The dynamics of the light adaptation of the human visual system; Subjective and electroretinographic analysis

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Abstract: The excitation of the visual system increases with increasing retinal illumination. At the same time, the sensitivity of the system decreases (light adaptation). Higher excitation automatically results in a lower sensitivity. This study investigates whether this parallelism between the excitation and the sensitivity also applies in the dynamic case, that is, during the transition to a higher excitation level after an increase in the retinal illuminance.

For this purpose, the courses of the subjective and the electroretinographic threshold during the transitional phase after a step of the adaptation illumination was determined by means of a special light-stimulation apparatus. As a measure of the course of the excitation during this time, the response ERG on the adaptation step was recorded with a special amplifier.

The threshold curve always has an overswing, which shows subjectively very strong differences. It can be concluded that the glare caused by a sudden increase in illuminance is subjectively very different. The comparison between the response ERG on the adaptation step and the course of the electroretinographic increment threshold during this time shows a broad agreement between the two courses.

It can thus be assumed that the sensitivity of the visual system follows the course of the excitation also in the dynamic case. In addition, the investigation shows that the glare experienced after a step in the illuminance clearly shows great subjective differences.

Keywords: rapid light adaptation; glare; discrimination threshold; increment threshold; direct current electroretinogram

1. Introduction

The sensitivity of the visual system finds its expression in the steepness of the relationship between the intensity of illuminance and the magnitude of excitation (also called the characteristic of the system). In the case of light adaptation, this slope and thus the sensitivity are reduced, the characteristic becomes flatter: The sensitivity follows the excitation, it decreases with increasing excitation. The reasons for this are photochemical and neuronal adaptation as well as the change in the pupil width. In addition, there are noise processes at the various stages of signal transmission. The correlation between sensitivity or rather stimulus threshold and stimulus intensity was extensively studied by Weber [16] and especially for the visual system by Barlow [2]. The relation to the strength of the excitation was then established by Fechner [6]. For the visual system especially, studies by Thoss [15] are available. Our present work is based on the assumption that, even in the dynamic case, i.e. in the case of a sudden transition to higher illuminance, the threshold follows the course of the excitation. In this paper, we try to confirm our assumption by measuring the courses of the subjective and the electroretinographic threshold after a step of the adaptation light. As a measure of the course of the excitation, we recorded the ERG response on the adaptation step.

2. Results

2.1. Course of the subjective threshold

In Fig. 1, the mean values of the subjective thresholds and their confidence intervals (all subjects) are shown graphically.
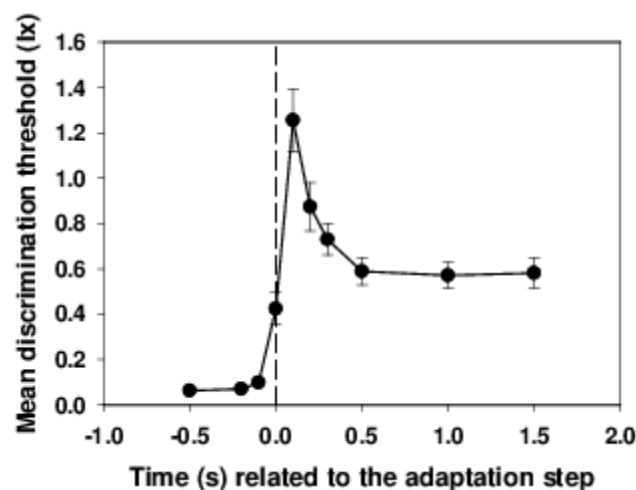

Fig. 1. Time course of the discrimination threshold, averaged for all 9 test subjects.

A very steep increase of the threshold is observed, which begins at -0.1 s (i.e. 0.1 s before the adaptation step). This value is already significantly different from the value measured at -0.5 s

(p <0.05). Already at +0.1 s the maximum is reached. Thereafter, a delayed decay takes place, which passes to the plateau of the new static threshold at +0.5 s.

2.2. Course of the electroretinographic threshold

In Fig. 2, the mean values and their confidence intervals for the electroretinographic thresholds of all subjects are shown.
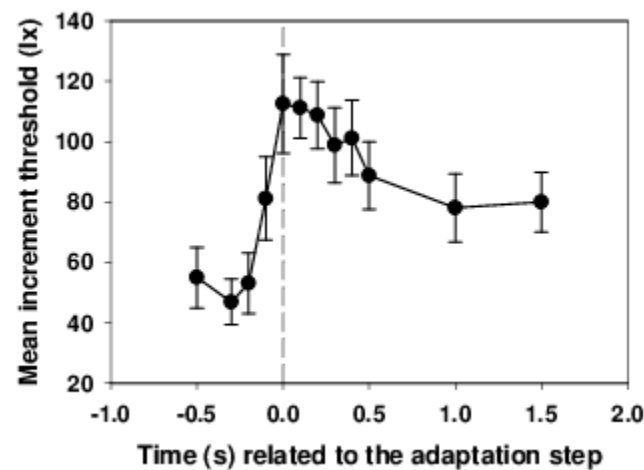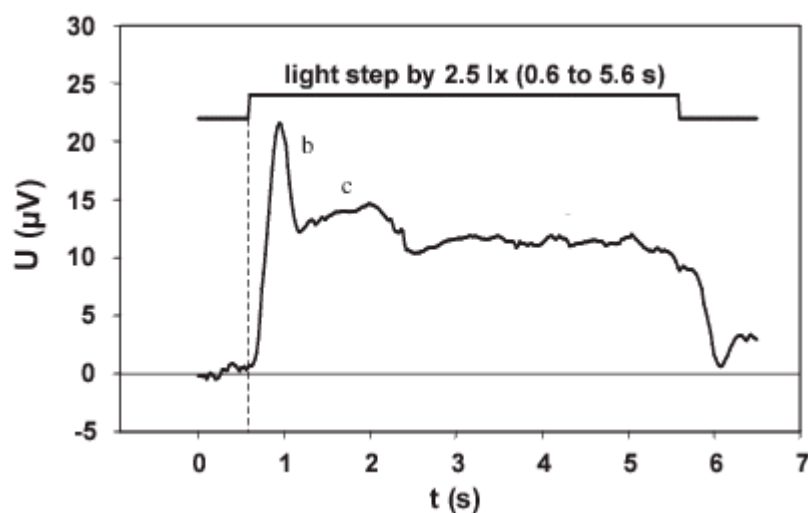

Fig.2. Time course of the electroretinographic increment threshold, averaged for all 12 test subjects.

While the value for -0.2 s is not yet significantly different from that at -0.3 s, the threshold at -0.1 s is significantly increased (p<0.05). The maximum is reached already at 0.0 s, the decrease to the end-plateau is broadened in comparison to the subjective threshold. The final threshold is reached only at 1.0 s. The high confidence intervals are an indication of the large individual differences in the course of the electroretinographic threshold.

2.3. The electroretinographic response to the 5 s adaptation pulse

Fig. 3 shows the electroretinographic response to the 5 s adaptation pulse.

Fig. 3. Electroretinographic response to the 5 s adaptation pulse (test subject 9, average course of 130 individual responses). The b- and the c-wave are clearly visible. The peak of the b-wave is located at about 0.3 s after the beginning of the adaptation pulse.

This electroretinogram was obtained by averaging 130 single runs, recorded in three sessions with twice 50 and once 30 runs, with the same subject. The course initially shows a pronounced b-wave, the maximum of which is reached at approx. 0.3 s after the step of the adaptation light. The b-wave is followed by a flat c-wave, which then passes into a plateau. This potential plateau ends with the end of the adaptation light pulse.

3. Discussion

3.1. The course of the subjective threshold (discrimination threshold)

In principle, our results are consistent with the results of Crawford [4], Baker [1], and Lingelbach et al. [10]. Approximately 0.1 s before the adaptation step a threshold rise starts, which quickly becomes very steep. As a rule, it reaches a maximum about 0.1 s after the step and then drops to a relatively constant value up to approx. 0.5 s after the step. This value is above the initial threshold, corresponding to the higher adaptation light. A closer comparison with the results of the authors mentioned is not possible, since their experimental conditions were different from ours and also from one another. Differences exist in the initial illuminance, the height and duration of the adaptation pulse, and in the stimulus field size.

The fact that the threshold is significantly increased already 0.1 s before the adaptation step (see Fig. 1) may cause that visual events, which happened actually before the glare, are not noticed. As early as 1961, Lisch [11] pointed out that this effect could have relevance for road traffic. Individual specialities in the transient behaviour of the discrimination threshold hardly exist in the dynamics of the course. Only the height of the peak as well as the position and stability of the subsequent plateau are different individually. The starting thresholds differ relatively little. They describe the respective subjective sensitivity at an adaptation illuminance of 0.5 lx. The maximum increase in the threshold caused by the adaptation light step or better the ratio of this value to the basic value (relative maximum increase) can serve as a measure of the magnitude of the individual glare effect. These values are extremely different for the different subjects (see Fig. 4).
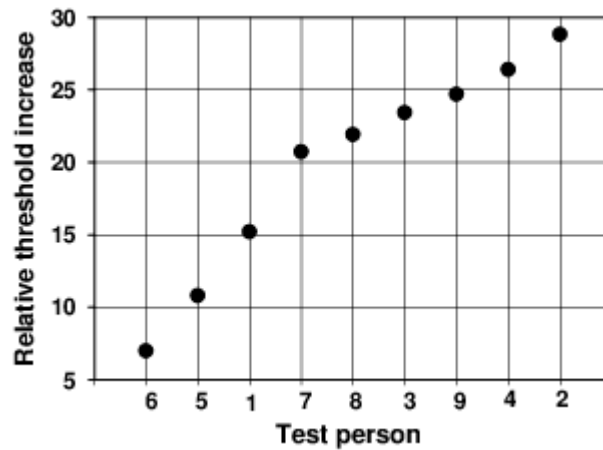
Fig.4. Ratio of the maximum value of the discrimination threshold to the basic value for all subjects (ordered by the magnitude of the effect).

The relative maximum increases cover the range between 7.0 and 28.8 already in this small group of test persons. It can be derived from this that, under similar external conditions, the degree of subjectively experienced glare is very different. The history of our subjects provides no explanation for these great differences.
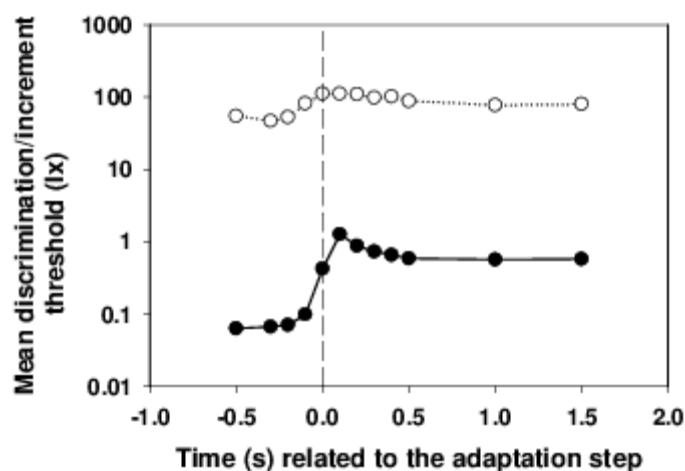
3.2. The course of the electroretinographic threshold (increment threshold)

The measurement of the electroretinographic thresholds was much more difficult for the subjects and the examiner, and above all more time-consuming than the determination of the subjective thresholds. For this reason, only one threshold course was obtained for each subject. The results for the single subjects are thus less secure than the subjective thresholds.

In contrast to the conditions at the subjective threshold, where the peak times were relatively constant at 0.1 s, there are strong differences for this parameter in the electroretinographic threshold. The values range from -0.1 s to 1.5 s. These large interindividual differences lead to a broadening of the peak in the mean course (see Fig.2).

3.3. Comparison between the dynamics of subjective and electroretinographic thresholds
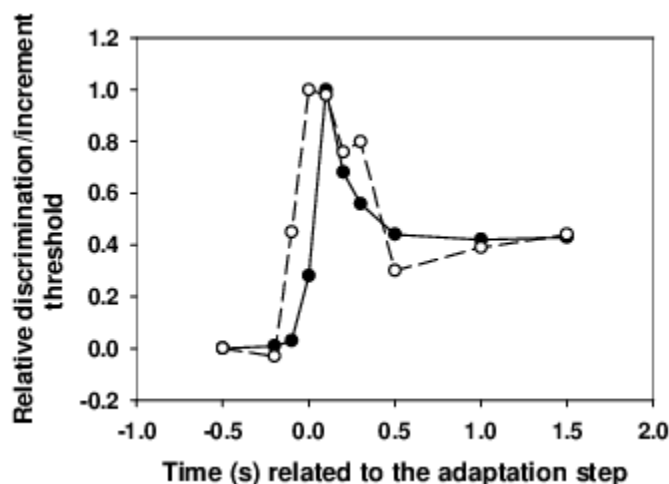
Fig. 5 shows the course of subjective and electroretinographic thresholds in the same diagram.

Fig. 5. Course of subjective (points) and electroretinographic (circles) thresholds in the same diagram. Because of the large range to be displayed, the ordinate was graduated logarithmically.

The difference between the two courses is about 3 orders of magnitude at the beginning, after the light step it is reduced to around 2 orders of magnitude. Thus the relative adaptation-induced sensitivity loss is significantly greater for the sensation than for the electroretinogram. This finding is consistent with the results of Dodt et al. [5]. They had measured the static thresholds in humans.

For a better comparison of the dynamics of the threshold courses, the values were standardized for the following figure. For this purpose, the initial values were subtracted and the remaining differences were divided by the maximum value.

Fig. 6. The courses of subjective (points) and electroretinographic (circles) thresholds. They were made comparable by subtracting the basic value and dividing by the maximum value. In both curves, the values at -0.1 s are already significantly different from the basic value of the threshold.

Fig. 6 shows the thus obtained normalized mean courses of the subjective and electroretinographic threshold. The first value, which is significantly different from the initial value, is that at -0.1 s for both courses. However, the course of the subjective threshold is

narrower. The maximum is in the band of the relatively wide electroretinographic maximum. The extent of the overswing is approximately the same for both courses.

3.4. The electroretinographic response to the 5 s adaptation pulse

The registration of the DC components of the electroretinogram in the waking human is extremely difficult because of the large number of interfering potentials which are also picked up thereby. Even if the subject is able to prevent blinking for a long time, the signal is superimposed by slow potentials generated in the head and body. Thus, it is certainly a consequence of these difficulties that the registration of the slow potentials was carried out either in narcotized animals [7,13], narcotized humans [8], or in the isolated retina (e.g. [17,18]). Kawasaki et al. [9] published results obtained on the waking man. However, the time constant of their amplifier was too low (0.6 s) in order to be able to speak of DC potentials.

The shape of our signal is in principle identical with the courses recorded by other authors. However, the special course is determined by the strength and shape of the stimulus, the position of the electrodes, and possibly also additional subjective factors. It becomes apparent in particular by the work of Hanitzsch et al. [8]. There the dependence of the human DC electroretinogram on the stimulus intensity (however, in the case of dark adaptation) is shown in Fig. 3. The potential generated at 3.6 cd/m^2 is very similar to the potential recorded by us. At lower stimulus levels, the initial overshoot (b-wave) decreases more and more, while at higher stimuli the plateau becomes lower and finally even negative (prevailing PIII). With regard to the c-wave, Granit [7] had already in 1933 described very strong individual peculiarities for the cat.

3.5. The relationship between the course of the electroretinographic threshold and the excitation

Our assumption stands to reason that the dynamics of the threshold changes are determined by the course of excitation. In order to be able to verify this for the electroretinographic increment threshold in connection with an adaptation step, the corresponding excitation, namely the electroretinographic response to the adaptation step, had to be recorded. In the next figure our assumption is checked.

In Fig. 7, the first part of the electroretinogram (Fig. 3) and the course of the electroretinographic threshold for subject 9 are shown together with the adaptation step.
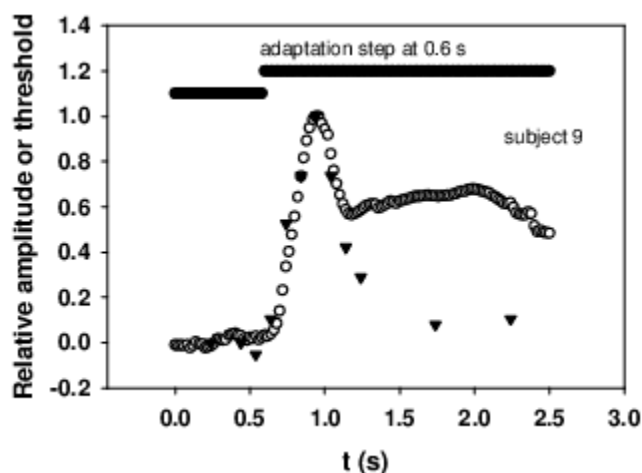
Fig. 7. Electroretinogram (circles) and electroretinographically determined increment thresholds (triangles) for subject 9 (both courses standardized). The threshold curve has been shifted in such a way that the maximum coincides with the maximum in the electroretinogram (peak of the b-wave). This displacement to the right (to higher times) is 0.1 s.

The maximum of the electroretinogram is at about 0.3 s, the maximum of the threshold is at 0.2 s after the adaptation step. In order to be able to compare the shapes, the course of the electroretinographic threshold was shifted by 0.1 s to the right. In addition, in order to may better compare the dynamics, the initial values were subtracted and the amplitudes divided by the remaining maximum values. The result is an almost identical course of the two curves. It can not be expected that the end values (the plateaus) will also accord, since the magnitude of the remaining threshold change depends on the nonlinearity of the ERG characteristic.

An attempt is made now to explain why the threshold increase precedes the response ERG by approximately 0.1-0.2 s. Crawford [4] assumed that the excitation caused by the strong adaptation step "overtakes" the excitation caused by the test stimulus. This explanation is not possible for our results, since in our case the threshold test stimuli were always stronger than the adaptation step. Rather, it can be assumed that a threshold increase occurs when the responses to the test stimulus and to the adaptation step begin to overlap. From then on, due to the nonlinearity of the characteristic curve, the increase in b-wave amplitude generated by the test stimulus is lower, respectively the test stimulus amplitude must be increased in order to achieve the same gain of b-wave. If we assume approximately the same latencies for the responses to the adaptation step and the test stimulus, the overlay begins as soon as the time between test stimulus and adaptation step becomes smaller than the duration of the response to the test stimulus, that is the duration of the b-wave. The width of the b-wave triggered by our test stimuli was actually about 0.1 - 0.2 s. This also explains why the electroretinographic threshold already rises before the adaptation step and this explanation also applies to the rise of the visual threshold.

If the threshold follows approximately the course of the excitation, it can be assumed that the course of the threshold also roughly describes the course of the excitation. Thus the course of the discrimination threshold should also reflect the course of the visual excitation. From this it can be concluded that the same mechanisms which determine the course of excitation are also responsible for the change in sensitivity.

4. Method

4.1. Light stimulation equipment

Fig. 8 shows the equipment for generating adaptation and stimulus light.
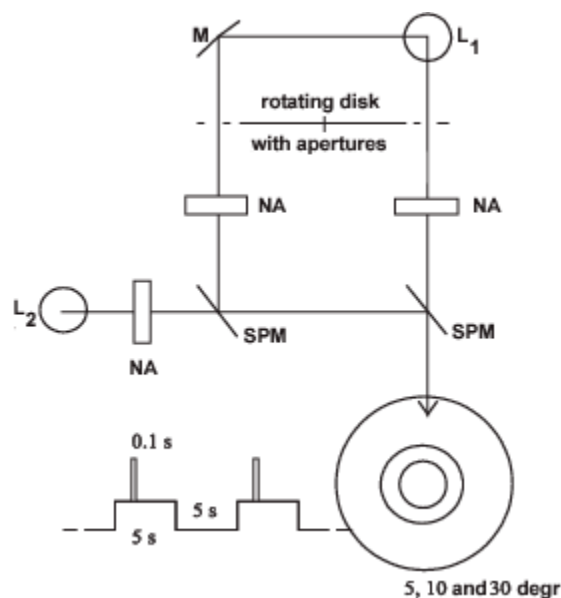
Fig. 8. Equipment for generating adaptation and stimulation light. The light source L_1 generates the adaptation pulse via the mirror M and also the test stimulus directly. The respective strengths are set by neutral filters at NA, the field sizes of 10 and 5 degrees by diaphragms. The light source L_2 generates the continuous adaptation light. Its intensity is again adjusted by a neutral filter at NA and its field size (30 degrees) by a diaphragm. The beam paths are combined at the semi-transparent mirrors SPM. L_1 and L_2 are 12 V, 50 W incandescent lamps.

The time course of adaptation pulse (5 s) and test stimulus (0.1 s) were generated by the rotating disk shown in Fig. 9.

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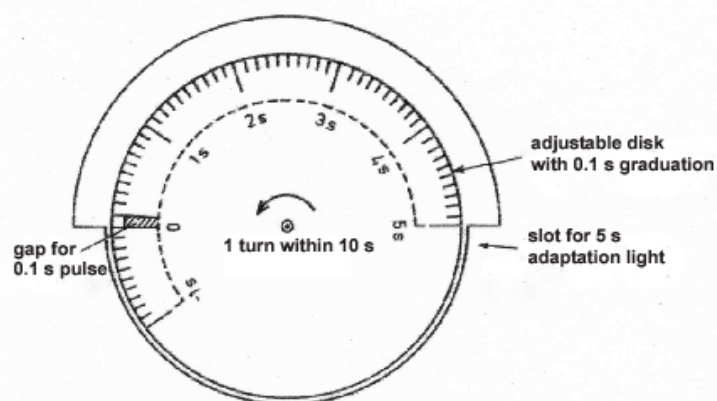
Fig. 9. Disc combination for the generation of adaptation pulse and stimulus light. The disc makes one revolution in 10 s, thereby giving free the beam path for the adaptation pulse for 5 s, that for the stimulus light for 0.1 s. The disc consists of 2 single discs. Their twisting against each other makes it possible to change the time interval between adaptation step and stimulus light from -1.0 s (stimulus light 1 s before adaptation step) up to +5.0 s (stimulus light 5 s after adaptation step).

This type of disk combination had already been used by Crawford [4].

The examination room was lit only by a weak red light. The subject was sitting in front of the equipment with the left eye on the eyepiece. When passing through the pupil, the bundle of light was so narrow that the pupil reaction had no influence on the illuminance on the retina (Maxwellian view, for example [3]). On the retina of the test person fell a constant adaptation light of 0.5 lx and an adaptation light step of 2.5 lx. (For the transparency of the eye media, a value of 0.8 was assumed for the wavelength range in question.) The test person fixed the crosshair in the eyepiece during the entire examination. Thus it was ensured that the test stimuli were mapped on the Macula lutea with the centre in the Fovea centralis.

4.2. Measurement of the subjective threshold

4.2.1. Subjects

The selection of subjects was arbitrarily, the only prerequisite for participation in the tests was a normal visual system. Myopia and/or hyperopia were corrected by the ocular of the device. A total of 9 subjects (7 female, 2 male) participated in the experiments. The age ranged between 21 and 49 years.

4.2.2. Procedure of the tests

The adaptation to the test conditions took place during 15 minutes before the threshold measurement was started. The brightness of the test stimulus was initially selected in such a way that it was clearly recognized by the subject. The stepwise reduction was then performed by means of neutral filters always to about 70% of the previous test strength. Each test stimulus

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was presented to the subjects 13 times. The first 3 presentations were used to adapt to the test situation. Then the test person replied to every stimulus that she/he perceived with "seen" or "yes". The threshold was achieved when 5 yes replies were made [12].

The threshold was identified for the following times before and after the step of the adaptation light:

-0.5; -0.2; -0.1; 0.0; +0.1; +0.2; +0.3; +0.5; +1.0; +1.5 s

The times indicate the time interval between test stimulus and adaptation light step. 0.0 s means synchronicity of the two events. The negative sign means that the test stimulus appeared by the specified time before the adaptation light step. The number behind the positive sign indicates how much later the test stimulus appeared as the adaptation step. These time intervals were adjusted by rotating the diaphragm disks (Fig. 9).

As a rule, one measurement run (all specified test times) could be completed in one session (approx. 90 min). The entire measurement was performed five times for each of the 9 subjects. All measurements were made at the left eye of the test persons. The experiments took place in the late morning hours.

4.2.3. Evaluation of the data

In general, the threshold stimuli had to be determined by interpolation, since only in exceptional cases exactly 5 yes responses were given at a specific test intensity. As a rule, after a test stimulus I_1 with more than 5 yes responses followed I_2 with less than 5. The threshold strength I_s was then calculated according to the formula:

$$I_s = I_2 + (I_1 - I_2) \bullet (5 - n_2) / (n_1 - n_2)$$

Where: n_1 number of yes responses at I_1; n_2 number of yes responses at I_2

The mean values and the range of confidence of the mean values for each test person were calculated from the 5 values for the threshold intensity obtained for each test time. This approach is justified because it can be assumed that the discrimination thresholds are normal distributed [14]. The averaging of the individual time courses then gave the mean course of the discrimination threshold for all subjects. The t-test was used to test for significant differences between the threshold values.

4.3. Electroretinographic studies

4.3.1. Determination of the electroretinographic threshold (increment threshold)

4.3.1.1. Equipment

The system described in chapter 2.1. was used to generate constant adaptation light, adaptation light pulse, and test stimuli. The ERG was recorded at the left eye of the subject with the help of a sub lid electrode. This was a filament electrode consisting of approximately 10 metal-

vaporized fibres (DTL ERG thread, UniMed Electrode Supplies, Farnham, England). The reference electrode was fixed at the left lateral corner of the eye and the mass electrode at the left earlobe. In order to reduce the skin resistance, the skin under the reference electrode was roughened somewhat. After degreasing this site and the earlobe with alcohol, a thin layer of conductive paste was applied and then the Ag/AgCl electrode was attached. In most cases electrode resistances (different and indifferent electrode to ground) of less than 3 kΩ could be achieved. If the resistance was more than 5 kΩ, the procedure of applying the electrode was repeated. The electroretinograms were recorded with a two-channel amplifier and recorder for sum potentials. The amplifier of the system had an input resistance of 200 MΩ. The measurements were carried out with a sensitivity of 25 μV/cm, an upper cut-off frequency of 20 Hz and a lower cut-off frequency of 0.1 Hz. The gain could still be changed during the evaluation of the recorded signals.

4.3.1.2. Subjects

A total of 12 subjects participated in the tests (4 female and 8 male). The age ranged between 20 and 59 years. They were, with two exceptions, other persons than in recording the discrimination threshold because of the great temporal distance. Apart from slight refractive anomalies, which were corrected during the adjustment of the device, all had a normal visual system.

4.3.1.3. Procedure of the tests

After the electrodes were placed, the subject was positioned in front of the device (Fig. 8), where the basic light (0.5 lx) was set. The optical system was adjusted so that the test person saw the fixation cross sharply. Then she/he adapted to the prevailing light conditions in the course of 15 minutes. Only then the measurement did begin. Because of the relatively strong fluctuations of the ERG amplitudes, mean values from 10 stimulus responses were recorded. For this the averager of the system was triggered by the test stimulus. The stimulus intensities were chosen in such a way that the b-wave amplitudes were as close as possible above and below 10 μV (threshold value), so that the threshold strength could be determined later on by interpolation. The duration of the investigation was limited to 60 min. because of the limited concentration capacity of the subjects. Test times were

-0.5; -0.3; -0.2; -0.1; 0.0; 0.1; 0.2; 0.3; 0.4; 0.5; 1.0 and 1.5 s

before and after the step of the adaptation light.

To measure an entire run from -0.5 s to + 1.5 s, 2-3 sessions were necessary.

4.3.1.4. Evaluation of the data

Already during the experiment average courses were calculated from 10 electroretinograms. The resulting b-wave amplitudes were plotted as a function of the stimulus intensity. By linear interpolation the stimulus intensity was determined at which the b-wave amplitude did correspond to the threshold value of 10 µV. This value represents the increment threshold at the actual time relative to the adaptation step.

The threshold determination was carried out for all examination times and all subjects. Thereafter, the mean course for all 12 subjects was calculated. The t-test was used to test for significant differences between the threshold values.

4.3.2. Measurement of the electroretinographic response to the 5 s adaptation pulse

4.3.2.1. Special features of the equipment

In order to obtain a true response to the 5s light pulse, a DC amplifier or an AC-amplifier with a very low lower cut-off frequency is required. We used an AC EEG amplifier with a lower cut-off frequency of 0.005 Hz. This corresponds to a time constant of about 30 s. In this way, we could be sure that the ERG response to the 5 s light pulse would be recorded correctly. The remaining settings were: upper cut-off frequency 10 Hz, sensitivity 0.2 mV/V. Due to the low lower cut-off frequency and the long measuring time, the signal was superimposed by strong low-frequency fluctuations. For this reason, as many individual responses as possible had to be recorded and then averaged.

4.3.2.2. Subjects

Since the adaptation pulse was a relatively weak stimulus (2.5 lx, adaptation field 10°) and therefore only a small signal (approx. 20 µV) was to be expected, interference potentials by eye and blink movements had to be avoided as completely as possible. Because of the long duration of a single run (10 s) and the relatively large number of required runs, the investigation could only be carried out on a subject who was able to avoid blinking during a long period of time. This was subject 9.

4.3.2.3. Procedure of the test and evaluation of the data

The preparation of the subject was carried out analogously to the description given in 4.3.1.1. The ERG response to the 2.5 lx, 5 s adaptation light pulse, which was repeated in the interval of 10 s, was recorded. A total of 3 sessions were performed with twice 50 (test duration 8.3 min) and once 30 (test duration 5 min) adaptation pulses. The electroretinograms were averaged during each test already. The final result was obtained by a second weighted (50 respectively 30) averaging of these mean courses.

4.4. Ethics

All subjects gave their informed consent for inclusion before they participated in the study. The study was conducted in accordance with the Declaration of Helsinki, and the protocol was approved by the Ethics Committee of the Medical Faculty of the University of Leipzig.

Acknowledgements

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