A practical method of measuring the human temporal contrast sensitivity function

Billy R. Wooten, Lisa M. Renzi, Robert Moore, and Billy R. Hammond, Jr. 2,*

¹Walter S. Hunter Laboratory, Department of Psychology, Brown University, 89 Waterman Street, Providence, RI 02912, USA ²Vision Science Laboratory, Department of Psychology, University of Georgia, Athens, GA 30602, USA *bhammond@uga.edu

Abstract: One of the more significant indicators of neural age-related loss and disease is reduced temporal processing speed. It would, therefore, be useful to have an accurate and practical device that measures the full range of an individual's temporal processing abilities (characterized as the temporal contrast sensitivity function, TCSF). 70 subjects (15-84 yrs) were tested. A small tabletop device utilizing electronic control of light-emitting diodes (LEDs) was constructed that delivered a 1-degree, 660 nm test (the modulation depth of which could be adjusted directly by the subject) centered within a 10-degree 660 nm surround. The method provided a TCSF that had a shape consistent with past studies (peaking around 8 Hz). Also consistent with past work, the largest age-decline was found at the highest frequencies and for the central fovea (r = 0.47, p < 0.0001, ~2 Hz per decade). Psychophysical assessment of temporal vision offers an easy and dynamic measure of central visual function.

©2010 Optical Society of America

OCIS codes: (120.0120) Instrumentation, measurement and metrology; (107.0170) Medical optics and biotechnology; (220.0220) Optical design and fabrication; (230.0230) Optical devices; (330.0330) Vision, color and visual optics.

References and links

- 1. A number of terms have been used to describe human temporal sensitivity. An early, and still relatively common, usage was the temporal modulation transfer function. Such a term, however, refers to physical characteristics of the stimulus not to the psychophysical response. Even with respect to the latter, the "modulation transfer function" is more aptly used to refer to the ability of a lens or optical system to faithfully transmit an image (in terms of its contrast, etc). "Contrast sensitivity" is the most descriptive term because it directly describes the actual values one obtains. Of course, contrast can be varied in either the spatial or temporal domains so this must also be specified (to wit, the SCSF or the TCSF).
- H. de Lange, "Experiments on flicker and some calculations on an electrical analogue of the foveal systems," Physica 18(11), 935–950 (1952).
- 3. A. B. Watson, "Temporal sensitivity," in *Handbook of perception and human performance*, K. R. Boff, L. Kaufman, & J. P. Thomas, eds. (Wiley, New York, NY, 1986).
- D. H. Kelly, "Spatio-temporal frequency chracteristics of color-vision mechanisms," J. Opt. Soc. Am. 64(7), 983–990 (1974).
- M. J. Mayer, C. B. Y. Kim, A. Svingos, and A. Glucs, "Foveal flicker sensitivity in healthy aging eyes. I. Compensating for pupil variation," J. Opt. Soc. Am. A 5(12), 2201–2209 (1988).
- C. W. Tyler, "Two processes control variations in flicker sensitivity over the life span," J. Opt. Soc. Am. A 6(4), 481–490 (1989).
- W. H. Seiple, V. Greenstein, and R. Carr, "Losses of temporal modulation sensitivity in retinal degenerations," Br. J. Ophthalmol. 73(6), 440–447 (1989).
- 8. M. J. Mayer, S. J. Spiegler, B. Ward, A. Glucs, and C. B. Kim, "Foveal flicker sensitivity discriminates ARM-risk from healthy eyes," Invest. Ophthalmol. Vis. Sci. 33(11), 3143–3149 (1992).
- 9. M. J. Mayer, S. J. Spiegler, B. Ward, A. Glucs, and C. B. Kim, "Preliminary evaluation of flicker sensitivity as a predictive test for exudative age-related maculopathy," Invest. Ophthalmol. Vis. Sci. 33(11), 3150–3155 (1992).
- 10. U. T. Keesey, "Variables determining flicker sensitivity in small fields," J. Opt. Soc. Am. 60(3), 390-398 (1970).
- 11. A. Peters, "Structural changes that occur during normal aging of primate cerebral hemispheres," Neurosci. Biobehav. Rev. 26(7), 733–741 (2002).

- 12. C. W. Tyler, "Specific deficits of flicker sensitivity in glaucoma and ocular hypertension," Invest. Ophthalmol. Vis. Sci. 20(2), 204–212 (1981).
- K. Neelam, J. Nolan, U. Chakravarthy, and S. Beatty, "Psychophysical function in age-related maculopathy," Surv. Ophthalmol. 54(2), 167–210 (2009).
- M. J. Mayer, B. Ward, R. Klein, J. B. Talcott, R. F. Dougherty, and A. Glucs, "Flicker sensitivity and fundus appearance in pre-exudative age-related maculopathy," Invest. Ophthalmol. Vis. Sci. 35(3), 1138–1149 (1994).
- J. A. Phipps, T. M. Dang, A. J. Vingrys, and R. H. Guymer, "Flicker perimetry losses in age-related macular degeneration," Invest. Ophthalmol. Vis. Sci. 45(9), 3355–3360 (2004).
- C. W. Tyler, "Analysis of normal flicker sensitivity and its variability in the visuogram test," Invest. Ophthalmol. Vis. Sci. 32(9), 2552–2560 (1991).
- R. Granit, and P. Harper, "Comparative studies on the peripheral and central retina: II.Synaptic reaction in the eye," Am. J. Physiol. 95, 211–228 (1930).
- 18. E. S. Ferry, "Persistence of vision," Am. J. Sci. 44, 192-207 (1892).
- 19. T. C. Porter, "Contributions to the study of flicker, II," Proc. R. Soc. Lond. 70A, 31–329 (1902).
- C. W. Tyler, and R. D. Hamer, "Analysis of visual modulation sensitivity. IV. Validity of the Ferry-Porter law,"
 J. Opt. Soc. Am. A 7(4), 743–758 (1990).
- M. A. García-Pérez, and E. Peli, "Luminance artifacts of cathode-ray tube displays for vision research," Spat. Vis. 14(2), 201–215 (2001).
- A. J. Zele, and A. J. Vingrys, "Cathode-ray-tube monitor artefacts in neurophysiology," J. Neurosci. Methods 141(1), 1–7 (2005).
- M. Bach, T. Meigen, and H. Strasburger, "Raster-scan cathode-ray tubes for vision research--limits of resolution in space, time and intensity, and some solutions," Spat. Vis. 10(4), 403–414 (1997).
 A. B. Metha, A. J. Vingrys, and D. R. Badcock, "Calibration of a color monitor for visual psychophysics,"
- A. B. Metha, A. J. Vingrys, and D. R. Badcock, "Calibration of a color monitor for visual psychophysics," Behav. Res. Methods Instrum. Comput. 25, 371–383 (1993).
- C. W. Tyler, "Analysis of visual modulation sensitivity. II. Peripheral retina and the role of photoreceptor dimensions," J. Opt. Soc. Am. A 2(3), 393–398 (1985).
- B. R. Hammond, Jr., and B. R. Wooten, "CFF thresholds: relation to macular pigment optical density," Ophthalmic Physiol. Opt. 25(4), 315–319 (2005).
- 27. B. Winn, D. Whitaker, D. B. Elliott, and N. J. Phillips, "Factors affecting light-adapted pupil size in normal human subjects," Invest. Ophthalmol. Vis. Sci. **35**(3), 1132–1137 (1994).
- 28. The results for our age analysis were limited by the fact that we did not sample equally across ages (there are more young subjects) and six of our oldest subjects could not detect flicker at the highest frequency even at maximum contrast (hence, the age-reduction may be greater for the highest frequencies). It should also be noted that we used a different field size in the two locations which also could have contributed to the differences in age-loss we report.
- D. H. Kelly, "Visual responses to time-dependent stimuli. I. Amplitude sensitivity measurements," J. Opt. Soc. Am. A 51(4), 422–429 (1961).
- J. M. Rovamo, and A. Raninen, "Critical flicker frequency and M-scaling of stimulus size and retinal illuminance," Vision Res. 24(10), 1127–1131 (1984).
- J. R. Jarvis, N. B. Prescott, and C. M. Wathes, "A mechanistic inter-species comparison of flicker sensitivity," Vision Res. 43(16), 1723–1734 (2003).
- P. J. B. Barten, Contrast sensitivity of the human eye and its effects on image quality. (SPIE Optical Engineering Press, Washington, 1999).
- 33. J. M. Rovamo, A. Raninen, and K. Donner, "The effects of temporal noise and retinal illuminance on foveal flicker sensitivity," Vision Res. 39(3), 533–550 (1999).
- 34. J. A. Joseph, B. Shukitt-Hale, N. A. Denisova, D. Bielinski, A. Martin, J. J. McEwen, and P. C. Bickford, "Reversals of age-related declines in neuronal signal transduction, cognitive, and motor behavioral deficits with blueberry, spinach, or strawberry dietary supplementation," J. Neurosci. 19(18), 8114–8121 (1999).

1. Introduction

Spatial vision is often characterized by measuring sensitivity to contrast as a function of spatial frequency (the spatial contrast sensitivity function, SCSF, i.e., sensitivity vs. spatial frequency). In a similar way, temporal vision can be characterized by measuring sensitivity to contrast (i.e., modulation depth) as a function of time (the temporal contrast sensitivity function, TCSF, i.e., luminance sensitivity vs. temporal frequency) [1]. To obtain such a function, one must present stimuli that vary sinusoidally over time (analogous to grating stimuli that vary sinusoidally over space). The visibility of these temporally modulated stimuli is dependent both upon the rate of presentation and the depth of modulation (the difference between the maximum and minimum luminance of stimuli presented in sequence). Also like the SCSF, temporal sensitivity decreases sharply at high frequencies and less sharply at low frequencies for most stimulus conditions. Early interpretations of this curve implicitly

assumed a single, unitary process. The shape was modeled as reflecting serial filters with low and high pass characteristics [2]. Later, more complex models (for a review see Watson, 1986 [3]), tended to interpret the TCSF, not as a unitary process, but, rather, as reflecting some number of more narrowly defined parallel sub-channels. Hence, the widely held view that the TCSF is an envelope (analogous to the luminosity function, which is an envelope of the three cone curves) of more narrowly-defined channels each type being based on a combination of low-and-high pass filters and noise. There is still debate about the number and properties of the sub-channels that form the TCSF. It is also unlikely that the temporal channels operate in isolation. For example, there are clear interactions between spatial, temporal, and even chromatic channels (e.g., Kelly, 1974 [4]): lower spatial frequency channels, for instance, appear to be more responsive to higher temporal frequencies than higher spatial frequency channels. What is clear is that the TCSF is a dynamic measure that appears to be strongly influenced by age [5,6] and degenerative disease [7–9] as well as stimulus features (e.g., size of field, the presence of surrounds, etc.) [10].

Visual processing, like other aspects of neural processing, undergoes significant slowing with age and at various stages of disease processes. This general slowing is due to the numerous anatomical/physiological changes that occur with age and disease. For example, the conduction rate of neuronal axons is reduced, in part, due to a general age-related breakdown of myelin [11]. Tyler (1981) [12] has shown that temporal-based measurements are particularly sensitive indicators of optic nerve damage in patients with open angle glaucoma (a condition that is difficult to diagnose using standard perimetry).

Given that visual processing deficits are seen with advancing age and during disease processes, and that the TCSF is a sensitive assay of visual processing ability, changes in the TCSF may be expected to correspond to, and perhaps predict, these deficits. A large body of data is consistent with this interpretation (recently reviewed by Neelam et al., 2009) [13]. The precise nature of changes in the TCSF is often prognostic. For example, evidence suggests that the high frequency channel of the TCSF is most strongly impacted by normal aging and disease [14]. Losses at low-to-moderate frequencies have been found to be correlated with early clinical changes such as drusen and/or RPE atrophy [14] and appear to predict AMD development with high accuracy. Phipps et al. (2004) [15] recently reported, for instance, that 84% of their subjects with early AMD had flicker abnormalities in their central foveal region. As noted by Tyler (1991) [16], the full TCSF is a valuable early diagnostic particularly since it may assess a potentially reversible component of an individual's overall susceptibility to visual disease.

Many factors must be considered, however, to meaningfully interpret the full TCSF. TCSF, like any visual function, is determined by several stimulus features including size (e.g., as described for CFF by the Granit-Harper law [17]), luminance (e.g., as described for CFF by the Ferry-Porter law [18-20]), and retinal location. As with many visual tasks, it is often difficult or impossible to separate these variables (e.g., stimulus size and retinal location are inextricably linked). Precise control of these factors can also be challenging. For example, 100% modulation is difficult when using a cathode-ray tube (CRT) display that utilizes phosphors without sharp temporal cutoffs [21,22]. Even modern CRTs have issues with limited spectral options (e.g., red, green, and blue guns often with about a 100 nm bandpass), calibration difficulties, phosphor decay rates, etc (for a review of the general limitations of modern CRTs see Bach et al., 1997) [23]. Refresh rates, for instance, vary widely depending on user settings and video card type. Sensitivity to flicker is strongly related to luminance (described by the Ferry-Porter law) [18-20] and luminance inhomogeneities are commonly found in CRT displays [24]. CRTs are also becoming increasing difficult to acquire because they are being largely replaced by liquid crystal displays (LDDs) which have even slower response times and can be strongly affected by viewing angles. Since TCSF measurement is critically dependent on these very features that are hardest to calibrate and standardize across monitors, interpretation is frequently difficult. At a minimum, any method for measuring temporal vision should enable detection of the better known characteristics of the system, such as the band-pass shape of the TCSF and its previously-established changes with age and disease.

Such considerations guided our selection of the stimulus characteristics we used when devising a practical method for measuring the TCSF. For example, we chose a one-degree target in the fovea (a size that is often used when assessing foveal function) but a two-degree stimulus in the parafovea for ease of viewing and to roughly correct for the cortical magnification factor [25]. We used a surround as opposed to a background since a background obviously affects modulation depth. We imposed a small gap between the test target and surround because past research [10] has shown this gap is necessary to achieve a band-pass shape to the curve.

This paper then had two major goals. The first was simply to demonstrate proof of concept. The second was to assess changes in the TCSF with age and retinal location. To address the first goal, we describe a simplified tabletop device for measuring the full TCSF. The device allows for specific control of the test stimulus, small fields for testing purely central foveal function (flicker sensitivity changes quickly across the central retina), and fixation points that allow parafoveal regions to be evaluated. To address the second goal, we measured the complete TCSF in the fovea and parafovea in a sample of healthy subjects with a wide range of ages.

2. Methods

2.1 Subjects

A total of 70 subjects, ranging in age from 15 to 84 years (mean = 33 years, SD = 18.8 years) was recruited from the University of Georgia and from the Athens-Clarke Co. community. Approximately 70% of the sample was female, and the majority of subjects (93%) were Caucasian. All subjects reported good ocular health and had visual acuity correctable to at least 20/40. The study was reviewed and approved by the Institutional Review Board at the University of Georgia and the tenets of the Declaration of Helsinki were adhered to at all times.

2.2 Assessment of temporal modulation sensitivity

2.2.1 Procedure

All measurements were made in the right eye. The stimulus consisted of a one-degree, 660 nm target on a 5.5-degree 660 nm surround, used to favor the long-wave cone system (with small contributions from the mid-wave system) (under our conditions) and to minimize absorption of the stimulus by the anterior media and macular pigment. To obtain the foveal TCSF, subjects were asked to fixate a point in the center of a circular target diagrammed in Fig. 1.

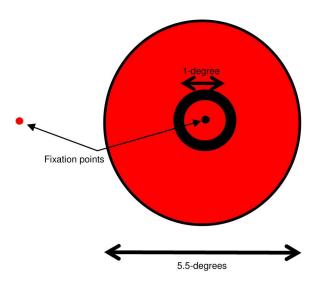


Fig. 1. A schematic of the stimulus used to measure the central TCSF.

To obtain a parafoveal TCSF, the fixation point was placed at 7-degrees nasally. An ascending method of adjustment was used to obtain thresholds, beginning at 0% modulation. Subjects were instructed to turn a rotary knob that controlled the depth of modulation until the appearance of flicker was just-noticeable. The following frequencies were tested in both the center and the parafovea for each subject: 2.5, 4, 6.3, 10, 12.6, 15.8, 20, 25, 32 Hz. Frequencies were presented to subjects in a random order. Five trials were assessed for each subject on each frequency in both center and periphery. Contrast values were derived based on the Michelson ratio.

Most subjects were assessed in one experimental session. For a subset of subjects (n=20), however, we measured the TCSF over two sessions to assess the reliability of the measurements. These subjects were experienced psychophysical observers and were only tested for the center condition and completed 10 trials per frequency. The test-retest correlations ranged from 0.80 to 0.97 and were not systematically related to frequency. This level of reliability is consistent with that obtained for CFF values (a Cronbach's alpha of 0.95) by Hammond and Wooten (2005) [26].

2.2.2 Stimulus and Apparatus

The entire target-surround arrangement is diagrammed in Fig. 1. The space between the target and surround was four arc-minutes and served the purpose of reducing small fixation errors while making it simpler to align than a contiguous center-surround configuration. As originally shown by Keesey (1970) [10], a center surround with contiguous edges (no gap) also yields a curve without the expected low-frequency fall off.

The target and surround was presented in free view with an average luminance of 25 cd/m². A schematic of the system is provided in Fig. 2.

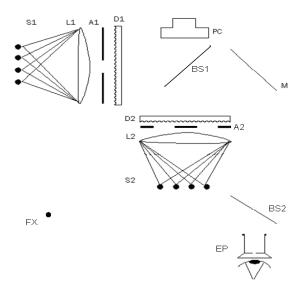


Fig. 2. A schematic of the optical system used to measure the TCSF. A1-A2, apertures; BS1-BS2, cover slip beam splitters; PC, photocell; M, mirror, D1-D2, diffusers; S1, S2, LED light sources; L1-L2, planoconvex lenses; FX, fixation point light source; EP, eye piece with the artificial pupil.

The light for the target (S1) and surround (S2) was formed by four LEDs (Nichia Corp., Mountville, PA) with peak energy at 660 nm and 20 nm half-widths. The lenses of these LEDs were embedded in epoxy resin that has the same refractive characteristics as the material encasing the LED thereby allowing the LED lens to be optically removed and direct view of the active element of the LED (creating a more uniform area of illumination across the LED heads). The LEDs for the target channel were electronically driven by a waveform generator (TTi TG-330 Function Generator; Thurlby-thander Instruments LTD, Cambridge, UK) that allowed both sine-and-square wave presentations (the latter can be used to obtain a cutoff value for the TCS curves; CFF thresholds). The LEDs are driven by a high frequency train of one usec wide constant current pulses. This is modulated by Pulse Repetition Frequency (PRF) and is not the usual method of LED brightness control using Pulse Width Modulation (PWM). In our application, the PRF may range as high as 300,000 Hz. (the minimum frequency we use is at least one order of magnitude above the CFF as measured under our conditions). A voltage controlled oscillator circuit was used to set the PRF. This circuit responds in a linear fashion to an applied voltage.

The function generator produced a modulation voltage signal which varied from 1 to 1000 mvolts which, with suitable rescaling, could be translated to read directly as modulation depth (0-100%). Subjects could directly change modulation depth at any frequency using a control knob with a logarithmic taper potentiometer to allow for small changes in percent modulation. Light from S1 and S2 was collimated with planoconvex lenses (L1 and L2, respectively) before passing through polycarbonate diffusers (D1 and D2, respectively; high-efficiency holographic type, Physical Optics Corp., Torrance, CA). The size of the test stimulus was determined by a circular aperture, A1, which yields a one-degree stimulus for the foveal condition and a two degree stimulus for the parafoveal condition. The configuration of the surround was determined by an aperture, A2. Light from both channels was combined with a cover slip beam-splitter (BS1) that channeled part of each beam to a photocell (PC). This photocell (Model Pin-10; UDT Sensors, Hawthorne, CA) was used for daily calibration of the target and surround. The combined field was reflected by a right angle first-surface mirror (M) to the eyepiece. Another beam splitter (BS2), made from an oversized coverslip, brought in the small (5 arc-min) red fixation light used for the parafoveal condition. The entire optical

system was enclosed in a black box (18.5X8-inch) on a tilt-base that was used to adjust for differences in subject height. Subjects looked into the apparatus through an eye piece (EP) containing the 3-mm artificial pupil. The artificial pupil was used to control variation in the luminance of the stimulus caused by changes in the size of the natural pupil. The natural pupil does not typically get smaller than 3 mm when using our stimulus conditions. For example, Winn et al. (1994) [27] measured the pupil size of 91 subjects (ages 17-83 years) while viewing a 10-degree circular disc varying in luminance (9-4400 cd/m²). As expected, pupil size decreased, on average, as luminance increased. At 9 cd/m², no subjects were under 3 mm. At 44 cd/m², only one subject (an 82 year old) dropped below 3 mm. Therefore, at our luminance level (25 cd/m²), it was unlikely that any subject had a pupil smaller than 3 mm.

3. Results

Figure 3 shows the average foveal and parafoveal data. These data reflect the TCSF for each subject as assessed during one experimental session. The curves shown in Fig. 3 peak in the mid-frequency range (approximately 8 Hz) and are generally consistent with the TCSF obtained under similar conditions [10]. One obvious feature of the curves is their similar sensitivity at higher frequencies and disparity at middle and lower frequencies (~0.45 log units). Another important difference between the foveal and parafoveal curves is how they relate to age.

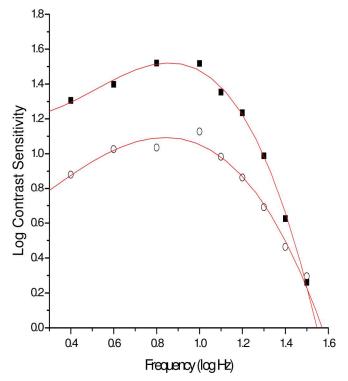


Fig. 3. The average TCSF (n=70) as measured with a foveal target (one-degree diameter, centrally fixated) and a parafoveal target (two-degree diameter, seven degrees, temporal retina). The associated standard deviation values for the fovea (from high to low frequency) were 0.23, 0.25, 0.28, 0.28, 0.26, 0.34, 0.35, 0.27, and 0.22. The associated standard deviation values for the parafovea (from high to low frequency) were 0.38, 0.21, 0.24, 0.22, 0.23, 0.19, 0.22, 0.19, and 0.19. The smooth lines are 3rd order polynomial fits.

These results are shown in Figs. 4–7. As can be seen in the figures, individual subjects vary quite widely. For example, the young subjects (18-22 yrs, who were most heavily sampled) varied by about 0.8 log units. Similar to past studies, we also found age-related

declines. See Figs. 4 and 5. The magnitude and pattern of the decline, however, was specific to retinal location [28]. When testing the fovea, significant (p<0.025 or lower) losses were found at all frequencies but the largest decline was found at the highest frequency. See Fig. 4. The magnitude of the age-related losses at the lower frequencies (see Fig. 5) was about half of what was seen at the higher frequencies. The highest rate of age decline in the parafovea was more near the peak of the function (e.g., at 10 Hz, Y = 0.26 – 0.003X, r = -0.38, p<0.001). See Fig. 6. In fact, the highest rate of decline for the parafovea was for the middle frequencies (~6-20 Hz, all significant at p<0.05) and was attenuated at the low-and- highest frequencies (see Figs. 6 and 7).

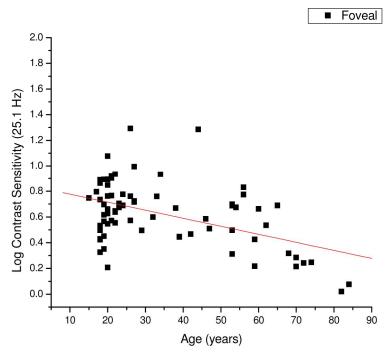


Fig. 4. The relation between age and TCS as measured in the fovea at 25. 1 Hz (Y = 0.84 - 0.006X, r = -0.48, p<0.0001).

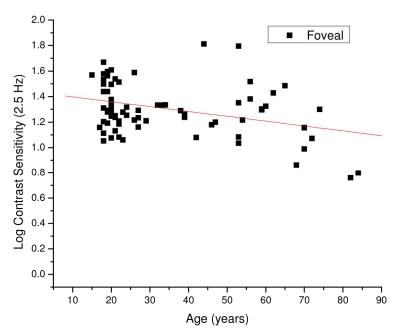


Fig. 5. The relation between age and TCS as measured in the fovea at 2.5 Hz (Y = 1.44 - 0.004X, r = -0.33, p <0.01).

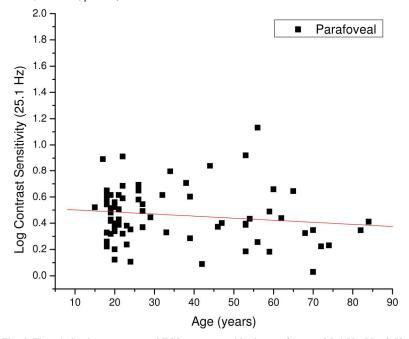


Fig. 6. The relation between age and TCS as measured in the parafovea at 25. 1 Hz (Y = 0.52 - 0.002X, r = -0.15).

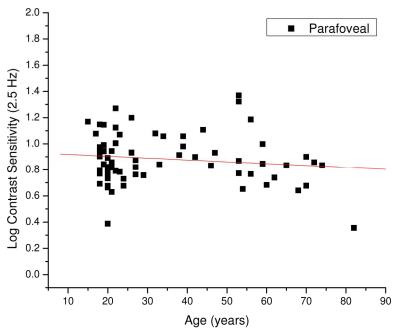


Fig. 7. The relation between age and TCS as measured in the parafovea at 2.5 Hz (Y = 0.94 - 0.001X, r = -0.15).

4. Discussion

As can be seen in Fig. 3, our simplified device provides temporal functions that are consistent with those that have commonly been reported that have used similar conditions [10]. For example, most curves tend to peak around 8-10 Hz and drop off gradually at low frequencies and sharply at high frequencies. Other shapes, however, are found that relate to specific stimulus conditions. For example, the expected fall-off at the low-frequency end of the curve is not obtained when using a contiguous surround [10]. Also, for example, the low-frequency decline is often not found when low luminance levels are used [29]. Another important stimulus condition, as shown in Fig. 3, is the change in shape that occurs when testing different regions in the central retina. Such shape differences are potentially a function of two inextricable factors, size and retinal location (retinal location varies as one varies size). Of course, with increasing eccentricity, the retina becomes increasingly homogeneous but the anatomy changes rapidly in the center. Hence, although we used stimuli that roughly equated the two retinal areas with respect to cortical magnification [25], the shape and overall sensitivity of our foveal and parafoveal curves was quite different. This difference was most exaggerated at the lowest frequencies. This result is consistent with past data on CFF thresholds that has shown that when stimuli are equated for retinal illuminance and scaled according to the cortical magnification, the CFF tends to be independent of retinal location [30]. Presumably the differences in shape at low frequencies reflect a difference in the relative weighting factors between the subchannels specific to the two sites and/or with respect to fields of different sizes. If this interpretation is true, then temporal stimuli can be equated across the central retina but change has to be specific to frequency.

The method described in this paper describes an easy and reliable method of obtaining TCSFs that is similar to those reported in previous studies. This is valuable because, with proper models, it can further our understanding of visual aging and disease. Changes in the shape of the curve and overall sensitivity for a given group (compared to normative values), for instance, lend insight into the nature of the deficits driving their condition. This requires a fairly complete understanding of the underlying mechanisms that drive the TCSF. A number

of specific and plausible models have been developed that allow a fuller interpretation of the entire TCSF (i.e., allows one to relate shape changes to the underlying biology). A common approach is to treat the eye as a linear system whereby input is the waveform of the stimulus and output is an internal, temporal response that determines the psychophysical response. One can then define an impulse response to a very brief stimulus pulse. From the impulse response, the visibility of any stimulus waveform can be evaluated. Watson (1986) [3] has described a model that allows the derivation of the impulse response from any TCSF. This procedure can be used to characterize the underlying changes in sensitivity and timing implied by differences in the TCSF.

Although the derivation of the impulse response function provides a succinct way to characterize potential response slowing that alters the TCSF, a more analytical approach is needed to define which underlying processes account for the observed changes. Jarvis et al. (2003) [31] reviewed the two most prominent models of flicker sensitivity: Barten, 1999; and Rovamo et al. 1999 [32,33]. Both models do an excellent job of providing a quantitative account of the human TCSF and, with altered free parameters, those of other species (goldfish, chicken, tree shrew, ground squirrel, cat, and pigeon). Barten's model is slightly superior in that the low-frequency decline is clearly better fit than the model of Rovamo. If Barten's model is used as a way of relating changes in the TCSF to the underlying biological mechanisms, the following terms can be derived:

t₁, which relates to photoreceptor response time;

t₂, which relates to the response time of the inhibitory neural stage;

N_{it}, the neural noise.

Roughly speaking, lower values for t₁ would appear as higher-frequency loss, lower values for t₂ would be reflected in relative decreases in sensitivity at low temporal frequencies, and increases in N_{it} would result in lower sensitivity at all frequencies (and an increase in variability). Applying this model to our own results would, for example, lead to the following interpretations. There were age-related reductions in sensitivity at all frequencies when testing at both the foveal and parafoveal sites. The magnitude of the loss was greatest when testing the highest frequencies in the fovea (Fig. 4). This pattern was quite different in the parafovea where the greatest losses were at and around the peak of the curve (6-20 Hz) and were attenuated at the low-and-high frequencies (Figs. 6 and 7). The fact that there were declines at all frequencies at both sites, suggests that neural noise increases with age. A slowing of photoreceptor response times (t1) with age appears to be most evident in the fovea (high frequency loss was double that of low frequency loss). As shown by the averaged values in Fig. 3, the timing constant, t2, appears to be most affected by retinal site: photoreceptor response times are nearly equal (t1) but there are fairly large average differences at the lowest frequencies. This latter effect (t2) implies differences in postreceptoral mechanisms (i.e., inhibition is crisper in the fovea). One difficulty, as noted earlier, when comparing the fovea and parafovea is that we used different field sizes (1 and 2 degrees, respectively). As noted by Barten, field size does change both time constants. If the differences in our results are linked to field size, however, it is clear that field size influenced t2 much more than t1.

Ultimately, proper interpretation of the TCSF would lead to better understanding and prediction of visual deficits. This would allow interventions that might affect these declines. Static functions, especially in the elderly or in patients with retinal disease, are probably much less likely to change as a result of interventions. For example, if scotopic sensitivity is primarily mediated by rods, no intervention can replace the millions of rods lost over a lifespan. In contrast, dynamic functions, such as temporal processing, might be more amenable to improvement. Reversals in age-related declines in neuronal signal transduction,

for instance, have been found with dietary supplementation of carotenoid-rich foods such as spinach in rat models [34].

Acknowledgements

This project was partially funded by Cognis Gmbh.