Electrodynamics of visible-light interactions with the vertebrate retinal rod

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Received December 21, 1992

We report the initial investigation of the electrodynamics of visible-light interaction with the outer segment of the vertebrate retinal rod based on detailed, first-principles computational electromagnetics modeling. The computational method employs a direct time integration of Maxwell's equations in a two-dimensional space grid for both transverse-magnetic and transverse-electric vector-field modes. Detailed maps of the optical standing wave within the retinal rod are given for three illumination wavelengths: 714, 505, and 475 nm. The standing-wave data are Fourier analyzed to obtain spatial frequency spectra. Except for isolated peaks, the spatial frequency spectra are essentially independent of the illumination wavelength.

For many years there has been interest in the optical properties of photoreceptors. 1-6 These studies addressed a variety of questions concerning the optical functioning of the photoreceptors. The goal of the research reported here differs from the earlier studies in at least one important aspect: We have sought to understand the interaction of the photoreceptor with light from a fundamental electrodynamics perspective. Our working hypothesis is that the detailed physical structure of a photoreceptor impacts the physics of its optical absorption and, thereby, vision. In this Letter we consider one such photoreceptor, the vertebrate retinal rod. The bulk structure of the retinal rod exhibits the physics of an optical waveguide, while the internal disk-stack periodic structure adds the physics of an optical interferometer. These effects combine to generate a complex optical standing wave within the rod, thereby creating a pattern of local intensifications of the optical field.

We employ a robust direct time-integration approach for Maxwell's vector-field equations, implemented on a two-dimensional space grid, to obtain the electrodynamics of the retinal rod at optical frequencies. The computational approach, designated as the finite-difference time-domain (FD-TD) method, 7-10 employs second-order accurate spatial central differences and leapfrog time stepping to implement the space and time derivatives of Maxwell's time-dependent curl equations. FD-TD is a highly efficient means to model full-vector impulsive or sinusoidal electromagnetic wave interactions with arbitrary one-, two-, or three-dimensional inhomogeneous material structures. Originating from defense applications in the radar cross-section area, FD-TD is becoming widely used for modeling radio frequency and microwave scattering, penetration, and radiation interactions with industrial and biomedical structures of realistic complexity.

Recently, the range of FD-TD modeling of electromagnetic wave interactions has been expanded to linear and nonlinear dispersive optical materials and structures, including linear opticaldirectional couplers¹¹ and femtosecond optical pulses and solitons. 12,13 The upper-frequency bound of FD-TD modeling (equivalently, the lower bound on grid cell size) is predicated by the proper incorporation of quantum effects into the macroscopic $\chi^{(1)}$ susceptibility function that relates the Maxwell displacement flux D to the electric field E as a function of frequency ω .

In our study we have implemented two separate two-dimensional models of the isolated outer segment of the retinal rod; a traverse-magnetic (TM) model and a transverse-electric (TE) model. The TM model involves the vector-field mode having H_x and H_y as the magnetic-field unknowns and E_z as the electricfield unknown, while the TE model involves the mode having E_x and E_y as the electric-field unknowns and H_z as the magnetic-field unknown. For both models, the optical excitation is a monochromatic incident plane wave propagating in the +y direction parallel to the major axis of the rod, which is assumed to be infinite and unchanging in the z direction. Three different free-space optical wavelengths λ_o have been investigated: 714 nm (red), 505 nm (green), and 475 nm (blue). The rod is assumed to have cross-section dimensions of 2000 nm \times 20,000 nm, ¹⁴ corresponding to $(3.8-5.7\lambda_d) \times (38-57\lambda_d)$ over the range of wavelengths used in the model, where λ_d is the optical wavelength within the rod's dielectric media.

A uniform Cartesian space grid having 5.0 nm × 5.0 nm unit cells is utilized in the computational model. This provides a wavelength resolution of $\lambda_d/70$ to $\lambda_d/105$, depending on the incident wavelength. The overall grid includes 2.1×10^6 cells, corresponding to 6.3×10^6 vector-field unknowns. Reliable

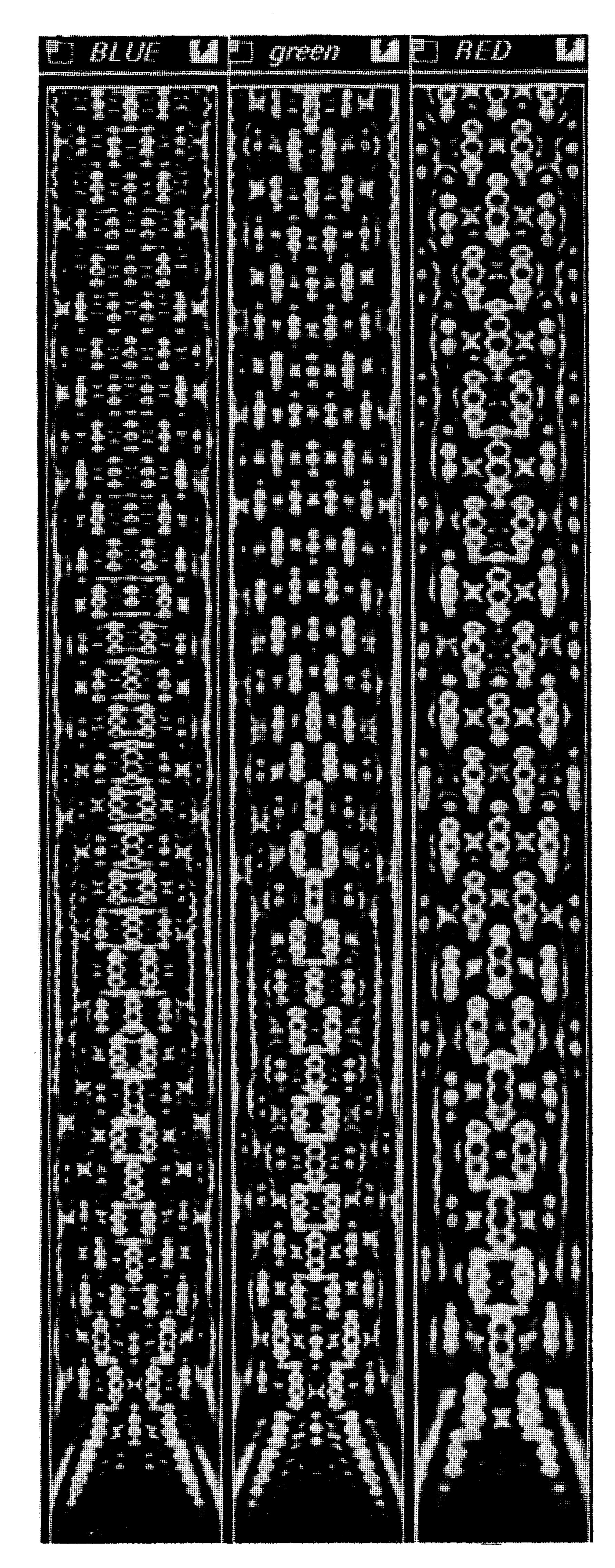


Fig. 1. Visualization of the magnitude of the electric-field values of the optical standing wave within the retinal rod for TM illumination relative to 1 V/m incident at 475, 505, and 714 nm. White areas, standing-wave peaks; dark areas, standing-wave nulls. The maximum amplification for the TM mode is 2.3.

second-order radiation boundary conditions⁹ are implemented at the outer grid boundaries to simulate the rod embedded in an infinite fluid region. Thus any computed wave reflections are virtually exclusively due to interface effects within and at the surface of the rod. There is little contribution to the computed optical standing wave owing to reflections from the outer grid boundary.

The 5-nm resolution of the space grid permits detailed modeling of the 15-nm-thick outer wall membrane of the rod and the 15-nm-thick internal disk membranes. There is assumed to be 799 of the latter distributed uniformly along the length of the rod, separated from each other by 10 nm of fluid and separated from the outer wall membrane by 5 nm of fluid. The index of refraction for the membrane n_m was chosen to be 1.43, and the index of refraction for the fluid n_f was chosen to be 1.36, in accordance with generally accepted physiological data.

The computational procedure involves launching a sinusoidal plane wave of the desired optical frequency in the +y direction and integrating Maxwell's equations in time as the wave penetrates the rod, propagates all the way to its back end (maximum y coordinate), rebounds, and propagates all the way to its front end (minimum y coordinate), rebounds again, and then repeats the front-to-back-to-front traversal one additional time. It should be understood that electromagnetic wave diffraction in all directions in the x-y plane is computed during this process in accordance with Maxwell's equations. At the conclusion of the time integration, the standing wave of the time-dependent optical electric field is obtained. Convergence studies involving extension of the integration period to allow a variable number of front-to-back-to-front traversals of the wave have been conducted and indicate that the sinusoidal steady state is essentially achieved after the first two complete traversals. Approximately 1.6 h of singleprocessor Cray Y-MP time is required to model one such integration at the 505-nm incident wavelength.

Figure 1 is a visualization of the computed magnitude of the normalized electric-field values of the optical standing wave within the retinal rod for TM polarization at $\lambda_o = 714$, 505, and 475 nm. A similar visualization is observed for TE polarization. To assist our understanding of the physics of the retinal rod as a complex optical waveguiding structure, we performed the following reduction of the standingwave magnitude data at each λ_o . First, at each transverse plane located at a given yo in the rod, we integrated the electric-field values $E(x, y_o)$ of the optical standing wave over the x coordinate to obtain a single number, $E_{int}(y_o)$. Second, we performed a discrete spatial Fourier transform of the resulting distribution $E_{\rm int}(y)$ over the y coordinate. The results are shown in Fig. 2 for the TM case and in Fig. 3 for the TE case. With the exception of isolated peaks unique to each λ_o , the spatial frequency spectra for each polarization are essentially independent of

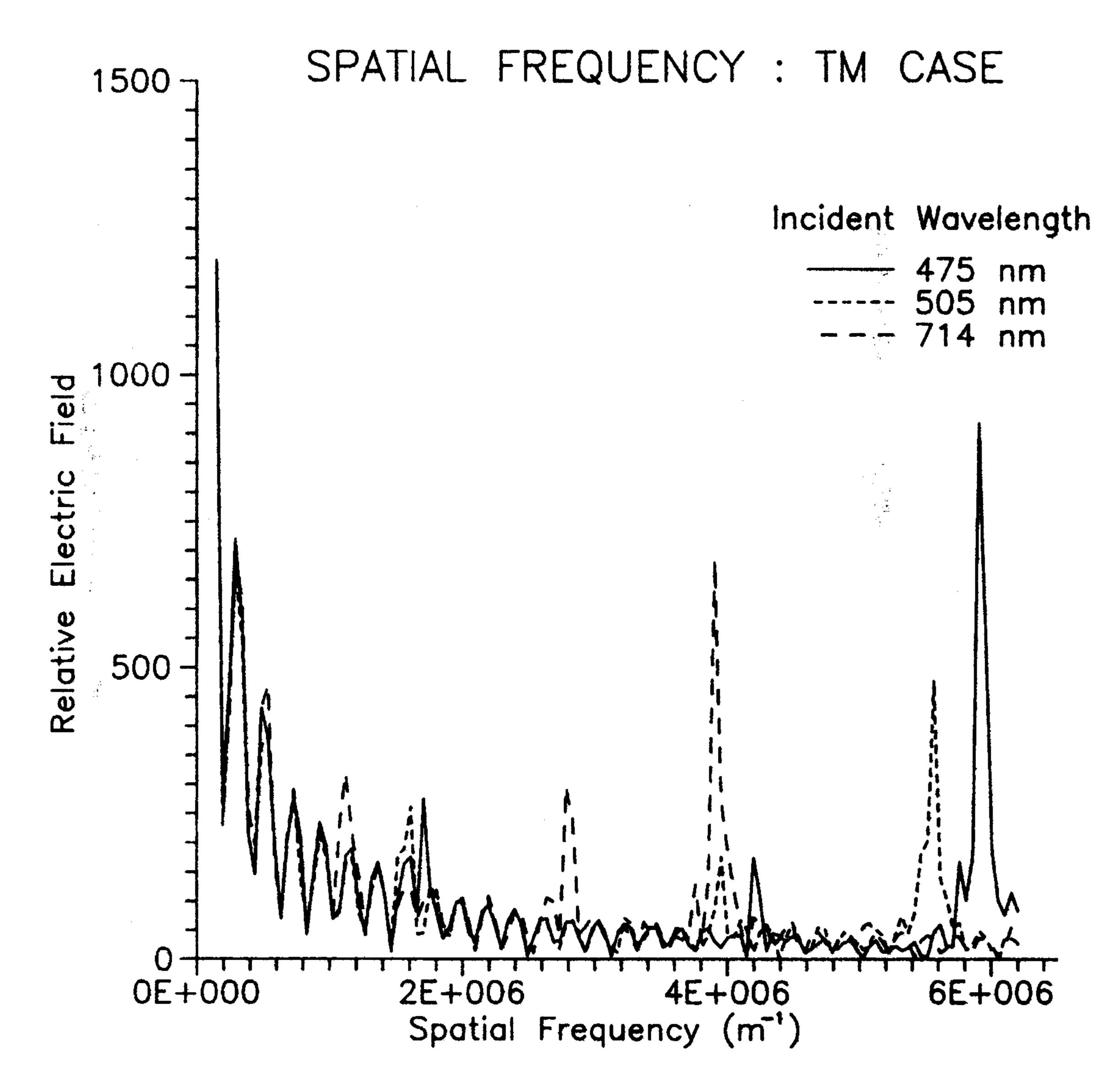


Fig. 2. Spatial frequency spectra of the transverse integrated optical standing wave for TM illumination at 714, 505, and 475 nm.

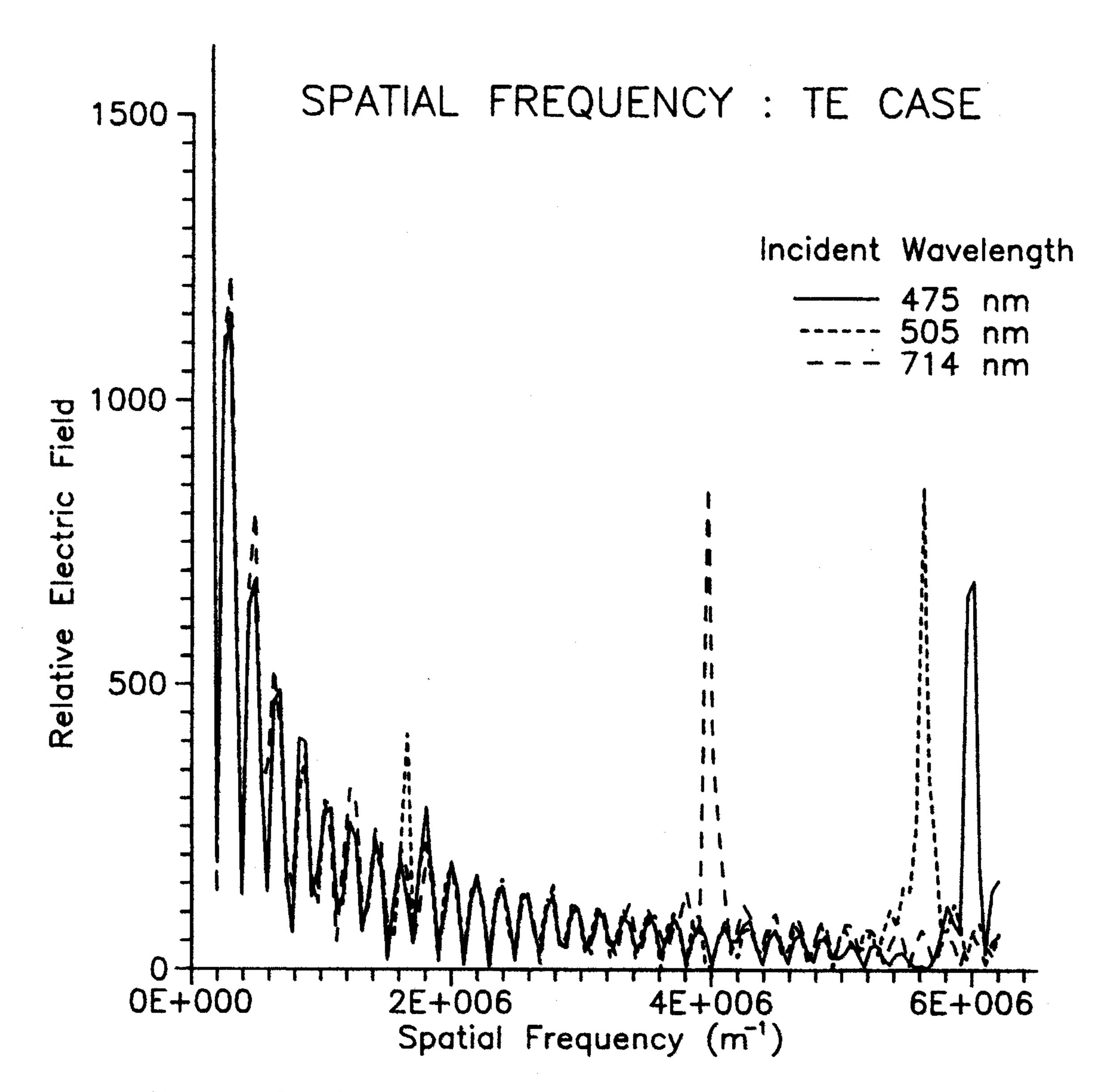


Fig. 3. Spatial frequency spectra of the transverse integrated optical standing wave for TE illumination at 714, 505, and 475 nm.

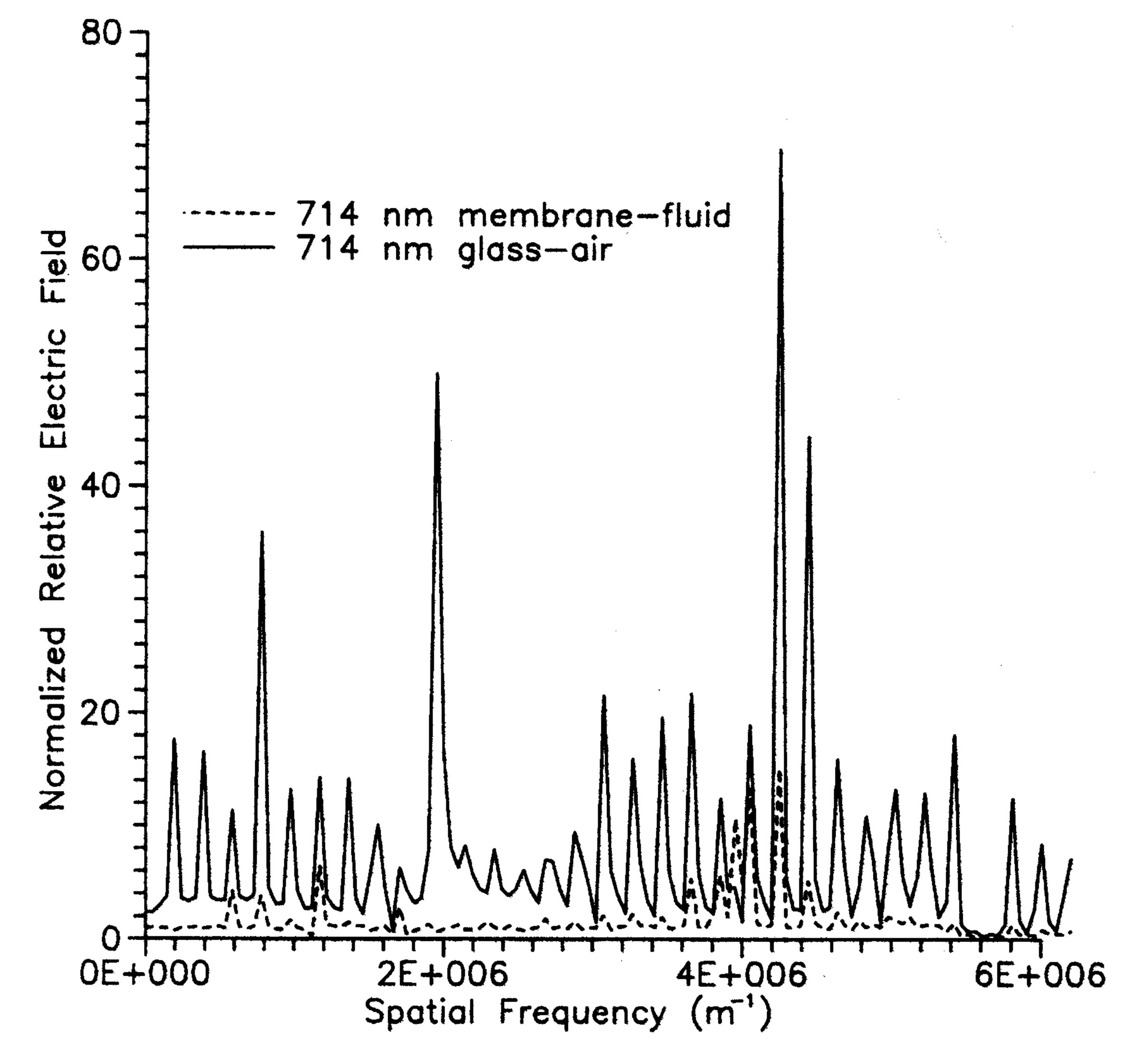


Fig. 4. Spatial frequency spectra for the membrane-fluid structure and the glass-air structure at 714 nm normalized to the spatial frequency spectrum of the respective structures at 505 nm.

the illumination wavelength. The retinal rod thus appears to exhibit a type of frequency-independent electrodynamic behavior.

The agreement of the spatial frequency spectra for the three incident wavelengths for each polarization was so remarkable that we tested our overall procedure for computational artifacts. The test involved perturbing the indices of refraction of the membrane and fluid from those of the vertebrate rod to those of glass and air. Figure 4 graphs the spatial frequency spectra at $\lambda_o = 714$ nm for the membrane-fluid structure and the glass-air structure, as normalized to the spectrum of the respective structures at $\lambda_o = 714$ nm for the membrane-fluid

505 nm. We see that the normalized glass—air spectrum exhibits little correlation, i.e., numerous sharp high-amplitude oscillations over the entire spatial frequency range considered. On the other hand, the normalized membrane—fluid spectrum varies in a tight range near unity through spatial frequencies of 3.6×10^6 m⁻¹. We conclude that the agreement of the spatial frequency spectra for the vertebrate retinal rod indicates a real physical effect that is dependent on the proper definition of the indices of refraction of the components of the rod structure.

The observed independence of the spatial frequency spectrum of the optical standing wave within the retinal rod structure relative to λ_o supports the hypothesis that the electrodynamic properties of the rod contribute little if at all to the wavelength specificity of optical absorption. From an electrical engineering standpoint, frequency-independent structures have found major applications in broadband transmission and reception of radio-frequency and microwave signals. There is a limited set of such structures, and it is always exciting to find a new one. We speculate that some engineering application of frequency-independent retinal-rod-like structures may eventually result for optical signal processing.

We thank M. Friedman for his initial suggestion to investigate computationally the electromagnetic properties of the vertebrate retinal rod. We thank P. Anvin for assisting in the visualization and A. Komaromi for assisting in the data reduction. This study was supported by National Science Foundation grant ASC-8811273, Office of Naval Research contract N00014-88-K-0475, and Cray Research, Inc.

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