followed by an interstimulus interval of 1000 ms. Mean illumination at full contrast (0.87) was 240 cd/m². We do not believe that the responses to rotation are rotation specific as shown by microelectrode recordings.

Results

General observations. In response to the standard stimulus (see above), retina and cerebral potentials of about 5–10 μV were recorded to the onset rotation of the sectored disc. Potentials to continuous and offset rotation were
occasionally seen but not systematically investigated. As shown in Fig. 1B, the ERG to onset rotation raised from the baseline (p) to an earlier positive potential (q50) with a peak time of about 45–70 ms (depending on luminance), followed by a late negative potential (r) N95, resembling the ERG to pattern onset and pattern reversal. Onset of windmill rotation produced two different types of VEP, with a dominance of either a positive peak (latency of about 100 ms), which is comparable to P100 in pattern-reversal VEP (Fig. 2, I) or a negative peak N1 corresponding to the motion-onset-specific component recorded in linear motion stimulation [3] (Fig. 2, III). While the pattern-reversal positive peak in response to rotation was highest at O2 the motion-onset-specific negative peak was usually lateralized with a maximum amplitude at about 5 cm right or left from O2. In eight of our 20 subjects, types of response (II) were recorded in one of the above-specified locations. Seven displayed dominant positivity (I), and five, dominant negativity (III). In the individual subject shown in Fig. 2 (right), the decrease of windmill cycles caused a change in the VEP from type I to type III. Such changes were seen also at different contrasts (type I at high contrast and type III at low contrast) and at different velocities of rotation (type I at high velocity and type III at low velocity). The predominance of early positive or later negative VEP components is discussed elsewhere [3, 4].

We are aware of the problem of interpeak amplitude measurements when each peak likely has different physiologic significance. However, this is the only way to evaluate the size of reactions (group mean values) in different stimulus conditions, when the shape of rotary VEP was interindividually substantially different (see Fig. 2). Therefore, we emphasize that the described variant of amplitude measurements was used to allow evaluation of the size of VEPs that have high interindividual variability in shape.

Since the VEP in the whole group reacted differently to the parameters of rotary stimulation, statistical evaluation was difficult. We therefore restricted the description of the VEP to rotary windmill stimulation mainly to the changes of motion-related negativity. No latency and amplitude differences were observed to clockwise and counter-clockwise rotation.

Effect of change of luminance. Changes of luminance of windmill rotation were investigated under standard conditions (see above) between 0.3 (0.005) and 240 cd/m². Changing the luminance level affected the amplitude of the ERG onset response more strongly than the VEP amplitude. Even at the lowermost luminance investigated (0.05 cd/m²), the VEP still showed its full amplitude, leaving the ERG unrecordable already at 1.5 cd/m² (Fig. 3A). The ERG/VEP amplitude and latency changes with luminance in six subjects are graphically depicted in Fig. 4A. Significant amplitude reduction
Fig. 3. Typical VEPs (left) and ERGs (right) to isoluminant windmill rotation showing the effect of luminance (A), contrast (B), velocity (C) and extent of rotation (D). Stimulus conditions: 16 dark and 16 light segments; field size, 33°; mean luminance, 240 cd/m² (except in A); contrast, 0.87 (except in B); velocity, 720°/s (except in C); extent of rotation, 0.5 cycle (except in D).

(paired t-test, p < 0.05) occurred at 10 cd/m² (ERG) and 0.3 cd/m² (VEP); significant latency prolongation occurred at 100 cd/m² (ERG) and 3 cd/m²
Fig. 4. VEP and ERG amplitudes (left) and latencies (right) to windmill rotation at different luminance (A), contrast (B) and velocity (speed of rotation, C). Field size, 33°; extent of rotation, one windmill segment (11.5° at 16 cycles).

(VEP). Related observations are reported on simultaneously recorded ERGs and VEPs to stationary pattern responses [5].

Contrast. Changes in luminance contrast between the light and the dark wings of the windmill were investigated at contrast levels between 0.07 and 0.87 under standard conditions, the mean illumination being 240 cd/m². Lowering the luminance contrast to 0.45 strongly decreased the ERG amplitude, while its latency remained constant. Different changes were seen in the VEP in Fig. 3B, where the latencies substantially increased without concomitant amplitude reduction. Statistical evaluation of data from eight subjects showed significant decrease in the ERG already at a contrast of 0.58. No distinct ERG was obtained at contrasts of 0.19 and 0.07. Significant reductions of VEP amplitude were seen at a contrast of 0.19 (Fig. 4B).
Velocity (speed of rotation). Lowering the speed of rotation from 720°/s to 30°/s without altering the extent of rotation increased the stimulus duration from 16 to 384 ms (Fig. 3C). Consequently, the time of rotation outlasted, at lower speed levels, the initial VEP/ERG components considerably. As a result, the responses increased their peak times and decreased their amplitudes. Moreover, the VEP was seen to split into several fast components that appeared as superimposed multiple wavelets during and after the first negativity and positivity, i.e., windmill rotation evoked, in addition to the onset potential, steady-state potentials during the whole length of the rotation period. Some of these changes were occasionally seen in the ERG but not studied systematically. Statistical evaluation of data from five subjects indicated significant ERG amplitude reduction at 500°/s and no significant changes of VEP amplitude. Significant latency prolongation was seen in the ERG at 370°/s and at 62°/s in the VEP (Fig. 4C).

Extent of rotation. Marked changes occurred in the ERG when the extent of windmill rotation was increased (Figs. 3D and 5). When the extent of rotation was increased from very small (0.72°, corresponding to 0.016 cycle) to high values (45.4°, 2.0 cycles of rotation), there were increases and decreases of response amplitude. The largest p-q and q-r ERG amplitude was at 11.5°, which (for a windmill of 32 light and 32 dark sectors) is equal to one segment (0.5 light and dark cycle) of the sectored disc. Further increases, irrespective of the extent of rotation (0.75 to 2.0 dark and light cycles), decreased the ERG amplitude to about half of its maximum.

The changes were widely independent of the number of windmill segments and highly significant (p < 0.001) in respect to the ERG amplitude, whereas the changes of VEP amplitude were not significant (Fig. 5B). Interestingly, the ERG latency of the positive component q (P45) stayed almost constant, whereas the VEP peak time monotonically decreased with the extent of rotation (Fig. 3D).

Field size, number of cycles. Other parameters relevant for the ERG to windmill rotation were the size of the retinal field stimulated and the number of windmill cycles (Fig. 6). Again, the VEP and ERG were similarly affected by these parameters, differences being mainly caused by the higher sensitivity of the VEP. Statistical evaluation indicated VEP amplitude saturation at eight cycles and no significant change of VEP latency, significant increase of ERG amplitude at more than four cycles and significant increase of ERG latency at less than four cycles (Fig. 6A). Significant reduction of ERG amplitude with field size occurred at a field of 20° or less, and decrease of VEP amplitude
Fig. 5. Stimulus display (A) and amplitude (B) of cerebral (VEP) and retinal (ERG) onset potentials (means ± SD of seven subjects) to windmill rotation of 16 cycles. Maximum response was obtained when the extent of rotation was equal to one windmill segment (see also Fig. 3D).

occurred at 5° field size; no significant changes of ERG/VEP latencies were seen with stimulus field changes (Fig. 6B).
Fig. 6. VEP and ERG amplitudes (left) and latencies (right) of onset responses showing the effect (A) of windmill rotation of various numbers of cycles at constant field size (33°) (A) and of windmill rotation stimulus field size at 16 cycles (B). Luminance, 240 cd/m²; contrast, 0.87; rotation velocity, 720°/s; extent of rotation, 11.5°.

Even at maximum field size (33°), almost no ERG was recorded at a windmill rotation of less than four cycles (Fig. 6A). Similarly, even at a high number of cycles, almost no ERG was recorded at a field diameter of less than 10° (Fig. 6B).

Discussion

Isoluminant retinal stimulation by windmill rotation of a symmetric sectored disc as employed in the present investigation can be regarded as a moving stripe pattern in which the element size increases with eccentricity, thereby providing a better fit to the diameter of the receptive field centers of the retina than a stripe pattern of fixed element size. Thus, windmill rotation can be regarded as a stimulus exciting the receptive field centers with stripes of increasing size with eccentricity. As long as the stripes are within the (excitatory) center of the receptive fields, the response amplitude increases, and then decreases to about half of the maximum as soon as the extent of rotation exceeds 0.5 cycle, which activates the inhibitory surround of the receptive field. This, however, is true mainly for the ERG windmill responses;
in the VEP windmill experiments, no statistically significant tuning was seen with variation of the extent of rotation.

From the present experiments, it is obvious why entoptic responses to polarized light (Haidinger's brushes) have been recorded successfully only at the higher visual brain centers (VEP). To record appreciable signals to windmill rotation in the ERG, the field diameter of the macula (2-3°), the number of contrast borders (two cycles per revolution), the luminance (4 cd/m^2) and the luminance contrast between the polarized and unpolarized parts (about 0.15) of the Haidinger's brushes are far too small.

What are the benefits of using a windmill instead of stationary pattern reversal? For stimulation of distinct regions of the retina, the use of pattern stimuli of constant element size (on-off of reversal) has been found to be inappropriate, since the size of the retinal receptive fields varies with eccentricity [6, 7]. So far, few data are available on the average size of the receptive field centers in relation to their surrounds at various eccentricities. In psychophysics, a relationship of 1:2 has been found for the size of the fovea versus the peripheral perceptive field centers [8] and according to microelectrode studies in monkeys the relationship of center/surround field sizes varies as much as 1:10 for small and 1:2 for large receptive field centers [9]. With more exact knowledge of the center/surround sizes of the receptive fields at different eccentricities, it would be possible to design a windmill that provides the best fit and the largest pattern responses to windmill rotation.

References


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