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Measurements of Human Sensitivity to Comb-filtered Spectra

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Using a novel stimulator that incorporates a liquid crystal display, the spectral modulation sensitivity function of the colour vision system was derived by measuring discrimination thresholds for comb-filtered spectra. This function shows a peak of sensitivity at 0.97 c/300 nm with a plateau that extends to 1.67 c/300 nm. Extrapolation of the curve gives an estimated high-frequency cut-off at 5 c/300 nm. The thresholds are also transformed to the CIE (1931) diagram and the elliptical isosensitivity contours thus obtained are compared with the classical discrimination ellipse of MacAdam for the corresponding region of colour space. Copyright © 1996 Elsevier Science Ltd.

Colour vision Comb-filtered spectra Psychophysics Spectral modulation sensitivity function

INTRODUCTION

More than 10 years ago H. Barlow (1982) suggested that the concept of Fourier transforms might be borrowed from spatial vision and applied to colour vision. He called for measurements of the sensitivity of the colour system using comb-filtered spectra,§ that is, sinusoidal modulations of radiant energy over the full visible spectrum. Sensitivity measurements for comb-filtered spectra for a range of frequencies will give an indirect estimate of the modulation transfer function (MTF) of the colour system in the same way that the contrast sensitivity function (CSF) determined by Campbell and Robson (1968) estimates the degree of demodulation imposed by the visual system on different spatial frequencies.

In applying Fourier analysis to colour vision, Barlow's original motive was to ask whether the dimensionality of the system (the number of types of receptors) was constrained by the low-pass filtering imposed by the spectral sensitivity curves of the cones. Subsequently, Benzschawel *et al.* (1986) and recently Romero *et al.* (1995a) showed that comb-filtered spectra could be used to distinguish different models of post-receptoral opponent processes. However, despite the potential interest of the frequency view of colour vision, it has not proved straightforward to develop an experimental set-up that generates sinusoidally modulated spectra. A first attempt to measure sensitivity to comb-filtered spectra was reported by Barlow *et al.* (1983), using a Michelson interferometer. This device was able to produce sinusoidal modulations, but did not allow frequency and phase to be controlled independently and did not allow frequency to be held constant over the entire spectrum. Bonnardel *et al.* (1991) developed another device based on a linear interference wedge and a cross-polarization filter system which avoided the previous limitations but produced square-wave modulations.

In the present experiment, we take advantage of liquid crystal display (LCD) technology to generate comb-filtered spectra that can be readily varied in frequency, phase and modulation depth. LCD technology offers a modern method of light modulation, but our device is similar in its principle to the early template colorimeters in which a mask was placed in the plane of the spectrum in order to obtain desired spectral profiles (Ives, 1921; Winch & Machin, 1940). Such instruments were primarily used for colour measurements, but more recently, colour discrimination experiments were carried out with the Spectral Colour Integrator where, according to the same principle, colour stimuli were produced by

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§Two considerations justify the term "comb-filtered spectra" adopted by H. Barlow. First, from an historical point of view, the term directly recalls an experiment of Newton where a comb was used to intercept some wavelength intervals while others were transmitted (Newton, 1704, Optick). His system served to demonstrate that the sensation of white was also elicited by a successive stimulation of coloured lights as long as the succession was fast enough. Second, from comb-filtered spectra, Barlow derived "comb-frequency" which is a convenient way to avoid any confusion with frequency of the electromagnetic radiations. In the present context although an actual comb would provide rectangular modulations the term is used to refer to sinusoidal spectral energy modulations.

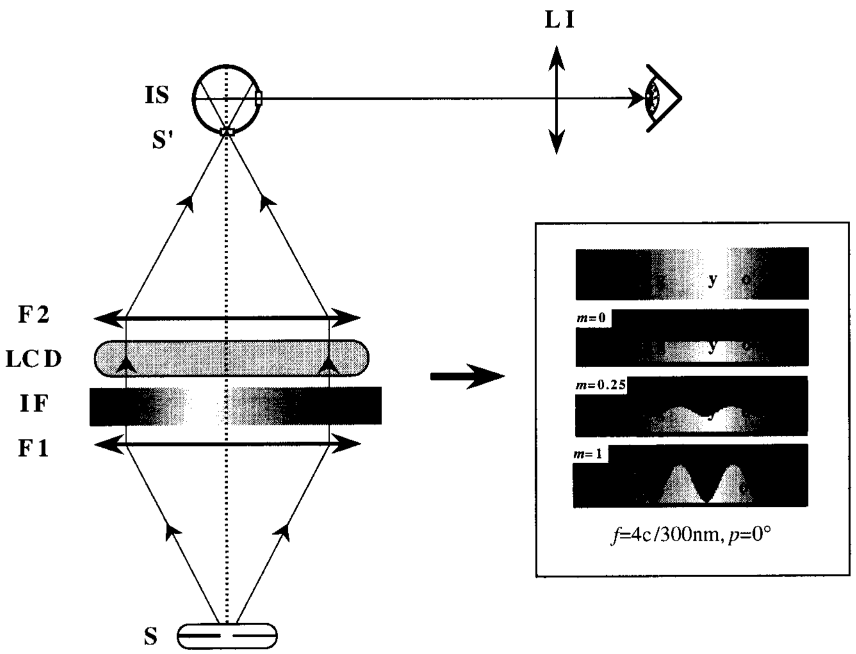

FIGURE 1. Experimental device. The light from the source (S) located at the focal point of a Fresnel lens (F1) is focused by a second lens (F2) to form a real image S′ of S at the aperture of the integrating sphere (IS). The LCD is mounted in the collimated beam, directly after the interference wedge (IF) which gives a continuous linear spectrum from 400 to 700 nm. The output of the integrating sphere, viewed through a lens (L1) in Maxwellian view, produces an homogeneous field of 2 deg diameter. The figure to the right shows examples of sinusoidal spectral modulations achieved by applying electronic masks to the spectrum (symbolized by the colour initials). The masks presented here have $f = 4$ c and $p = 0$ deg with three different levels of modulation. When the spectrum is unmodulated ($m = 0$), the spot is perceived as achromatic. When $m \neq 0$ the spot appears coloured and for a constant level of modulation its hue depends on the combination of frequency and phase, that is, the number and the position of the spectral bands that are transmitted.

cardboard masks applied to a large spectrum (Holtsmark & Valberg, 1969).

The threshold measurements presented here were performed for a large gamut of frequencies combined with a full range of phases, which allowed us to derive a spectral modulation sensitivity function (SMSF) for a normal trichromat observer. A particular advantage of comb-filtered spectra is that the chromaticity coordinates for a given frequency with a constant level of modulation describe an ellipse in the CIE (1931) diagram, when phase varies from 0 to 360 deg (Buchsbaum & Gottschalk, 1984). This convenient property allowed us to derive for the different frequencies a set of discrimination ellipses, which are compared to the classical MacAdam ellipse (MacAdam, 1943) for the corresponding region of chromaticity space.

METHODS

Experimental device

The luminous source is a short-arc Xenon Lamp (Osram XBO, 150 W), located at the focal point of a Fresnel lens (157 mm × 157 mm). The collimated beam illuminates an interference wedge, which yields a continuous spectrum (115 mm × 24 mm) that is linear in wavelength units. The rays are then collected by a second identical Fresnel lens, which forms a real image of the source at the aperture of an integrating sphere (50.8 mm in diameter). The output of the sphere, viewed through a lens in Maxwellian view, produces an homogeneous field of 2 deg diameter (Fig. 1). A LCD is mounted in the collimated beam, directly after the interference wedge. The LCD screen currently used is one commercially available as a peripheral for displaying computer-generated images with an overhead projector (Sayett Datashow 480). It is of the double super twisted nematic type and gives a contrast ratio of 15:1. The extinction ratio of the LCD screen (i.e. the transmission ratio of black and white pixels) is wavelength-dependent, showing the highest residual transmission in the short-wavelengths and the lowest in the 450–550 nm interval with a transmission of an intermediate level in the long-wavelengths. These characteristics slightly distort our empirical modulations measured with a spectroradiometer. However, this effect is small, as is indicated by the quality of fit found between the relative sinusoidal spectral distribution given by the ratio $E(\lambda)/E_0(\lambda)$ and the best-fitting sine function.*

The screen (211 mm × 158 mm) is a passive-matrix addressing system of 640 × 480 pixels on which sinusoi-

*For each relative sinusoidal spectral modulation at the threshold level, the parameters were determined by calculating the best fitting sinusoidal function over 400–696 nm. The curve fitting was done with Kaleidagraph–Macintosh software. For the overall 24 sinusoidal fittings the mean correlation is 0.98.

dal profiles are drawn in a rectangle whose size fits that of the continuous spectrum. The software application has been developed on an Apple Macintosh LC computer to display sinusoidal profiles of any frequency and phase. The level of modulation is set by the number of pixels corresponding to the width of the interference wedge at each wavelength (see inset, Fig. 1).

Thus, the LCD acts as an electronic mask imposing sinusoidal modulations over the spectral power distribution of the light source. The resulting illumination $E(\lambda)$ is expressed by the following formula:

$$E(\lambda) = E_0(\lambda)[1 + m\sin(fp(\lambda) + p_0)] \quad (1)$$

where $E_0(\lambda)$ is the spectral power distribution of the source measured in the absence of modulation; m is the level of modulation which varies from 0 to 1; f is the frequency expressed in cycles per 300 nm and denoted c; p_0 the starting phase which, by convention, is equal to 0 deg when for a maximal modulation the sinusoid increases from the mean level of modulation at the 400 nm end. $p(\lambda) = (1.2\lambda–480)$ scales the spectral interval in a 0–360 deg interval.

In the case of comb-filtered spectra, two interesting questions arise that do not find an obvious analogy in the case of spatial vision. The first is whether a CSF for colour vision should properly be based on modulations that are constant in wavelength units, or whether frequency or some other metric (such as log frequency) offers an appropriate basis. In this first study our choice is mainly dictated by practical considerations: our interference wedge is linear in wavelength, and the CIE (1931) chose this unit to describe spectral radiant power distributions. A second question concerns the distribution of the unmodulated spectrum. Should it, say, be flat in energy units or in quantum units or in luminance units? The last is certainly unrealistic if the results are to apply to naturalistic illuminants or visual signals. In the absence of any obvious theoretical consideration and in view of the difficulty of obtaining a flat equal-energy spectrum, we use here the spectral power distribution of the Xenon lamp after transmission through IR and UV filters.

Light measurements

Calibrations of the spectral power distribution and the chromaticity coordinates of the stimuli were made with a spectroradiometer (model PR-650, Photo Research). The manufacturer's calibration of the spectroradiometer was checked at the Laboratoire de Physique Appliquée, Muséum d'Histoire Naturelle (Paris) against a secondary luminance standard (Pefferkorn, 1993).

Since light levels were too low to measure the spectral distributions at the position of the subject's pupil, these calibrations were made at the extremity of an optic fibre (Oriel, liquid fibre, 8 mm in diameter), which fitted into the output of the integrating sphere. Before and after each experimental session the chromaticity coordinates for the unmodulated spectrum were recorded. For a total of 130 experimental sessions, the mean difference between these two chromaticity coordinates expressed as distance in the CIE (1931) diagram is 0.0029. This small variability testifies to the stability of the light source for the duration of the testing session (1.5 hr). However, a slight drift in the chromaticity coordinates over the period of the experiment was noticed. For 130 measurements the average chromaticity coordinates of the unmodulated spectrum are $x_0 = 0.284$, $y_0 = 0.372$ with SDs of 0.00675 and 0.0085. This variability displaced the locus of the unmodulated spectrum to noticeably different positions of the chromaticity diagram. To estimate the effects of this displacement on the sensitivity of the observer, the theoretical MacAdam ellipses (MacAdam, 1943) were computed for the two extreme colour centres recorded. The two ellipses show a size difference of only 4%, which is insignificant for our experiment.

Psychophysical procedure

The observer, her head resting on a chin-rest in dark-adapted conditions, saw the output of the integrating sphere in Maxwellian view as a homogeneous spot. The absolute luminance of the target was estimated at 5–6 cd/m^2 by visually matching it to a white spot of similar diameter viewed directly and not in Maxwellian view.

In a three-alternative temporal forced choice, the reference (unmodulated spectrum) appeared twice and the test (modulated spectrum) once in the three temporal windows (1 sec each) in a random fashion. The task was simply to indicate which stimulus differed from the other two by pressing one of the three keys. Between stimulus presentations the LCD was in its off state, giving a luminance level below 1 cd/m^2.

In order to ensure that the observer did not use brightness as a cue, the program introduced luminance variations by applying patterns to the electronic mask in a random fashion. Luminance variations between the three individual presentations of a trial were of the order of 25% for all frequencies except for 0.44 and 0.7 c for which they were double.

The threshold modulation difference between the test and the reference was determined by an adaptive staircase procedure (Cornsweet, 1962). Twelve frequencies (from 0.44 to 3.96 c) combined with the full range of phases (from 0 to 330 deg, in 30 deg steps) provided a total of 144 combinations of frequency and phase. Six threshold determinations were carried out for all frequencies except for 0.44–0.7 c where only five measurements were made after all the other data had been gathered.

The observer (VB) is a female with a normal colour vision according to a battery of clinical tests (Ishihara, Farnsworth-Munsell 100-Hue, Nagel anomaloscope).

RESULTS AND DISCUSSION

Spectral modulation sensitivity measurements

As has already been noted for the case of square-wave modulations (Bonnardel & Varela, 1991), if sensitivity is plotted against frequency for constant phase, the curves display several local minima and maxima. The bumpy profiles arise from a systematic change of direction in the

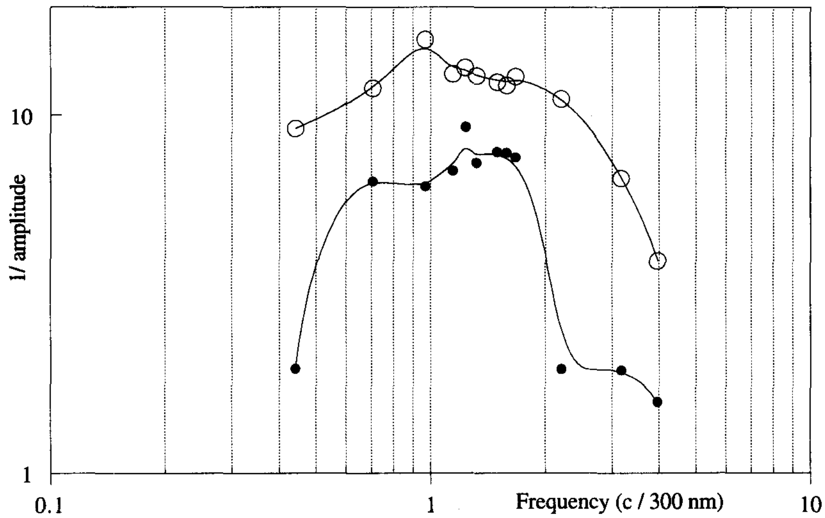

FIGURE 2. Spectral modulation sensitivity function. The parameters of the relative spectral sinusoidal modulations measured at the threshold level (E_t/E_0) were estimated by a fitting procedure. The reciprocal of the estimated amplitude is plotted against the frequency. The upper curve describes the sensitivity to optimal phases and corresponds to the SMSF whereas the lower curve corresponds to the sensitivity to pessimal phases. The SMSF peaks at 0.97 c and the lower curve at 1.23 c. Both curves display a maximum of sensitivity for the medium-range frequencies. The phase dependence of the colour system can be appreciated from the difference between the two curves.

CIE (1931) diagram for a given phase when frequency is varied, as illustrated for 0 deg phase in Fig. 4. Similarly, the sensitivity of the chromatic system shows a large dependency on phase, as can be seen in the jagged curves obtained by Barlow *et al.* (1983), whose interferometer produced phase changes concomitantly with frequency variations.

Because our intention was to estimate the MTF of the chromatic system, we choose to represent the upper limit of sensitivity, that is, for each frequency we plot the measurement for the optimal phase only. We also derive a similar curve describing the lower limit, which corresponds to the sensitivity measured at the least favourable or "pessimal" phase.*

Spectral modulation sensitivity function (SMSF). For each of 24 combinations of frequency and phase, we measured the spectral power distribution of the modulated spectrum at the threshold level, $E_t(\lambda)$, and of the corresponding unmodulated spectrum, $E_0(\lambda)$. The relative sinusoidal spectral modulation is given by $E_t(\lambda)/E_0(\lambda)$. A fitting procedure was then used to estimate the parameters of the best-fitting sinusoid and the reciprocal of the amplitude was plotted as a function of frequency (Fig. 2).

The upper curve, i.e. the SMSF peaks at 0.97 c with a shoulder at 1.67 c and decreases on either side of this interval. The high-frequency cut-off, estimated by extrapolating the curve to $y = 1$, is five cycles. At the lower frequencies the fall in sensitivity is less steep than at the higher frequencies. Because the threshold measurements at 0.44 and 0.7 c were performed after all the other data had been gathered, a practice effect may have led to overestimation of the sensitivity at these two frequencies.

Compared to the previous curve obtained with square-wave modulations for the same observer [see Fig. 5 in Bonnardel & Varela (1991)], the SMSF presented here shows a general improvement of sensitivity, owing to the method used (three-alternative forced choice vs adjustment). In the middle range of frequencies, the sensitivity curve for square-wave modulations displayed two clear peaks (0.8 and 1.8 c) which are not apparent in the SMSF. This last discrepancy was not expected and may need further experimental investigation.

With a peak at 1.23 c and a decrease below 0.7 c and beyond 1.67 c, the lower curve of Fig. 2 displays a clear band-pass profile. The residual sensitivity for the lowest frequency allows us to estimate a low-frequency cut-off near 0.4 c. The difference between the optimal and pessimal curves indicates the phase dependence of the colour system. The shift of phase necessary to switch from maximal to minimal sensitivity depends on frequency but always lies in the 60–120 deg interval. It is worth noting that a shift of 180 deg produces a colour stimulus of a complementary wavelength for which a comparable sensitivity can be assumed, as shown in discrimination threshold measurements for complementary colours performed by Holtsmark and Valberg (1969) with the Spectral Colour Integrator.

Remark on the spectral profile of stimuli included in 0.97–1.67 c interval. Profiles of the relative spectral modulations for the 0.97–1.67 c interval corresponding to optimal and pessimal phases are plotted on two different graphs (Fig. 3, right) and, within each category, it can be seen that the seven different spectral power distributions show clear similarities. The optimal spectral profiles display three lobes approximately centred on 420–430,

*This neologism is borrowed from Weale (1951).

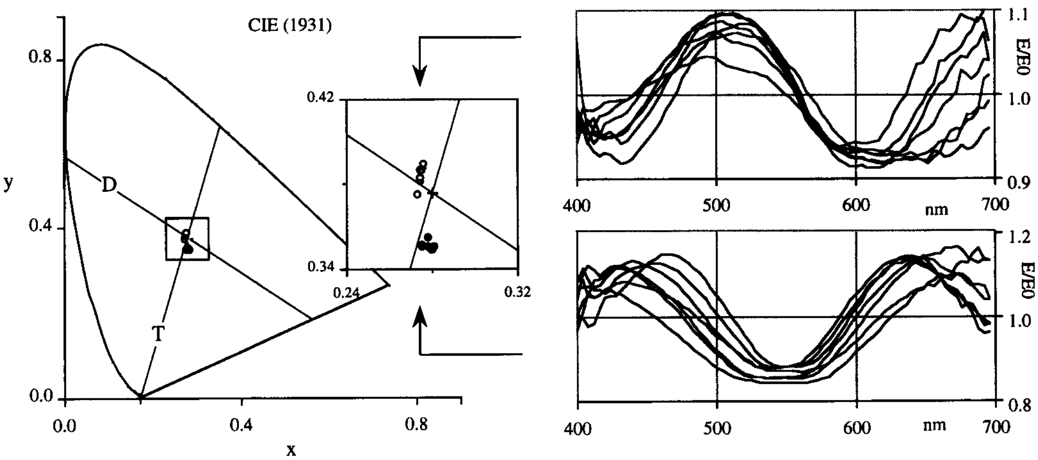

FIGURE 3. Spectral profiles of stimuli included in the 0.97–1.67 c interval. Right, relative spectral modulation of optimal (top) and pessimal (bottom) stimuli. Left, the chromaticity coordinates of the corresponding spectral power distributions plotted in the CIE (1931) diagram form two distinct clusters. The chromaticity coordinates of the pessimal stimuli are located on an axis slightly tilted from the tritanopic axis and the chromaticity coordinates for optimal SPDs form a cluster roughly in the deutan direction. T and D lines correspond to the dichromatic confusion lines (T, Tritan; D, Deutan) passing though the locus of the unmodulated spectrum (cross) which is located for these measurements at $x_0 = 0.28$ and $y_0 = 0.376$.

500–510 and 600–610 nm, and one of the crossovers occurs in a tight interval at 560 nm. With three lobes occurring where the crossovers of the optimal profiles are observed, the pessimal profiles exhibit a reverse profile. Correspondingly, the chromaticity coordinates of the corresponding spectral power distribution are shown to be clustered in two distinct groups in the CIE (1931) diagram (Fig. 3, left).

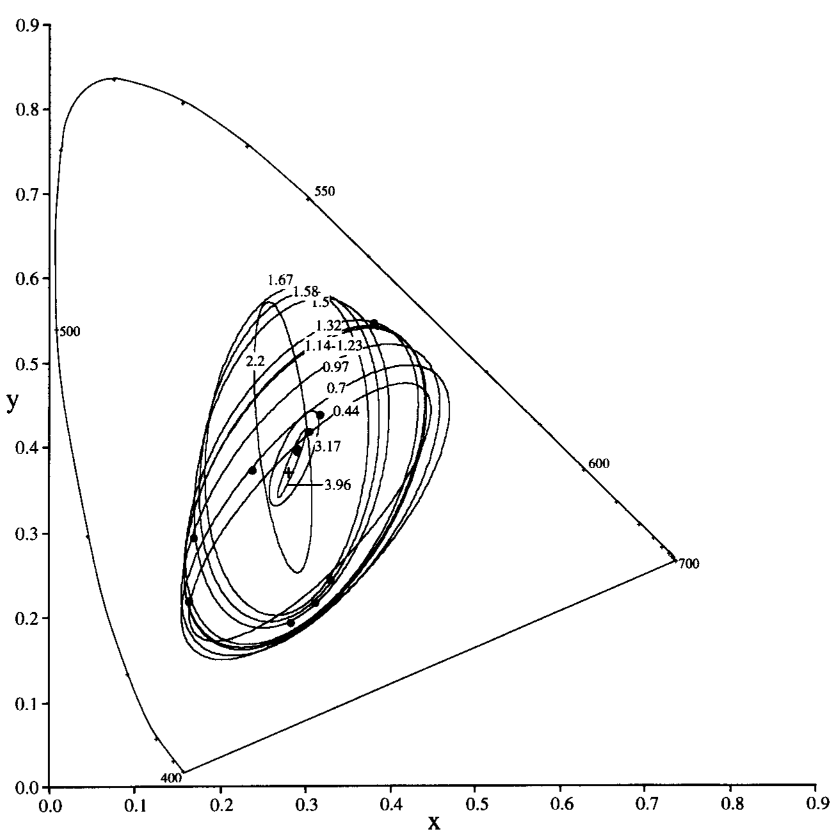

FIGURE 4. Elliptical representation of fully modulated spectra in the CIE (1931) diagram. The elliptical contours fitted to the chromaticity coordinates measured for the 12 frequencies at 30 deg steps are drawn in the CIE (1931) diagram. The axis ratio, the orientation and the colour centre of best-fitting ellipses vary with frequency. For each frequency the 0 deg starting phase is indicated (dots). Variation in depth of modulation corresponds to movement along a line that joins the unmodulated spectrum (cross) to an elliptical contour in a given direction i.e. for a given phase. For these measurements the locus of the unmodulated spectrum is $x_0 = 0.277$, $y_0 = 0.365$.

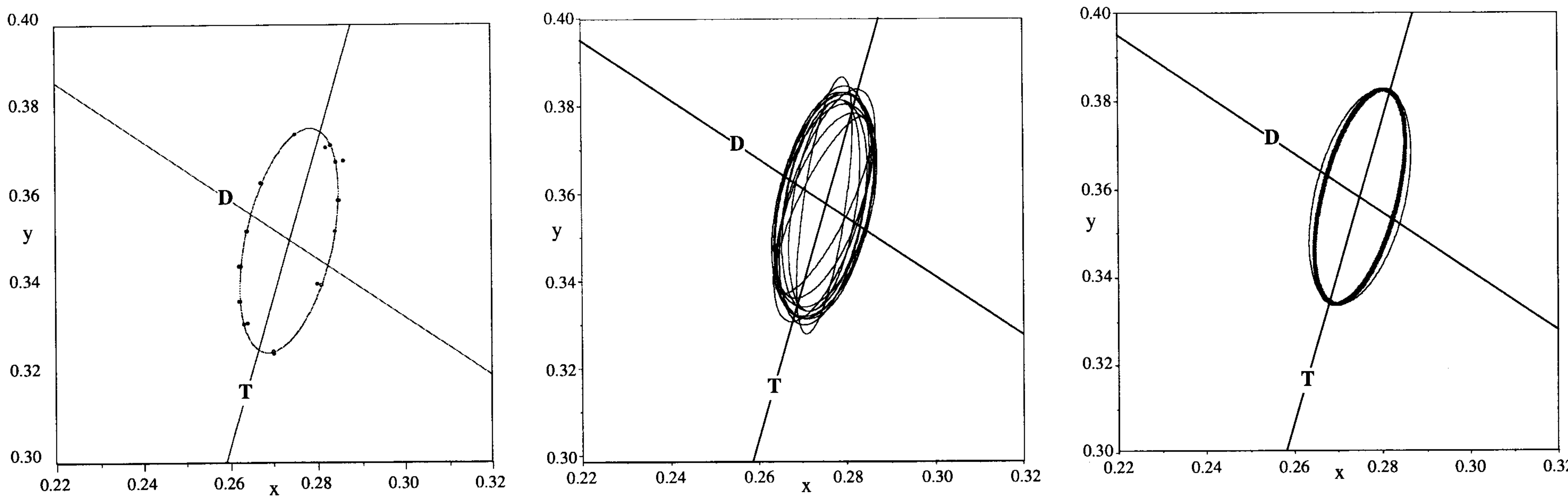

FIGURE 5. Experimental discrimination ellipse compared to MacAdam ellipse. Left, an elliptical contour is fitted to the chromaticity coordinates measured for frequencies from 0.7 to 3.2 c at the modulation threshold as shown here for 1.23 c. Centre, for comparison, the ellipses are centred on the same colour centre ($x_0 = 0.275$; $y_0 = 0.358$) and plotted on the same graph. Right, a mean experimental discrimination ellipse (in bold) is derived and compared to the MacAdam ellipse computed for the same colour centre. The absence of substantial orientation difference between the two ellipses sugests an equivalent relative sensitivity; however, the sevenfold magnification of the axes of the MacAdam ellipse indicates a difference in absolute sensitivity (see Table 1 for the parameter values).

TABLE 1. Parameters and coefficients of correlation (ρ) of the best fitting ellipses to the chromaticity coordinates measured at threshold values

Frequency (c)	Semi-axis a	Axis ratio	Angle (deg)	ρ
0.44	0.022	0.257	63.5	0.980
0.7	0.024	0.299	80.6	0.969
0.97	0.022	0.364	69.3	0.996
1.14	0.026	0.390	77.5	0.995
1.23	0.023	0.436	75.0	0.983
1.32	0.026	0.398	79.0	0.985
1.5	0.026	0.420	76.8	0.991
1.58	0.024	0.365	79.6	0.989
1.67	0.027	0.330	78.9	0.992
2.2	0.027	0.308	72.1	0.987
3.17	0.029	0.164	81.5	0.999
Average	0.025	0.339	75.8	
σ	0.002	0.076	5.2	
MacAdam	0.00358	0.407	76.2	

For comparison the parameters of the MacAdam ellipse computed for the same colour centre ($x_0 = 0.275$, $y_0 = 0.358$) are also given.

In summary, in spite of large differences in experimental procedures, the present data show features in common with the empirical measurements of the SMSF previously published for normal trichromats (Barlow *et al.*, 1983; Gemperlein *et al.* 1990; Bonnardel & Varela, 1991): sensitivity decreases at the lower frequencies and exhibits an optimum for the intermediate frequencies, while a high-frequency cut-off is observed between 4 and 6 c.

This high-frequency limit is also consistent with that based on the Fourier transform of Smith and Pokorny's fundamentals (Smith & Pokorny, 1975) computed by Barlow (1982) or that computed more recently by Romero *et al.* (1992) from the colour matching functions. Although total demodulation is observed at different frequencies according to the type of receptor, the critical frequency does not exceed 6 c. The conclusion that Barlow derives from his analysis of individual cones is here confirmed empirically for the whole colour system.

Elliptical representation of sensitivity

Chromaticity coordinates of fully modulated spectra. In order to determine the area covered in the CIE (1931) diagram by frequency-limited functions, that is, functions that have no harmonic higher than a given order when resolved by Fourier methods, Buchsbaum & Gottschalk (1984; see also Buchsbaum, 1985) computed the chromaticity coordinates of sinusoidal spectral power distributions (SSPDs) with $0 \leqslant f \leqslant 1.5$ c. For a given frequency with a constant modulation, they showed that chromaticity coordinates of SSPDs describe an elliptical contour in the CIE (1931) diagram as phase varies from 0 to 360 deg.

By referring to Wolter's theorem (Wolter, 1950), Brill and Benzschawel (1985), provided their own demonstration that the chromaticity coordinates of SSPDs must describe an ellipse in the chromaticity diagram. Thus, whatever the frequency, an elliptical contour can be perfectly fitted to the data points, as in fact was the case with the chromaticity coordinates we measured for fully modulated spectra (Fig. 4).

Chromaticity coordinates of minimally modulated spectra. Full discrimination ellipses were also derived by measuring the chromaticity coordinates at the threshold modulation. Since at least in one direction the sensitivity measurements were limited by the maximum modulation available, the highest frequency was removed from this analysis. The actual chromaticity coordinates are the means of the chromaticity coordinates of the six threshold determinations (or five for 0.44 and 0.7 c) recorded after each set of experimental data had been gathered (Fig. 5, left).

The best-fitting ellipses form a quite homogeneous set with an axis ratio variation of 22% and an orientation variation of 5.2 deg with a mean of 75.8 deg (see Table 1 for values). Because the measurements were made at different times there were small variations in the colour centre of the ellipses. However the centres of the ellipses estimated by our elliptic regression algorithm always corresponded to the chromaticity coordinates of the unmodulated spectrum. For the purpose of comparison, a mean colour centre is computed and the full set of ellipses is plotted on the same graph (Fig. 5, centre).

From this set, a mean ellipse is derived and compared to the MacAdam ellipse computed for the same colour centre. To match the size of our ellipse, the MacAdam ellipse in Fig. 5 (right) is enlarged seven times its actual value. It should be noted that the MacAdam ellipse represents the standard deviations of chromaticity matches. Thus, the size difference can be partly attributed to the measure of discrimination used (standard deviation of matches vs mean of thresholds for discrimination), and partly to the difference between successive and simultaneous methods. Several studies have shown that the capacity to discriminate colour is impaired in successive comparison tasks (Uchikawa & Ikeda, 1981; Romero *et al.* 1986).

Finally, it is worth comparing the present results with those of Romero *et al.*, (1995b) where, in contrast to our empirical method, the spectral modulation sensitivity curves are computed from the MacAdam discrimination ellipses. For each combination of frequency and phase, Romero and his collegues calculated the amplitude of modulation needed to bring the chromaticity coordinates of each SSPD to the elliptical threshold contour. Two sets of curves were derived corresponding to thresholds of either three or ten MacAdam units. For the wider tolerance, the maximal sensitivity function displays a cut-off frequency at 4.125 c with a peak at 1.5 c, whereas the narrower tolerance shows a peak value at 1.35 c and a high-frequency cut-off at 6 c. Our empirical estimate of 5 c for the high-frequency cut-off is thus consistent with an absolute sensitivity corresponding to seven MacAdam units.

CONCLUSION

An LCD template offers the visual scientist a convenient way of generating colour stimuli with any required spectral power distributions and thus is an alternative to traditional colorimeters with three monochromatic primaries. The reliability of the stimulator was tested by measuring discrimination thresholds to sinusoidal spectral modulations and these results were consistent with classical discrimination data. From these measurements an estimate of the MTF was derived describing the filtering properties of the entire chromatic system in the frequency domain.

REFERENCES

Barlow, H. B. (1982). What causes trichromacy? A theoretical analysis using comb-filtered spectra. *Vision Research, 22*, 635–643.

Barlow, H. B., Gemperlein, R., Paul, R. & Steiner, A. (1983). Human contrast sensitivity for comb-filtered spectra. *Journal of Physiology, 340*, 50p.

Benzschawel, T., Brill, M. H. & Cohn, T. E. (1986). Analysis of human color mechanisms using sinusoidal spectral power distributions. *Journal of the Optical Society of America A, 3*, 1713–1725.

Bonnardel, V., Martinoya, C. & Varela, F. J. (1991). Une méthode de mesure de la sensibilité aux modulations périodiques d'énergie lumineuse spectrale chez l'Homme. *Comptes Rendus de l'Académie des Sciences, Paris, 312*, 695–700.

Bonnardel, V. & Varela, F. J. (1991). A frequency view of color: Measuring the human sensitivity to square-wave spectral power distributions. *Proceedings of the Royal Society London, B, 245*, 165–171.

Brill, M. H. & Benzschawel, T. (1985). Remarks on signal-processing explanations of the trichromacy of vision. *Journal of the Optical Society of America A, 2*, 1794–1796.

Buchsbaum, G. (1985). Chromaticity coordinates of frequency-limited functions: erratum. *Journal of the Optical Society of America A, 2*, 95.

Buchsbaum, G. & Gottschalk, A. (1984). Chromaticity coordinates of frequency-limited functions. *Journal of the Optical Society of America A, 1*, 885–887.

Campbell, F. W. & Robson, J. G. (1968). Application of Fourier Analysis to the visibility of gratings. *Journal of Physiology (London), 197*, 551–566.

Cornsweet, T. N. (1962). The staircase method in psychophysics. *American Journal of Psychology, 75*, 485–491.

Gemperlein, R., Paul, R. & Steiner, A. (1990). Fourier Interferometric Stimulation (FIS): The method and its applications. In Blakemore C. (Ed.), *Vision: Coding and efficiency*. Cambridge: Cambridge University Press.

Holtsmark, T. & Valberg, A. (1969). Colour discrimination and hue. *Nature, 224*, 366–367.

Ives, H. E. (1921). A proposed standard method of colorimetry. *Journal of the Optical Society of America, 6*, 469–478.

MacAdam, D. L. (1943). Specification of small chromaticity differences in daylight. *Journal of the Optical Society of America, 33*, 18–26.

Pefferkorn, S. (1993). Rapport étalon de luminance. In Photométrie mésopique, convention de recherche BNM 91-2-46-0027 (personal communication).

Romero, J., Hita, E. & Jimenez Del Barco, L. (1986). A comparative study of successive and simultaneous methods in colour discrimination. *Vision Research, 26*, 471–476.

Romero, J., Jimenez del Barco, L. & Hita, E. (1992). Mathematical reconstruction of color-matching functions. *Journal of the Optical Society of America A, 9*, 25–29.

Romero, J., Nieves, J. L., García-Beltrán, A. & Hita, E. (1995a) Analysis of colour-vision mechanisms in the chromatic frequency domain. *Journal of Optics (Paris), 26*, 9–15.

Romero, L., Nieves, J. L. & García-Beltrán, A. (1995b) Human processing of colour information in the chromatic-frequency domain. *Vision Research, 35*, 867–871.

Smith, V. C. & Pokorny, J. (1975). Spectral sensitivity of the foveal cone pigments between 400 and 500 nm. *Vision Research, 15*, 161–171.

Uchikawa, K. & Ikeda, M. (1981). Temporal deterioration of wavelength discrimination with successive comparison method. *Vision Research, 21*, 591–595.

Weale, R. A. (1951). *Journal of Physiology (London), 13*, 115–122.

Winch, J. T. & Machin, C. F. (1940). The physical realisation of the C.I.E. average eye. *Transactions of the Illuminating Engineering Society of London, 5*, 93–104.

Wolter, H. (1950). Physikalische Begründung eines Farbenkreises und Anzätze einer physikalischen Farbenlehre. *Annalen der Physik, Ser 6, 8*, 11–29.

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