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Bacterial bioelectricity, the first 15 years: developments, tools, and remaining questions

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Fifteen years after the first optical recordings of fast cell membrane-potential ("Vm") transients in *Escherichia coli* using a genetically encoded rhodopsin-based reporter, bacterial bioelectricity has matured from a provocative observation into a quantitative, multi-scale research program. Early work established that bacterial Vm is dynamic and can exhibit spike-like events correlated with rapid ion efflux, suggesting that electrical state participates in regulating transport and stress responses. Subsequent studies revealed that ion channels can mediate long-range electrical communication in *Bacillus subtilis* biofilms via propagating K^+ waves that coordinate metabolic states across millimeter scales. In parallel, theory and experimental work formalized how community heterogeneity and spatial organization determine signal transmission, and how electrical dynamics can influence cell behaviors such as motility and recruitment into biofilms. Most recently, the field has entered a "perturb-and-measure" phase: optical, bioelectronic, and impedance-based platforms now enable controlled stimulation and more mechanistic tests of causality in bacterial electrophysiology, with emerging translational directions in antimicrobial control. Here we review these developments, highlight competing interpretations of bacterial "excitability," identify key measurement and mechanistic gaps (especially absolute Vm quantification and causal linking to phenotype), and outline future opportunities at the interface of photobiology, bioelectronics, and microbial physiology.

KEYWORDS
bacterial bioelectricity, bacterial electrophysiology, bacterial signalling, ion channel dynamics, membrane potenial

1 Introduction

Bacterial membranes maintain electrochemical gradients that power respiration, ion and nutrient transport, and cell motility, yet for decades these gradients were treated largely as homeostatic background variables rather than dynamic signals. A core barrier was methodological: bacteria are small and often motile, they possess a thick peptidoglycan envelope, and electrical dynamics can occur on timescales that are difficult to capture without specialized probes and imaging platforms. As a result, much of early bacterial "electrophysiology" relied on indirect, ensemble measurements—growth phenotypes, ion flux assays, or population-averaged dye readouts—rather than direct measurements of membrane potential (Vm) dynamics in single cells or structured communities. The last decade has forced a re-evaluation, with reviews now explicitly arguing that standard biophysical theories and measurement practices need adaptation for bacterial contexts, and that Vm dynamics can play signaling roles in cell–cell interaction and stress adaptation

(Benarroch and Asally, 2020; Mancini et al., 2020; Lo et al., 2024; Pater et al., 2021; Paternò, 2024; Roy et al. 2025; Krasteva, 2011; de la Viuda et al., 2025; Bertolotti et al., 2025).

A widely recognized turning point occurred in 2011, when Kralj and colleagues engineered a voltage-sensitive fluorescent protein based on a proteorhodopsin scaffold (PROPS), using it to image electrical spiking in *Escherichia coli* at up to ~1 Hz. Importantly, spiking was sensitive to perturbations and coincided with rapid efflux of a small-molecule fluorophore, hinting at a functional link between electrical state and membrane transport machinery (Kralj et al., 2011). In the years that followed, bacterial bioelectricity expanded to greater scales: from single-cell Vm transients to biofilm-wide potassium ion (K^+) waves coordinating metabolism, and onward to inter-community coupling and "memory-like" electrical states (Prindle et al., 2015; Liu et al., 2017). In parallel, photobiology has become increasingly central, not only for readout (fluorescent reporters and dyes), but also for perturbation (photoactive membrane modulators and optical transducers), enabling causal experiments that were previously impractical (Gao et al., 2020; de Souza-Guerreiro et al., 2023).

This Mini Review focuses on the developments since 2011 with an emphasis on (i) bacterial Vm dynamics and measurement approaches, (ii) how electrical signaling integrates with community physiology and metabolism, (iii) how optical and bioelectronic toolkits are reshaping the field, and (iv) discussion of controversies, gaps, and future directions most relevant to a photobiology readership.

2 Concepts and measurement of Vm

2.1 What is bacterial bioelectricity?

In bacteria, Vm is one component of the proton motive force (PMF), coupled to ΔpH and ion gradients that depend on cell respiration, transport, and envelope properties. While it was known already that bacteria have membrane potential, the crucial conceptual update from the last 15 years is that Vm can be dynamic, can be measured at a single cell level and be heterogeneous across cells, and can be responsive on timescales relevant to physiology and collective behavior (Benarroch and Asally, 2020; Roy et al. 2025; Hennes et al., 2023; Akabuogu et al., 2025). It is useful to distinguish three related but non-identical domains: (i) transmembrane voltage dynamics (Vm fluctuations and excitability-like transients), (ii) ionic signaling in communities (e.g., extracellular K^+ waves that depolarize neighbors), and (iii) electrochemical interactions at interfaces (including electrode-based stimulation and impedance phenotyping). Vm fluctuations are often referred to, in literature, as a signal of a bacterial excitability. In neuroscience to fulfill excitability a system must have the capacity to produce a stereotyped, amplified response when a threshold stimulus is exceeded, followed by a refractory period before the following event. Despite promising results, particularly on large colonies and biofilms (Masi et al., 2015; Martinez-Corral et al., 2019), whether bacteria can fulfill strictly this definition is still debated, for this reason, to compel with the existing literature we will refer to this phenomena as "excitability-like". Even though there is overlap in the experimental measures of these different phenomena, they can be mechanistically distinct; conflating them is a recurring source of confusion in the field. Bacterial Vm typically lies in a 70 mV range between −75 and −140 mV (ref Stratford) with a strong dependence on growth medium, growth phase but also inter and intraspecies. Roy et al, for example, show how a same *Bacillus subtilis* strain might vary between −65 and −127 mV if moving from a rich to a minimal medium. Measurement of Vm in bacteria remains the main bottleneck and driver of controversy (Mancini et al., 2020). The 2020 review from Benarroch and Asally explicitly emphasizes that many classical voltage probes and calibration assumptions were developed for eukaryotic membranes and must be re-validated for bacterial envelopes and growth conditions (Benarroch and Asally, 2020). Likewise, the recent 2024 Annual Review on bacterial electrophysiology from Lo et al. stresses the need for bacterial-specific theory and standardization of methods, including careful reporting of medium composition, growth phase, probe concentration, illumination dose, and validation by multiple experimental approaches where feasible (Lo et al., 2024).

2.2 The 2011 milestone: optical access to single-cell Vm dynamics

The PROPS study showed that genetically encoded optical reporters can work in bacteria and can reveal fast Vm dynamics that were previously inaccessible (Figure 1). Two aspects were field-shaping (Kralj et al., 2011). First, the signal itself: electrical "spikes" in bacteria invited comparisons to action potentials, even if mechanisms and scales differ. Second, the hypothesis space: correlation of spikes with rapid dye efflux suggested that Vm transients might couple to transport/efflux activity and thus potentially influence drug susceptibility or stress responses. The work also implicitly seeded a central controversy: are Vm transients a cause, or an aftereffect of fluctuating cell conditions?

Since 2011, optical readout has diversified into (i) improved genetically encoded indicators, (ii) bacterial-adapted small-molecule probes, and (iii) combined platforms pairing stimulation with live imaging. The general trajectory moves from merely observing bioelectrical dynamics to triggering and quantifying them. This trajectory is particularly important for photobiology because both the readout and many perturbations are light-driven and thus susceptible to confounds (phototoxicity, heating, intrinsic non-photosynthetic light sensitivity and reactive oxygen species) (Cianflone and Paternò, 2025) unless dose and controls are treated as first-class experimental variables.

2.3 Non-optical approaches to Vm measurement

Non-optical approaches have a double and crucial role in bacterial bioelectricity measurements; on one hand they can corroborate optical results avoiding potential biases (such as phototoxicity or an over-measurement of the probe); on the other hand, they can bypass the constraints of optical access and access to different timescales (Akabuogu et al., 2024; Biquet-Bisquert et al., 2024). Complementary non-fluorescent, single-cell "physical voltmeters" can help triangulate electrophysiological state: Krasnopeeva and colleagues developed an electric-circuit analogue, linking PMF, membrane electrical properties, and catabolism, and used the flagellar motor as a rapid single-cell

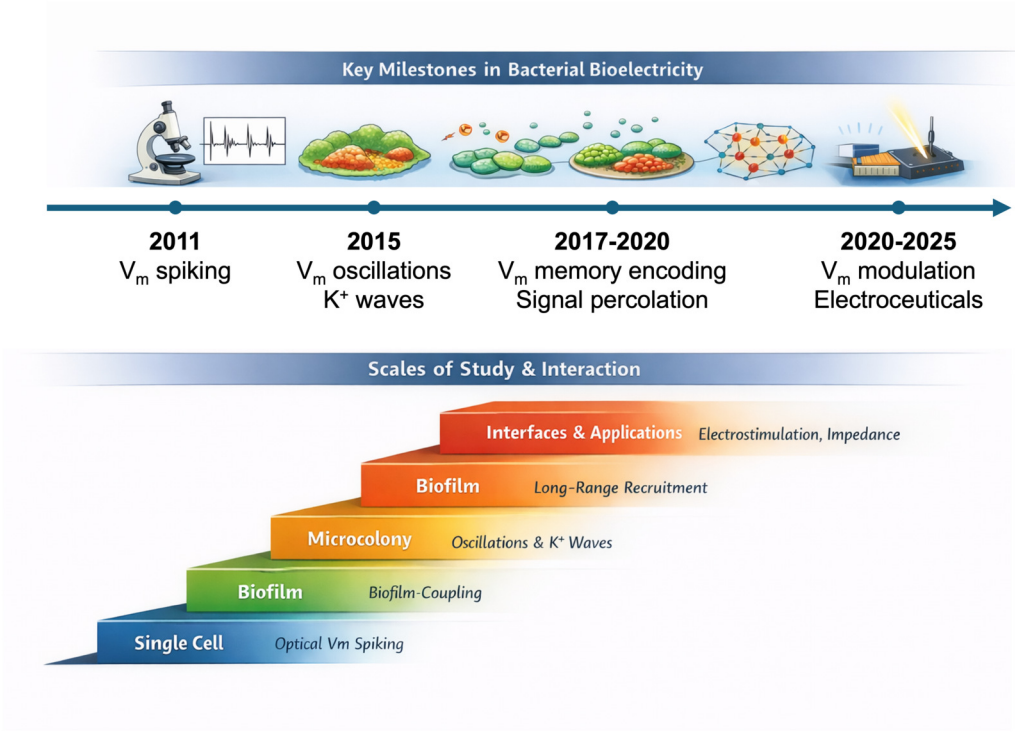

FIGURE 1
Timeline and scale ladder of key milestones in bacterial bioelectricity (2011–2024). Top: Conceptual timeline highlighting major advances enabled by optical readouts and, more recently, by controlled perturbation platforms. Milestones include optical detection of fast membrane-potential (Vm) dynamics in single cells (2011), emergence of biofilm-scale oscillatory physiology and K^+-mediated electrical signaling (2015), biofilm coupling and recruitment phenomena (2017), and the development of interface-driven control strategies (2019–2024), including photonic transducers, electrical stimulation, impedance-based phenotyping, and electroceutical approaches. Bottom: Scale ladder summarizing how the field expanded from single-cell Vm dynamics to microcolony/biofilm collective behaviors and finally to biointerfaces and applications, where electrical and optical stimuli can be used to probe causality and modulate bacterial physiology.

readout under dynamic stresses (Krasnopeeva et al., 2019). Their approach was able to separate stressors that enact a change in Vm (as an ionophore would) from those that cause membrane damage. Notably, they highlighted that shorter-wavelength light can induce electrophysiological impairment (Cianflone and Paternò, 2025), an observation that reinforces the need for rigorous wavelength and dose controls in photobiology-driven bacterial electrophysiology. Another approach for single cell Vm measurements came from Biquet-Bisquert et al. (2024); their study of PMF dynamics enabled ms resolution in Vm variations. A practical takeaway is that most bacterial Vm studies are strongest when they (a) report relative dynamics robustly (timing, frequency, spatial propagation, cell-to-cell heterogeneity) and (b) avoid overclaiming absolute Vm values unless calibration is explicitly demonstrated.

3 Community bacteria electrophysiology and behavior

3.1 Biofilm electrophysiology: K^+ waves, metabolic oscillations, and community coordination

As introduced in Section 2.1, the K^+ waves phenomena discussed in what follows are primarily in the domain of the extracellular ionic signaling rather than single-cell Vm dynamics. Nonetheless, the two phenomena are both effective at the cell membrane level through depolarization. A second inflection point came from biofilm studies in *B. subtilis*, where electrical and metabolic dynamics were shown to be coupled at community scale. Liu et al. (2015) described long-range metabolic codependence between peripheral and interior biofilm cells as a mechanism to resolve a growth–protection conflict, producing collective oscillations (Liu et al., 2015). In the same year, Prindle et al. demonstrated that ion channels can conduct long-range electrical signals in biofilms through spatially propagating K^+ waves; a metabolic trigger induces K^+ release, the increased extracellular K^+ then depolarizes neighboring cells, and a depolarization wave coordinates metabolic states across the biofilm (Prindle et al., 2015). These papers jointly established that bacterial communities can exhibit structured dynamics reminiscent of excitable media, but with metabolism as a core driver rather than a background condition.

Crucially, these findings extended beyond a single biofilm. Liu et al. (2017) showed coupling between distant biofilms: 2 *B. subtilis* biofilm communities undergoing oscillations can become synchronized through electrical signaling, with consequences for competition and nutrient utilization ("nutrient time-sharing") (Liu et al., 2017). This raised an ecological interpretation of bacterial electrophysiology, namely electrical coupling as an interaction channel between spatially separated populations.

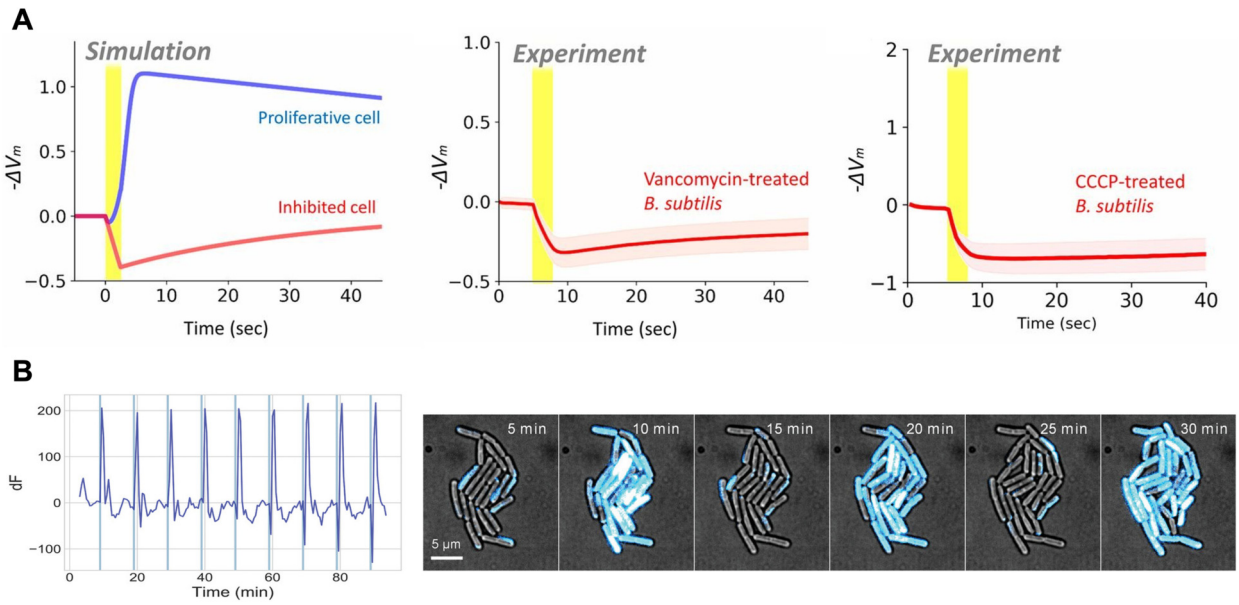

FIGURE 2
State-dependent electrical excitability in *Bacillus subtilis* and photodriven oscillatory voltage responses induced by a membrane-targeted azobenzene. **(A)** Model prediction (left) and experimental measurements (middle/right) of stimulus-evoked membrane-potential changes (reported as $-\Delta V_m$) following a brief electrical stimulus (yellow bar). The simulation illustrates that identical stimulation can yield qualitatively different polarization dynamics depending on cellular state (proliferative vs. inhibited), while experiments show corresponding responses in *B. subtilis* under pharmacological perturbations (vancomycin or CCCP), highlighting strong state dependence in bacterial electrophysiology. **(B)** Repeated optical stimulation in the presence of the membrane-targeted photoswitch Ziapin2 elicits recurring oscillations in voltage-sensitive fluorescence (dF; left), linked to potential hyperpolarisation. Representative time-lapse images (right; 5–30 min; scale bar 5 µm) show coordinated fluorescence activity within a local cell group across successive illumination cycles, consistent with photomodulated membrane-voltage dynamics and suggesting the potential for intercellular coupling under these stimulation conditions. Figure 2A is adapted from ref. (Stratford et al., 2019),Copyright National Academy of Sciences (2020). Figure 2B is adapted from ref. (de Souza-Guerreiro et al., 2023), Copyright Wiley (2023).

Theory has also matured. A percolation-based framework linked signal propagation to community heterogeneity and spatial organization, providing a quantitative language for when long-range transmission becomes possible and how near-critical organization can facilitate it (Larkin et al., 2018). Complementarily, a spatial reaction–diffusion model explicitly combined metabolic and electrical components and supported the view that metabolic stress can be transmitted via a K^+ wave, offering a mechanistic bridge between the "metabolism-first" and "channel-first" intuitions that often appear as competing schools of thought (Martinez-Corral et al., 2019). These findings have also found preliminary coincident results on different Gram-negative bacteria such as *Escherichia coli* or *N. gonorrhoeae*. For the first, Akabuogu and colleagues (Akabuogu et al., 2025), demonstrated Vm oscillations in *E. coli* biofilms; for the latter Hennes et al. (2023) showed that the polarization behavior transitions from individual to collective dynamics beyond a critical biofilm size.

3.2 From community signals to behavioral outputs: recruitment, motility, and second messengers

A key step toward "function" is demonstrating that electrical signals are not only internally coordinating within a connected group of bacteria but can influence behaviors of cells outside the community as well. Humphries et al. used microfluidics to show that K^+ channel–mediated electrical signaling generated by a *B. subtilis* biofilm can attract distant motile cells, and that recruitment can be species-independent (Humphries et al., 2017). Interestingly, this recruitment was even observed to target cell behavior; an electrical stimulus was able to preferentially promote the proliferation of motile over the matrix-producing *B. subtilis* cells (Comerci et al., 2022). Modeling and experiments supported a mechanism in which extracellular K^+ alters the Vm of distant cells, biasing motility and accumulation near the biofilm. This is a particularly photobiology-relevant result because it provides a conceptually clean Vm → behavior linkage that can, in principle, be tested causally with optical perturbations.

At the single-cell level, bacterial electrophysiology has also been connected to downstream signaling-like processes. In *E. coli*, voltage transients were shown to induce calcium influx, supporting the idea that bacteria can couple voltage dynamics to intracellular ionic signaling and potentially treat Ca^{2+} as a second messenger (Bruni et al., 2017). While the mechanistic and evolutionary interpretations can be debated, the result expands the field beyond "membrane energetics" toward "electrophysiology as information routing," where Vm dynamics can gate other cellular processes. For example, in *B. subtilis*, Kikuchi et al. observed that fluctuations in Vm were linked to a tailored "awakening" from a dormant metabolic state; sporulated bacteria were able to accumulate K^+ ions through an "integrate and fire" mechanism, exiting the dormant state once a certain threshold was reached (Kikuchi et al., 2022).

4 Toolkits for exploring causality and emerging concepts

4.1 Perturb-and-measure platforms: optical, electrical, and hybrid

The past few years have shifted the field from observation to intervention. For photobiology, the most important development is the emergence of nongenetic optical control of bacterial Vm. A membrane-targeted azobenzene (Ziapin2) (Paterno et al., 2020; Paternò et al., 2020) was shown to photomodulate Vm in *B. subtilis*, positioning photopharmacology-like strategies as practical tools for bacterial electrophysiology without the need for genetic manipulation (de Souza-Guerreiro et al., 2023). This matters not only as a method but as a conceptual bridge: it enables experiments where Vm is controlled by defined temporal patterns and then linked to transport, stress responses, or community dynamics.

In parallel, structured photonic materials can act as optical transducers for bacteria. Multiscale structured silicon was developed as a nongenetic optical transducer capable of modulating activities of single bacterial cells and biofilms at high spatiotemporal resolution, addressing the long-standing lack of localized physical perturbation tools in microbial communities (Gao et al., 2020). These approaches suggest a future in which light patterns become "stimuli" for bacterial systems in the same way they are used in optogenetics, while remaining mindful that photothermal, photochemical, or intrinsic photobiological responses must be experimentally separated from genuine electrophysiological modulation (Cianflone and Paternò, 2025; Van Der St et al., 2015; Perlova et al., 2019; Blee et al., 2020).

Electrical stimulation platforms are also becoming more sophisticated. A microfluidic/electrode-based approach from Stratford et al. showed that identical electrical stimuli can produce opposite polarization dynamics depending on the proliferative capacity of the cells, emphasizing that bacterial electrical responses are state-dependent and that heterogeneity must be treated as an intrinsic variable, not noise (Stratford et al., 2019). At the translational end, a "drug-free" bioelectronic strategy from Kim et al. exploited selective excitability of *Staphylococcus epidermidis* and demonstrated reduced colonization on a porcine skin model using an electroceutical patch (BLAST) (Kim et al., 2024).

Finally, electrophysiology is broadening beyond fluorescence. Electrical impedance spectroscopy by Akabuogu et al. revealed that *E. coli* biofilms can exhibit stable negative capacitances at low frequencies under small DC bias and implicated the voltage-gated K^+ "Kch" using knock-down mutants. This work showed how electrical phenotyping can connect macroscopic electrical signatures to specific channel machinery in living biofilms (Akabuogu et al., 2024).

4.2 Emerging concepts: "memory" and programmability in biofilms

One of the more provocative post-2015 directions is that bacterial communities may encode persistent electrical states. Yang et al. (2020) demonstrated that transient optical perturbations generated a long-lasting K^+-channel-mediated change in Vm within a biofilm, such that exposed cells responded out of phase relative to unexposed cells during subsequent oscillations (Yang et al., 2020). This was interpreted as a type of Vm-based "memory" in a microbial community. This tangible phenomenon has implications for programmability and information storage in bacterial collectives.

This behavior is consistent with bistable dynamics within the metabolic-electrical network as for the coupled reaction-diffusion framework showed by Martinez-Corral et al. In their work the different components of the phenomenon are discretized in an experimental-backed reaction-diffusion scheme proving the role of K^+ waves in the diffusion of information within a dense colony and showing the persistence of those signals. These results are relevant as a foundation to move from the observation of bistable dynamics towards the measurement of bistable states in a bacterial population.

This line of work connects naturally to percolation and reaction–diffusion models: if transmission depends on network organization and metabolic/electrical coupling, then persistent state changes could arise from bistability and feedback within these coupled systems (Larkin et al., 2018). For photobiology, the main opportunity is methodological: optical perturbation can write states, optical readout can track them, and spatially structured illumination can test whether "writing" is local, propagative, or dependent on community connectivity..

5 Discussion

5.1 Different schools of thought and controversies

Are bacterial "spikes" action potentials, or something else? The PROPS-era discovery of ~Hz spiking in *Escherichia coli* understandably triggered analogies to neuronal action potentials. However, bacteria lack the canonical architecture of excitable membranes found in neurons, and spike-like events may represent a mixture of processes (transport transitions, metabolic switching, channel activity, envelope constraints) that can generate rapid Vm excursions without a single conserved mechanism. The controversy here is less about whether spikes exist, and more about how much explanatory power is gained by importing neuronal language *versus* developing bacteria-native descriptors anchored in metabolism and transport physiology.

Is biofilm electrical signaling "channel-first" or "metabolism-first"? Prindle et al. provide a channel-mediated, K^+-wave mechanism that clearly links metabolic triggers to propagating depolarization and coordinated states. Liu et al. emphasize metabolic codependence and oscillatory growth dynamics as an emergent resolution to spatial resource conflicts. The most productive synthesis is that metabolism and electrophysiology are coupled layers of the same dynamical system, as formalized in models explicitly combining metabolic and electrical components and validated by perturbations.

Correlation *versus* causality in phenotype links (e.g. efflux, motility, tolerance). The original observation that spikes coincide with fluorophore efflux motivates hypotheses about electrical regulation of transport. Yet correlation is expected whenever both

Vm and transport respond to shared metabolic or stress drivers. The field's current challenge is to elevate such claims with perturb-and-measure designs: drive Vm independently (optically or electrically), and test whether efflux, motility, or survival phenotypes change in a direction and timescale consistent with a causal mechanism. The primarily objective of a realistic experiment should be to perturb and manipulate Vm through the use of a molecular actuator (such as Ziapin2 in ref 32) or a generic electrical stimulus and then measuring the effects on their physiology as well as on the motility or survival. These readouts must compel to the direction and timescale of an electrophysiological mechanism and differ substantially from the metabolic behavior.

5.2 Current research gaps

Optical probes limitations. Most of the frequently used Nernstian indicators (ThT, DiBAC, TMRM and many others) tend to measure the steady-state Vm rather thant fast transients; furthermore, their signal might be altered by membrane permeability changes, the activity of the efflux pump or other variations in the membrane physiology independent from the Vm. These dyes, even at low concentrations might also influence bacterial growth. On the other hand, PROPS-like indicators require genomic modifications and are not suitable for clinic applications.

Quantitative Vm and calibration standards. Many studies excel at dynamics but remain limited in absolute Vm quantification, and cross-lab comparability is hindered by differences in probes, media, growth state, and illumination protocols. Calls for bacterial-specific standardization are now explicit in the field's synthetic reviews.

Mechanistic mapping to molecular actors. For biofilms, K^+ channels are clearly implicated, but broader mapping to transporters, respiratory chain states, and envelope properties is incomplete. Impedance spectroscopy that links macroscopic electrical signatures to specific channels (e.g., Kch) is a promising complement to fluorescence-based approaches.

State dependence and heterogeneity. The same external electrical stimulus can produce opposite Vm dynamics depending on cell proliferative capacity and metabolism. This implies that cellular state is not a confounding variable, but rather an important control parameter. Future work must treat state variables (growth phase, nutrient limitation, stress history, spatial position in biofilms) as integral to electrophysiological interpretation.

Separating electrical signaling from other long-range interactions. Electrical coupling in biofilms can be entangled with chemical gradients, mechanical structure, and extracellular matrix effects. Percolation-style and reaction–diffusion models offer testable predictions but require more standardized datasets with single-cell resolution and defined perturbations.

The relation between Vm and antibiotic tolerance. Despite the large body of work linking Vm fluctuation and antibiotic tolerance, there remains a lack of consensus on how hyper-*versus* depolarization impacts antibiotic effects. An extensive investigation of different bacterium-stimulus-antibiotic combinations is required to comprehend and consider electrophysiology a useful tool to face this issue (Hennes et al., 2023; Jin et al., 2023; Lee et al., 2023; Lee et al., 2019; Whittle et al., 2024; Bruni and Kralj, 2020).

5.3 Potential future developments

Photobiology-enabled causality at scale. Nongenetic optical Vm modulators point toward bacterial "all-optical electrophysiology" experiments where stimulation patterns are as controllable as in modern optogenetics, but with bacterial-appropriate mechanisms and controls. The near-term opportunity is not merely new tools, but a change in experimental logic: use light to write defined Vm perturbations and then quantify downstream effects on motility, recruitment, efflux, and signaling.

Hybrid bioelectronic–photonic platforms and translational control. Bioelectronic stimulation devices that exploit bacterial excitability (e.g., BLAST) suggest antimicrobial strategies that are drug-sparing and can be localized to interfaces such as skin or implanted materials. Combining such approaches with optical readout could accelerate mechanism-guided parameter optimization (waveform, dose, pH/ionic environment) and help define which phenotypes are truly "electrically addressable."

Tailored bioelectricity enhancement. An additional, potentially interesting, future path could be the use of exogenous modulators to obtain a willingly incrementation of the bioelectrical response. It has been shown that supplement of Tricarboxylic Acid Cycle Intermediates (such as glutamate, fumarate or pyruvate) might boost the PMF, amplify $\Delta\Psi$ and impact the uptaking of aminoglycoside antibiotics increasing their effect and proving how Vm control has a relevant clinical framework (de Souza-Guerreiro et al., 2023; Lee et al., 2023; Allison et al., 2011; Meylan et al., 2017). This enhancement might also be use synergistically with chemical phototransducers as Ziapin2 to achieve a double-edged control on the potential.

Interrogation-driven phenotyping and diagnostics. A near-term opportunity is to move from passive observation to standardized interrogation protocols, defined optical or electrical stimuli paired with time-resolved, single-cell and community-level readouts, to generate reproducible "response fingerprints" of bacterial physiological state. Such stimulus–response phenotyping could enable diagnostic and screening strategies for clinically relevant phenotypes that are otherwise hard to assay, including antibiotic tolerance, persister formation, and dormancy, by capturing how membrane energetics and excitability-like dynamics reshape under challenge.

Programmability and memory in microbial collectives. Persistent Vm state changes induced by transient optical perturbations highlight a plausible route toward programmable bacterial communities, where electrical state acts as a distributed variable for encoding history or coordinating future responses. A key future step is to determine generality across species and environments and to map the minimal circuits (channel types, feedback loops, metabolic couplings) required for such state storage.

Author contributions

EC: Conceptualization, Visualization, Writing – review and editing. HK: Writing – review and editing. NS: Writing – review and editing. GP: Conceptualization, Writing – original draft, Writing – review and editing.

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