Coupling electrodynamic fields to phonons in helical structures

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Helical structures like alpha helices, DNA, and microtubules have profound importance in biology. It has been suggested that these periodic arrangements of the constituent units could support collective excitations similarly to crystalline solids, which display a continuous spectrum and localized excitations. Here, we examine the interaction between such constructs and oscillating dipoles, and evaluate the role of the helical structure in the coupling between electrodynamic fields and phonons. Based on an eigenfunction analysis, we found that the helical configuration couples the azimuthal and axial degrees of freedom of the modes, which, in turn, leads to a discrete spectrum and delocalized excitations. Quasistatic eigenpermittivities are usually negative but we show here that in the case of anisotropic structures with cylindrical symmetry they are positive. This suggests a strong electrodynamic response in naturally occurring structures such as microtubules. The new type of dielectric quasistatic resonances identified here may help explain the role of electrodynamic fields in the diverse functionality of cytoskeletal microtubules in the cellular environment.

Microtubules (MTs) are tubular helical structures that self-assemble from their constituent tubulin-protein units. MTs are critical for the development and maintenance of the cell shape, transport of vesicles and other components throughout cells, cell signaling, division, and mitosis. Because of their distribution of charges and the large dipole moments associated with tubulins [1], the microtubules have unique electric properties, which may affect the interactions with surrounding molecules, also beyond the common short-range Coulomb and van der Waals interactions [2].

It has been conjectured that due to the large dipole moment of tubulins [3,4], MT vibrations could generate electric field in its vicinity [5-7]. The source of energy for this process could be the hydrolysis of GTP, motor proteins that move along the microtubule, and energy released from the mitochondria [6]. Microtubules were also analyzed in the context of robust-edge topological vibrational modes [8] and their vibrational modes were calculated using a hollow-cylinder model [9].

MTs have a highly regular helical shape that is very rare in nature. Their constituent units are identical, even more than in DNA and alpha helices, whose elementary units have different residues. It is certainly of interest to understand how this exquisite geometry may affect various oscillatory phenomena of MTs such as vibrations and electromagnetic excitations. This would obviously relate to microtubules absorption and emission properties as well as to their ability to couple with external fields. In a broader sense, one can ask if this property is critical for the diverse functionality of MTs in biology. The unique helical structural, which appears like a shifted crystal, and the electrical properties of the MTs may suggest that electromagnetic field can couple to phonons across a microtubule. Of particular interest would be to understand if surrounding molecules could excite phonons in the helical structure and if the structure modes have any particular extent and frequency properties.

In the following, we attempt to answer these questions to some extent by developing an eigenfunction analysis for the interaction between a microtubule and an oscillating point dipole in a host medium via phonons. To that end, we consider a dielectric structure consisting of units disposed in a helical arrangement and embedded in a host-medium. These units can vibrate in a collective manner and have internal vibrational and electronic excitations. We consider a dipole in proximity to this structure that emits radiation with a wavelength much larger than the relevant length scales and therefore the interaction can be analyzed in the quasistatic approximation. In this regime, the electric and magnetic fields are decoupled and the electric field, which oscillates in time, obeys Poisson’s equation [10-12]. In the case of an infinitely long helix, the relevant length scales are the diameter of the helix and the distance between the dipole and the helix, which are usually of the order of tens of nanometers. The excitation wavelength is assumed to be at least hundreds of nanometers. In these circumstances, we derive the eigenfunctions that couple to axial helical vibrations. To model such vibrations, we assume an anisotropic permittivity inside the inclusion and calculate the eigenpermittivities.

In our formulation, an eigenstate of the quasistatic potential couples to longitudinal vibrations of the structure. We assume that each protafilament behaves as a one-dimensional crystal. In order to have a synchronic motion in the helical structure laterally adjacent units are required to move together or, in other words, the protafilaments are non-interacting. To impose this movement, we require that the eigenfunctions will be symmetric to continuous translation along a helical orbit. As detailed in Supplementary Material (SM) Sec. 1, this means that the eigenfunctions will be of the form

\[ \psi_m = \frac{1}{\sqrt{A_{1m}K_m}} \frac{A_{1m}K_m}{A_{2m}I_m + A_{3m}K_m} \begin{cases} \rho > \rho_2, \\
\rho_2 < \rho < \rho_1, \\
\rho < \rho_1 \end{cases} \]

where \( \phi, z, \rho \) are cylindrical-coordinates variables, \( K_m \) and \( I_m \) are the modified Bessel functions, \( \rho_1, \rho_2 \) are the internal and external inclusion radii and the ‘\( \ell \)’ symbol denotes ‘or’. Note that upon continuous translation along a helical orbit \( \psi_m \) remains constant i.e., \( \hat{R} \psi_m = \psi_m \), where \( \hat{R} \) is the translation operator, and therefore the eigenvalue of \( \psi_m \) is 1. Invariance of the potential to discrete lateral translations along the helix results in the same potential distribution in each constituent unit and coordinated movement. Such modes have high spatial frequencies characterized by \( k_d b \), where \( b \) is the number of units per helical round. In principle, these modes can be excited when the
dipole is very close to the helical structure (typical interaction distance is $2\pi/k_{\rho} b$) and the field impinging on the structure has very high spatial frequencies.

Figure 1: The physical system: an oscillating dipole emitting electromagnetic fields is placed in the proximity of a microtubule composed of tubulin dimers. Part of the electric field couples to phonons in the microtubule (a). There are two possibilities for the configuration of the coupled field with respect to the units of the helical structure: helical arrangement (b) and standard longitudinal arrangement (c). In response to the field, the tubulins deform and translate such that tubulin movement synchronously (d) or asynchronously (e), a situation less favorable energetically.

Microtubules are composed of tubulin dimers disposed in a helical arrangement as depicted in Fig. 1 (a). The electric field can be in a helical and standard longitudinal arrangements relative to the constituent units, as suggested in Fig. 1 (b) and (c). After the field is applied, the tubulin units can change their size and move as shown in (d) and (e), respectively. In a helical field arrangement, laterally adjacent units will move together. Also when they move together, they generate field in a helical arrangement. The movement with adjacent tubulins that are not aligned as in Fig. 1(e) is less favorable energetically compared with the aligned state in Fig. 1(d), and therefore in this situation the movements will be damped considerably. Tubulins have large dipoles moments [2] and we examine which mode couples to their oscillation. To that end, we model the tubulin dipoles by placing charges with alternating signs at $k_{\rho} x = \frac{3\pi}{4}, \frac{5\pi}{4}, \frac{7\pi}{4}$ and observe that they oscillate in response to the $m = 1$ cosine mode. This mode is therefore expected to be dominant.

We note that the form of the eigenfunctions in Eq. (1) is similar to that of a subgroup of terms in a simpler case of the electrostatic potential generated by charges in a helical arrangement in DNA with a uniform permittivity inclusion [14]. Our system is much more complex as the inclusion (the MT construct) is anisotropic, charge-free, and composed of many atoms. We also consider excitations of vibrations by electrodynamic field. In Ref. [14] the potential expansion includes solutions of Laplace’s equation in cylindrical coordinates that are invariant to discrete lateral translations and solutions of Poisson’s equation to account for the net charge. In the present case, we assume that the constituent units cannot move laterally. In addition, since the eigenstates are polarization states we only have solutions of Laplace’s equation and not a potential that is generated by a charge distribution inside the inclusion.

Let us now analyze the scaling of $\psi_{m}$ for small and large radial arguments. Since

$$\lim_{x \to 0} K_{m}(x) = \begin{cases} \frac{\Gamma(n)}{2} & m = 0 \\ \frac{\ln(\frac{x}{2}) + 0.5772}{2} & m \neq 0 \end{cases}$$

and the potential is finite, the $m = 0$ mode, for which $x \to 0$, is associated with $l_{m=0}(x)$ and is constant everywhere and therefore can be omitted. However, this mode plays a role in the full electrodynamic analysis that is relevant for the far field. From the full electrodynamic solution for an infinite cylinder [15] it can be seen that $k = m = 0$ and $\rho_{2} \ll k$ the dominant term outside the helical inclusion has the form

$$E_{z} TM_{m=0} \propto k H_{0}(k p), \quad H_{0}(k p \gg 1) = \frac{2}{\pi k p} e^{ik p p / 4},$$

where $k = \omega / c$. Interestingly, this mode extends far from the helical structure with a $\sqrt{k/\rho}$ magnitude scaling.

Now we examine the scaling of the $m \geq 1$ modes. For $p \gg a$

$$a \lim_{p \to a} K_{m=1}(p) = \frac{1}{\sqrt{2mk_{\rho}}} \sqrt{\frac{2}{\pi}} e^{-mk_{\rho}p},$$

from which one can see that the typical interaction distance is of the order of the size of the axial period. Inside the microtubule, the modes scale like

$$\lim_{x \to 0} l_{m}(x) = \frac{1}{\Gamma(n+1)} \left( \frac{mk_{\rho}}{2} \right)^{n}, \quad \Gamma(n) \sim (n - 1)!$$

Importantly, the modes are discrete and the $m = 1$ modes are dominant for $p_{0} - p_{2} > 1/k_{\rho}$, where $p_{0}$ is the dipole radius. This means that the helical structure is highly selective in $k$. Since each $k$ is associated with an eigenpermittivity (see SM, Sec. 2), and the physical permittivity depends on $\omega$, it implies high selectivity in frequency. In addition, when a constituent unit is situated outside the helical structure, the $m = 1, 2$ modes spatially match the tubulin dipoles, which may indicate spatial selectivity. The fact that the modes are well separated in $k$-space implies also delocalization. Similar properties have been recently observed in DNA [16]. While the DNA structure is quite different from that of microtubules, its backbone is helical and the coupling of the field to phonons can be via the same form of eigenfunctions. Interestingly, the singularities in the electronic density of states and their energy separations for an armchair carbon nanotube attached to a substrate, which resembles the MT, are discrete in energy [17]. While this requires quantum-mechanical treatment, it would make sense that helical field patterns drive transitions between these electronic states.

Let us briefly analyze additional forms of vibrations. Radial movements are expected to be damped due to the environment [6] since they involve movements of a relatively large volume of liquid. While the vibrations of helical structures are different from vibrations of a spring, a spiral motion may also be less favorable mechanically since it involves movements of long helical chains of dimers. Moreover, in the context of microtubules, the azimuthal dipole moment is small and at the macroscopic level the particles are identical along the helix, which usually relates to acoustical modes [18].

An eigenpermittivity is a permittivity of an inclusion of a composite medium for which the electric field can exist without a source [10-13]. For propagating waves, this requires gain and constructive interference in the inclusion as in laser. However, for evanescent waves the eigenpermittivities are real and can be approached more naturally [10], see SM Sec. 2. When the inclusion permittivity approaches an eigenpermittivity, the system responds resonantly. Eigenpermittivities are exact resonances since the imaginary part can also be incorporated in the physical parameter. This differs from eigenfrequencies for which only the real part can be realized. Finally, we note that an eigenpermittivity calculation is based on the geometrical properties of the system. At the same time, a bulk dispersion relation can be derived based on the interactions between the physical parameters of all constituents. A physical resonance occurs when both requirements are satisfied.

To analyze the eigenpermittivities and the form of the eigenfunctions in the region $p_{1} < p < p_{2}$, we assume that the inclusion behaves like a crystal and its permittivity can be expressed as $\varepsilon(\omega, k)$. In the case of a microtubule, this
form of $\epsilon(\omega, k)$ is justified because the period length $\alpha$ is 8nm and therefore $(\lambda_0/\alpha)^2 \gg 1$, where $\lambda_0 = c/\omega$ is the vacuum wavelength [19]. Note that in the derivation in Ref. [19] it is assumed that inside the inclusion $\rho_{\text{ext}}(\omega, k') = 0$, $J_{\text{ext}}(\omega, k') = 0$ where $k' = k_z + n k_x$, which is satisfied in our case since the charges in the tubulin and tubulin dimers oscillate only as a response to an external excitation and can therefore be defined as polarization [19,20]. Also, eigenstates are defined for the system without a source. Another argument is that for sources at distances larger than the typical interaction distance of the $m = 2$ mode, the $m > 1$ modes that are emitted from the dipole have a negligible effect on the polarization of the inclusion.

We further assume an anisotropic inclusion with an axial permittivity $\varepsilon_x$ and $\varepsilon_y = \varepsilon_z = \varepsilon$, where $\varepsilon$ is the host-medium permittivity and solve Laplace’s equation in cylindrical coordinates inside the anisotropic inclusion. This allows us to find the argument of the functions $I_{m\lambda}$ for $\rho_1 < \rho < \rho_2$ and then calculate the eigenvalues. Substituting the form of $\psi_m$ from Eq. (1), we write Laplace’s equation inside the inclusion

$$\varepsilon_2 \frac{1}{\rho} \frac{\partial}{\partial \rho} \left( \rho \frac{\partial \psi_m}{\partial \rho} \right) - \varepsilon_2 m^2 \frac{1}{\rho} \psi_m - k_z^2 \varepsilon_2 \psi_m = 0,$$  \hspace{1cm} (4)

and get

$$\psi_m = \cos(m(\phi - k_z z))/\sin(m(\phi - k_z z))F_m(km\rho),$$

$$F_m(km\rho) = \begin{cases} A_{2m}I_{m}(km\rho) & \rho > \rho_2, \\ A_{2m}I_{m}(km\rho) + A_{2m}I_{m}(km\rho) & \rho_1 < \rho < \rho_2, \\ A_{2m}I_{m}(km\rho) & \rho < \rho_1 \end{cases}$$

To obtain the contribution of a mode in the potential expansion, $\psi_{m\lambda}$ must be multiplied by $C_{m\lambda} \propto \psi_{m\lambda}(r_0)q$ for a point charge and $C_{m\lambda} \propto \psi_{m\lambda}(r_0)$ for a point dipole, and $4\pi \varepsilon_s s_{m\lambda} = e_{\lambda} s_{m\lambda}(k_0) = e_{\lambda}(k_0)$, and $e_{\lambda}(k)$ is the physical axial permittivity (see SM, Sec. 2). By imposing continuity of $E_\rho |_{D_1}$ one can calculate the eigenpermittivities $\varepsilon_{1m\lambda}$. To incorporate the time dependency we also multiply $\psi_m$ by $e^{i\omega t}$ and analyze the resulting waves. After normalizing $\psi_m$, it can also be shown that $A_{1m} \propto \frac{1}{K_{m2}(km\rho)}$, $A_{4m} \propto \frac{1}{K_{m2}(km\rho)}$.

**Figure 2** Normalized $K_m(\rho \rho)$ outside the microtubule. The interaction distance is of the order of the axial period of the helix.

In Fig. 2 we present the radial dependence of the first modes outside a microtubule. The modes have a typical interaction distance of the size of the axial period of the helix, which is larger than the Debye distance of 1nm [2], and the $m = 1$ mode dominates at large distances. Note that these functions have $m$ in the radial argument unlike the cylindrical modes. Two isopotential surfaces of $\psi_{m=1}(r)$ outside the helical structure are shown in Fig. 3. As can be seen, the mode dominates in sign and extends over distances of the order of $a$ away from the microtubule. When a dipole is at distances $\rho > a/4$, the most dominantly excited mode is $\psi_{m=1}(r)$. Since the modes are discrete, an excitation of several modes leads to spatially delocalized excitation as follows from simple Fourier Transform arguments.

To calculate the eigenpermittivities, we imposed continuity of $\phi$ and $D_z$ at the boundaries for the eigenfunctions in Eq. (5) (see SM Sec. 3). The resonances of the far-field mode in Eq. (3) depend on $\omega$ and can be obtained by requiring continuity of $E_\rho$ and $B$. In Fig. 4 (a) we present the eigenpermittivity ratios $\varepsilon_{1m\lambda}(k)/\varepsilon_s$ for the first quasistatic modes in Eq. (5). The host-medium permittivity $\varepsilon_s$ is assumed to be positive and the sign of $\varepsilon_{1m\lambda}(k)/\varepsilon_s$ equals the sign of $\varepsilon_{1m\lambda}(k)$. The damping of the vibrations by the environment is expected to introduce an imaginary part to the physical permittivity $\varepsilon_{1m\lambda}(\omega)$ and the resonances can be approached when the real parts of $\varepsilon_{1m\lambda}(\omega)$ and $\varepsilon_{1m\lambda}(\omega)$ are equal. In the quasistatic regime for a uniform inclusion or anisotropic permittivity in Cartesian coordinates, the eigenpermittivities are negative and correspond to plasmonic resonances [8-10, 16]. Interestingly, in our case the ratios $\varepsilon_{1m\lambda}(\omega)/\varepsilon_s$ is positive. This suggests that anisotropic cylindrical structures, which can occur naturally, exhibit evanescent-wave resonances similarly to polar materials, graphene, and metals [22-24]. In contrast, when these materials are infinitely long and have losses, they exhibit localized excitations [11,24] and non-selectivity in frequency. Our result is in accordance with the response expected from biological media, which is dielectric in nature. Note that this type of positive-permittivity resonance is relevant to all interactions (e.g., optics) in which the permittivity is anisotropic and in cylindrical coordinates. Note also that for a crystal $\varepsilon(k) = \varepsilon(k + mk_s)$ is expected that implies a more selective spectrum and that on the other hand the spectrum can be composed of several modes.

The modes become dominant at different permittivity ratios that correspond to different frequencies, which implies selectivity in frequency. Also, there is an asymptotic degeneracy of the high-order modes, which means that at close proximity to the helical structure several modes can be excited at once, leading to a strong response. The situation is similar to the accumulation point at $\varepsilon_{2m\lambda} = -\varepsilon_4$ for metal inclusions in a dielectric host medium [8-10]. For comparison, we also calculated the first eigenpermittivities for the longitudinal-cylindrical eigenfunctions (see Fig. 1(c)). In this case the spectrum is continuous and the eigenvalues are negative. The same behavior was observed for the high-order modes.

To exemplify the significance of the eigenpermittivity results we consider a system close to the $m = 1$ resonance at a frequency $\omega_{1z}$. For instance, if $\varepsilon_z(\omega_{1z}) = 80$ and $\varepsilon_1(\omega_{1z}) = 87 \pm 0.5\i$, it follows that $\varepsilon_1/\varepsilon_z \equiv \varepsilon_{1m1}/\varepsilon_z = 1.1$, and the $m = 1$ mode will dominate. In these conditions, at frequency $\omega_{1z}$ there will be a large collective response of the entire helical structure, which is likely to affect the MT functionality. These results for the eigenpermittivities depend on the dimensions of the structure (radii and $k_z$) and the mode contribution in the field expansion is subject to the physical value of the permittivity $\varepsilon_{1z}$ (see SM Sec 2). Since the size of the structure and
$\varepsilon_{1z}$ determine $\omega_1$, this resonant frequency may enable to distinguish between different helical structures. For example, the C-terminal tail of tubulins varies across species and is a target for post-transcription modification [26]. Since it is highly polar [25], it should modify the dispersion relation of the structure, thereby affecting $\varepsilon_{1z}$ and $\omega_1$.

![Diagram](image-url)

Figure 4 Eigenpermittivity ratios $\varepsilon_{1z}(k)/\varepsilon_2$ for helical (a) and cylindrical-longitudinal (b) eigenfunctions. The ratios for the helical eigenfunctions are positive and discrete and the ratios for the cylindrical-longitudinal eigenfunctions are continuous and negative. The illustrations show that $k = k_m m$ are allowed when imposing a helical field arrangement.

Incorporating the time dependency $\cos \omega t$, which is implicit in the expressions for the quasistatic potential, we obtain traveling potential waves of the form $\cos((\phi - k \cdot z) + \omega t) = \cos((k_z (z \pm \nu t) - \phi))$, $\nu = \omega/k_z$. This means that the field can be viewed as a standing wave or as composed of two traveling waves. Since the dipole is free to move, it is conceivable that the forces acting on the dipole due to the interaction with the helical structure will cause the dipole to move. We can use the traveling-wave description to analyze the motion of a dipole as a response to the field generated by a fixed dipole or by itself (it can be shown that the same arguments apply also for the second case). In order for a dipole to ride the wave that it generates it is required that $\omega = \nu k_z$. Thus, knowing the value of $\nu$ or $\omega$ will enable us to obtain the other. We calculate the thermal velocity of a tubulin dimer using Boltzmann distribution [27] $\langle \nu \rangle = \frac{2}{3} \sqrt{\frac{2 \varepsilon_2}{m}} \approx 2.7 \frac{\text{m}}{\text{s}}$, where $m$ is a tubulin-dimer mass. Then, since in order for the force to be dominant the velocity should satisfy $\nu \gg \nu_0$, we approximate the angular frequency as $\omega \gtrsim 2 \text{GHz}$. Importantly, this frequency is of the same order of magnitude of frequencies, which affect the MT function [28,29]. Interestingly, a recent work found that nanosecond pulses might affect the tubulin structure and its polarizability [25]. For completeness, we also calculate $E_{\text{res}}$. In the SM, Sec. 4 we show that the axial component dominates $E_z > E_y > E_\phi$, which means that the dipole will tend to align almost parallel to the helical structure.

In conclusion, we analyzed the effect of the helical arrangement of the constituent units of a structure on the coupling between the structure phonons and electromagnetic fields and oscillating dipole. In standard longitudinal modes there is no coupling between the spatial degrees of freedom (or the longitudinal and transverse modes) and the spectrum is continuous or close to continuous. Here, phonons are coupled to the electrodynamic field via helical eigenfunctions in which the $z$ and $\phi$ degrees of freedom are coupled. This results in a spectrum that is discrete and excitations that are delocalized. We note that a recent experiment has identified delocalized modes in DNA structures [16].

We found that the zero-order mode is long-range and has a $1/\sqrt{p}$ scaling while the other ones are helical and quasi-static with a typical interaction distance of the size of the axial period of the helical structure. At this short separation distance, a few modes dominate and, therefore, the structure has high frequency selectivity. In these circumstances, a single dipole oscillating at a resonant frequency can excite the whole structure and may affect its function. The fact that the spatial distribution of the $m = 1$ mode is correlated with the constituent units of a microtubule may imply spatial selectivity and be relevant for processes of self-assembly and induced polymerization. Quasistatic eigenpermittivities are usually negative [8-10, 16]. However, we found that for anisotropic constructs with cylindrical and helical symmetry, they are positive and correspond to dielectric resonances. This may suggest that naturally occurring structures such as microtubules have strong resonances associated with evanescent fields similarly to polar materials, metals, and graphene [22-24].

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