

Visual perception in space and time – mapping the visual field of temporal resolution

Dorothe A. Poggel and Hans Strasburger

Generation Research Program (GRP), Human Science Center, Ludwig-Maximilians University Munich, Prof.-Max-Lange-Platz 11, 83646 Bad Toelz, Germany

Abstract. To characterize temporal aspects of information processing in the human visual field, we studied the topographical distribution of temporal and non-temporal performance parameters in 95 normally sighted subjects. Visual field maps of double-pulse resolution thresholds (DPR) (the minimum detectable temporal gap between two light stimuli) and simple visual reaction times (RT) (measuring the speed of reaction to a light stimulus) were compared to maps of luminance thresholds determined by standard perimetry. Thus, for the first time, the topography of a visual variable without temporal constraints (perimetry) could be compared to visual variables in the temporal domain, with (RT) and without (DPR) motor reaction. The goal of the study was to obtain and to describe the pattern of co-variation of performance indicators. In all three measures, performance was best in the central visual field and dropped significantly towards the periphery. Although the correlation between DPR and RT was significant, shared variance was low, and we observed large topographical differences between these two temporal-performance variables. In contrast, DPR and perimetric thresholds correlated more substantially, and visual field maps were similar. The Gestalt of DPR maps shares characteristics of basic visual processing (e.g., light sensitivity), but it also reflects top-down influences, i.e., from spatial attention. Although the correlation between DPR and RT suggests common characteristics between these two temporal variables, the topographic distributions reveal significant differences, indicating separate underlying processing mechanisms.

The correspondence should be addressed to H. Strasburger, Email: Strasburger@uni-muenchen.de

Key words: temporal processing, visual function, mapping, topography, visual field, double-pulse resolution, reaction time, perimetry

INTRODUCTION

Time plays a fundamental role in all perceptual processes. Processing of temporal aspects of information is obviously a highly complex function of the brain. Like attention, it is crucial for virtually all cerebral input and output processes of an organism, but there seems to be no unitary process or "sensory organ" for temporal processing. Instead, it is heavily interwoven with perceptual functions and motor processes (Rubia and Smith 2004, Wittmann 1999, Wittmann and Fink 2004). However, the interaction of basic sensory functions with mechanisms of processing temporal information is usually not taken into consideration in studies on time perception, either because this relationship is still largely unknown, or because it is taken for granted and performance parameters are assumed to be constant within the experimental context. For instance, age-related changes in temporal processing (Bao et al. 2004) may be confounded with modulations of sensory performance parameters over the life span, but the latter are rarely measured in detail.

Trying to understand the way in which temporal processing is connected with visual functions requires a detailed comparison of a range of variables. In most psychophysical studies, foveal vision (i.e., vision in the very center of the visual field) is exclusively assessed. However, the functional properties of the visual system are not homogeneous across the visual field. Indeed, performance on virtually all visual parameters - ranging from visual acuity and light sensitivity to more complex processes like color vision or motion perception - depends heavily on the visual field position (for reviews see Drasdo 1991, Pointer 1986, Strasburger 2002, Strasburger et al. 1994). Those behavioral measures yield valuable information on the functional architecture of the visual system. The topographic distribution of such variables across the visual field and neuronal networks in the visual brain, respectively, is quite specific for each function, i.e., the pattern of performance within a specific visual field map depends on the demands of the visual task. The recognition of fine-grain patterns and the identification of form at low contrast between stimulus and background is mainly carried out by foveal vision, where the architecture of the visual system allows best performance (Strasburger 2002, Strasburger and Rentschler 1996). Many visual functions show a systematic decline in performance with increasing retinal eccentricity (for reviews see Drasdo 1991, Strasburger 2002). Other visual functions, however, like flicker detection (Tyler 1987) seem more efficiently accomplished by the periphery of the visual field.

The topographic distribution of visual variables reflects not only the functional architecture within a processing structure of the visual system (e.g., visual acuity is related to the size of receptive fields of retinal ganglion cells), but it also contains information on the interaction between different levels of processing in the visual system (e.g., lesions on different levels of the visual system cause characteristic patterns of visual field loss). Hence it is necessary to investigate the full topography of visual functions, not only to assess the interrelations between different visual variables in the intact brain, but also to properly evaluate changes of performance in the lesioned visual system.

Most studies on temporal processing in the visual domain (with few exceptions; see Tyler 1987) do not take into account the interaction of temporal variables and visual parameters. Therefore, it is unclear whether the effects reported in those studies are merely epiphenomena of visual processes (e.g., a loss of light sensitivity in elderly subjects) or whether they originate in the mechanisms which mediate the processing of temporal information (e.g., a change in temporal resolution in those subjects). Hence it is unclear whether the variation of performance in tasks within the temporal domain over the life-span is simply a result of reduced visual performance of older subjects. Also, for instance, divergent results between studies on time perception might be affected by the presentation of stimuli at different visual field positions so that the results are not directly comparable.

The aim of our study was therefore to explore and to describe the topography of different variables of visual and temporal processing. This description should serve as a first step towards a systematic investigation of the relationship between basic visual processes like light detection and performance in the temporal domain that is mediated by visual perception, e.g. the temporal resolution of light pulses and the reaction time to simple light stimuli.

The mapping of light sensitivity across the visual field is routinely done in perimetric measurements. Quantifying the detectability of light, this topographic variable reflects the basic functional characteristics of the visual system and yields information on the quality of transmission of neural information (and hence possible defects) along the primary visual pathway (retina, optic nerve, lateral geniculate, radiatio, primary visual cortex). Double-pulse resolution (DPR) is a measure that also relies on the detection of light stimuli, but additionally yields information on the processing speed or sluggishness, respectively, of the visual system without being contaminated by temporal processing in the motor domain. Finally, the measurement of simple reaction times (RT) to light stimuli is a standard measure of processing speed applied in many perceptual and cognitive experiments. Here we mapped RT across the visual field which presumably reflects purely sensory influences since the motor components of reaction times should be independent of the stimulus position in the visual field. Both, DPR and RT, are conceptually related to processing speed in the visual system, in particular on the lower level. Thus we expected co-variation of the two measures. Additionally, the comparison of their topographic characteristics was performed to gain more information about possible common mechanisms involved, finally aiming at a clearer definition of temporal processing and its underlying mechanisms. Furthermore, this approach of detailed spatial description of functional characteristics was chosen based on clinical considerations. The new visual field maps can serve as normative data for neuropsychological studies: lesions of the visual system typically result in visual field loss which is, at present, exclusively diagnosed by perimetry, i.e., the measurement of light detection thresholds. Other visual functions - e.g., parameters of temporal processing - are not routinely assessed, although they may have massive effects on performance in everyday life of patients with visual impairment. The data of the study presented here thus also provide a basis for a more complete assessment of visual field defects, and thereby allow describing the interaction of temporal and visual processing in the lesioned visual system. Finally, the information can be useful for the evaluation of treatment -e.g., training of compensatory eye movements or vision restoration approaches - in the context of visual rehabilitation.

METHODS

Sample

A sample of 95 volunteers (26 male and 69 female subjects) was investigated to obtain normative data on visual and temporal brain functions. The age range of the sample was 10 to 90 years. All subjects had normal or corrected-to-normal vision. Severe dementia, impairments of attention or other mental functions, depression or other psychiatric disorders as well as any brain lesion and/or visual impairment were exclusion criteria for the present study.

All subjects (or their parents for subjects below an age of 18, respectively) gave their informed consent for participation and were paid for taking part in the study. The experimental design had been approved by our local ethics committee.

Double-pulse resolution

Thresholds of double-pulse resolution were determined using an apparatus and a psychophysical technique developed by Treutwein (Treutwein 1989, 1995, 1997, Treutwein and Rentschler 1992; for an introduction to psychophysical methods see Gescheider 1997). The test is performed as a nine-alternative forced-choice task and determines the minimal duration of a gap between two light pulses that the subject can just detect by identifying one non-continuous stimulus out of eight continuous stimuli. Testing was done under standardized conditions in a darkened room, i.e., under mesopic light conditions, with a room illuminance of 1.5 lx. Subjects were positioned at a distance of 30 cm from a screen (background luminance: 0.01 cd/m^2), so that the eyes were located opposite the center of the stimulus display. Viewing was binocular in all cases. The subject's position was kept constant by using a chin rest.

Before the beginning of a trial, the subject saw a dim cross-hair on black background that indicated the center of the display and also showed the main meridians of the visual field where the stimuli were to be presented. The onset of a trial was triggered by the experimenter. A trial consisted of the simultaneous presentation of nine rectangular white light stimuli (luminance = 215 cd/m^2 , size = 1.15° visual angle), one stimulus located in the center of the display, the other eight arranged on a circle around it at the intersections with the main meridians (horizontal, vertical and the 45° oblique meridians) (see Fig. 1), i.e., the peripheral stimuli were presented all at the same eccentricity in the visual field that was defined by the radius of the circle.

Within a trial, eight stimuli were presented continuously, and one stimulus, the target, was presented as a double pulse, i.e., it was interrupted by a gap interval of defined length. Provided that the gap duration was above threshold, the subject perceived the difference between the target and the other eight stimuli as a short flicker of the target. The subject's task was to verbally indicate the target position either in terms of directions on the display (middle, left, upper right etc.) or positions on a clock face (middle, nine o'clock, two o'clock etc.). The subject's responses were entered by the experimenter on the computer keyboard, and the next trial was started by the experimenter pressing the enter key. Subjects were instructed to keep their eyes fixated at the central position of the cross hair displayed between trials and to indicate the target position on each trial. They were asked to guess when they were not sure of the answer or when they had not perceived the flicker.

The gap duration between the two light pulses of the target stimulus was varied, controlled by a maximum-likelihood adaptive procedure (YAAP) (Treutwein 1989, 1995), starting from an initial gap duration of 80 ms. To gather an initial a-priori response distribution (a means of stabilizing the maximum-likelihood procedure) the first ten trials of a block were presented according to the method of constant stimuli. Only then, the YAAP-algorithm proper started, and the threshold at each stimulus position was determined independently of the other locations. The target position was selected randomly for each trial so that attention could not be focused on the target location, but had to cover all stimulus positions. The duration of light pulses was asymmetric: the first pulse was 280 ms long, the second 80 ms (differing from Fig. 1). The non-target stimuli were presented simultaneously with the target, i.e., their duration was 280 ms + gap duration + 80 ms. Target and non-targets were matched in



Fig. 1. Time course of stimulus display within one trial of double pulse resolution measurement: stimulus display (top), stimulus onset, and timing of continuous non-target stimuli and double-pulse target stimulus (bottom). Differing from the graph, the leading pulse was the longer one (modified from Treutwein 1989).

brightness according to Bloch's law. This pattern of stimulation had been tested in earlier experiments and was chosen for this study to allow comparison with results from previous experiments (Sachs 1995, Treutwein 1989). Stimuli were presented on a 17" screen of an x-y-z-oscilloscope (HP 1310) that was controlled by a point plot buffer (G. Finlay, Edmonton, Canada) which in turn was receiving input from an IBM compatible PC. This setup allowed presentation of stimuli and adaptation of the gap duration between double pulses with microsecond accuracy since it circumvents raster-scan technology (see Bach et al. 1997).

A block was ended when all nine thresholds were determined to a previously specified confidence interval, defined as containing the threshold at 85% probability, which took approximately 140-280 trials (test duration ranged between ten and twenty minutes). All subjects performed ten blocks of trials. After each block, the radius of the circle, i.e., the eccentricity of the peripheral stimulus positions, was changed (see the test grid in Fig. 3). The position of the stimuli in the subsequent block was presented to the subjects on the screen prior to the first trial of each block. The first block was carried out with stimuli arranged on a circle of 2.5 degrees visual angle. Subsequently, the test trials were repeated with eccentricities of 5°, 10°, 15°, and 20° visual angle, respectively. When the maximum eccentricity was reached, the sequence of blocks was repeated in reverse order (starting from 20° down to 2.5°) so that each block was presented twice to the subject. This procedure was chosen both to balance out sequence effects and to get more reliable threshold estimates by using more trials.

Subjects determined the speed of the test by answering in a self-paced manner. Participants also were allowed to take breaks whenever they wished. Except for an initial short block of practice trials, no feedback was given once the subject had learned to recognize a target.

Raw threshold values (of individual subjects or averaged data of the complete sample, see Results section) were entered into statistical software (Microsoft Excel and SPSS) for analysis. The 3-D-plots were prepared with a Matlab script originally programmed by Lutz (see Gothe et al. 2000, Strasburger et al. 2000) and modified for the present purpose to get a graphic display of the double-pulse resolution map (Mathworks, Version 5.3).

Reaction times

For assessment of reaction time maps, a high-resolution computer-based campimetric test was used (Nova Vision, Magdeburg). Testing was done under standardized conditions in a darkened room (see section on double-pulse resolution above). The subject was seated in front of a 17"-computer screen, the head stabilized with a chin rest at a constant viewing distance of 30 cm. Viewing was binocular in all subjects.

In the visual field test (Nova Vision, Magdeburg) (see Kasten et al. 1997), round white light stimuli (luminance = 96 cd/m², size = 0.76° , presentation time = 150 ms, ISI = 1000 ms) were presented in random order at 474 positions, in a grid of 25×19 stimulus locations on a grey screen (luminance = 26 cd/m^2) (see Fig. 2). The subject was instructed to press the space bar on the computer keyboard upon detection of a stimulus. Feedback on correct detection and false positives was provided by a high vs. low tone, respectively. Fixation was controlled by having the subjects report an equiluminant change of the fixation point's color, e.g., from bright green to bright yellow, that could not be perceived with eccentric fixation. The subject had to fixate throughout the test and was instructed to press the space bar of the computer keyboard upon detection of the color change. Additionally, eye position was controlled by the experimenter observing the subject's fixation behavior in a mirror. Inter-stimulus intervals were randomized to prevent guessing and hence random hits. Total duration of the visual field test was approximately 20 minutes.

The numbers of hits, misses, and false positives, as well as reaction times for each detected stimulus were recorded. Reaction times were displayed as a complete map (see Fig. 2), but for the statistical analysis of reaction times and comparison of reaction time maps with the maps of double-pulse resolution, only the RT values at those positions used in the DPR testing were considered. Raw reaction times at these positions were entered into statistical software (see section on double-pulse resolution above), and graphic maps were generated using the Matlab scripts mentioned above. Since the RT motor requirements are constant under all conditions, these maps, which show the variation of RT across the visual field, can be considered to reflect the variation of the RT's sensory component only (Teichner and Krebs 1972).

Perimetry

Subjects were examined with two standard perimetric tests implemented in the Octopus 101 Perimeter (InterZeag/ Haag Streit): firstly, all participants performed a screening test (Program No. 07) separately for each eye to get an overview of the complete visual field up to 90° visual angle and to exclude subjects having visual field defects. The subject's task was to detect static light stimuli presented in a pre-defined test grid in pseudo-random order. The subject's head rested on a chin rest. Fixation was controlled with an infrared-sensitive camera that gave feedback about the eye position to the perimetric software and stopped the program automatically whenever the subject looked away from the central cross-hair position, or closed the eye, respectively.

Subsequently, the thresholds of light sensitivity were assessed with a finer test grid (Program No. G2) within the inner 30° radius of the visual field. Again, the test was done monocularly using static test stimuli. Fixation



Fig. 2. Left: monitor display for the campimetric reaction time test. The fixation point (middle) is continuously present, and subjects react to 474 supra-threshold white light stimuli appearing in random order on a dark screen. Right: reaction time map from the campimetric test.

control was identical to that of the perimetric screening test described above. The subject's head rested on a chin rest. He/she had to press a response button upon detection of a stimulus. Each trial was announced by an acoustic stimulus (a beep), but there were also catch trials interspersed so that the number of false positives served as a criterion for the reliability of the examination. The test uses a simple adaptive procedure by which the luminance of the test stimuli at 59 positions was varied to determine luminance thresholds at each position independently. Results are stated in dB attenuation from maximum luminance (10 000 asb = 3 183 cd/m²). Test duration for the examination of one eye was approximately 10-12 minutes.

Raw threshold values were converted into an Excel format and subsequently modified to generate a graphic display using the Matlab scripts mentioned above.

Data Analysis

Initially, all visual field maps were analyzed separately using the quantitative raw data of each test. To compare the maps of different visual/temporal functions, particularly to obtain an overview of the graphic displays, all data were plotted within the test grid of double-pulse resolution described above (see Fig. 3). The grid contained 41 stimulus positions: one central



Fig. 3. Grid of stimulus positions used in the double-pulse resolution tests, campimetric reaction time mapping, and perimetric threshold measurement.

position and five circular arrays with different radius (= eccentricity), each consisting of eight stimulus positions. For the reaction time maps which had a much higher spatial resolution than those of the DPR, data points were extracted from the original map only at the positions of the double-pulse resolution grid as described above. Since in the perimetric map of light sensitivity thresholds the stimulus positions did not correspond to the DPR-positions, the values at the norm-grid positions were determined by interpolation.

Statistical analysis was done with the SPSS program, using non-parametric methods of correlation and comparison of means (oneway ANOVA). All tests were performed with an alpha level of 0.05 (two-tailed).

RESULTS

Double-pulse resolution

Average threshold values of double-pulse resolution (DPR) increased markedly and significantly with increasing eccentricity of the stimulus positions (oneway ANOVA: F=19.5, df = 4, P<0.001, main factor eccentricity) (see Fig. 4A, left column). There was further a substantial and highly significant correlation of DPR threshold with the subject's age (Spearman's Rho: r = 0.67, P<0.001).

The average threshold, over all subjects and positions, was 49.74 ms (SD = 13.58 ms) (average map shown in Fig. 4A, left column). Subject 004 (female, age 21) showed the best performance in the DPR test (mean DPR threshold = 27.50 ms) (see Fig. 4A, middle column), and subject 084 (female, age 82) had the highest average DPR thresholds (mean = 97.96 ms) (Fig. 4A, right column).

Comparison with the average map (average threshold of all subjects) shows the high variability of data in the sample. Nevertheless, the form of the DPR map showed the same characteristic in all subjects: performance in the center of the visual field was best, and with increasing eccentricity the thresholds increased, i.e., temporal resolution performance declined towards the periphery of the visual field. The increase was most pronounced between the central position and the 2.5° radius, but there was a further significant elevation of temporal thresholds in the zone between 2.5° and 5.0° visual angle. Beyond 5°, performance almost leveled out with just a moderate gradient up to the maximum tested eccentricity of 20° visual angle.



Fig. 4. Topographic maps of (A) double pulse resolution, (B) reaction times, and (C) standard perimetry. Left column: average map over all subjects and trials (top view, profile, and 3D-map). Middle column: mapping of performance of the best subject. Right column: mapping of performance of the lowest-performing subject.

Reaction time campimetry

Reaction time also increased from the center of the visual field toward the periphery (oneway ANOVA: F=3.69, df=4, main factor eccentricity: P=0.006). However, performance did not drop as rapidly with increasing eccentricity as in the distribution of DPR thresholds (see Fig. 4B, left column). Particularly in the visual field center, there was only a moderate increase of RT. Reaction times were considerably longer in older subjects, and age and reaction time correlated significantly (Spearman's Rho: r = 0.30, P=0.003). The best average reaction time was observed in a young female, 14 years of age (subject 057, mean = 273 ms) (Fig. 4B, middle column). A female subject of 72 years had the longest average reaction times (subject 011, mean = 689 ms) (Fig. 4B, right column).

The topographic map of average reaction times of the complete sample (mean = 370.9 ms, SD = 69.3 s) (Fig. 4B, left column) was much flatter than the DPR map as already indicated by the quantitative analysis of reaction time data, with high variability within and between subjects.

Reaction times correlated significantly but surprisingly not substantially with DPR thresholds. This was true for the correlation of average RT over all subjects and positions with average DPR values (Spearman's Rho: r = 0.38, P < 0.001), but also for the correlation of RT and DPR data averaged along any particular meridian (correlations between r = 0.36 and r = 0.19). Thus, the two measures of temporal performance shared only about 14% common variance.

Perimetry

Luminance sensitivity for light detection as assessed by standard perimetry was highest (best) in the center of the visual field and dropped significantly (oneway ANOVA: F=17.0, df = 6, main factor eccentricity: P<0.001) (Fig. 4C, left column) towards the periphery of the visual field. Light detection performance also decreased significantly with age (oneway ANOVA: F=12.5, df = 7, main factor age: P<0.001). The best performance in the perimetric test was observed in a 38-year-old female (subject 003, mean = 34.5 dB) (Fig. 4C, middle column). An 82-year-old woman showed the lowest values (subject 084, mean = 16.6 dB) (Fig. 4C, right column).

Individual maps, as well as the average map of all subjects in the sample (mean = 26.9 dB) (Fig. 4C, left column) were much more similar to those for DPR than the reaction time maps. This is also evident from the correlations. Average perimetric thresholds of all subjects and stimulus positions correlated substantially and significantly with DPR thresholds (Spearman's Rho: r = -0.52, P < 0.001; the correlation was negative because higher perimetric threshold values but lower DPR values, respectively, corresponded to better performance).

In summary, the graphic results confirmed the quantitative analysis described above: the two temporal variables, DPR thresholds and RT, correlated significantly but not substantially, and the distribution of the two parameters over the visual field was quite dissimilar. In contrast, DPR thresholds and perimetric thresholds correlated substantially, and the highly significant interaction of both variables was also mirrored by the similar patterns of visual field maps.

DISCUSSION

In this study, we investigated the interdependencies of temporal and non-temporal visual performance parameters and their topographical distribution in a sample of 95 normally sighted subject spanning a large spectrum of ages from 10 to 90 years. Thresholds of double-pulse resolution (DPR), reaction times (RT), and perimetric luminance-increment thresholds were mapped across the visual field. Older subjects generally showed somewhat lower performance, but interindividual variability of data was high for all three parameters and in part exceeded this systematic trend. Performance was best in the central visual field and dropped significantly and systematically towards the periphery in all three variables. Comparison of the maps showed a significant but surprisingly low correlation between DPR and RT, and large topographical deviations between these maps. In contrast, DPR and perimetric thresholds correlated more substantially and visual field maps were similar.

Even though both, DPR and RT, are parameters characterizing temporal processing, the correlation as well as the shared variance between the two measures is low. Thus, although conceptually a common basis might be assumed for what is reflected in DPR and RT – since both are measures of temporal performance of information processing in the millisecond range – our data rather point to the involvement of different mechanisms.

DPR and RT differ in their involvement of the motor system: DPR is not speeded and involves only verbal responses of the subject, whereas RT requires a speeded motor reaction to a visually presented stimulus. However, different motor requirements cannot be the cause for the deviations between DPR and RT; since motor requirements were constant for all stimulus positions during RT measurement, only sensory factors can explain the topographic distribution of RTs in the visual field.

RT is clearly dependent on transmission speed along the neural pathways, including the visual afferent and the motor efferent path. The topography of simple visual RT reflects differences in information processing speed across the visual field since the motor component is constant over all positions. DPR differs from RT not only quantitatively but also with regard to the topographical map. Presumably DPR does not simply reflect (sensory) information processing speed but rather the ability of the visual system to segregate units of visual information that may be largely independent of processing speed per se. On the neuronal level, the resolution of light pulses might be mediated not exclusively by the transmission speed along the visual pathways, which is expected to introduce a certain delay but leave the gap information intact, but rather by the efficiency of readout mechanism processing patterns of neural activation. Light pulses presumably are coded in the afferent pathway as bursts of action potentials, and the ability to separate two bursts of activation and thus to identify two light stimuli as separate might depend on the overlap between the first and second burst of action potentials, and thus the signal-to-noise ratio and its time course, rather than on the speed of conveying the information to processing units higher up the visual pathway.

In contrast, the correlation between DPR thresholds and perimetric data as well as the similarity of visual field maps was quite high. In standard perimetry, the performance decrease towards the periphery is, of course, what would be expected, but with respect to double-pulse perimetry that decrease is surprising in light of earlier findings (Otto 1987, Tyler 1987) which show that temporal resolution as assessed by flicker fusion is mostly independent of, or even improving with eccentricity. The difference is probably explained by the fact that we did not use size scaling – be it according to ganglion receptive field size or to the cortical magnification factor. The constant size of the stimuli used for our study may thus account for the lower resolution performance in the periphery: constant-size stimuli will stimulate less receptive field area and less cortical area at eccentric positions. Additionally, the luminance of double pulse stimuli was not adjusted to more peripheral positions - as would be required to equalize performance across different eccentricities. Some decrease of performance might thus also be caused by the weaker light sensitivity in the periphery of the visual field. However, since DPR stimuli were far above detection threshold, we presume this latter influence of luminance had only minor consequences in our experiment.

The reduced DPR performance in older subjects can be explained by lower retinal illumination in those subjects: the reduced transparency of the lens, together with a systematic decrease of the size of the pupil (senile miosis) decreases the retinal illuminance on average by about a factor of three from the twenties to the age of sixty (Weale 1963, cited from Owsley et al. 1983). According to the Ferry-Porter law, this age-related reduction of retinal illuminance can be expected to systematically and substantially lower temporal resolution (a decrease of illumination by a factor of three will decrease the flicker fusion frequency by about 8 Hz) (see Tyler and Hamer 1993).

Factors mediating double-pulse resolution

The low coherence of RT and DPR data suggests that performance parameters are not generally mediated by a unitary mechanism determining temporal characteristics of neural information processing that exerts a general influence on all visual processes. In contrast, the substantial shared variance and topographical similarity of DPR thresholds and perimetric thresholds indicates that the ability to resolve light pulses is strongly influenced by the visual field architecture, possibly the anatomy of the earliest processing levels of the visual system, as Tyler (1985) concluded for the case of flicker fusion.

Nevertheless, even with the substantial correlation between DPR values and light sensitivity, in absolute terms only a small part of the variance of DPR thresholds can be explained. Hence, there must be other significant factors mediating the pattern of DPR maps. Preliminary data from studies with normally sighted subjects and clinical studies suggest two sources. Firstly, there seems to be a top-down influence of spatial attention on DPR thresholds: focusing attention at a specific visual field location changes the thresholds dramatically, and also the size of the attention focus exerts an influence on DPR performance (Poggel et al. unpublished results). Secondly, data from patients with lesions at higher levels of the visual pathway, e.g., the optic radiation or the primary visual cortex, show a pronounced increase of DPR thresholds in partially blind zones of the visual field (Poggel et al. unpublished results). Hence it is likely that temporal resolution is mediated also - and perhaps to a large part - by higher-level processes: on the one hand, processing of visual stimuli in the primary visual cortex plays an important role for the temporal resolution mapped in the visual field as preliminary clinical results show. On the

other hand, cortical areas believed to be involved in the allocation of spatial attention, supposedly frontal and parietal regions of the brain, modify basic processing steps by a top-down regulation of visual and temporal processes (Pouthas and Perbal 2004, Rubia and Smith 2004).

CONCLUSIONS

In conclusion, our data allow a detailed characterization of the visual field with respect to the role of temporal characteristics of information processing. The visual field maps presented here complement and extend previous attempts of mapping visual functions which mainly concentrated on non-temporal aspects. We showed that topographical maps differ not only between visual functions that are measured on different physical dimensions, but also between those that reflect temporal aspects of visual information processing. In particular the sensory component of simple visual reaction times, and double-pulse resolution, seem to reflect separate temporal characteristics of visual information processing. There is thus not a unitary system of temporal processing mediating all aspects of time and timing.

Similar to the situation in perimetry, the retino-cortical architecture shows its characteristics in the topography of the variables. However, the patterns of interdependencies in the data, particularly the topography of double-pulse resolution maps, cannot be explained by retino-cortical architecture alone. The correlations as well as the topographical comparisons between maps indicate a complex combination of factors mediating temporal aspects of information processing in the visual system: double-pulse resolution certainly depends on basic processes at lower stages of the visual system, like receptor sensitivity, receptive field size, and areal summation. These influences are indicated by the dependence of resolution performance on the size and the luminance of the stimuli and are captured by the classical Granit-Harper law (for stimulus size) and Ferry-Porter law (for retinal illuminance), respectively (see Hartmann et al. 1979, Treutwein 1989, Tyler 1985, 1987, Tyler and Hamer 1990, 1993). However, DPR is also modified by cortical processing, and we have collected preliminary data pointing at top-down influences on double-pulse resolution.

The data of our study show that there is additional information on mechanisms of temporal information processing in interaction maps of different visual and temporal functions. Hence, in research on time and timing, not only the dimension of time but also the dimension of space should be considered.

ACKNOWLEDGEMENTS

The authors would like to thank Dr. Bernhard Treutwein for providing the DPR technique, Dipl.-Psych. Claudia Calmanti, Andrea Geyer, and Luise Schulze for their help with data acquisition, Dr. Kai Lutz and Dr. Jan Churan for helping to program the Matlab scripts. The work was supported by a grant of the Deutsche Forschungsgemeinschaft (STR 354/3-1) to Hans Strasburger.

REFERENCES

- Bach M, Meigen T, Strasburger H (1997) Raster-scan cathode ray tubes for vision research - limits of resolution in space, time and intensity, and some solutions. Spat Vis 10: 403-414.
- Bao Y, Zhou J, Fu L (2004) Aging and the time course of inhibition of return in a static environment. Acta Neurobiol Exp (Wars) 64: 403-414.
- Drasdo N (1991) Neural substrates and threshold gradients of peripheral vision. In: Limits of vision (Eds. J.J. Kulikowski, V. Walsh and I.J. Murray). Macmillan Press, London, p. 250-264.
- Gescheider GA (1997) Psychophysics: the fundamentals. Lawrence Erlbaum Association, Mahwah, 177 p.
- Gothe J, Strasburger H, Lutz K, Kasten E, Sabel BA (2000) Recognition of low-contrast characters by subjects with cerebral visual-field defects. Perception 29 (Suppl): 45.
- Hartmann E, Lachenmayr B, Brettel H (1979) The peripheral critical flicker frequency. Vis Res 19: 1019-1023.
- Kasten E, Strasburger H, Sabel BA (1997) Programs for diagnosis and therapy of visual field deficits in vision rehabilitation. Spat Vis 10: 499-503.
- Otto E (1987) Multifactorial dependency of the critical flicker fusion frequency relationship of physical and physiological variables (in German). Z f Psychol 195: 261-281.
- Owsley C, Sekuler R, Siemsen D (1983) Contrast sensitivity throughout adulthood. Vis Res 23: 689-699.
- Pointer JS (1986) The cortical magnification factor and photopic vision. Biol Rev Camb Phil Soc 61: 97-119.
- Pouthas V, Perbal S (2004) Time perception does not only depend on accurate clock mechanisms but also on unim-

paired attention and memory processes. Acta Neurobiol Exp (Wars) 64: 367-385.

- Rubia K, Smith A (2004) The neural correlates of cognitive time management: a review. Acta Neurobiol Exp (Wars) 64: 329-340.
- Sachs H (1995) The detection of temporal double pulses in the central visual field: basic research and clinical application. (Dissertation) (in German). Akademischer Verlag, München, 91 p.
- Strasburger H, Rentschler I (1996) Contrast-dependent dissociation of visual recognition and detection fields. Eur J Neurosci 8: 1787–1791.
- Strasburger H, Rentschler I, Harvey LO (1994) Cortical magnification theory fails to predict visual recognition. Eur J Neurosci 6: 1583-1588.
- Strasburger H, Gothe J, Lutz K (2000) The healthy visual field of recognition. Perception 29 (Suppl): 84-85.
- Strasburger H (2002) Indirect vision: recognition of form in the central and peripheral visual field (in German). Hogrefe Verlag, Göttingen, 296 p.
- Teichner WH, Krebs MJ (1972) Laws of the simple visual reaction time. Psychol Rev 79: 344-358.
- Treutwein B (1989) Temporal aspects of visual information processing (Dissertation) (in German). Kyrill & Method Verlag, München, 95 p.
- Treutwein B, Rentschler I (1992) Double pulse resolution in the visual field: The influence of temporal stimulus characteristics. Clin Vis Sci 7: 421-434.
- Treutwein B (1995) Adaptive psychophysical procedures. Vis Res 35: 2503-2522.
- Treutwein B (1997) Yaap: yet another adaptive procedure. Spat Vis 11: 129-134.
- Tyler CW (1985) Analysis of visual modulation sensitivity. II. Peripheral retina and the role of photoreceptor dimensions. J Opt Soc Am 2: 393-398.
- Tyler CW (1987) Analysis of visual modulation sensitivity. III. Meridional variations in peripheral flicker sensitivity. J Opt Soc Am 4: 1612-1619.
- Tyler CW, Hamer RD (1990) Analysis of visual modulation sensitivity. IV. Validity of the Ferry-Porter law. J Opt Soc Am 7: 743-758.
- Tyler CW, Hamer RD (1993) Eccentricity and the Ferry-Porter law. J Opt Soc Am 10: 2084-2087.
- Weale R (1963) The aging eye. Lewis, London, 200 p.
- Wittmann M (1999) Time perception and temporal processing levels of the brain. Chronobiol Internat 16: 17-32.
- Wittmann M, Fink M (2004) Time and language critical remarks on diagnosis and training methods of temporal-order judgment. Acta Neurobiol Exp (Wars) 64: 341-348.

Received 26 January 2003, accepted 19 March 2004