Some paradoxes, errors, and resolutions concerning the spectral optimization of human vision

Bernard H. Soffer
665 Bienveneda Avenue, Pacific Palisades, California 90272

David K. Lynch
The Aerospace Corporation, P.O. Box 92957, Los Angeles, California 90009

The peak brightness of the solar spectrum is in the green when plotted in wavelength units. It peaks in the near-infrared when plotted in frequency units. Therefore the oft-quoted notion that evolution led to an optimized eye whose sensitivity peaks where there is most available sunlight is misleading and erroneous. The confusion arises when density distribution functions like the spectral radiance are compared with ordinary functions like the sensitivity of the eye. Spectral radiance functions, excepting very narrow ones, can change peak positions greatly when transformed from wavelength to frequency units, but sensitivity functions do not. Expressing the spectral radiance in terms of photons per second, rather than power, also causes a change in the shape and peak of the distribution, even keeping the choice of bandwidth units fixed. The confusion arising from comparing simple functions to distribution functions occurs in many parts of the scientific and engineering literature aside from vision, and some examples are given. The eye does not appear to be optimized for detection of the available sunlight, including the surprisingly large amount of infrared radiation in the environment. The color sensitivity of the eye is discussed in terms of the spectral properties and the photo and chemical stability of available biological materials. It is likely that we are viewing the world with a souvenir of the human evolutionary voyage. © *1999 American Association of Physics Teachers.*

I. INTRODUCTION

Many people believe that evolution has produced a human eye whose color sensitivity roughly matches the sunlight spectrum.[1–9] Some authors only hint but others state the case even more strongly, i.e., that both the solar spectrum and the color sensitivity of the eye peak very nearly together at around 560 nm in the green. Such an agreement could hardly be accidental, so the implication and reasoning goes, and therefore the human eye must have evolved to possess a near-optimum color sensitivity. The framed text insert shows a sampling of quotes from the vision literature, illustrating how pervasive this idea has become. Many more authors cause this idea to spread by further quoting and paraphrasing these ideas, without sufficient reflection, in fresh publications of their own. For example, Sekuler and Blake paraphrase Mollon[2] in their textbook ''Perception.''[10]

We will show that the apparent wavelength coincidence between the solar spectral radiant power (radiant power per unit bandwidth)[11] and the eye's spectral sensitivity, its spectral ability to elicit a visual response, is artificial and often misleading. It results from the choice of units in which the solar spectrum is plotted. Comparing spectral radiant power to sensitivity is like ''comparing apples and oranges.'' they are fundamentally different quantities and their shapes and peaks should not be compared with one another (even though they can legitimately be *multiplied* together for some purposes, as we will show). In particular, we will show how the wavelength of peak emission depends on the units used in computing and displaying a spectral distribution. Furthermore, we will demonstrate that, on the contrary, the spectral sensitivity of the eye does not depend on the units used, and suggest that the eye is poorly optimized to take full advantage of all the visible and the enormous amount of infrared

light that is available in the environment. We will the discuss evolution as it relates to color vision. Examples of similar confusions from fields other than vision will also be given.

CAVEAT LECTOR

''The peak of [the solar spectral irradiance[11]] curve is located at the visible wavelengths we see with our eyes.''[1]

''For the main business of vision...most mammals depend on a single class of cone, which has its peak sensitivity near the peak of the solar spectrum, in the range 510–570 nm.''[2]

''Figure 1.3 compares the spectral content of light... with the spectral sensitivities of the rod and cone systems of human vision.''[3]

''Sunlight comprises wavelengths ranging from... 300 nm through 800 nm... For humans visible light ranges from approximately 400 to 700 nm.''[4]

''The spectral response of the human eye is closely matched to the peak of the sun's radiation. (5500 Å) in daylight.''[5]

''This shows that the eye is sensitive to a region of the spectrum where the radiation reaching the earth from the sun is most plentiful.''[6]

''Note that the maximum available energy from sunlight peaks in the same region of the spectrum where the eye is most sensitive. This coincidence is probably not accidental, but is more likely the product of biological evolution.''[7]

''It is no accident that this [human cone] sensitivity is centered on the peak of the energy distribution of light from the sun; evolution of the eye has obviously taken advantage of the spectral character of daylight.''[8]
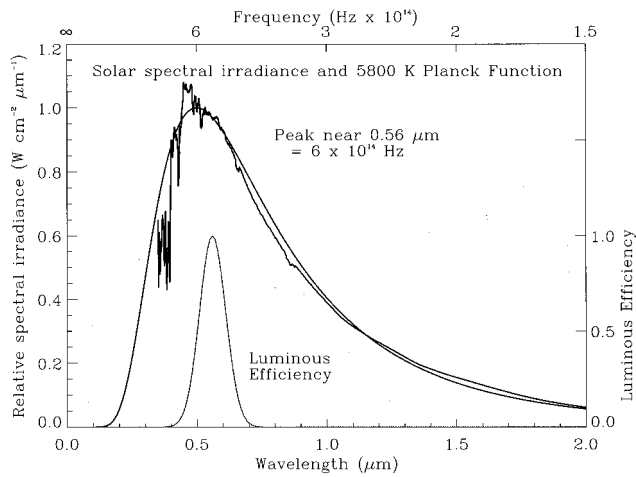

Fig. 1. The solar spectrum plotted in wavelength units peaks near 500 nm. Also shown is an approximate fit of a 5800 K Planck function that has been scaled to match the solar spectrum. This shows that the solar spectrum is roughly Planckian in the optical part of the spectrum. The luminous efficiency of the eye peaks at 560 nm. All three curves appear to peak near 500–560 nm, a wavelength region generally perceived as being green.

II. SPECTRAL RADIANT DENSITY DISTRIBUTIONS CONTRASTED WITH SENSITIVITY

Figure 1 shows the spectrum of the sun[12] at sea level for a daytime midlatitude summer with the sun at the zenith and with nominal values for Rayleigh scattering, water vapor absorption, boundary layer, and stratospheric aerosols etc. Also shown in Fig. 1 is a 5800 K Planck function scaled to approximately match the sunlight. We concentrate on sunlight rather than daylight because that is what all the authors referred to above have done. Daylight, of course, is highly variable, and has been much studied.[13] It depends on many factors, including, the direction and degree of sky exposure, weather conditions, time of day, and polarization. The reflected spectrum of the statistically broadband reflectivity of the natural visual scene is, of course, extremely dependent upon the spectrum of the sunlight that illuminates the scene.

Several aspects of the solar spectrum are noteworthy. First, sunlight shows significant departures from a Planck function. The features are due to absorption by the Earth's atmosphere and to absorption in the solar photosphere. Figure 1 also shows that the brightest part of the spectrum seems to occur in the green near 0.5 μm (500 nm.) But rather than being a pronounced peak here, there is a broad one between 450 and 610 mm. This plateau is due to the combined influence of thousands of solar and atmospheric absorption lines, which, though not resolved here, serve to alter the shape from a pure blackbody.

Let us examine the position of the peaks. Figure 1 shows the Sun's spectral irradiance plotted in units that are most commonly used for visible spectra, i.e., W cm^{-2} μm^{-1} vs μm (wavelength units). In these units the peak of the solar spectrum is unquestionably at a wavelength that by itself would appear green. Also shown in Fig. 1 is the normalized spectral sensitivity of the eye, or equivalently, its normalized "luminous efficiency;" i.e., its relative spectral ability to evoke a visual sensation, adapted from Judd and Wyszecki.[14] The peak of the luminous efficiency is also in the green and peaks at 560 nm.
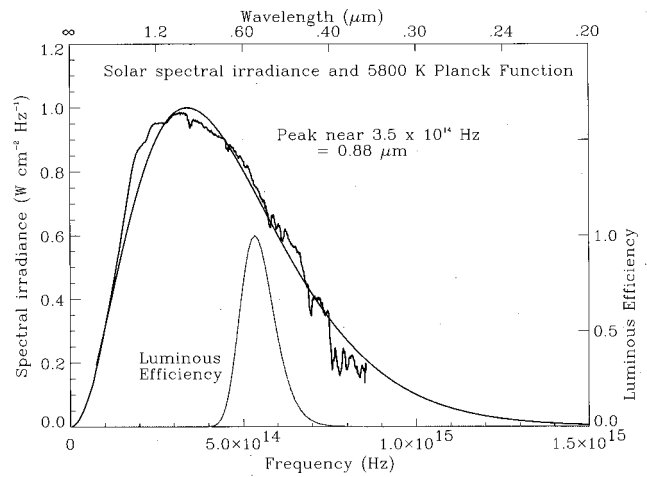

Fig. 2. The same data shown in Fig. 1 except plotted in frequency units. Here the sun and Planck functions peak near the wavelength equivalent to 880 nm in the near-infrared while the luminous efficiency curve still peaks at 560 nm. The solar irradiance and Planck function transform differently than the luminous efficiency.

The spectrum can also be plotted in frequency units, i.e., W cm^{-2} Hz^{-1} as a function of frequency (Fig. 2). In this case, the spectrum no longer peaks in the green but rather in the near infrared close to a wavelength equivalent to 0.88 μm (880 nm). Yet the peak of the luminous efficiency of the eye remains in the green. As frequency and wavelength distributions are both equally valid representations of the very same physical phenomenon, we *seem* to be left with the following question: "Where does the solar spectrum 'really' peak, in the green or in the near infrared?"

The answer is that it depends on the choice of independent variable for the bandwidth. To see this, let us first approximate the solar spectrum by a Planck function because it is analytic and closely matches the solar spectrum. The arguments will hold for the solar spectrum as well.

In wavelength units the Planck function spectral radiant power $B_\lambda(T)$ is

$$B_\lambda(T) = 2hc^2\lambda^{-5}/(e^{hc/\lambda kT}-1), \tag{1}$$

in units of power per unit area per unit wavelength interval. As Wien's displacement law says, the wavelength of peak emission is $0.2897/T = 0.2897/5800 = 4.99\times10^{-5}$ cm=500 nm, corresponding to a frequency ν of $\nu = c/\lambda = 6\times10^{14}$ Hz. This is in the green part of the spectrum and agrees with most people's idea of the shape and peak of the solar spectrum. Wien's law with the conventional constant, however, only works when the spectrum is plotted *per unit wavelength* interval. When the same spectrum is plotted *per unit frequency* interval W cm^{-2} Hz^{-1},

$$B_\nu(T) = 2h\nu^3 c^{-2}/(e^{h\nu/kT}-1), \tag{2}$$

the distribution peaks at 3.4×10^{14} Hz, corresponding to 8.8×10^{-5} cm($=0.88$ μm$=880$ nm). The peak wavelength of the Planck distribution in frequency is easily shown to be 1.76 longer than the peak of the wavelength distribution for any temperature. See Figs. 1 and 2.

Although Eqs. (1) and (2) are equivalent representations, converting one to the other is not simply a matter of making the substitution $\nu = c/\lambda$. This is because the Planck function is a density distribution function and is defined differentially.
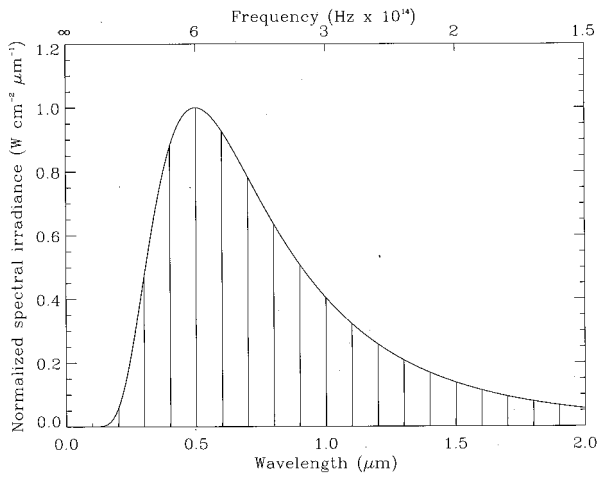
Fig. 3. A 5800 K Planck distribution function divided into equal 100 nm wavelength intervals.

$B_\lambda \, d\lambda$ represents the power in the differential bandwidth $d\lambda$ while $B_\nu \, d\nu$ represents the power in the differential bandwidth $d\nu$. If the variables correspond, the powers must be equal and

$$B_\lambda \, d\lambda = B_\nu \, d\nu. \tag{3}$$

This is simply conservation of energy. Since $d\nu/d\lambda = -c/\lambda^2$ [and ignoring the minus sign because it is merely an artifact of the directions of integration of Eq. (3)], then

$$B_\lambda \, d\lambda = B_\nu c/\lambda^2 \, d\lambda, \tag{4}$$

and thus $B_\lambda = B_\nu c/\lambda^2$, or, conversely, $B_\nu = B_\lambda \lambda^2/c$. The apparent ''shift'' in peak wavelength between B_λ and B_ν is not simply due to a substitution of variables, $\nu = c/\lambda$, but to the $1/\lambda^2$ Jacobian weighting factor as well. This is a necessary result of the differential nature of the Planck distribution function.

The relation between B_λ and B_ν is illustrated in Figs. 3 and 4. Figure 3 shows a 5800 K Planck function as a wavelength distribution and Fig. 4 shows the same function as a
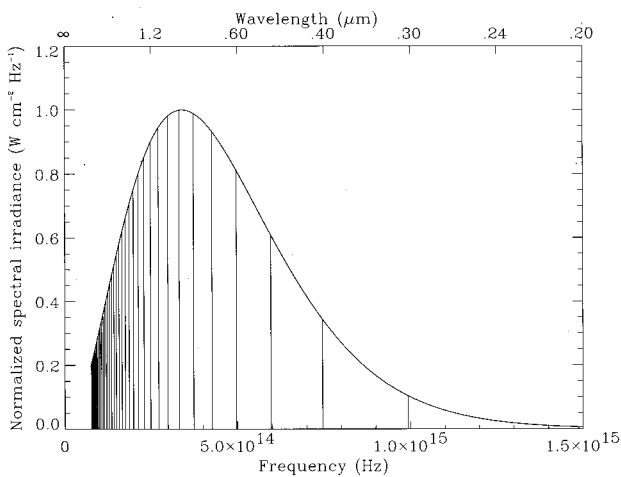

Fig. 4. The same Planck function and wavelength intervals as Fig. 3 transformed into frequency intervals. Note that the frequency intervals are not equal.

frequency distribution. Figure 3 is divided into equal intervals of wavelength in the amount of 0.1 μm. The same intervals are marked in frequency units in Fig. 4. In Fig. 4 they clearly are unequally spaced because there are more wavelengths per unit frequency at longer wavelengths than at shorter ones. Conversely, there are more frequencies per unit wavelength at shorter wavelengths. Clearly then, a plot of irradiance per unit frequency would skew the curve to longer wavelengths, which is exactly what we have just seen happen (Figs. 1 and 2).

We have used Planck's function only as a convenient example. Most distribution function would suffer some change in shape depending, not only on the transformation itself, but also on the original shape and width of the distribution to be redistributed as well. For example, a very narrow distribution with little to redistribute such as a spectral line would shift much less than 1.76 times its wavelength. A function broader than the Planck distribution could shift more.

Another commonly used representation of irradiance functions describes the spectral irradiance in terms of the number N of photons per second (rather than in Watts) per unit bandwidth. The transformation to photons per second by itself engenders a change in the shape and a shift in the distribution's peak position. This is an additional and separate consideration from the distortions from the Jacobian weighting effects that would occur upon changing bandwidth representations, say from wavelength to frequency, as described above. The distribution function with power represented by photon number has a different form and a different dependence on the independent variable. For example, for the Planck distribution function, $B_\lambda(N)$, in terms of the number of photons per second, per unit wavelength, noting that N = power/$h\nu$ and $B_\lambda(N) = B_\lambda/h\nu$, we have

$$B_\lambda(N,T) = 2hc^2\lambda^{-4}/(e^{hc/\lambda kT} - 1), \tag{5}$$

and the distribution $B_\lambda(N,T)$ stretches vertically *nonlinearly* by the factor of λ in comparison to the distribution $B_\lambda(T)$. Wien's displacement law for the distribution in terms of photon number has a different constant: $\lambda T = 0.3670$. The peak of the 5800 K. Planck spectrum shifts to 633 nm in this representation.

There are myriad ways of representing a density distribution function. Each one represents the function with equal mathematical validity and without loss or gain of information, even though each has a different shape. The meaning and usefulness of the representation chosen depends entirely on the intention, interest, and the convenience of the user. One could plot a valid spectral distribution, for example, versus the square root of frequency. This might seem unnatural or ''unphysical'' to some but perfectly reasonable and useful to someone concerned with the figure of merit D^*, which is expressed in those units and is often used to describe infrared detectors. Spectroscopists may prefer frequency, as quantum mechanical transitions occur between states or bands of states whose energy is proportional to frequency, but spectra can also be studied profitably, although more cumbersomely, even in a wavelength representation, as did Balmer and then Bohr when he conceived his classic theory. Naturally, those concerned with photon counting detection issues may prefer the photon number distribution.

The result of plotting the Planck distribution semilogarithmically, as is often done, is shown for 5800 K in Fig. 5. It reveals yet a different shape and a different peak, this time
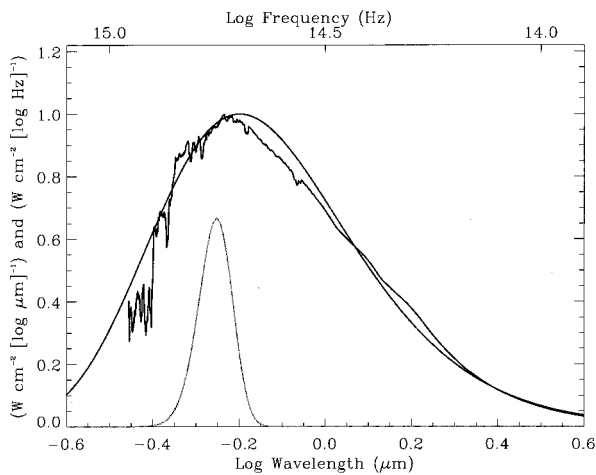
Fig. 5. Relative spectral irradiamce. A semilogarithmic plot of the Planck function and solar spectrum compared with the luminous efficiency of the eye.

near 720 nm, for either log wavelength or log frequency. The Jacobians for these logarithmic transformations are $1/\lambda$ and $1/\nu$ respectively. The wavelength–frequency pair of these two semilogarithmic representations of Planck's function, or any other distribution function using these variables including sunlight, have exactly the same left–right mirrored functional form. This can easily be seen by noting that $d(\log \lambda) = -d(\log \nu)$ and again ignoring the minus sign, then $B_{\log \lambda} = B_{\log \nu}$. No special physical significance should be attached to this curious symmetry nor should the logarithmic form be singled out as a preferred physical or physiological representation.[15]

The spectral behavior of optical filters and detectors is not described by density distributions and so they transform in a much simpler way. Spectral sensitivity of any detector including the eye is expressed in units of Amps/Watt, Volts/Watt, or in the case of the eye, Lumens/Watt, each *at a given wavelength*. Filter transmission, being a unitless ratio between zero and one *at each wavelength*, behaves identically. This is fundamentally different than spectral irradiance which, by virtue of being a density distribution function, is expressed per unit bandwidth, for example, as a *value per unit wavelength interval*. Consequently, sensitivities possess no Jacobian differential weighting factor as when transforming the representation of the eye's sensitivity from wavelength intervals to frequency intervals. One need only use the substitution $\nu = c/\lambda$. This is why the peaks in the sensitivity curve remain at the same frequency (and wavelength) when plotted in either frequency or wavelength units (Figs. 1 and 2).

The fact that all measurements are necessarily made with instruments that must have finite bandwidth resolution or, expressed in conjugate space, finite convolutional spread functions, may cause some confusion about the distinction we are making. Measuring the spectral transmission of a filter, for example, will result in apparent values measured in finite bandwidth intervals, but this is merely a sampling issue. The measured values in the intervals are averages for the finite intervals and represent the transmission at each point in the interval. This does not make the measured transmission in any sense a density distribution.

The eye's spectral response can be likened to a filter. The

spectral absorption of the eye is nearly linear. It is nearly intensity independent over many orders of magnitude, and each absorbed photon is equally effective, although only about 10% of the incident photons are absorbed.[5] So we can treat the eye's spectral sensitivity just like the transmission of a colored linear filter. Multiplying the sensitivity by the Planck function will result in the spectral radiance that gets through the filter (i.e., the radiance actually detected by the eye and appropriately weighted). This is an example of when it is perfectly legitimate to multiply, point by point, an ordinary function and a distribution function in order to get the desired resultant distribution function. Yet, as we have seen, it can be very misleading to compare shapes and peaks and draw inferences from them.

This explanation may leave some people feeling a little uneasy. If we are designing a detector of broadband light and want to know at what wavelength to position a filter of a fixed bandwidth in order to transmit the most power, intuition might say to put it at the peak of the source's spectrum. Yet we seem to be saying that this mental procedure of sliding the filter back and forth to maximize power near the peak would not work, as the peak's position is ambiguous and somewhat arbitrary. What's going on here?

The answer is that for a fixed filter bandwidth in wavelength, maximizing in wavelength space is not the same as maximizing in frequency space. What may not be apparent is that as the wavelength filter is sliding back and forth, its width in frequency space is changing. Consider a filter (like the eye) whose bandwidth is 100 nm centered at 520 nm, which just happens to be near the maximum in the wavelength representation of sunlight. The same filter is not near the peak in frequency space. If we were to take the filter in frequency space with the same fixed wavelength bandwidth that was used to optimize in wavelength space, and move it instead as a fixed frequency bandwidth filter toward smaller frequencies to attempt to further maximize the signal, we would find that its width in wavelength space had increased. We would also find a maximum where the filter and source spectrum align, but it would be a *different* maximum than found before because the optimization constraint was different. This is all a result of the relation $d\lambda = -c \, d\nu/\nu^2$. An optimization somewhat similar to the one described above was done analytically for the Planck distribution by Benford.[16]

In summary, thus far we have shown that the peak wavelength of the solar spectrum depends on how the spectral distribution is plotted. The fact that in wavelength units the spectrum roughly agrees with the peak sensitivity of the eye is an accidental and meaningless quirk involving the units in which the spectrum is plotted. Computing it in frequency units, for example, is just as valid and results in a peak near the equivalent of 880 nm, well away from the peak sensitivity of the eye. There is, however, no paradox or inconsistency in this. While we firmly believe in the modern theory of evolution, we wish to warn others, including one of the authors of this article,[8] of the dangers of glibly assigning Darwinian significance to what is merely an accidental wavelength coincidence—and to their readers as well.

The paradoxes, errors, and confusions that arise when density distributions are involved are ubiquitous, pervading the entire scientific literature. The potential for these problems to arise exists not only for spectral power density distributions, but for spatial power and spatial frequency power distributions as well. It is also a general issue for all *statistical* den-
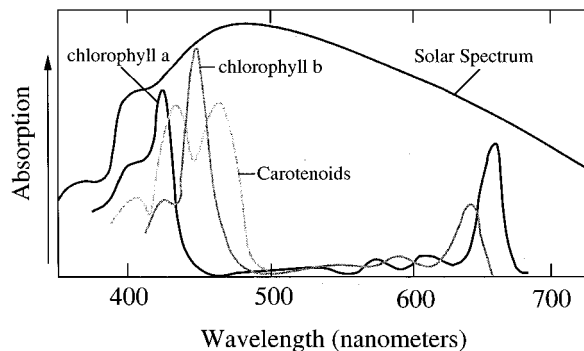
Fig. 6. The absorption spectra of various chromophores involved in photosynthesis compared with the solar spectrum as a function of wavelength. After Szalai and Brudvig.[18]

Fig. 7. The sky noise power density distribution at galactic latitude 10°, scaled by the square root of frequency, plotted as noise temperature versus frequency, showing the minimum in the free space microwave window.

sity distributions in whatever discipline they may arise. There is a very close parallel between the paradox we have described and the famous Bertrand paradox in probability theory that hinges on the arbitrariness of choosing the *a priori* uniformly random distribution, or, putting it another way, of choosing the *a priori* equally likely states. Different choices result in probability density functions with different shapes and peak positions that denote different answers to the problem at hand. Statistical distributions of great interest include all the important quantum mechanical probability density distributions and their relative, the Wigner function. Similarly, this general issue exists for the Ambiguity function, the Spectrogram, and other related two-dimensional phase space representations that are useful in radar, communications, and signal processing. To end this section we will give two examples, from different scientific disciplines, of the error that we have been describing.

The first comes from the study of photosynthesis. The error in this example[17] is rather close to the immediate subject of our paper. Here the authors plot the absorption spectra of various chromophores involved in photosynthesis together with the solar spectrum in wavelength units (Fig. 6). In the wavelength representation the curves happen to overlap strongly. The authors incorrectly conclude: ''...almost the entire spectrum of light coming from the sun can be absorbed for use in photosynthesis.''

The second example concerns the so-called microwave window. Radio astronomers are interested in determining the most transparent spectral region where they might best hope to receive weak signals. The radio sky has many noise components that would interfere with detection. Their density distribution spectra are plotted separately and added together in Fig. 7. Variants of this figure are so ubiquitous as to defy making a proper original attribution. One fascinating place to find it is in the Project Cyclops[18] study for detecting extraterrestrial intelligent life. The spectral noise power densities are described by their ''noise temperatures,'' which relate to the Planck distribution function. These density distributions are here further scaled by the square root of frequency. The three noise sources, galactic nonthermal, the 2.7 K cosmic background, and the quantum noise of coherent detection, define a broad minimum called the free space microwave window. The location and shape of this minimum in the density distribution will depend on the choice of representation in the same ways as we described at length above. The common error is to locate the emission frequency of some
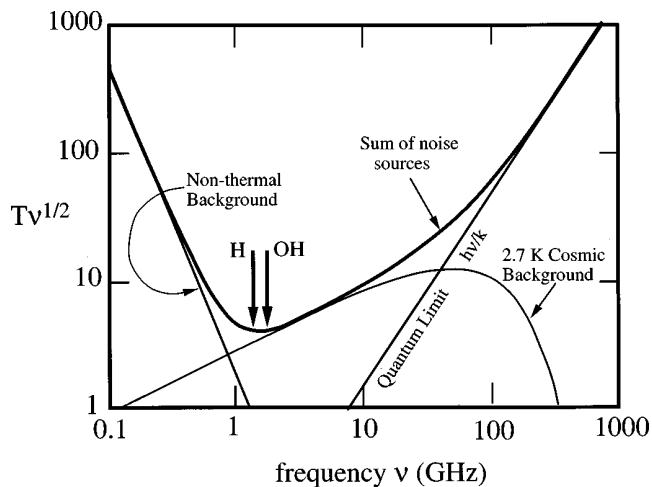
hoped to be detected narrow line, such as the 21 cm H hyperfine line or the OH line, in that window, as we do with the arrows in the figure. Being very narrow spectral distribution lines, their position would *not* change significantly with a change in representation as would the broader distributions. In that way the narrow lines do not behave like density distribution functions under transformation, and it is not legitimate to compare them with distributions, as we have explained. Granted that the errors in this particular case are trivial and have not much practical consequence, they are nevertheless errors in principle.

III. REGARDING EVOLUTION

The many opinions in the literature noted earlier about the evolution of color vision were based in part on a simple misunderstanding about density distribution functions. But there is another underlying bias that we would like to mention. The consensual, canonical belief in the power of evolution to optimize absolutely, globally, and without constraint is so strongly held that it is sometimes invoked as a sufficient causal explanation of whatever the facts at hand may be. The opinion has been expressed that visible light has just the right wavelengths to reflect light from objects in useful ways, and to permit the evolution of the eye.[19] This is a Panglossian view of evolution, a modern Darwinian reading of Liebnitz's world view: the eye is the best of all possible optimizations and every thing about it has sufficient cause. In fact, evolution has historically traced many irreversible pathways to reach its present state. Any potentially more favorable global optimum might be too energetically difficult to achieve and would thus be very unlikely to ever occur. A quantitative measure of the optimization of spectral utilization that has been achieved by the eye can be obtained by integrating under the curves shown in Fig. 1 to get the fraction of the available light between 320 nm (the atmospheric transmission cutoff) and 1400 nm (the thermodynamic noise limit[20]) detected by the eye. It is only 19%, hardly optimal in a spectral sense. There is also the question of the availability of suitable biological materials that would posses the necessary photochemical and thermochemical stability to achieve a more optimum state. All of these factors

have mediated and constrained the process of the evolution of the eye and its optimization to the Sun's light.

Sight is clearly a survival advantage, and so it seems reasonable to suppose that the better one sees, the more able one is to survive. It might be expected that a very efficiently optimized eye should be able to see both longer and shorter wavelengths with greater sensitivity. There is considerable solar radiation in the near infrared that the eye does not detect. The full width at half-maximum of the solar spectrum in wavelength units (Fig. 1) is ~500 nm while that of the eye is only 100 nm. Should not an optimized eye be very sensitive to radiation longward of 700 nm? After all, during the day there is plenty of sunlight at these wavelengths and at night the OH airglow[21] between 0.6 and 1.2 μm would light up the landscape tremendously. Thermal excitations in the retina only begin to compete with any incoming photons at wavelengths longer than 1.4 μm at the absolute threshold of vision.[20] Sensitivity in the infrared 600–1200 nm range would seem like an obvious advantage with significant evolutionary potential. Pirenne[22] has suggested that strong infrared sensitivity would be undesirable because the infrared in the eyeball, the body's own heat radiation, would cause the external world to be obscured by a luminous fog of this radiation. This is precisely why we do not expect to see beyond 1.4 microns. That is where the fog would begin to manifest itself strongly. But this effect does not rule out the possibility of some near-infrared sensitivity up to 1.4 microns. Similarly, there would also seem to be some advantage to having a greater blue and ultraviolet sensitivity. Yet neither of these things happened in humans. Why? If our vision is not well matched to the light of our present environment, including the large infrared component bathing us now, could we be mired in some evolutionary backwater, where once we were indeed better adapted? This may put a damper on the enthusiasm of those who prefer a story of continual linear progress, but those familiar with the evolution of the vertebrate eye and how its structure and function mirror its evolutionary history will not be surprised at the following compelling suggestion by Duke-Elder:[23]

"So far as the evidence goes, the eyes of all vertebrates including man are stimulated by approximately the same range of the spectrum (760 mμ–390 mμ) with the highest sensitivity at a band with a wavelength varying between 500 and 550 mμ; it is no coincidence that this corresponds roughly with the transmission spectrum of water. The visual mechanism of Vertebrates was first evolved in water and their photopigments were presumably developed as sensitizers to allow their possessors to leave the brightly-lit surface and penetrate more deeply into the darker depths of the sea; and it would be surprising if their descendants discarded a mechanism which their ancestors had found of such value."

This opinion was echoed very recently,[3] however, mistakenly illustrating the point by wrongly superposing spectral densities and cone color sensitivities, a comparison that we have explained is not appropriate! It is, however, perfectly legitimate and appropriate to compare transmission and sensitivity, as we do in Fig. 8, as they are neither one density distributions. Figure 6 shows the transmission of water through different pathlengths, plotted together with the luminous efficiency of the eye. Note how much narrower the water's transmission curves are in comparison to the solar
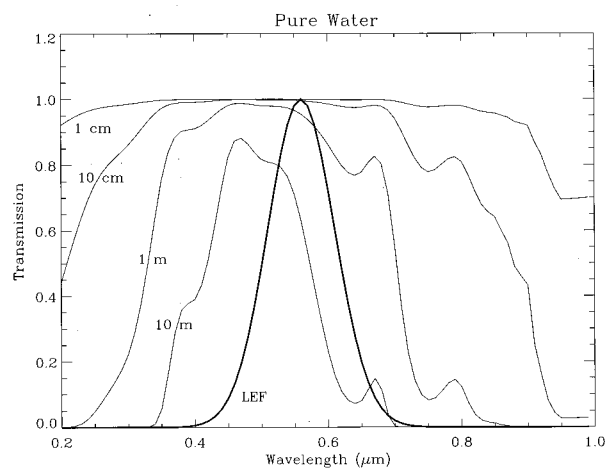

Fig. 8. The transmission of pure water compared with the luminous efficiency function (LEF) of the eye. This calculation was done for absorption, and scattering was ignored.

spectrum. As a result, water imposed a tighter constraint on the vision's original spectral evolution than did sunlight. This filtered sunlight illumination was itself the original natural scene for vision long before visual imaging evolved. The historical channel of evolution often prevents deviation to a more optimum course. Later, when object and scene discrimination, including color discrimination, exerted evolutionary pressure, and constraint, the general bearing had already been charted.

Other constraints on the optimization of the visual spectral response come from the properties of available biological materials. To get sensitivities further in the infrared via photoisomerization, larger molecules with longer conjugated chains, which would have their first electronic excited states at lower energies, would be needed. But such large molecules are unstable and subject to dissociation and bleaching by thermal processes at body temperature, where the thermal energy kT is comparable to the excited state energies.[24–26] This is why it is extremely difficult to produce stable photographic sensitizing dyes or laser giant pulse Q-spoiling dyes at wavelengths longer than 1 micron in aqueous solutions. Although the tails of animal photopigment sensitivity become uselessly small, except under artificially extreme brightness conditions, beyond about 850 nm,[27] organic dye molecules have been synthesized with longer peak wavelength sensitivities. They, however, are unstable in aqueous media, all the more so when traces of oxygen species and free radicals are present.

At the short wavelength side, all organic molecules are susceptible to direct UV damage or indirect damage from UV-generated free radicals in their proximity. Those are not promising prospects for evolutionary candidates. People who have had their corneas or lenses removed can see a bit farther in the UV, but they often develop UV-related ocular damage and dysfunction.[28] Interestingly, many insects, animals, and birds do see a bit farther in the UV and IR than we do.[29] For instance, compared to other frogs, *Rana Tempoaria* has high sensitivity down to 330 nm,[30] which coincidentally corresponds very nearly to the atmospheric short-wavelength transmission sharp cutoff at 320 nm.

IV. SUMMARY

We have shown that, contrary to the belief expressed by many authors, the eye is only weakly optimized to take full advantage of the available solar spectrum. The erroneous belief often arises from a blind faith in the power of evolution to optimize absolutely, coupled with a misunderstanding of the nature of density distribution functions. That misunderstanding appears in a diverse range of scientific literature. Other constraints upon the eyes' evolutionary optimization besides the Sun's radiance were also important, such as the historically significant influence of the transmission of water, the susceptibility of potentially available biological materials such as photopigments to UV damage, and the instability of possible infrared sensitive photopigments. Contemplating why we did not evolve to use other mechanisms to produce a broader band visual sensitivity, as for an unlikely example electron–hole pair generation, would seem to be a futile exercise in a counterfactual history of evolution. But the question of how and why our vision evolved to employ its equally unlikely photoisomerization scheme for vision remains an interesting and open issue.

[1] Keneth R. Lang, *Sun Earth and Sky* (Springer-Verlag, Berlin, 1995), p. 210.

[2] J. D. Mollon, ''The Uses and Origins of Primate Colour Vision,'' J. Exp. Biol. **146**, 21–38 (1989).

[3] James T. McIlwain, *An Introduction to the Biology of Vision* (Cambridge UP, Cambridge, 1996), pp. 5–6.

[4] Evan Thompson, *Colour Vision* (Routledge, London and New York, 1995), pp. 51, 169.

[5] Albert Rose, *Vision Human and Electronic* (Plenum, New York and London, 1973), pp. 49–50.

[6] Robert M. Boynton, *Human Color Vision* (Holt, Rienhart and Winston, New York, 1979), p. 51 This misleading statement is repeated in Peter K. Kaiser and Robert M. Boynton, *Human Color Vision*, 2nd ed. (Optical Society of America, Washington, DC, 1996), p. 6.

[7] Robert M. Boynton, ''Human color perception,'' in *Science of Vision*, edited by K. N. Leiboveic (Springer-Verlag, New York, 1990), p. 218.

[8] David K. Lynch and William Livingston, *Color and Light in Nature* (Cambridge UP, Cambridge, 1995), p. 222.

[9] Laurie White, *Infrared Photography Handbook* (Amherst Media, Amherst, New York, 1996), pp. 28–32.

[10] Robert Sekuler and Randolph Blake, *Perception*, 3rd ed. (McGraw-Hill, New York, 1994), p. 201.

[11] Several confusingly similar sounding but distinct spectral radiometric quantities: spectral radiant power; spectral radiant emittance; spectral irradiance; spectral radiant intensity; and spectral radiance are all employed to describe spectral density distributions. They differ in whether or not they are intensities per unit area, per unit solid angle, both together or neither one, and whether the radiation is emanating from an emitter or impinging on a surface. Many of the papers we quote from, and refer the reader to, do use these different quantities for their purposes, and make the errors we describe using them. As these quantities are all are spectral densities, i.e., quantities per unit bandwidth interval, e.g., per unit wavelength interval or per unit frequency interval, they all illustrate the argument of this paper equally well. They all suffer exactly the same peak shifts and distortions that we describe. For the thesis of this paper we may normalize these quantities by setting all areas and solid angles equal to one and use all of these terms interchangeably without fear of spoiling our argument. Furthermore, for the purposes of this paper we make all powers relative and normalize them as well. Separate from the thesis of this paper, however, it should be pointed out that in spite of the efforts of many international committees to standardize the polyglot nomenclature of radiometry and photometry, not many seem to abide strictly by the naming standards. The confusion in the set of quantities that are intensities per unit area is even more than a matter of naming them, as some authors use projected area, including the cosine obliquity factor, and some others, using the same nomenclature, do not. All this is yet another reason to exclaim *CAVEAT LECTOR.*

[12] Gail P. Anderson *et al.*, ''MODTRAN2: Evolution and applications,'' Proc. SPIE **222**, 790–799 (1994).

[13] Stanley Thomas Henderson, *Daylight and its Spectrum* (American Elsevier, New York, 1970).

[14] D. B. Judd and G. Wyszecki, *Color in Business, Science and Industry*, 3rd ed. (Wiley, New York, 1975), p. 71. We reluctantly introduce the photometric quantity relative ''luminous efficiency'' at this point only because the vision literature to which we refer the reader, almost exclusively, uses it to describe the eye's sensitivity. It is the perceptual sensitivity of human photopic, or cone vision to quasimonochromatic light, relative to its maximum sensitivity, usually as a function of wavelength, represented by the fictitious eye of a standardized observer. It is a good practical model for the bright-light adapted eye and it is proportional to the spectral power sensitivity over a large gamut of power. It is not a density distribution function. We do not really need to consider, for the argument of this paper, the sophisticated subtleties of photometry, how many lumens per watt there may be, or even what a lumen might be. Older synonymous terms for luminous efficiency, still to be found, are ''visibility factor'' and ''luminosity factor.''

[15] Incidentally, human hearing, on the other hand, does have a physiologically preferred spectral representation. We have an intrinsic logarithmic spectral response to acoustic radiance. This can be appreciated by noticing that we associate essentially the same musical pitch and note ''name'' to all the n octaves (2^n multiples) of a given note's frequency. If we pick, for example, middle C$=256$ Hz, the frequency of the note one octave higher, by definition, is 512 Hz. We hear all those n higher octave notes, ignoring intensity-dependent effects, still as a kind of replica of C, although higher in pitch. In representing musical spectral power or noise density distributions, the very same representational issues that we have been discussing for optical power naturally arise. But here, if the intention is to represent human perceptual hearing, then the logarithmic representation is clearly to be preferred and thus, by settling on it, many of the representational pitfalls and paradoxes can be avoided. Audio engineers have introduced several spectral logarithmic measures and quantities. For example, the logarithmic equivalent of equally distributed, or so-called ''white,'' noise is called appropriately ''pink'' noise. It preferentially weights the lower frequencies logarithmically, thereby putting equal noise power into each octave. To the ear, pink noise sounds uniformly distributed.

[16] Frank Benford, ''Laws and corollaries of the black body,'' J. Opt. Soc. Am. **29**, 92–96 (1939). He solved for the maximal power, relative to the total radiated power, in the neighborhood of a given wavelength of interest, λ_M, at which the absorption (or sensitivity) is highest. In the wavelength representation this occurs when $\lambda_M T_M = 0.3666$. Note that the optimum wavelength, for a given temperature, does not coincide with the peak of the Planck distribution. Benford was the same person whose name has come to be associated what is variously referred to as the ''Dirty [first pages of the] Logarithm Table Phenomenon,'' ''the Anomalous Distribution of First Digits,'' or more usually ''Benford's Law,'' though this empirical law may have been first noticed at least a century ago by Simon Newcomb [Am. J. Math. **4**, 39–40 (1881)]. See Frank Benford, ''The Law of Anomalous Numbers,'' Proc. Am. Philos. Soc. **78**, 551–572 (1938). The first digits of naturally occurring numbers, such as of the physical constants, expressed in scientific or floating point notation, are not distributed uniformly randomly as naively might be expected, but rather they have the ubiquitous reciprocal, or inverse probability density distribution. This is all the more pronouncedly so, when many disparate kinds of quantities are examined all together. The integrated cumulative probability is thus logarithmic, and, by subtraction, the probability of a first digit N occurring is $\log(N+1) - \log N$, favoring small Ns. Many theoretical and empirical studies of this law have been published, but one simple and direct way of proving and appreciating it is to realize that the inverse probability density distribution, with its strong fractal invariance properties, satisfies the requirement of being independent of the arbitrary choice of scale or units, and the base or modulus, that the numbers are expressed in. Benford's Law is thus seen to be a property of our number system.

Those with a taste for paradox will savor this result and many may be tempted to make wagers with the unwary.

[17]Veronika A. Szalai and Gary W. Brudviig, ''How plants produce dioxygen,'' Am. Sci. **86**, 542–551 (1998).

[18]Project Cyclops CR 114445, revised ed., NASA/Ames Research Center, Moffett Field, California, 1973, p. 41.

[19]Boynton, Ref. 6.

[20]Albert Rose, Ref. 5, p. 50.

[21]V. I. Krasovsky, N. N. Shefov, and V. I. Yarin, ''Atlas of the airglow spectrum 3000–12400 Å.,'' Planet. Space Sci. **9**, 883–915 (1962).

[22]M. H. Pirenne, ''The thermal radiation inside the eye and the red end of the spectral sensitivity curve,'' J. Physiol. (London) **106**, 25 (1947); or Proc. Physiol. Soc. **106**, 25 (April, 1947). Pirenne's old numerical estimates differ markedly from Rose's analysis.

[23]S. Duke-Elder, *The Eye in Evolution* (C. V. Mosby Co., St. Louis, 1958), p. 619.

[24]Ricardo C. Pastor, Hiroshe Kimura, and Bernard H. Soffer, ''Thermal stability of polymethine *Q*-Switch solutions,'' J. Appl. Phys. **42**, 3844–3847 (1971).

[25]Ricardo C. Pastor, Bernard H. Soffer, and Hiroshe Kimura, ''Photostability of polymethine saturably absorbing dye solutions,'' J. Appl. Phys. **43**, 3530–3533 (1972).

[26]M. A. Ali, ''Temperature and vision,'' Rev. Can. Biol. **34**, 131–186 (1975).

[27]See, e.g., A. Knowles and H. J. A. Dartnall, in *The Eye*, edited by Hugh Davson, 2nd ed. (Academic, London, 1977), Chap. 8.; and Boynton, in Ref. 6, pp. 104, 107.

[28]Frederick J. G. M. van Kuijk, ''Effects of ultraviolet light on the eye: Role of protective glasses,'' Environ. Health Perspect. **96**, 177–184 (1991).

[29]James K. Bowmaker, ''The evolution of vertebrate visual pigments and photoreceptors,'' in *Vision and Visual Dysfunction*, edited by John R. Cronly-Dillon and Richard L. Gregory (CRC, Boca Raton, 1991), pp. 63–81.

[30]V. I. Govardovskii and L. V. Zueva, ''Spectral sensitivity of the frog the in the ultraviolet and visible region,'' Vision Res. **14**, 1317–1321 (1974).

[31]Bernard H. Soffer and David K. Lynch, ''Has evolution optimized vision for sunlight?,'' Annual Meeting of the OSA, Long Beach CA, 12–17 October 1997, SUE4, p. 70; David K. Lynch and Bernard H. Soffer, ''On the solar spectrum and the color sensitivity of the eye,'' Optics and Photonics News, March, 1999; Bernard H. Soffer and David K. Lynch, ''The spectral optimization of human vision: Some paradoxes, errors and resolutions,'' *Trends in Optics and Photonics*, edited by Toshimitsu Asakura, International Commission for Optics Book 4 (Springer-Verlag, Heidelberg and New York, 1999).

LECTURING STYLE

There was something about Professor Turgot that I found immensely appealing. He was a big bearlike man, fortyish, beginning to bald, stoop-shouldered, whose shirttails always drooped down behind him. He was not at all the absentminded professor. He could fix me and all I was thinking with one eagle glance. When he lectured in the classroom, he addressed the blackboard rather than his students, as if he were having a private conversation with some mythical being living in the world he had created in equations and diagrams. I knew that this lecturing style was deficient, but it conveyed a lifelong fascination with his subject.

Alan Lightman, *Dance for Two* (Pantheon Books, New York, 1996), p. 163.