JPhys Photonics

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To cite this article before publication: Lea Gassab *et al* 2026 *J. Phys. Photonics* in press https://doi.org/10.1088/2515-7647/ae3ee8

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Optical Properties of the Cytoskeleton: A Review of Light-Matter Interactions, Quantum Effects, and Biological Implications

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Abstract. Traditionally viewed as a structural and motile framework, the cytoskeleton is now emerging as a platform for complex electromagnetic and optical interactions in the cell. In this review, we explore recent advances that position cytoskeletal filaments, particularly microtubules, not only as mechanical scaffolds but also as dynamic participants in light–matter interactions. We examine classical optical phenomena such as birefringence, dielectric anisotropy, and waveguiding, alongside growing experimental and theoretical evidence for quantum optical effects, including exciton transport, Fano resonances, and superradiance. These findings suggest that microtubules may support coherent energy transfer and exhibit collective electromagnetic behavior under physiological conditions. By integrating perspectives from biophysics, quantum biology, and cellular optics, this review highlights the potential of cytoskeletal systems to mediate biological photonic processes and inspire novel applications in biomedical imaging, nanophotonics, and quantum biomaterials.

1. Introduction

The cytoskeleton is a dynamic network of protein filaments that supports cellular structure, enables intracellular transport, and coordinates essential biological functions such as division, migration, and signaling [1, 2, 3, 4]. Although traditionally studied from a biomechanical perspective [5, 6], recent research suggests that cytoskeletal elements, particularly microtubules, may also exhibit significant electromagnetic and optical properties. This positions them as active mediators of light–matter interactions within living cells [7, 8].

Microtubules, composed of highly ordered arrays of α- and β-tubulin dimers [9, 10], exhibit several features conducive to optical activity: structural regularity, high dielectric contrast, and the presence of optically fluorescent aromatic residues

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such as tryptophan (Trp), tyrosine, and phenylalanine. These features enable classical interactions with light, including birefringence [11, 12], scattering, and waveguiding [13, 14]. The similarity of microtubules to engineered photonic structures has inspired models of the latter property of waveguiding, in which they act to guide and direct electromagnetic fields [15, 16]. Taken together, these optical and structural properties suggest that microtubules could support guided electromagnetic modes and excitonic energy transport on cellular length scales, positioning them as candidate architectures for nanoscale light transport and biological nanophotonic functions.

Experimental studies have shown that microtubules reorganize in response to specific light wavelengths [17, 18, 19, 20], and Raman spectroscopy has revealed light-induced conformational transitions in tubulin, such as an α-helix to β-sheet shift upon near-infrared exposure [21]. This evidence highlights the responsiveness of cytoskeletal proteins to photonic stimuli and suggests functional links between the cytoskeletal architecture and the optical environment.

Beyond classical optics, microtubules have also been proposed to support quantum optical phenomena. Theoretical and computational models suggest the possibility of exciton formation and migration [22, 23], quantum interference (e.g., Fano resonance [24]), and collective emission effects such as superradiance [25, 26]. Spectroscopic studies have even hinted at ultraviolet (UV) superradiant emission from Trp networks embedded in cytoskeletal proteins [27]. Kalra et al. have further demonstrated excitations with coherent length scales that outperform classical models [28]. These data raise the possibility that microtubules may facilitate coherent energy transfer or modulate quantum states relevant to cellular signaling.

This expanding body of research aligns with the broader field of quantum biology, which explores how phenomena such as quantum coherence, tunneling, and entanglement may influence biological processes [29, 30]. Once considered speculative, quantum effects have now been established in systems such as photosynthetic complexes and are increasingly being examined in the context of the cytoskeleton and neural signaling [23, 31]. Recent two-dimensional electronic spectroscopy and open-quantum-system simulations in light-harvesting complexes further demonstrate that long-lived excitonic coherences can enhance energy-transfer efficiency even under ambient, noisy conditions [32, 33].

In contrast to earlier reviews that have primarily focused on quantum coherence in photosynthetic complexes or on speculative links between quantum effects and brain function, our aim here is to provide a focused and data-driven account of optical and quantum phenomena in cytoskeletal structures, with an emphasis on microtubules. We bring together classical electromagnetic properties (refractive index, birefringence, and waveguiding), residue-level excitonic and superradiant models, and recent spectroscopic evidence (including quantum-yield measurements, diffusion lengths, and Fano line shapes), and we discuss how these ingredients constrain plausible quantum-mechanical scenarios in this specific biological context. In addition, we highlight concrete experimental observables and emerging quantum-technology tools that can discriminate

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genuine quantum-coherent or collective effects from purely classical photo-physical mechanisms in future work.

In this review, we synthesize current knowledge on the optical and quantum properties of cytoskeletal structures. Section 2 examines the structural architecture of the cytoskeleton. In Section 3, we explore how microtubules interact with light in the classical regime. Section 4 discusses their quantum properties, while Section 5 considers the biological implications of these phenomena. Section 6 addresses the experimental and theoretical challenges in identifying quantum properties in microtubules, and Section 7 outlines key open questions for future research. Finally, Section 8 concludes the review by summarizing the discussion.

2. Structural Architecture of the Cytoskeleton

The cytoskeleton is a complex but highly organized network of protein filaments that gives cells their shape, supports internal organization, and enables transport and movement. It is made up of three main components: microtubules, actin microfilaments, and intermediate filaments. Figure 1 summarizes this hierarchical organization in neurons, from the cellular architecture down to individual tubulin dimers and their aromatic residues.

Microtubules are rigid, tube-like structures about 25 nanometers in diameter, assembled from repeating units of α- and β-tubulin [34]. These tubulin dimers line up in a head-to-tail fashion, giving the filament a directional "polarity" that is essential for moving cargo in specific directions inside the cell [2, 35].

In mature neurons, microtubules are not organized by a central hub, like a centrosome, but instead form through localized assembly at sites such as Golgi outposts and endosomes [36, 37]. This decentralized system allows for precise control of microtubule orientation and growth throughout the cell. In axons, microtubules are generally aligned with their fast-growing ends pointing outward. Dendrites, in contrast, show a mix of orientations that supports bidirectional transport [4].

Microtubules are constantly switching between phases of growth and shrinkage, a behavior known as dynamic instability, which is driven by GTP hydrolysis on β-tubulin [34]. This dynamic nature is especially important at synapses, where temporary microtubule extensions can influence synaptic strength and the movement of receptors [38]. However, to maintain the stability and organization of the soma and main bodies of the axon and dendrites, microtubules are regulated by structural microtubule-associated proteins (MAPs). These MAPs bind along the microtubule lattice to modulate their assembly and spatial arrangement. In neurons, Tau and MAP2 are two key MAPs that help maintain compartment-specific cytoskeletal architecture [39]. Chemical modifications to tubulin, such as acetylation, detyrosination, or polyglutamylation, fine-tune the properties of microtubules. For example, acetylation of α-tubulin in lysine 40 increases resistance to mechanical stress, which helps to maintain the structure of long neuronal projections [35, 2, 40].

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Actin filaments are thinner and more flexible than microtubules. They are formed by the polymerization of globular actin (G-actin) into filamentous actin (F-actin) and are especially concentrated just below the plasma membrane [41]. Actin filaments support cell shape and form specialized structures such as filopodia, lamellipodia, and dendritic spines. At synapses, they interact with microtubules to coordinate structural changes and local transport [38].

The connections between the cytoskeleton and the plasma membrane are maintained by specific proteins, including spectrins, ankyrins, and members of the ERM family (ezrin, radixin, and moesin) [42, 43]. These proteins link cytoskeletal filaments to membrane proteins, helping to stabilize the cell surface and organize distinct regions of the membrane. In polarized cells such as neurons and epithelial cells, this organization is essential for function and may also influence how the cell responds to physical or electromagnetic cues.

The arrangement of cytoskeletal elements can produce unique structural patterns. In axons, for example, actin and spectrin form a repeating ladder-like structure with a spacing of around 190 nanometers [44]. This periodic architecture not only reinforces the axon's mechanical strength but may also shape how light travels through the intracellular environment by affecting refractive properties.

Intermediate filaments (IFs), such as neurofilaments in neurons and vimentin in glial cells, provide additional structural support. These filaments are less dynamic but form networks that help maintain the cell's shape and position organelles [3]. Recent studies suggest that, due to their density and arrangement, IFs may also play a role in modulating how light interacts with the intracellular space.

Altogether, the cytoskeleton forms a versatile and dynamic scaffold that underpins cell structure, movement, and intracellular organization. Its unique architectures and molecular diversity also create a complex physical environment that can shape how light behaves inside cells, which is an important consideration when exploring the optical properties of the cytoskeleton.

3. Classical Light-Matter Interactions in the Cytoskeleton

3.1. Electromagnetic Response of Microtubules

Microtubules, essential components of the cytoskeleton, display significant electromagnetic properties that allow them to interact with light in biologically meaningful ways. Key characteristics such as electric dipole moment, dielectric constant, and refractive index determine how they scatter, absorb, and guide light. In this subsection, we emphasize how specific optical and electromagnetic experiments interrogate and control microtubule behaviour through their interaction with incident fields. Tubulin dimers, the building blocks of microtubules, have strong permanent dipole moments, estimated to be up to 1740D, indicating their strong response to external electric fields [45]. Studies using techniques such as refractometry and surface plasmon resonance (SPR) have

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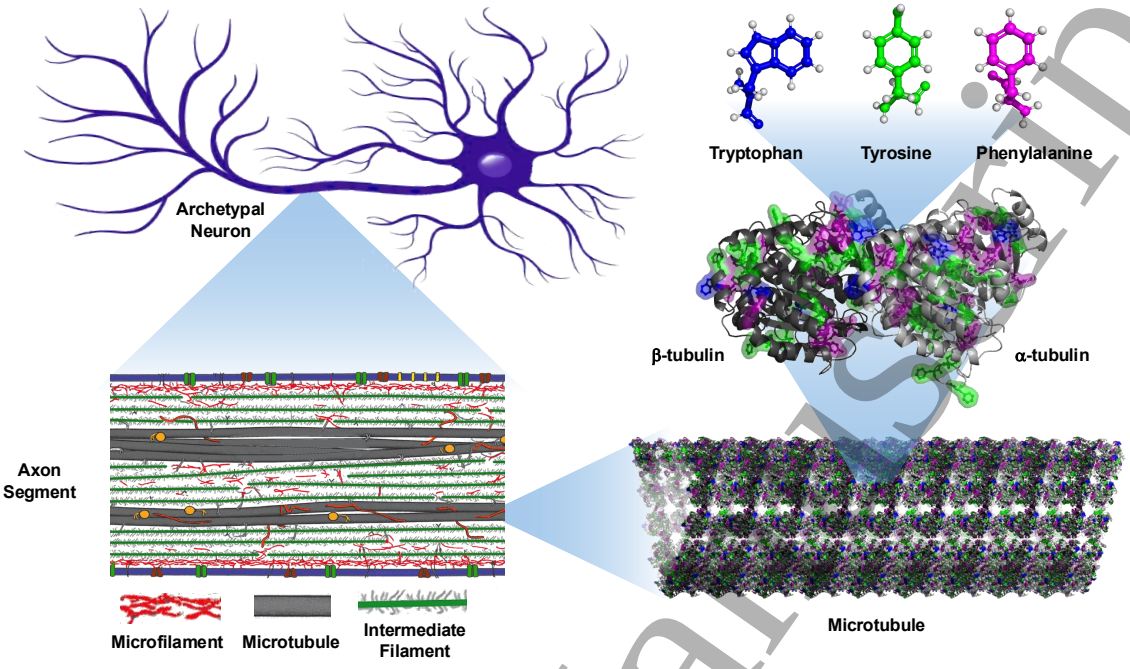

Figure 1. Multiscale organization of the neuronal cytoskeleton and aromatic chromophores in tubulin. A schematic of an archetypal neuron (upper left) emphasizes that microtubule bundles extend along neurites, motivating a multiscale "zoom-in" from the cellular level to the molecular building blocks. The neuronal cytoskeletal cartoon (lower left) places microtubules in the context of other filament systems (e.g., actin microfilaments, and intermediate filaments) and microtubule-associated proteins that regulate spacing, stability, and organization. Microtubules are a polymerized lattice (lower right) of the $\alpha\beta$-tubulin dimer protein (middle right). At the molecular scale (upper right), the main aromatic residues found in tubulin (i.e., tryptophan, tyrosine, and phenylalanine) form an extended, ordered/disordered chromophore network within the microtubule wall. This aromatic lattice provides the physical basis for UV absorption and intrinsic fluorescence, motivating models of excitonic energy transport and collective light–matter effects in microtubule assemblies.

shown that tubulin has a high refractive index ($n_{\mathrm{tub}} \sim 2.90$) and dielectric constant ($\kappa_{\mathrm{tub}} \sim 8.41$) [45, 46]. Similarly, a quantitative phase imaging-based microscopy approach found a high microtubule refractive index ($n_{\mathrm{MT}} \sim 2.36$ with corresponding $\kappa_{\mathrm{MT}} \sim 5.57$) [47]. While these results seem to be consistent, the high refractive index remains controversial with an additional experiment suggesting lower values ($n_{\mathrm{tub}} \sim 1.6$ with corresponding $\kappa_{\mathrm{tub}} \sim 2.56$) [48]. Regardless of the exact value, these values indicate that microtubules can act as nanoscale birefringent structures, capable of influencing how light moves through the cell. In the context of system–light experiments, these parameters are probed by directing well-defined optical fields onto tubulin solutions or microtubule layers and measuring their absorption, fluorescence, reflectivity, and phase retardation. As summarized schematically in Fig. 2, panel (a) corresponds to conventional solution spectroscopy, whereas panels (b) and (c) illustrate the refractometry/SPR and quantitative phase-imaging configurations that underlie the high-n and

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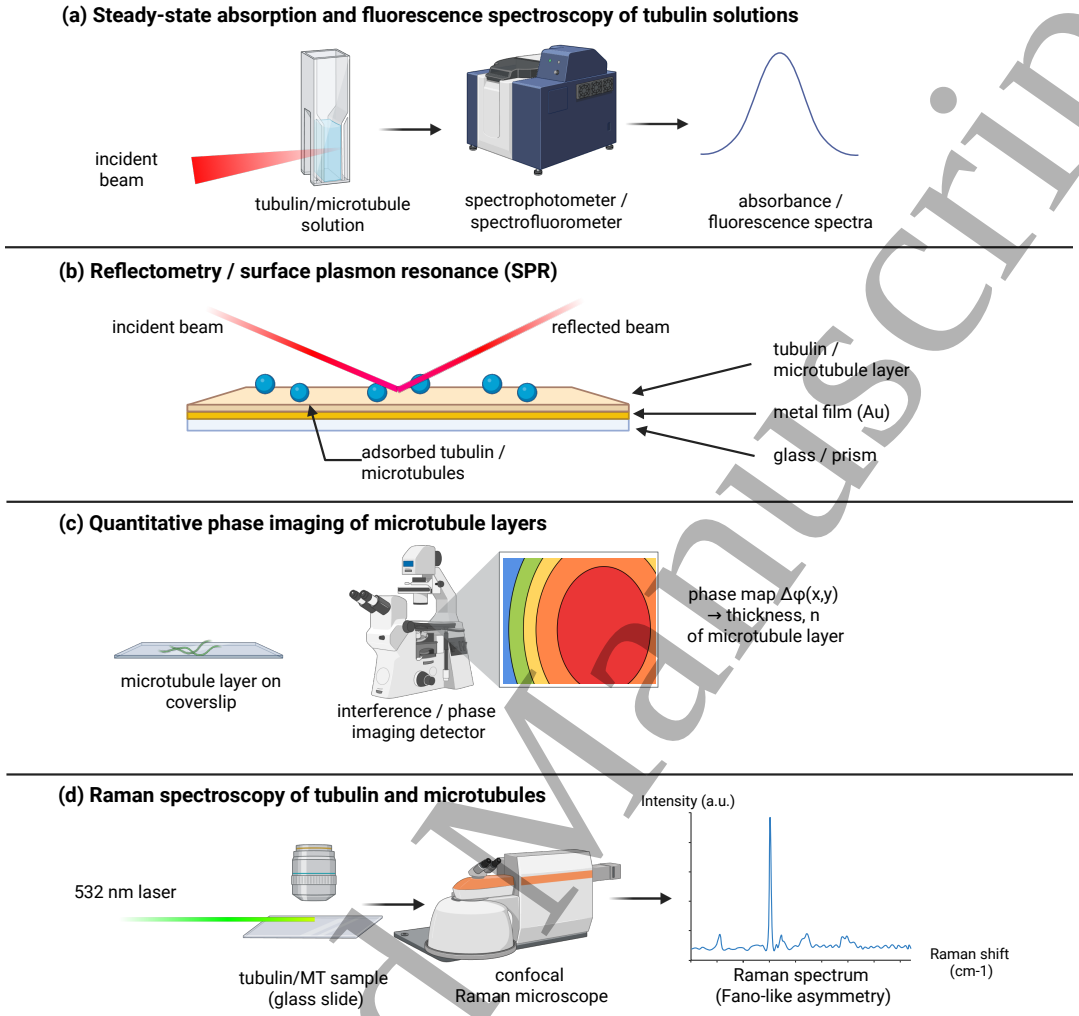

Figure 2. Representative optical measurement configurations for cytoskeletal systems. (a) Steady-state absorption and fluorescence spectroscopy of tubulin or microtubule solutions in a cuvette, using a spectrophotometer or fluorimeter to record absorbance and emission spectra. (b) Reflectometry and surface plasmon resonance (SPR) measurements, where an incident beam is reflected from a metal film supporting an adsorbed tubulin or microtubule layer; fitting the angular or spectral dependence of the reflected intensity yields the complex refractive index of the protein layer. (c) Quantitative phase imaging of microtubule layers on a coverslip, in which interference-based microscopy produces phase maps $\Delta\phi(x, y)$ that report on layer thickness and refractive index. (d) Confocal Raman microspectroscopy of tubulin and microtubules under laser excitation (e.g., 532 nm), yielding Raman spectra in which asymmetric (Fano-like) line shapes can indicate interference between discrete vibrational modes and an electronic or excitonic continuum. Created in BioRender. Gassab, L. (2026) https://BioRender.com/g4qz00a.

high-κ estimates reported here.

This electromagnetic sensitivity allows microtubules to actively respond to optical and electric stimuli. For example, Vacek et al. [49] showed that intense pulsed electric fields (PEFs), with strengths in the megavolt-per-meter range, can alter microtubule

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structure and stability. These fields can reorient dipole moments, affect the assembly of microtubules, and disrupt their organization, as supported by both experiments and computer simulations [50, 51, 52]. These results indicate that microtubules can act as sensors and transducers of electromagnetic fields in biological systems. Although these experiments employ strong electric fields rather than optical beams, they rely on the same large dipole moments and dielectric response that govern light–microtubule coupling and therefore provide a benchmark for the magnitude of field-induced structural changes that optical fields might, in principle, achieve.

In living cells, such responsiveness is evident in light-dependent rearrangements of the cytoskeleton. Sambade et al. [18] found that light can change the orientation of microtubules in *Arabidopsis* plant cells. Depending on the light conditions and hormonal signals, microtubules reorganize from longitudinal to transverse patterns, passing through intermediate "star" configurations. In these experiments, microtubules are visualized by fluorescence microscopy under controlled illumination protocols, so that both the spectral composition and the directionality of the incident light can be related directly to the observed reorientation dynamics. These observations emphasize how the electromagnetic properties of microtubules allow them to mediate interactions with light and influence cellular structure and behavior. Similar effects have been documented in mammalian systems. Zamansky and Chou showed that ultraviolet irradiation disrupts microtubule organization in fibroblasts [19], and later work revealed that keratinocytes undergo simultaneous reorganization of microtubules, actin filaments, and intermediate filaments under UV exposure [53]. In plants, Krasylenko et al. reported that UV-B radiation induces dose-dependent microtubule reorganization and cell death [54], while in vitro experiments by Zaremba et al. demonstrated that 280 nm light directly impairs tubulin polymerization [20]. Across these studies, a dedicated UV illumination arm (lamp or laser with appropriate filters) is combined with an imaging or detection arm that records cytoskeletal architecture or polymerization state before and after exposure, making the dependence of microtubule organization on wavelength and dose explicit and allowing the construction of quantitative dose–response curves.

Recent literature provides extensive insight into the electromagnetic response of microtubules. Studies have shown that microtubules are not only polar and highly charged structures, but they also support vibrational modes that can generate electric fields in the kHz to GHz range [55, 56, 57]. These oscillations may be coherently excited via GTP hydrolysis, motor protein activity, or mitochondrial energy fluxes. Such coherent vibrations have been proposed to influence processes like mass transport, polymerization, and even long-range intracellular signaling [7, 57]. It is important to note that these GHz-scale vibrational resonances are based primarily on theoretical models and simulations, and remain speculative in the absence of direct experimental confirmation. From the viewpoint of light–matter interaction, these models effectively treat microtubules as nanoscale resonators whose mechanical and electrical modes could couple to optical or terahertz fields, even though explicit pump–probe or terahertz spectroscopy measurements on these putative resonances are still lacking.

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Moreover, external electromagnetic fields (EMFs), whether static or alternating, have been shown to alter the mechanical and electrical properties of tubulin assemblies. Static magnetic fields (SMFs) in the 100–300 mT range were shown to affect tubulin polymerization, surface potential, and secondary structure [50]. These findings are further complemented by experimental data demonstrating light- and EMF-induced deformation or alignment of microtubules [52, 58]. In alignment experiments, for example, polarized light or combined electric and magnetic fields are used to bias microtubule orientation in solution or on surfaces, and the resulting alignment is quantified by scattering, birefringence, or fluorescence readouts, providing a direct link between the imposed field geometry and cytoskeletal organization.

Molecular dynamics simulations also show that nanosecond-scale pulsed electric fields can destabilize or alter tubulin conformation [59], corroborating the idea that microtubules can transduce field energy into structural or organizational changes. In that study, Marracino et al. performed all-atom simulations of tubulin exposed to intense nanosecond electric pulses and found field-induced rotations of the tubulin dipole, local rearrangements of secondary-structure elements, and a redistribution of charged residues at the protein surface. These conformational changes modify both the magnitude and direction of the tubulin dipole moment and can weaken dimer–dimer contacts, offering a microscopic mechanism for how strong external fields can influence microtubule stability and dielectric response. As a motivation for this pronounced field sensitivity, Fig. 3 reproduces their comparison showing that tubulin exhibits unusually large net charge and dipole moment relative to a broad set of proteins in the PDB [59]. In light of this, microtubules have been described as biological analogues of nanoscale conductors, capable of supporting ionic transport, charge storage, and signal amplification [8, 60, 61]. This idea remains largely theoretical, motivated by modeling and analogy to engineered systems, but it illustrates how their experimentally observed electrical responsiveness could inspire future bioelectronic applications. By modifying charge distributions and conformations, strong fields change the effective refractive-index landscape and scattering cross sections of microtubules, which in turn influences how they guide and modulate light at the nanoscale.

Altogether, the literature converges on the idea that microtubules are not just passive scaffolds but active participants in the cell's electrical and optical environment. Their response to electromagnetic stimuli supports roles in cellular signaling, morphology regulation, and possibly bioelectromagnetic communication. The set of experiments discussed in this subsection therefore illustrates not only that microtubules respond to fields, but also how specific optical and electromagnetic configurations probe scattering, refractive index, alignment, and structural stability of the cytoskeleton during its interaction with light.

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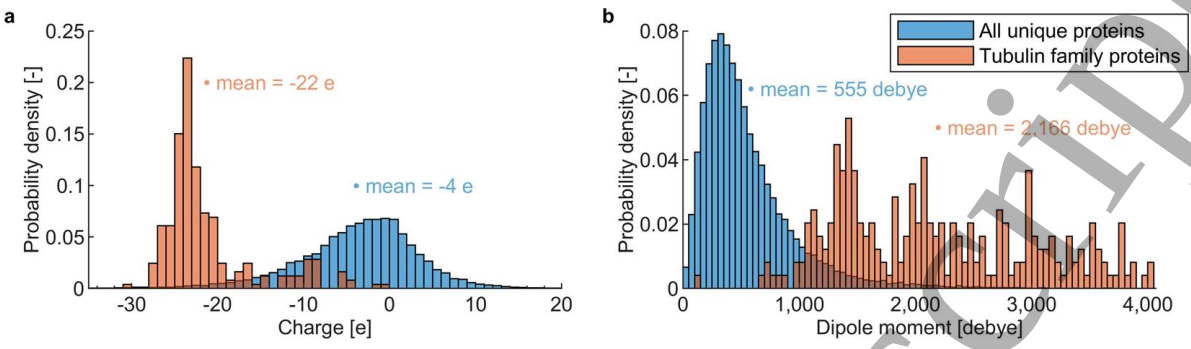

Figure 3. Electrical properties of tubulin. The figure compares the distribution of net charge and dipole moment for tubulin against a large reference set of PDB proteins, highlighting tubulin as an outlier with relatively large charge and dipole. The inset shows an $\alpha\beta$-tubulin dimer structure with highlighted C-terminal tail regions implicated in the field response. Figure and caption reproduced from Marracino et al. [59] under the Creative Commons Attribution 4.0 International License (CC BY 4.0)(http://creativecommons.org/licenses/by/4.0).

3.2. Spectroscopic Features

Cytoskeletal proteins, including tubulin, show characteristic absorption and fluorescence signals in the UV range due to the presence of aromatic amino acids like Trp, tyrosine, and phenylalanine [27, 28, 54, 62]. These molecules serve as natural chromophores, or light-absorbing units, and their electronic interactions may allow for energy transfer between sites, similar to exciton behavior seen in photosynthetic complexes [63]. As such, spectroscopy offers insights into how energy may move through the cytoskeleton. In measurements on polymerized microtubules, elastic scattering can substantially complicate spectral interpretation, so careful baseline correction and scattering controls are often required (see Sec. 6).

UV exposure affects microtubule function. For instance, Zaremba et al. [20] showed that 280 nm UV light can disrupt the ability of tubulin to form polymers, underscoring the photochemical sensitivity of microtubule assembly. In plants, UV-B radiation causes microtubule reorganization in a dose-dependent manner, which is linked to processes such as cell death and developmental changes [54].

Fluorescence studies have further highlighted the sensitivity of these aromatic residues to their environment. For example, Chen measured fluorescence quantum yields (QY) of 0.13 for Trp and 0.14 for tyrosine in water at 23°C, indicating notable light emission efficiency [64]. Callis and Liu used quantum mechanics/molecular mechanics (QM/MM) simulations to show that the local electric field, influenced by nearby charges and protein structure, can tune the energy levels of these chromophores, influencing how they emit light [65].

Given the abundance of these light-responsive residues in both tubulin and actin, it is likely that the cytoskeleton is naturally adapted for UV absorption and possibly for energy transfer through quantum-coherent mechanisms [27, 28, 31]. This opens

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up engaging possibilities for cytoskeletal proteins participating in biologically relevant photonic and quantum processes.

Recent research has expanded the understanding of how low-intensity light beyond the UV range can modulate cytoskeletal structure, particularly through the technique of photobiomodulation (PBM). PBM typically employs visible red to near-infrared (NIR) light to induce physiological effects. While red light (660 nm) has been shown to modulate inflammatory responses and brain function, recent spectroscopic studies have focused on the effects of NIR light on tubulin and microtubules. Di Gregorio et al. [21] used Raman spectroscopy to demonstrate that pulsed NIR light (810 nm, 10 Hz) induces a significant conformational change in polymerized tubulin, marked by a transition from α-helices to β-sheets, which may destabilize microtubules and facilitate cytoskeletal remodeling. Complementary work by Staelens et al. [66] used fluorescence microscopy and turbidity assays to show that PBM can modulate microtubule polymerization dynamics in a concentration-dependent manner and even destabilize Taxol-stabilized filaments. Additionally, Albrecht-Buehler demonstrated that pulsed near-infrared light (835 nm) accelerates the disassembly of centrosome-nucleated microtubule asters in cultured cells, suggesting that microtubules may transmit stability-altering signals in response to light [67]. This evidence reveals that cytoskeletal proteins are not only spectroscopically active but also structurally responsive to low-intensity optical fields in the visible and NIR regions, suggesting new avenues for optical control of cell architecture.

3.3. Birefringence and Anisotropy

Microtubules possess an inherent optical anisotropy known as birefringence, stemming from their highly organized, cylindrical structure. This means they can split light into two polarized beams traveling at different speeds. Advanced imaging techniques like polarized light microscopy (e.g., Pol-Scope) have directly measured this property, resolving changes in optical retardation as small as 0.02 nm in single microtubules [11]. The observed increase in birefringence with the number of microtubules in a bundle suggests that the effect originates primarily from their geometric arrangement, a phenomenon known as form birefringence [11].

In tissues such as the retinal nerve fiber layer (RNFL), microtubules are key contributors to optical anisotropy. When microtubules are depolymerized using colchicine, RNFL birefringence decreases sharply, demonstrating that microtubules are the main structural elements responsible for the birefringent properties of the RNFL [12]. The birefringence of assembled microtubules differs significantly from that of individual tubulin dimers, indicating that their tubular structure enhances their interaction with light [68]. The alignment of dipole moments, repeating lattice, and hollow cylindrical form all promote resonant interactions with electromagnetic waves, potentially enabling them to act as biological antennas.

Further evidence of light-sensitive microtubule organization comes from studies in

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plant guard cells. Lahav et al. [17] showed that microtubule bundles become more stable and organized under white or blue light but appear disordered in darkness or red light. This suggests that cells can use light to control cytoskeletal anisotropy, which is important for waveguiding and birefringence-based cellular processes.

Beyond geometric arrangement, the birefringence of microtubules is also influenced by intrinsic anisotropy in their molecular polarizability. The ordered alignment of electric dipoles along the microtubule axis results in direction-dependent light interaction [8]. Theoretical models further suggest that microtubules support coherent vibrational modes in the GHz range [55, 56], which may resonate with specific optical frequencies, subtly modulating birefringence. These physical properties highlight how microtubules not only guide light structurally but also engage with it at a fundamental electromagnetic level.

3.4. Waveguiding Properties

Due to their hollow cylindrical structure and crystalline lattice, microtubules have been proposed to function as biological waveguides, which are structures that channel electromagnetic waves within cells. Their geometry, dielectric contrast, and symmetry make them resemble artificial optical waveguides used in photonics [15]. These similarities have led to models proposing that microtubules can support guided optical modes in the UV-visible spectrum through the central lumen or outer shell [13, 14]. It should be emphasized that these waveguiding properties are theoretical predictions based on modeling and analogy and have not yet been directly observed in experiments with living cells.

Computer simulations and continuum electromagnetic models show that microtubules can sustain low-loss optical modes, especially in the high-frequency regime typical of cellular light exposure [16]. Their unique dielectric structure, composed of a low index lumen, a tubulin shell, and the surrounding cytosol, provides a natural configuration for trapping and guiding light, much like coaxial cables in electronics. Their rigidity and precise lattice organization have also been proposed to help stabilize such modes and potentially reduce sensitivity to intracellular fluctuations [15]. Structural similarities with carbon nanotubes, which are well known for their waveguiding and conductive properties, strengthen the argument. Both structures share nanoscale diameters, cylindrical symmetry, and high mechanical strength [15]. This has prompted interest in the use of microtubules as inspiration for future nanophotonic, biosensing, or quantum computing applications.

Altogether, these studies portray microtubules not only as static structural components but as dynamic conduits for optical and electromagnetic information within living cells.

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4. Quantum Optical Phenomena in the Cytoskeleton

4.1. Exciton Formation and Transport

4.1.1. Theoretical Framework: In residue-level models, microtubules are treated as excitonic systems in which excitation energy can propagate via dipole–dipole interactions among aromatic residues. Networks of aromatic amino acids, primarily tryptophan (Trp) and tyrosine, have been proposed as pathways for exciton formation and transport [22, 23]. These residues are chromophoric and can absorb UV photons, including ultraweak photon emission (UPE) produced by reactive oxygen species (ROS) in cells.

At the level of a closed excitonic system, the density operator $\rho(t)$ obeys the von Neumann equation

$$\frac{d\rho}{dt} = -\frac{i}{\hbar}[H_{\text{exc}}, \rho], \tag{1}$$

which describes unitary quantum dynamics generated solely by the system Hamiltonian H_{exc}. To include environmental noise and irreversible loss channels, one typically models the reduced dynamics of the system as Markovian and extends this description to a Lindblad-type master equation. The quantum dynamics of this transport are modeled using the Lindblad master equation,

$$\frac{d\rho}{dt} = -\frac{i}{\hbar}[H_{\text{exc}}, \rho] + \sum_k \gamma_k \left(L_k \rho L_k^\dagger - \frac{1}{2}\{L_k^\dagger L_k, \rho\} \right), \tag{2}$$

with the Hamiltonian,

$$H_{\text{exc}} = \sum_i \varepsilon_i |i\rangle\langle i| + \sum_{i \neq j} J_{ij} (|i\rangle\langle j| + |j\rangle\langle i|), \tag{3}$$

where ε_i are site energies of individual residues and J_{ij} are inter-residue couplings. In many treatments, J_{ij} is evaluated in the electric-dipole (point-dipole) approximation in terms of transition dipole vectors $\hat{\mu}_i$ and $\hat{\mu}_j$ separated by the displacement direction $\hat{R}_{ij}$,

$$J_{ij} \approx \frac{\mu_i \mu_j}{4\pi\varepsilon_0 \, n^2 \, R_{ij}^3} \left[\hat{\mu}_i \cdot \hat{\mu}_j - 3(\hat{\mu}_i \cdot \hat{R}_{ij})(\hat{\mu}_j \cdot \hat{R}_{ij}) \right], \tag{4}$$

where μ_i and μ_j are dipole magnitudes, R_{ij} is the site separation, and n is an effective refractive index accounting for dielectric screening (equivalently one may write $J_{ij} \propto \kappa_{ij}\mu_i\mu_j/R_{ij}^3$ with orientation factor κ_{ij}). Using this type of coupling model (with structure-derived geometries and dielectric assumptions), simulations have estimated J_{ij} values between 60 and 330 cm^{-1} [23]. These values are comparable to those in light-harvesting complexes, suggesting that weakly coherent energy transfer could be possible across short distances of up to two tubulin dimers, or about 16 nm. However, coherence lengths extending beyond a dimer remain speculative and are not yet supported by direct experimental evidence. In Eq. 2, the first term on the right-hand side encodes the coherent evolution generated by H_{exc}, while the second term collects decoherence and dissipation processes through the jump operators L_k with rates γ_k. Typical choices include pure-dephasing operators $L_i = |i\rangle\langle i|$ (Haken–Strobl dephasing), which

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randomize phases without changing populations, and relaxation or trapping operators that transfer population to lower-energy, sink, or ground states. Throughout this section, H_{exc} is understood in the single-excitation manifold spanned by the site basis $\{|i\rangle\}$, and the couplings J_{ij} are evaluated in the electric-dipole approximation. The Lindblad master equation is used under the standard assumptions of weak system–bath coupling and a broadband bosonic environment. In this Markovian limit, bath correlation times are assumed short compared to the excitonic dynamics and memory effects can be neglected. Within this framework, multi-exciton processes and exciton–exciton annihilation are ignored, and the resulting dynamics should be regarded as an effective description valid for low excitation densities and on timescales beyond the bath correlation time.

Förster resonance energy transfer (FRET) generally limits singlet exciton diffusion to approximately 0.8 nm [69], while in the specific case of tubulin, Kalra et al. have calculated a Förster radius of $\sim$ 1.54 nm [28]. Dexter-type triplet transfer, which requires direct orbital overlap, predicts even shorter diffusion distances under physiological conditions [28, 70]. Despite these classical limits, coherence-assisted hopping mechanisms have been proposed to enable longer-range energy transfer, but might overestimate it at this stage. In the language of the Lindblad equation above, such mechanisms correspond to regimes where the interplay between coherent hopping (set by J_{ij}) and moderate dephasing (set by appropriate L_k and γ_k) can enhance net transport efficiency compared to both the fully coherent and the strongly overdamped limits.

Earlier theoretical models have proposed that microtubules, owing to their cylindrical geometry and periodic arrangement of $\alpha\beta$-tubulin dimers, may act as biological analogues of quantum electrodynamic (QED) cavities [71, 72]. In this perspective, coherent electromagnetic modes (often termed dipole quanta) can arise from interactions between the electric dipoles of ordered water molecules and the quantized electromagnetic field within the microtubule interior. These cavity-like modes may couple to the electric-dipole transitions of tubulin dimers and potentially enable phenomena analogous to vacuum-field Rabi splitting and other cavity-QED effects. Such interactions have been hypothesized to support quantum coherent states and energy-transfer mechanisms in microtubules, even under ambient biological conditions. In the present review, we briefly summarize these cavity-inspired proposals here and return to a more explicit Hamiltonian formulation in Sec. 4.2.1, where we discuss their implications for superradiant emission.

Some recent theoretical work has gone further to explore entanglement dynamics between Trp residues, treating microtubules as spin or excitonic networks and analyzing their quantum correlations over time [31]. These models provide tools to evaluate entanglement lifetimes, or the extent of spatial correlations, though their biological significance remains speculative. Follow-up studies by Shirmovsky and co-workers extend this spin-network perspective to single-excitation migration and entanglement transfer along tryptophan chains, as well as to the quantum relaxation of coupled tubulin

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dipoles under Markovian and non-Markovian environmental dynamics. Together, these works frame microtubules as potential quantum communication channels subject to realistic decoherence [73, 74, 75, 76, 77].

Another line of work, using open quantum system models, has suggested that environmental noise need not always destroy coherence. Under certain conditions, noise-assisted transport may occur, where moderate dephasing helps excitons overcome energetic traps, enhancing net energy migration [78]. This mechanism has been studied in photosynthetic systems and applied to microtubules to explore whether similar transport benefits might exist under biological conditions. More speculative proposals invoke error-correcting surface codes or entangled mitotic spindles to connect cytoskeletal degrees of freedom with objective-reduction–type mechanisms [79, 80].

Beyond these residue-level excitonic models, very recent theoretical work has approached microtubules as nonlinear lattices with both nearest- and next-nearest-neighbor couplings. This framework predicts the emergence of localized excitations, or breathers, whose stability and propagation depend sensitively on homodimer coupling [81]. Although still in the early stages, such models broaden the theoretical landscape by highlighting how nonlinear lattice effects may contribute to microtubule energy transport.

Together, these models, which range from cavity-level descriptions of tubulin to detailed simulations of residue-level exciton dynamics, highlight multiple theoretical possibilities for photonic and excitonic processes in microtubules. Whether such effects are functionally relevant in living systems remains an open question, but their investigation continues to offer insight into the intersection of quantum physics and cellular biology.

4.1.2. Experimental Evidence: Empirical support for exciton-based transport in microtubules is emerging, with particularly notable contributions from Kalra et al., who provided direct experimental evidence for long-range energy migration in cytoskeletal polymers [28]. In their study, purified tubulin was polymerized in vitro into stabilized microtubules, and samples were probed using time-resolved optical spectroscopy under ambient buffer conditions. Short near-UV pump pulses selectively excited the aromatic network, and the subsequent decay of triplet-state absorption and phosphorescence was recorded on nanosecond to microsecond timescales. By globally fitting these transients with diffusion–reaction models that include triplet–triplet annihilation and trapping, the authors extracted effective exciton diffusion coefficients and associated diffusion lengths. In practical terms, their measurements used a cuvette-based optical geometry similar to the tubulin/microtubule solution spectroscopy setup schematized in Figure 2a, but implemented in a time-resolved pump–probe and phosphorescence-detection mode rather than in steady-state absorption or fluorescence. Using this approach, they demonstrated that triplet excitonic migration can occur over distances as long as 6.6 nm in microtubules. This observation significantly exceeds classical predictions based on Förster theory, which estimates singlet diffusion lengths for tryptophan in tubulin at

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only about 1.54 nm [28].

These results were obtained through detailed kinetic modeling and spectroscopic analysis of tubulin assemblies, which suggest energy propagation characteristics consistent with delocalized excitonic states. This transport was observed under physiological-like conditions, without the need for cryogenic temperatures, highlighting the potential biological relevance of such processes. It is important to note, however, that the extracted migration lengths depend on the assumed kinetic scheme and on accurate separation of singlet and triplet contributions, so further experiments using complementary observables (e.g., site-selective quenchers, single-molecule measurements) will be valuable to test the robustness of these conclusions.

In a separate line of experimental evidence, Raman spectroscopy studies have reported the presence of Fano resonances in tubulin [24] (Fig. 2d). Fano resonances arise from the interference between discrete vibrational modes and a continuum of electronic states, a signature of strong light–matter coupling and a hallmark of quantum coherence. Experimentally, Zhang et al. recorded spontaneous Raman spectra of tubulin and microtubules in both dry powder and aqueous solution using a confocal Raman microscope with a 532 nm excitation laser, high-resolution grating, and a 50× objective. After baseline correction and subtraction of the water spectrum, individual vibrational bands were fitted with Breit–Wigner–Fano line shapes to extract the asymmetry parameter q, which quantifies the strength and phase of coupling between discrete phonon modes and an electronic continuum. The observation of such resonances is consistent with the presence of coherent vibronic coupling and suggests that coherent optical processes may occur within microtubules, in line with theoretical models that treat them as cavity-like environments capable of supporting coupled excitonic and photonic dynamics. At the same time, the interpretation of asymmetric line shapes as genuine Fano resonances relies on model-dependent fitting and careful control of experimental artifacts, so additional studies that vary excitation wavelength, polarization, and environmental conditions will be needed to fully establish the microscopic origin of these features.

These early experimental successes serve as a crucial bridge between abstract quantum models and biological function, suggesting that microtubules may indeed participate in nontrivial quantum energy transport phenomena within living systems. To aid comparison, Table 1 summarizes excitonic diffusion lengths predicted by different mechanisms (Förster, Dexter, coherence-assisted).

4.2. Superradiance and Collective Effects

4.2.1. Theoretical Framework: Superradiance refers to the collective emission of light by an ensemble of quantum emitters, such as atoms or molecules, whose dipoles couple through a shared electromagnetic field and interfere constructively. This interaction results in a radiative decay rate Γ that significantly exceeds that of isolated emitters (γ) [82, 83, 84, 85]. First proposed by Dicke in the 1950s, this phenomenon arises when

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Table 1. Comparison of excitonic diffusion lengths for tryptophan in tubulin, predicted by different mechanisms.

Mechanism	Diffusion length	Notes / References
Dexter (triplet transfer)	<1 nm	Requires orbital overlap [70]
Förster (singlet transfer)	1.54 nm	Calculated exciton hopping [28]
Coherent energy transfer (singlet)	<96 nm	Theoretical upper bound [23]
Experimental	6.6 nm	Measured exciton diffusion [28]

excitation becomes delocalized across multiple emitters, creating a coherent collective state that couples strongly to the radiation field [82]. In its ideal form, the enhanced decay rate can be approximated by

$$\Gamma \sim N\gamma, \tag{5}$$

where N is the number of coherently coupled emitters.

In microtubule-inspired cavity-QED proposals, the interior of the microtubule is treated as a high-Q electromagnetic cavity, and tubulin (or ordered water) dipoles are taken as effective quantum emitters. As a generic representative of cavity–emitter models, one may write the standard cavity–matter Hamiltonian (Jaynes–/Tavis–Cummings type) [86, 87],

$$H = \sum_{\mu} \hbar\omega_\mu a_\mu^\dagger a_\mu + \sum_{j} \hbar\omega_j \sigma_j^+ \sigma_j^- + \sum_{\mu,j} g_{\mu j}(a_\mu^\dagger \sigma_j^- + a_\mu \sigma_j^+), \tag{6}$$

where a_μ annihilates a confined electromagnetic mode of frequency ω_μ, $\sigma_j^\pm$ are raising and lowering operators for the relevant dipole transition of the jth emitter with transition frequency ω_j, and $g_{\mu j}$ is the mode–dipole coupling set by the local field and transition dipole moment. In microtubule cavity scenarios, such as those proposed by Michette and co-workers and by Mavromatos and collaborators [71, 72, 88], the confined modes are associated with the microtubule lumen and/or structured ("ordered") water, while the emitters correspond to tubulin or water dipoles. The 2025 review by Mavromatos, Mershin and Nanopoulos summarises this cavity-QED program and makes its key modelling assumptions explicit: ordered water in the lumen is treated as supporting coherent dipolar modes that couple to tubulin dimer electric dipoles, with decoherence argued to be limited primarily by leakage of the coherent cavity-like modes through the imperfect microtubule wall. Within this picture, they estimate characteristic decoherence times (coherence windows) on the order of 10^{-7}–10^{-6} s for the dipolar dynamics under physiological conditions, while emphasising that such estimates are parameter-dependent and require experimental validation [88]. The earlier Mavromatos–Mershin–Nanopoulos work also used this cavity analogy to motivate proposed biological consequences such as effectively dissipationless energy transfer along microtubules. They further discuss speculative state-teleportation protocols in microtubule networks, which remain experimentally unverified [72].

Under near-resonant conditions and within the rotating-wave approximation, Eq. (6) can be cast in a Tavis–Cummings–type form in which many dipoles are

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collectively coupled to a small number of cavity-like modes. A central experimental signature discussed in Ref. [88] is vacuum-field Rabi splitting (mode hybridization) in the optical response, with a splitting that in such models scales as $\Delta\omega \propto \sqrt{N}$ for N coherently coupled dipoles (and related plasmon-based probe concepts are also proposed) [88]. In this way, cavity-induced collective coupling provides a microscopic route to superradiant and subradiant emission channels in microtubule assemblies. Early cavity-type proposals by Jibu et al. [89] fall into this class, attributing collective emission to coherent photon exchange with ordered water dipoles within the microtubule lumen.

A closely related but explicitly one-dimensional variant is the waveguide quantum electrodynamics (wQED) framework introduced by Nishiyama and co-workers [90]. There, tryptophan residues along a protofilament are treated as two-level data qubits coupled to photon modes propagating along a one-dimensional waveguide formed by the microtubule lattice, with surrounding water molecules modeled as Josephson quantum filters (JQFs). Their starting point is the Hamiltonian

$$H = \sum_j \omega_j \, \sigma_j^\dagger \sigma_j + \int_0^\infty dk \, k \, c_k^\dagger c_k + \sum_j \int_0^\infty dk \left(\xi_{jk} \, \sigma_j^\dagger c_k + \xi_{jk}^* \, c_k^\dagger \sigma_j \right), \tag{7}$$

where $\sigma_j^\dagger$ and σ_j are raising and lowering operators for the jth qubit, $c_k^\dagger$ and c_k create and annihilate photons with wavevector k, and ξ_{jk} is the position-dependent qubit–photon coupling. In their model this coupling is chosen as

$$\xi_{jk} = \sqrt{\frac{\gamma_j}{\pi}} \, \cos(k r_j + \theta), \tag{8}$$

where γ_j is the decay rate of the jth qubit, r_j is its position along the waveguide, and θ encodes boundary conditions [90]. Using the Heisenberg equations of motion derived from Eqs. (7)–(8), Nishiyama et al. obtain time-evolution equations for qubit populations and photon distributions at zero and finite temperature, and show within their model the emergence of subradiant states with strongly suppressed decay when tryptophan data qubits are entangled with JQF-like water degrees of freedom. This wQED approach thus provides a concrete implementation of super- and subradiant channels in a microtubule-based geometry. These QED-inspired models include both cavity-like descriptions (discrete confined modes) and waveguide-QED descriptions (propagating 1D modes). In contrast, the residue-level non-Hermitian framework used below targets Trp-network superradiance and enables direct comparison to UV fluorescence quantum-yield measurements.

To model radiative decay and cooperative emission in a way that is directly comparable to fluorescence experiments, Celardo and co-workers introduced an effective non-Hermitian Hamiltonian for Trp networks in microtubules and related architectures [25]. In this residue-level excitonic picture, the relevant quantum emitters are localized Trp excitations on the microtubule lattice (see Figure 4), whose dense packing and large transition dipoles enable coherent coupling and collective optical response. The effective Hamiltonian is written as

$$H_{\text{eff}} = H_0 - \frac{i}{2} \Gamma, \tag{9}$$

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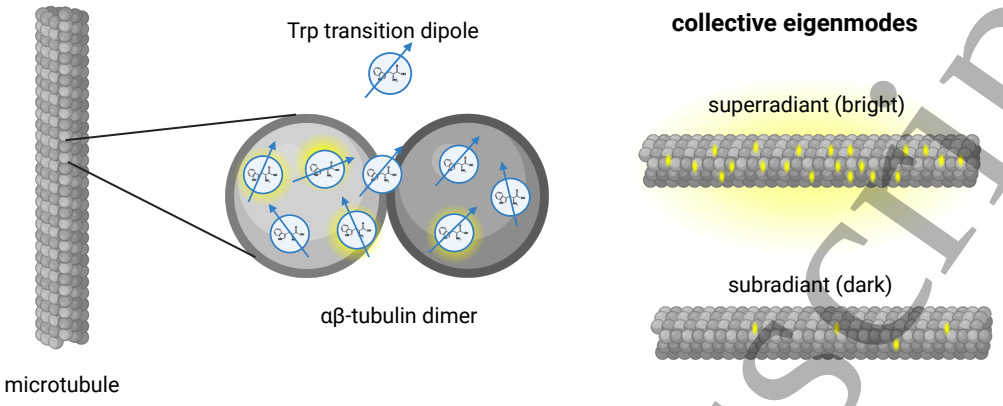

Figure 4. Schematic representation linking microtubule architecture to collective aromatic excitations. The left panel shows a cylindrical microtubule composed of repeating α- and β-tubulin heterodimers, with a representative heterodimer indicated as the molecular building block. The central panel zooms into the $\alpha\beta$-tubulin dimer, where α- and β-tubulin are distinguished by shading and tryptophan (Trp) residues are depicted as aromatic side chains; arrows indicate the Trp transition dipole orientations. These Trp chromophores form a dense network of coupled dipoles that can support excitonic delocalization and cooperative light–matter interactions. The right panel provides a qualitative illustration of collective eigenmodes in a microtubule segment, where constructive interference among many dipoles yields superradiant (bright) emission, while destructive interference yields subradiant (dark), longer-lived modes. Created in BioRender. Gassab, L. (2026) https://BioRender.com/4ar6k6o.

where H_0 describes coherent exciton dynamics and Γ is a decay-rate matrix capturing radiative coupling to the electromagnetic field. In the site basis $\{|n\rangle\}$ of localized Trp excitations, H_0 is taken in a tight-binding form within the single-excitation manifold,

$$H_0 = \sum_n \varepsilon_0 \, |n\rangle \langle n| + \sum_{n \neq m} \Delta_{nm} \, |n\rangle \langle m| \,, \tag{10}$$

with ε_0 the Trp site energy and Δ_{nm} the coherent light-mediated dipole–dipole coupling between sites n and m [25]. The decay matrix has diagonal elements $\Gamma_{nn} = \gamma$ (the single-Trp radiative rate) and off-diagonal elements Γ_{nm} encoding radiative cross-coupling between distinct sites. Diagonalization of H_{eff} yields complex eigenvalues $E_n - i\Gamma_n/2$, so that each collective eigenstate carries a well-defined radiative width Γ_n: modes with $\Gamma_n > \gamma$ are superradiant (bright, fast emission), whereas modes with $\Gamma_n < \gamma$ are subradiant (dark, long-lived). In finite disordered microtubule segments, key questions are how the eigenmodes of H_{eff} distribute over the lattice and how their Γ_n scale with system size and disorder, since these features directly determine emission lifetimes and effective quantum yield.

Within this non-Hermitian description, Trp networks are treated as open quantum systems whose collective modes naturally partition into bright (superradiant) and dark (subradiant) channels. This becomes particularly relevant when microtubule dimensions are comparable to or larger than the emission wavelength, where cooperative emission

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and radiative cross-couplings can dominate over a simple pairwise dipole picture. In this setting, delocalized superradiant modes can emerge through supertransfer coupling between smaller Trp subunits and can remain robust to moderate static disorder, suggesting the possibility of ultrafast, long-range photoexcitation transport under physiological conditions [25].

Further theoretical development by Patwa et al. [27, 26] extended these insights by calculating thermally averaged QY across various Trp-rich protein architectures, including microtubules, actin bundles, and amyloid fibrils. Building directly on the mode-resolved decay rates Γ_j obtained from diagonalizing H_{eff}, they related cooperative radiative enhancement to experimentally observable fluorescence quantum yield. Here we use QY to denote the fluorescence quantum yield Φ, defined as

$$\Phi = \frac{k_{\text{rad}}}{k_{\text{rad}} + k_{\text{nr}}}, \tag{11}$$

where k_{rad} and k_{nr} are the effective radiative and non-radiative decay rates of the excitonic system. Under collective emission, k_{rad} becomes effectively state-dependent through the distribution of Γ_j across superradiant and subradiant modes, so that changes in delocalization and cooperativity feed directly into the measured quantum yield. The thermal QY was expressed as

$$\langle \text{QY} \rangle_{\text{th}} = \frac{\langle \Gamma \rangle_{\text{th}}}{\langle \Gamma \rangle_{\text{th}} + \gamma_{\text{nr}}}, \tag{12}$$

where the thermally averaged radiative decay rate is

$$\langle \Gamma \rangle_{\text{th}} = \frac{\sum_j \Gamma_j e^{-E_j/k_B T}}{\sum_j e^{-E_j/k_B T}}, \tag{13}$$

and γ_{nr} is the non-radiative decay rate of Trp in solution. This formulation emphasizes that low-energy superradiant states, being more heavily weighted in the Boltzmann distribution, dominate the emission behavior. Their analysis showed that such collective excitonic modes are remarkably robust to thermal fluctuations and structural disorder, suggesting they could play a role in photoprotection and signaling in biological systems. In applying this non-Hermitian and thermal-averaging formalism to Trp networks, we work in the single-excitation manifold of the underlying excitonic Hamiltonian H_0 and construct the radiative coupling matrix Γ within the electric-dipole approximation for spontaneous emission into a broadband photonic environment. The resulting H_{eff} describes an open system weakly coupled to this bath, so radiative loss is encoded in the imaginary parts of the eigenvalues $E_j - i\Gamma_j/2$ in a Markovian limit. The non-radiative rate γ_{nr} entering the thermal quantum-yield expressions is taken as a phenomenological parameter (typically the Trp non-radiative rate in solution), while multi-exciton effects, exciton–exciton annihilation, and explicit vibrational back-action are neglected; $\langle \Gamma \rangle_{\text{th}}$ and $\langle \text{QY} \rangle_{\text{th}}$ should therefore be interpreted as effective, low-excitation descriptions valid on timescales longer than the bath correlation time.

Additionally, general principles of superradiant light absorption and excitonic transport, inspired by photosynthetic systems, have been explored in engineered light-harvesting networks. These studies underscore the universal relevance of cooperative

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quantum effects for efficient energy capture and transfer, and offer theoretical frameworks that help interpret recent biological observations [91].

Within this broader landscape, the wQED description introduced above provides a complementary, explicitly one-dimensional realization of cooperative emission and subradiance in microtubules, in which tryptophan qubits and water-based JQFs jointly determine the effective decay channels. Together with cavity-inspired QED pictures and non-Hermitian excitonic models, it illustrates how different levels of description—from field-theoretic to residue-resolved—can be used to analyze superradiant and subradiant behavior in the cytoskeleton.

4.2.2. Experimental Evidence: Expanding on this theoretical foundation, Babcock et al. [27] provided the first experimental evidence for superradiance in microtubule assemblies. By measuring fluorescence QY under UV excitation, they observed that QY increased significantly with the size of the Trp network, reaching values up to 70% higher than those of free Trp or isolated tubulin dimers. This finding indicates the presence of cooperative light–matter interactions. Experimentally, Babcock et al. [27] prepared solutions of Trp, tubulin dimers, and taxol-stabilized microtubules in BRB80 buffer at comparable Trp concentrations and recorded UV–visible absorption and steady-state fluorescence spectra in 1 cm UV-grade cuvettes, using a cuvette-based geometry closely matching the tubulin/microtubule solution spectroscopy setup schematized in Figure 2a. Using Trp in water as a reference standard and applying the standard relative-quantum-yield method at 280 and 295 nm excitation, with Rayleigh-like scattering subtracted for microtubules, they extracted Trp-specific fluorescence quantum yields for each architecture. These measurements show that the Trp-network QY is lower in tubulin dimers but increases markedly in microtubules, with an apparent enhancement of up to $\sim 66\%$ for microtubules relative to tubulin. This largest value is obtained from the 280 nm dataset after applying an additional treatment to isolate the Trp contribution (since absorption at 280 nm is not exclusively Trp-specific) together with background/scattering subtraction; a consistent increase is also observed at 295 nm when background removal is applied. Importantly, in this experiment they compare a tubulin solution to a separate preparation of taxol-stabilized microtubules rather than measuring the same sample before and after polymerization. When compared with non-Hermitian radiative Hamiltonian simulations, which predict low-energy, spatially extended superradiant eigenmodes contributing strongly to emission, the experimental results show a qualitatively similar trend, although the predicted percent change is more modest (of order $\sim 6\%$). Changes in local chromophore environment, redistribution between radiative and non-radiative decay channels, and other classical photophysical effects may also contribute, so future studies combining QY measurements with time-resolved fluorescence lifetimes and ultrafast spectroscopy will be required to determine how much of the enhancement is attributable to cooperative emission versus classical mechanisms.

In parallel fields, light-harvesting nanotubes have shown that superradiance can be

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modulated by photochemically induced disorder. Studies by Doria et al. demonstrated that the radiative rate and QY of excitonic aggregates could be controlled by varying energetic disorder, further confirming the deep link between exciton delocalization and emission efficiency [92]. In those experiments, supramolecular dye nanotubes were subjected to controlled photochemical oxidation to introduce energetic disorder, and changes in absorption line shapes, fluorescence lifetimes, and quantum yields were monitored as a function of irradiation dose, thereby directly correlating the degree of structural disorder with the strength of superradiant enhancement.

4.3. Environmental Effects

The potential for microtubules to support quantum optical phenomena is closely linked to their interaction with the surrounding cellular environment. One proposed mechanism involves the emergence of ferroelectric ordering within microtubules, attributed to the polar nature of tubulin dimers [14, 68]. Theoretical models suggest that the aligned dipole moments of tubulin could generate macroscopic polarization fields, potentially stabilizing coherent excitations [14]. Under such conditions, it has been hypothesized that solitons, or non-dispersive wave packets, might propagate along microtubules, facilitating energy transfer with reduced dissipation [13, 93]. In these ferroelectric/dipole-chain models, the aligned tubulin dipoles are placed on the microtubule lattice and generate a self-consistent polarization field that is taken to enter the equations of motion (or an effective Hamiltonian) as a local field, thereby effectively renormalizing on-site terms and dipolar couplings along protofilaments. The associated soliton solutions then correspond to nonlinear, localized excitations of this dipole chain, providing a concrete mechanism by which energy could propagate while remaining partially protected from environmental decoherence. A representative nonlinear dipole-chain treatment is the classical pseudospin model of Nesterov et al., which incorporates cylindrical microtubule geometry and dipole–dipole interactions (including a radial-field contribution from the solvent). Within that classical framework, snoidal waves, solitons, kinks, and localized spike excitations arise as solutions of the resulting nonlinear equations of motion [94].

Another proposed mechanism for sustaining coherence involves the role of structured water layers adjacent to the microtubule surface. These interfacial water layers have been proposed to create a more ordered microenvironment that reduces effective fluctuations and supports sustained dipolar interactions, potentially extending the lifetime of quantum states [24, 95].

However, the cellular milieu presents a far more complex and dynamic environment. Variations in ionic strength, pH, temperature, mechanical forces, and the binding of microtubule-associated proteins all contribute to the dynamic and potentially decohering environment [2, 96]. Gaining a better understanding of how microtubules might mitigate or adapt to these influences is central to evaluating their capacity for quantum behavior in vivo.

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To capture these effects quantitatively, explicit modeling of both Markovian and non-Markovian environments in microtubules has reported transitions between more coherent and more strongly decohered regimes as a function of temperature and structural parameters, using a dipole model of tubulin dimers [77]. Using spectral densities chosen to mimic cytosolic and intra-lumenal noise, these studies identify temperature- and geometry-dependent crossovers between regimes with long-lived coherent oscillations of tubulin dipoles and regimes dominated by fast decoherence, thereby tying the abstract open-system formalism directly to specific microtubule structural parameters.

While not a direct observation of excitonic transport, recent experimental work by Di Gregorio et al. [21] demonstrates that photobiomodulation can induce conformational changes in polymerized tubulin, notably shifting its secondary structure from α-helical to β-sheet content. These light-induced structural changes may alter the electronic and dipolar landscape of the tubulin lattice, suggesting an indirect mechanism by which external illumination conditions could influence energy transport dynamics.

5. Biological Implications and Functions

5.1. Cellular Signaling and Energy Transport

If sustained, quantum transport mechanisms in the cytoskeleton could support novel signaling networks or energy transfer pathways. The ordered arrangement of chromophores within microtubules, combined with their ability to form extended networks throughout the cell, has motivated proposals for potential roles in long-range information transfer [28, 96]. Theoretical models suggest that, under specific assumptions, polarons and excitonic states in tubulin can propagate across microtubules with relatively long-lived coherence, implying a possible role in energy or information transport in cytoskeletal assemblies [93]. Furthermore, electromagnetic field generation and guidance along microtubules have been proposed as mechanisms for intracellular communication [14, 68]. Taken together, these proposals position cytoskeletal filaments as potential conduits for nanoscale light and energy transport, that is, as elements of a hypothesized internal biophotonic network superimposed on conventional electrochemical signalling pathways.

Interestingly, microtubules share key structural and functional similarities with carbon nanotubes, including their cylindrical geometry, mechanical robustness, and the potential to support both mechanical and electromagnetic signal propagation [15]. In carbon nanotubes, these properties are known to enable efficient one-dimensional transport of excitons, charge carriers, and guided optical modes, and they have been exploited as nanoscale interconnects and waveguides in optoelectronic devices. By analogy, the comparable dimensions, symmetry, and internal ordering of microtubules suggest that they could act as biological counterparts of such quasi-one-dimensional conductors and waveguides. This analogy therefore motivates the idea that microtubules

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might not only provide structural support but also furnish preferred pathways for directed energy and signal transport within the cytoplasm. This resemblance has inspired the use of microtubules as biological templates in the design of biomimetic nanomaterials and optoelectronic systems [97]. In this sense, microtubules represent both a candidate platform for native biological photonics and a blueprint for engineered nanostructures that perform similar functions in artificial devices. Clarifying to what extent these functional similarities reflect genuinely quantum-coherent transport, rather than purely classical mechanical or diffusive processes, remains an open question that will require combined theoretical and experimental investigation. Such analogies strengthen the view that microtubules could serve not only as mechanical scaffolds but also as dynamic elements in intracellular energy distribution and communication networks.

Finally, the possibility of efficient energy transport through cytoskeletal structures raises intriguing questions about cellular energetics. Quantum-coherent excitation transfer may offer alternative or complementary routes for energy redistribution within cells, potentially contributing to regulatory or signaling functions beyond conventional metabolic pathways [23]. If demonstrated, such routes would amount to an additional layer of control over how and where energy is delivered on nanometric length scales, with immediate relevance for biophotonic signalling, photoprotection, and light-driven regulation of cellular function.

5.2. Functional Implications of Superradiance

The implications of superradiance in microtubules extend beyond photophysics. The enhanced QY and radiative speed of collective states have been proposed to function as a natural photoprotective mechanism: by quickly re-emitting absorbed high-energy UV photons, cells can reduce the risk of photochemical damage and oxidative stress [27, 26]. This is especially relevant given the abundance of Trp residues in the cytoskeleton and the sensitivity of cellular signaling pathways to oxidative disruptions. In this view, cytoskeletal superradiance would complement classical photoprotective strategies (such as pigment screening and antioxidant scavenging) by providing a quantum-enhanced channel for rapid, radiative energy disposal.

Additionally, structured electromagnetic propagation within microtubules could support mechanisms akin to superradiance and provide natural photonic pathways through which energy or signaling is distributed efficiently across the cell [13]. If such cooperative emission and transport are confirmed in vivo, they would constitute a concrete example of biological light-harvesting and redistribution optimized at the mesoscale, with clear analogies to engineered superabsorbing and superemitting nanostructures.

Moreover, the possibility that excitonic energy can propagate over long distances through cooperative effects may suggest a role in cellular communication and regulation. The structural similarity between microtubules and photosynthetic antenna complexes

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underscores the potential for evolutionary convergence toward efficient energy-handling architectures in biology [91]. Theoretical models suggest that these mechanisms could influence processes such as neuronal signaling and cytoskeletal organization, both of which are affected in various neurodegenerative diseases where microtubule dysfunction is implicated [26].

Extending these ideas, recent theoretical work has proposed that not only superradiant but also subradiant states, characterized by suppressed emission and prolonged excitation lifetimes, may play a biologically relevant role. In particular, Nishiyama et al. [90] show within their model that such subradiant states can arise from entangled tryptophan–water systems in microtubules, potentially enabling robust quantum information retention. This mechanism may offer a novel layer of signal stability or memory-like behavior within the cytoskeleton, with implications for information processing and resilience to oxidative stress under physiological conditions. Although these proposals remain speculative, they point toward experimentally testable signatures, such as anomalously long-lived emission components or field-sensitive changes in cytoskeletal fluorescence, that could be targeted by emerging quantum-sensing and advanced bioimaging techniques.

5.3. Neurobiological Applications

The presence of organized microtubule arrays in synaptic regions, coupled with their optical and quantum properties, suggests possible roles in synaptic transmission and plasticity. The dynamic nature of cytoskeletal reorganization during synaptic events could modulate these quantum-optical properties, potentially contributing to information processing at synapses [38]. Modeling studies show that the geometric arrangement and dipole interactions within neuronal microtubules support exciton-based energy transport in ways that could influence neuronal communication [96].

While speculative, theories linking cytoskeletal quantum coherence to consciousness and cognitive function have garnered attention [89, 98, 99]. Experimental models indicate that anesthetics may disrupt terahertz oscillations in tubulin, potentially interfering with long-range coherent signaling in the brain [95, 100]. The ordered structure and the potential for quantum effects in neuronal microtubules provide a physical basis for exploring these connections, though definitive evidence remains elusive.

The concept of light-mediated communication within the nervous system has been explored in early theoretical frameworks that suggest microtubules may function as internal photonic channels. Grass et al. [101] proposed that neurons are well-suited for such mechanisms due to their minimal pigmentation, extensive arborization, and hollow microtubule structures. They argued that biophoton emission, possibly generated by mitochondrial activity and transmitted via cytoskeletal filaments, could facilitate a form of intra- and intercellular optical communication. In this context, they highlighted the strong fluorescence properties of key neurotransmitters like serotonin and dopamine, positing a role for these molecules in modulating optical signals. If substantiated,

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such mechanisms could reshape our understanding of the brain's computational architecture, with implications extending to models of consciousness and memory based on photonic and holographic principles. From an applied perspective, any confirmation of light-mediated signalling along neuronal cytoskeleton would immediately motivate new strategies for optical neuromodulation and quantum-enhanced neuroimaging that exploit these native photonic pathways.

6. Theoretical and Experimental Challenges

6.1. Experimental Barriers to Detecting Quantum Effects

Although theoretical and computational studies suggest that quantum effects may play a role in cytoskeletal systems, experimental evidence remains sparse and inconclusive. A few studies have reported interesting findings: Kalra et al. [28] observed excitonic energy transport over approximately 6.6 nm using fluorescence-based techniques, while Babcock et al. [27] identified spectral features consistent with superradiance. However, these remain isolated cases, and no systematic or reproducible demonstrations of quantum coherence or entanglement in cytoskeletal structures have been achieved to date. Moreover, the underlying mechanisms responsible for these observations have not yet been clearly identified or verified.

This lack of experimental evidence stems from substantial technical challenges. Quantum effects in biological systems are expected to be extremely fragile due to thermal noise, molecular fluctuations, and the inherently decohering environment of the cell. Detecting such effects at nanometer scales and femtosecond timescales requires instrumentation that can isolate subtle quantum signals from complex background noise, capabilities that are still emerging.

A further practical barrier, especially for optical tests of collective light–matter coupling in intact microtubules, is that microtubule (MT) suspensions are often highly turbid. Strong elastic scattering can dominate the measured optical density baseline and obscure weak absorption structure, making it difficult to distinguish true spectral features from scattering artifacts without careful controls and modeling. In the specific context of superradiance, this turbidity can also mask or distort the modest intensity changes expected from collective radiative channels, and can complicate comparisons between tubulin and MT samples when background subtraction or scattering models are required [27]. This is particularly relevant for cavity-inspired proposals that suggest searching for strong-coupling signatures (e.g. vacuum-field Rabi splitting) in optical spectra, which would likely require stabilized or immobilized microtubule formats, thin-film geometries, or complementary dielectric/reflectometric probes designed to suppress turbidity and improve spectral interpretability [88].

In this vein, one factor that confounds fluorescence-based measurements (as performed by [28, 27]) is the presence of guanosine nucleotide cofactors in tubulin. Each tubulin dimer binds two guanosine triphosphate (GTP) molecules, with one

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being hydrolyzed to guanosine diphosphate (GDP) upon polymerization, leading to conformational changes near Trp residues. This is an essential process to natural microtubule polymerization and can not be overlooked. As noted in [102], GTP absorbs in the 250–300 nm range, overlapping with Trp excitation wavelengths and potentially reducing available excitation energy. Furthermore, the hydrolysis from GTP to GDP has been shown to alter Trp emission intensity in GTPases, like tubulin, due to conformational effects [103]. These cofactor-related contributions could partly explain experiments in fluorescence lifetimes and QY reported in recent experiments and should be carefully considered in future studies.

6.2. Structural Sensitivity and Biological Variability

Theoretical models aiming to explain phenomena such as superradiance or excitonic transport often rely on highly idealized assumptions. In superradiance studies [25, 27, 26], the models use symmetrical and repetitive arrangements based on a single protein structure, commonly the 1JFF PDB file, to construct arrays of Trp residues. While these assumptions simplify calculations and demonstrate emergent behaviors, they do not consider that protein structures vary across species, physiological conditions, and even conformational states within a single cell. Small changes in residue orientation or spatial arrangement can drastically affect coupling strengths, coherence times, and energy transfer efficiency. As a result, the predicted quantum behavior may be an artifact of model symmetry rather than a robust biological feature. This structural sensitivity highlights the importance of validating quantum predictions across more realistic, heterogeneous biological geometries.

6.3. Modeling Limitations and Computational Challenges

To model excitonic transport in microtubules, master equation approaches such as the Haken-Strobl model [22, 23] have provided valuable preliminary insights. However, these models often rely on simplified treatments of system–environment interactions. More accurate descriptions would benefit from microscopically derived master equations that incorporate environmental effects in greater detail [104, 105].

In analogy to light-harvesting systems, the use of hierarchical equations of motion (HEOM) could also be extended to microtubule energy transfer, enabling a more realistic treatment of the structured bosonic environment [106, 107, 108]. Moreover, the biological environment is likely to exhibit non-Markovian behavior, where memory effects and environmental correlations influence system dynamics. Capturing such effects may require more advanced methods [77, 109, 110].

A major challenge, however, remains computational: simulating the full quantum dynamics of an entire microtubule is currently not feasible due to its size and structural complexity. Consequently, most studies are limited to the single-excitation regime or to small segments, which may not fully capture the behavior of the complete system.

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To provide an overview of these issues, Table 2 summarizes the main methodological challenges and experimental uncertainties discussed in this section and their implications for interpreting putative quantum signatures in cytoskeletal systems.

Table 2. Main methodological challenges and uncertainties in cytoskeletal quantum–optical studies (Exp. = experimental, Struct. = structural, Comp. = computational).

Challenge	Type	Brief description
Signal-to-noise	Exp.	Weak UV / biophotonic signals can be masked by background autofluorescence, detector noise, and scattering.
Optical turbidity / baseline	Exp.	Elastic scattering in MT suspensions distorts apparent "absorbance" baselines and can obscure weak spectral features unless corrected or mitigated (e.g. stabilized/immobilized or thin-film formats).
Sample control	Exp.	Mixed microtubule lengths, bundling, and concentration variability complicate quantitative comparisons across conditions.
Structural variation	Struct.	Small geometry changes can strongly modify dipole couplings, delocalization, and predicted collective radiative rates.
Polymerization effects	Struct.	Tubulin→MT assembly can alter local dielectric screening, chromophore/cofactor solvent exposure and flexibility.
Nucleotide / cofactors	Exp.	GTP/GDP and other chromophores can overlap UV excitation bands and influence Trp absorption/emission via conformational effects.
Photodamage	Exp.	High excitation powers can induce photobleaching, heating, or chemical modification that alters cytoskeletal structure and spectra.
Environment / decoherence	Exp.	Warm, wet environments introduce strong dephasing; isolating genuine coherence from classical dynamics and heterogeneity is difficult.
Temporal / spatial resolution	Exp.	Limited femtosecond timing and nanometre localization constrain direct detection of coherent transport in large, heterogeneous assemblies.
Models / computation	Comp.	Simplified bath models, parameter uncertainty, and finite system sizes can bias extracted coherence times, coupling strengths, and predicted scaling laws.

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7. Future Directions and Applications

7.1. Quantum Technologies for Cytoskeletal Research

Emerging spectroscopic and imaging technologies are revolutionizing our ability to probe cytoskeletal quantum dynamics at unprecedented resolution. Advanced quantum sensing platforms, particularly those based on nitrogen-vacancy (NV) centers in diamond and optically pumped magnetometers, are pushing the boundaries of detection sensitivity and spatial resolution in biological environments [111, 112, 113, 114, 115, 116]. Aslam et al. and related reviews show that NV centers and atomic magnetometers can detect magnetic fields and other physical quantities with sensitivities down to the sub-picotesla range and with spatial resolution from the cellular down to the nanoscale, in contexts such as magnetoencephalography, single-cell spectroscopy, and local thermometry [111, 112]. These demonstrated capabilities indicate that, in principle, similar platforms could be adapted to probe magnetic, electric, or strain signatures associated with cytoskeletal organization and dynamics, for example by positioning shallow NV layers beneath adherent cells or using internalized nanodiamonds as local probes in the vicinity of microtubules. Designing such experiments, and quantifying the expected signal amplitudes from any putative quantum-coherent or spin-dependent processes in the cytoskeleton, represents a concrete and testable future direction for the field. In addition to clarifying whether cytoskeletal processes genuinely require a quantum description, such quantum-sensing measurements could also open routes to functional bioimaging modalities that report directly on local field fluctuations and excitonic dynamics along cytoskeletal tracks.

7.2. Biomimetic and Hybrid Quantum Systems

Understanding the quantum-optical behavior of cytoskeletal elements could also inspire the development of novel biomimetic materials [16, 117, 118]. The natural organization, chirality, and electronic properties of these biological systems offer design principles for artificial light-harvesting arrays, quantum sensors, or hybrid photonic devices that operate at the interface of biology and quantum engineering [91, 93]. Experiments have already shown that microtubules and tubulin can act as templates for conductive nanostructures, including microtubule-based gold nanowires and hybrid bio-nanowires in which tubulin self-assembles with carbon-based nanomaterials [118, 117]. At the same time, theoretical work on engineered cooperative light-harvesting structures demonstrates that extended excitonic states and superabsorption can be exploited to enhance photon capture and sensing efficiency [91]. Together, these results suggest that cytoskeleton-inspired architectures could be used to realize artificial networks in which geometry, coupling strength, and disorder are systematically tuned to test how cooperative quantum effects such as superradiance, supertransfer, or subradiance influence transport and emission. Rather than directly serving as quantum computers, such biomimetic and hybrid systems are more realistically positioned as testbeds and

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components for light-harvesting, sensing, and imaging technologies where cytoskeletal design principles are translated into controllable quantum-optical functionality. In this way, the study of cytoskeletal quantum optics feeds back into nanophotonic device engineering, providing concrete design rules for robust, disorder-tolerant cooperative emission and absorption.

7.3. Theoretical Modeling and Quantum Simulation

From a theoretical standpoint, as mentioned in Section 6.3, more advanced models such as the hierarchically coupled equations of motion (HEOM) offer a promising approach for realistically capturing system–environment interactions by modeling the structured bosonic bath. Additionally, microscopic descriptions of the system itself could further improve accuracy in representing these interactions. Applied to Trp networks in tubulin or microtubules, HEOM and related open-quantum-system methods would allow one to calculate coherence lifetimes, transport efficiencies, and quantum yields as functions of temperature and environmental spectral density, providing observables that can be compared directly with steady-state and time-resolved spectroscopic measurements.

More recently, the development of quantum computing platforms has opened new possibilities for simulating biological systems at the quantum level [119, 120, 121]. Current proposals emphasize using small- to intermediate-scale quantum devices to simulate fragments of complex biomolecular systems that are classically expensive, such as strongly correlated electronic subsystems or simplified spin and exciton models [119, 120]. In the context of cytoskeletal quantum optics, this suggests that minimal models of excitonic or spin dynamics on microtubule motifs could eventually be mapped to qubit registers and evolved on quantum hardware to benchmark approximations used in classical simulations.

Moreover, artificial intelligence (AI) and machine learning (ML) can help bridge scales: by learning from simulations of small tubulin segments, ML models can approximate the behavior of full microtubules, optimize simulation parameters, reduce data dimensionality, and accelerate sampling, thereby making large-scale quantum simulations more tractable. Recent reviews further emphasize that combining ML with molecular simulation and, in some cases, emerging quantum algorithms can extend accessible time and length scales via surrogate models that reproduce key observables at a fraction of the computational cost. For cytoskeletal systems, such approaches could be used to learn effective Hamiltonians, spectral densities, or coarse-grained dynamical rules from high-level electronic-structure or HEOM calculations on small subsystems, and then deploy these learned models to explore excitonic or spin transport in larger, biologically realistic microtubule geometries [122, 123].

7.4. Interdisciplinary Opportunities

Advancing our understanding of putative quantum processes in the cytoskeleton requires coordinated efforts across quantum physics, molecular biology, structural chemistry,

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neuroscience, and bioengineering. In practical terms, progress will depend on combining excitonic and spin-based models with high-resolution structural data (e.g., cryo-EM or X-ray structures that resolve Trp environments), parameterizing these models using quantum-chemical and molecular-dynamics calculations, and validating their predictions through targeted biochemical and biophysical experiments on tubulin and microtubules in conditions that mimic the intracellular milieu.

Developing accurate quantum models of tubulin and microtubules requires input from chemists to refine electronic structure, excitonic couplings, and redox pathways for specific residues and cofactors, and from structural and cell biologists to incorporate polymerization state, post-translational modifications, and microtubule-associated proteins into these models. Bioengineers and experimental physicists can contribute by designing concrete measurement protocols—such as fluorescence quantum-yield and lifetime measurements on well-defined cytoskeletal assemblies, time-resolved spectroscopy of ultraweak photon emission, and quantum-sensing geometries that place NV centers or other probes near microtubule bundles—to test for quantum coherence, energy transfer, or spin-dependent processes in conditions that approach those of living cells.

If robust quantum signatures in the cytoskeleton are experimentally confirmed, they could reshape our understanding of intracellular signaling, especially in neurons where microtubule dynamics are closely linked to synaptic function and neurodegeneration [23, 38, 96, 124]. In that scenario, quantum-coherent or collectively enhanced energy and information transfer along neuronal microtubules might provide additional control layers for processes such as axonal transport, synaptic plasticity, or stress responses, and could suggest new readouts or intervention points for disorders in which microtubule disruption is a hallmark, including Alzheimer's and Parkinson's disease. At the same time, it remains essential to distinguish such possibilities from purely classical mechanisms; interdisciplinary collaborations will be crucial for designing decisive experiments that can tell whether the observed cytoskeletal phenomena truly require a quantum-mechanical description or can be fully explained within a classical biophysical framework.

8. Conclusion

The cytoskeleton has emerged as a remarkable candidate for mediating light–matter interactions and possibly hosting quantum phenomena in living systems. In this review, we have traced the evolution of this perspective, starting from classical optical properties such as birefringence and waveguiding to recent explorations into quantum-coherent processes, including exciton transport, Fano interference, and superradiance within microtubule networks.

At the crossroads of quantum physics, biophotonics, and cell biology, the cytoskeleton has presented a unique structural and electronic architecture capable of supporting sophisticated electromagnetic behavior. Classical studies have long

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established the cytoskeleton's optical anisotropy and its contribution to intracellular light scattering and guidance. Meanwhile, emerging experimental evidence, including light-induced conformational changes in tubulin and Raman-detected quantum coupling, has begun to validate theoretical predictions of quantum coherence and collective excitonic behavior.

Although confirming quantum effects in the cellular context has remained technically challenging, the convergence of simulation, spectroscopy, and biological modeling has built a strong case for continued inquiry. Advances in ultrafast spectroscopy, nanoscale imaging, and molecular simulations would be expected to play a critical role in disentangling these effects from classical noise and thermal decoherence. In particular, systematic time-resolved measurements on well-defined cytoskeletal assemblies, combined with quantum-sensing experiments using NV centers or optically pumped magnetometers near microtubule bundles, provide concrete routes to test the scenarios discussed here and to determine whether a genuinely quantum description is required.

The implications have been far-reaching. At the fundamental level, these interactions may have influenced intracellular signaling, energy transport, or structural regulation. At the applied level, cytoskeletal filaments could have inspired new biomimetic devices in nanophotonics, biosensing, and quantum engineering. Potential applications range from cytoskeleton-inspired light-harvesting and photoprotective materials, through quantum-enhanced bioimaging and neuromodulation schemes that exploit native biophotonic pathways, to hybrid bio–nano platforms where cytoskeletal templates are integrated with photonic and plasmonic components. Importantly, the interdisciplinary nature of this field has opened up exciting collaborations between physicists, biologists, chemists, and engineers.

In bridging quantum theory and cellular dynamics, the cytoskeleton may have ultimately offered a new framework for understanding life's physical basis. As research advances, microtubules and related filaments could prove not only to scaffold the cell but also to actively process optical and quantum information, representing a transformative view of their role in biology. Whether or not all of the quantum-optical mechanisms proposed to date are ultimately confirmed, the effort to test them experimentally is already yielding powerful new tools and concepts at the interface of quantum science and biology, with implications for both fundamental understanding and technological innovation.

9. Acknowledgements

This research was undertaken, in part, thanks to funding to TJAC from the Canada Research Chairs Program (CRC-2022-00204), and the University of Waterloo.

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