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Fundamentals and Control of Electron Transport at Cellular-Electronic Interfaces

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14. ABSTRACT
This AFOSR PECASE award led to major discoveries of the structure-function relationships and charge transport physics in metal-reducing bacteria across length scales – from individual metalloproteinase to bacterial nanowires, single cells, and multicellular biofilms. These discoveries include (i) describing a multistep electron hopping mechanism in cell surface cytochromes that allow biotic-abiotic electron exchange; (ii) the development of new computational and immersive visualization strategies for understanding electron transport dynamics in large redox networks;
(iii) discovering the structural basis of bacterial nanowires in an important environmental organism; and (iv) demonstrating multi-cell redox conduction. These discoveries were reported in 20 peer reviewed publications, fully or partially supported by this AFOSR
PECASE award.

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Final Report for AFOSR Award FA9550-14-1-0294

PECASE: Fundamentals and Control of Electron Transport at Cellular-Electronic Interfaces

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1. Summary

Electronic components that interface to biological systems will have vast implications for both studying and harnessing the activity of living cells. While much ongoing research focuses on applying traditional rigid nanomaterials to cells, this approach presents yet-unresolved mechanical and signal transmission compatibility issues. An alternative, pursued through this AFOSR PECASE award, is to understand the mechanisms behind solutions that life itself already evolved to interact with abiotic surfaces. The project focused on the biophysical and structural basis of long-distance (over micrometer length scales) extracellular electron transport (EET) by metal-reducing bacteria. These remarkable organisms have evolved direct charge transfer mechanisms (multiheme cytochromes and bacterial nanowires) to solid surfaces outside the cells, allowing them to use abundant minerals as electron acceptors for respiration, instead of oxygen or other soluble oxidants that would normally diffuse inside cells.

The project led to **major discoveries of the structure-function relationships and charge transport physics in metal-reducing bacteria** (using *Shewanella oneidensis* MR-1 as a model organism) across length scales – from individual metalloproteins to bacterial nanowires, single cells, and multicellular biofilms. These discoveries include (i) describing a multistep electron hopping mechanism in cell surface cytochromes that allow biotic-abiotic electron exchange; (ii) the development of new computational and immersive visualization strategies for understanding electron transport dynamics in large redox networks e.g. bacterial nanowires, whole cells, and biofilms; (iii) discovering the structural basis of bacterial nanowires in an important environmental organism; and (iv) demonstrating multi-cell redox conduction. These discoveries were reported in **20 peer-reviewed publications** (see Publications Section below), fully or partially supported by this AFOSR PECASE award, and collectively **already cited > 830 times** in the literature (as of December 2020). Importantly, these discoveries opened entirely new research directions for understanding and exploring the biotic-abiotic interface (e.g. the recent discovery of chiral induced spin selectivity in metalloproteins) and generated much of the PI's preliminary results that led to a large-scale MURI effort on living electronics.

Trainee outcomes. We note that this project **enabled the successful dissertations and/or publications of 7 PhD students, 4 postdoctoral scholars, and a high school student** (who went on to graduate from the University of Chicago). The graduated PhD students went on to postdoctoral positions (Caltech, MIT) and industry jobs (*Intel*). The completed postdoctoral scholars went on to permanent positions in academia (University of Hong Kong), scientific consulting (*BAH*/DARPA), and industry (*Cercacor*). It is impossible to overstate the impact that this presidential early career award had on both the career of the PI and his trainees.

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2. Full list of Publications Resulting (fully or partially) from AFOSR-PECASE Funding (*denotes trainees from El-Naggar's group)

1. S. Pirbadian*, M.S. Chavez*, M.Y. El-Naggar, *Spatiotemporal mapping of bacterial membrane potential responses to extracellular electron transfer*, Proceedings of the National Academy of Sciences of the United States of America, 117, 20171-20179, 2020
2. G.W. Chong*, S. Pirbadian*, M.Y. El-Naggar, *Surface-induced formation and redox-dependent staining of outer membrane extensions in Shewanella oneidensis MR-1*, Frontiers in Energy Research 7, 87 2019
3. M. Kaplan, P. Subramanian, D. Ghosal, C.M. Oikonomou, S. Pirbadian*, R. Starwalt-Lee, S.K. Mageswaran, D.R. Ortega, J.A. Gralnick, M.Y. El-Naggar, G.J. Jensen, *In situ imaging of the bacterial flagellar motor disassembly and assembly processes*, The EMBO Journal, e100957, 2019
4. M. Kaplan, D. Ghosal, P. Subramanian, C.M. Oikonomou, A. Kjaer, S. Pirbadian*, D.R. Ortega, A. Briegel, M.Y. El-Naggar, G.J. Jensen, *The presence and absence of periplasmic rings in bacterial flagellar motors correlates with stator type*, eLife 8, e43487, 2019
5. P. Chellamuthu, K.L. Naughton, S. Pirbadian*, K.P.T. Silva, M.S. Chavez*, M.Y. El-Naggar, J.Q. Boedicker, *Biogenic control of manganese doping in zinc sulfide nanomaterial using Shewanella oneidensis MR-1, Frontiers in Microbiology* 10, 938, 2019
6. S. Xu*, A. Barrozo, L.M. Tender, A.I. Krylov, M.Y. El-Naggar, *Multiheme Cytochrome Mediated Redox Conduction Through Shewanella oneidensis MR-1 Cells*, Journal of the American Chemical Society, 140, 32, 10085-10089, 2018
7. N.L. Ing, M.Y. El-Naggar, A.I. Hochbaum, *Going the distance: long-range conductivity in protein and peptide bioelectronic materials*, The Journal of Physical Chemistry, 122, 10403-10423, 2018 *ACS Editors Choice*.
8. G.W. Chong*, A.A. Karbelkar*, M.Y. El-Naggar, *Nature's Conductors: What can microbial multi-heme cytochromes teach us about electron transport and biological energy conversion?* Current Opinion in Chemical Biology, 47, 7-17, 2018
9. P. Subramanian, S. Pirbadian*, M.Y. El-Naggar, G.J Jensen, *The ultrastructure of Shewanella oneidensis MR-1 nanowires revealed by electron cryo-tomography*, Proceedings of the National Academy of Sciences of the United States of America, 115, E3246-E3255, 2018. Highlighted by *Nature Reviews Microbiology* and the American Society for Microbiology (*Small Things Considered* series), recommended in F1000 prime. Media coverage by multiple outlets.
10. Barrozo, M.Y. El-Naggar, A.I. Krylov, *Distinct Electron Conductance Regimes in Bacterial Decaheme Cytochromes*, Angewandte Chemie, 57, 6805-6809, 2018
11. H.W. Harris, I. Sánchez-Andrea, J.S. McLean, E.C. Salas, W. Tran, M.Y. El-Naggar, K.H. Nealson, *Redox Sensing Within the Genus Shewanella*, Frontiers in Microbiology, 8, 2568, 2018
12. L.A. Zacharoff*, M.Y. El-Naggar. *Redox Conduction in Biofilms: From Respiration to Living Electronics*, Current Opinion in Electrochemistry, 4, 182-189, 2017
13. N.P. Shroff, S. Xu*, J. Acevedo, J. Lima, M.Y. El-Naggar, S.E. Finkel, *A novel microenvironment for Shewanella oneidensis MR-1 exists within graphite felt electrodes*, Journal of The Electrochemical Society, 164, H3103-H3108, 2017
14. S.E. Barchinger, S. Pirbadian*, C. Sambles, C.S. Baker, K.M. Leung*, N.J. Burroughs, M.Y. El-Naggar and J.H. Golbeck. *Regulation of Gene Expression During Electron Acceptor*

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Limitation and Bacterial Nanowire Formation in Shewanella oneidensis MR-1, Applied and Environmental Microbiology, 82, 5428-5443, 2016

15. S. Xu*, Y. Jangir*, and M.Y. El-Naggar. *Disentangling the roles of free and cytochrome-bound flavins in extracellular electron transport from Shewanella oneidensis MR-1*, Electrochimica Acta, 198, 49-55, 2016
16. C. Masato Nakano*, E. Moen, H.S. Byun*, H. Ma, B. Newman, A. McDowell, T. Wei and M.Y. El-Naggar, *iBET: Immersive visualization of biological electron-transfer dynamics*, Journal of Molecular Graphics and Modelling, 65, 94-99, 2016
17. B.J. Gross* and M.Y. El-Naggar. *A combined electrochemical and optical trapping platform for measuring single cell respiration rates at electrode interfaces*, Review of Scientific Instruments, 86, 064301, 2015.
18. C. Masato Nakano*, H.S. Byun*, H. Ma, T. Wei, and M.Y. El-Naggar. *A framework for stochastic simulations and visualization of biological electron-transfer dynamics*, Computer Physics Communications 193, 1-9, 2015.
19. S. Pirbadian*, S. E. Barchinger, K.M. Leung*, H.S. Byun*, Y. Jangir*, R.A. Bouhenni, S.B. Reed, M.F. Romine, D.A. Saffarini, L. Shi, Y.A. Gorby, J. H. Golbeck, and M.Y. El-Naggar. *Shewanella oneidensis MR-1 nanowires are outer membrane and periplasmic extensions of the extracellular electron transport components,* Proceedings of the National Academy of Sciences of the United States of America, 111, 12883-12888, 2014. Highlighted by News & Views pieces in *Nature Chemical Biology* and *Nature Nanotechnology*. Cover feature about this work in March 2015 issue of *Microbe*. Media coverage by *Public Radio's Science Friday*, *Southern California Public Radio, Popular Science,* and *Smithsonian* magazine.
20. P. Atanassov, M.Y. El-Naggar, S. Cosnier, U. Schröder. *Biological fuel cells: cardinal advances and critical challenges*, ChemElectroChem, 1, 1702-1704, 2014.

3. Highlights from Select Publications

Here we describe selected highlights from the project's publications listed above. The publications highlighted in this section have already gathered > 640 citations in the literature during the project performance period (citation records from *Google Scholar* as of 12/10/2020):

Discovery of the Structural Basis of Bacterial Nanowires from *Shewanella oneidensis* MR-1
Pirbadian *et al. Proceedings of the National Academy of Sciences of the United States of America*, 111, 12883-12888, 2014

Prior to this study, intense debate surrounded the molecular makeup, identity of the charge carriers, and cellular respiratory impact of bacterial nanowires displayed by the model organism *Shewanella oneidensis* MR-1. In this work, using *in vivo* fluorescence measurements, immunolabeling, and quantitative gene expression analysis, we demonstrated that *S. oneidensis* nanowires are extensions of the outer membrane and periplasm, rather than pilin-based structures, as previously thought. We also demonstrated that the outer membrane multiheme cytochromes MtrC and OmcA localize to these membrane extensions (Fig. 1), directly supporting their role in electron transport through the nanowires; consistent with this, production of bacterial nanowires was correlated with an increase in cellular reductase activity.

Defining the role of flavins in extracellular electron transport from *Shewanella*
Xu et *al. Electrochimica Acta*, 198, 49-55, 2016

While flavins were known to enhance extracellular electron transport in *Shewanella*, there was intense debate surrounding the mechanistic basis of this enhancement. One hypothesis is that the

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bacterial multiheme cytochromes reduce secreted flavins that in turn function as indirect soluble shuttles between cells and external surfaces. A different hypothesis invoked a more intimate interaction and the formation of a flavocytochrome where the flavins enhance extracellular electron transport as redox cofactors bound to the multiheme cytochromes MtrC and OmcA. To address this controversy, we performed electrochemical measurements that captured the redox signatures of both free and cytochrome-bound flavins simultaneously in one experimental system for the first time, allowing us to compare their relative contributions while studying the impact of cell-removal, flavin addition, different culture conditions, and a mutant disrupted in flavin secretion. Our results indicated that endogenous flavins accelerate electron transport from *Shewanella* to electrodes primarily as cytochrome-bound cofactors, rather than free soluble shuttles.

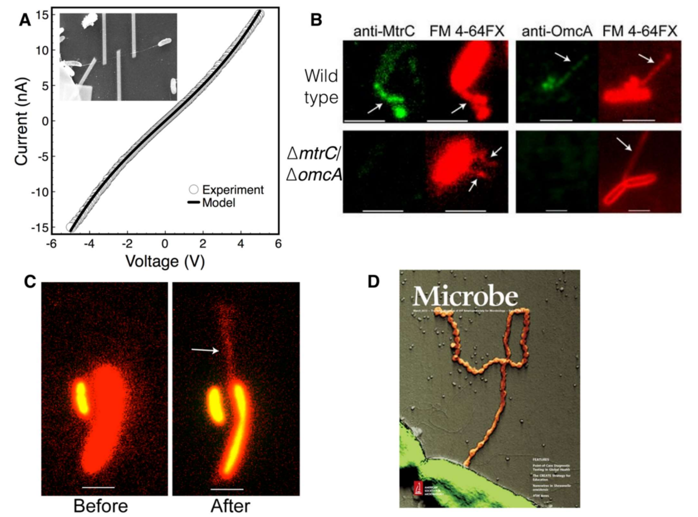

Fig. 1. (A) Measuring transport along *Shewanella* nanowires with nanoscale electrodes. (B) Labeling with antibodies against MtrC or OmcA and membrane fluorescence (FM 4-64FX) images of wild-type *S. oneidensis* MR-1 (top) compared to the *ΔmtrC/omcA* control strain (bottom). (C) Combined respiration (RedoxSensor, Green) and membrane (FM 4-64FX, red) fluorescence images of *S. oneidensis*, before and after the production of a bacterial nanowire. (D) *Microbe* cover image: atomic force microscopy showing that the nanowires originate from interconnected membrane vesicles. Images from El-Naggar *et al. PNAS* 2010 and Pirbadian *et al. PNAS* 2014.

Simulations and immersive visualization of large electron transport networks
Nakano *et al. Journal of Molecular Graphics and Modelling*, 65, 94-99, 2016
Nakano *et al. Computer Physics Communications*, 193, 1-9, 2015.

Our ability to understand complex, large-scale (> 1 μm), multidimensional electron transport pathways is severely limited when visualized in two dimensions on traditional computer monitors, especially when the individual elementary electron transfer steps occur over nm length scales. To provide a more accurate representation with enhanced depth perception, we developed and published an immersive biological electron transport framework to render molecular dynamics models of electron transfer in commodity virtual reality (VR) platforms (Fig. 2). Our publications described how scalable computational approaches to simulate electron transport in large redox networks (whole cells, nanowires, biofilms) can be coupled to these state-of-the-art VR tools for immersive visualization. This work was done in collaboration with the USC Collaboratory for Advanced Computing and Simulations and the USC Cinema School.

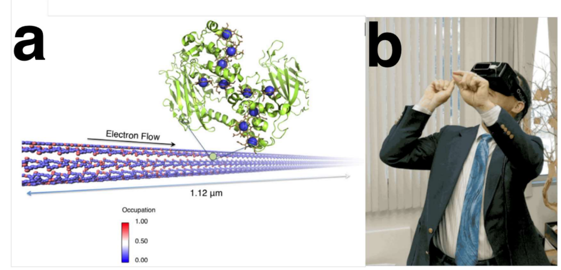

Fig. 2. (A) Simulations and (B) immersive visualization of electron transport networks. Adapted from Nakano *et al.* JMGM 2016 and Nakano *et al.* CPC 2015

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A new electrochemical/optical method for simultaneous electron transfer and bioenergetic measurements of electric bacteria

<u>Pirbadian *et al. Proceedings of the National Academy of Sciences of the United States of America*, 117, 20171-20179, 2020</u>

Up until this work studies on biotic-abiotic electron transfer by metal-reducing bacteria mainly employed bulk techniques, overlooking the subpopulation variation in electron transfer and the potentially complex spatial patterns of activity in microbial communities. Here, by performing simultaneous electrochemical and *in vivo* single-cell-level fluorescence microscopy, we demonstrated the link between extracellular electron transfer and the cell membrane potential (Fig. 3), revealing the utility of membrane potential as a single-cell-level bioenergetic indicator of cell-to-electrode electron transfer by *Shewanella oneidensis* MR-1 cells. This method, developed with AFOSR PECASE funding over the past few years, is now being applied in an ONR funded MURI project and paves the way for understanding the factors underlying extracellular electron transfer at a fundamental level, which could, in turn, lead to improvements in the design of living electronics that enhance their overall performance.

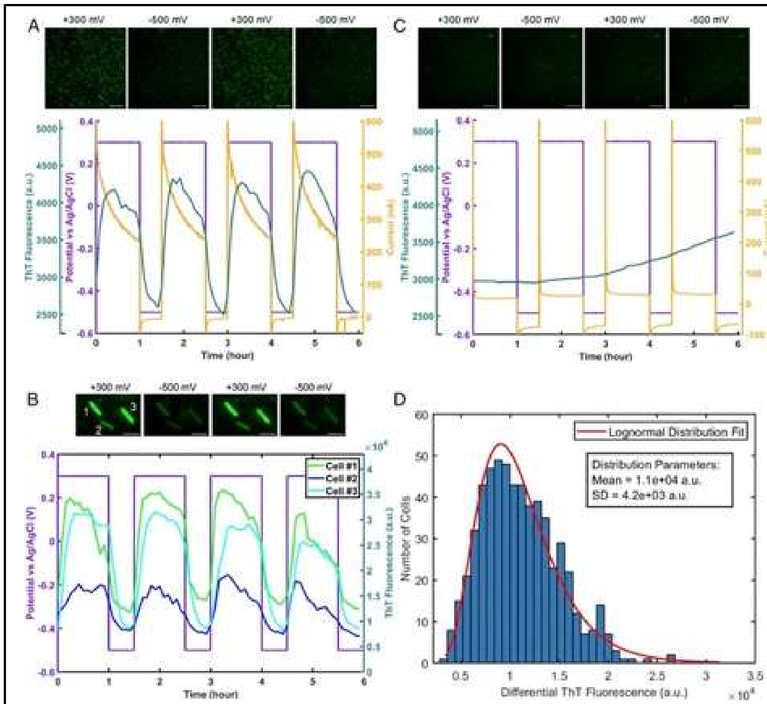

Fig. 3. Membrane potential in *S. oneidensis* is an indicator of extracellular electron transfer activity at the single-cell level. (*A*) Fluorescence images along with electrode potential, current, and average Thioflavin T (ThT) fluorescence plots of *S. oneidensis* cells on the ITO working electrode of a bioelectrochemical reactor during a two-step potential sequence (1 h at +300 mV, 0.5 h at −500 mV vs. Ag/AgCl 1 M KCl). (Scale bars, 20 µm.) (*B*) Fluorescence images along with electrode potential and fluorescence plots of three individual *S. oneidensis* cells from *A*, highlighting the cell-to-cell variability in the larger population. (Scale bars, 2 µm.) (*C*) Images and plots of the ΔMtr/Δ*mtrB*/Δ*mtrE* mutant during an identical two-step potential sequence. The mutant strain lacks genes encoding eight periplasmic and outer membrane cytochromes. (Scale bars, 20 µm.) (*D*) Histogram of the difference in ThT fluorescence between positive and negative potential steps in 592 cells, as well as the lognormal distribution fit with the corresponding distribution parameters. Image from Pirbadian *et al.* PNAS 2020.

Nanoscale mapping and understanding the distribution of electron transport proteins in bacterial nanowires

<u>Subramanian *et al. Proceedings of the National Academy of Sciences of the United States of America*, 115, E3246-E3255, 2018.</u>

Up until this work, a detailed understanding of the architecture and electron transport mechanism along bacterial membrane nanowires was lacking. To address this knowledge gap, we measured and published the electron cryo-tomography ultrastructure of bacterial nanowires from the *S. oneidensis* MR-1. In addition to revealing the dynamic nature of nanowires as chains of interconnected membrane vesicles (with various degrees of tubulation), we

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reported a full 3-dimensional map of the multiheme cytochrome (MtrC/F, OmcA and MtrA/D) distribution, pointing to a mixed collision-exchange mechanism that combines hopping and inter-protein electron transfer steps to facilitate long-distance conduction. To test this hypothesis, we are now measuring the diffusive dynamics of cytochromes by single-molecule imaging studies tracking the trajectories of quantum-dot labeled MtrC/OmcA. Our preliminary results (unpublished) revealed dynamics fast enough to allow frequent collision-exchange events and significant electron transport along nanowires and whole cell surfaces.

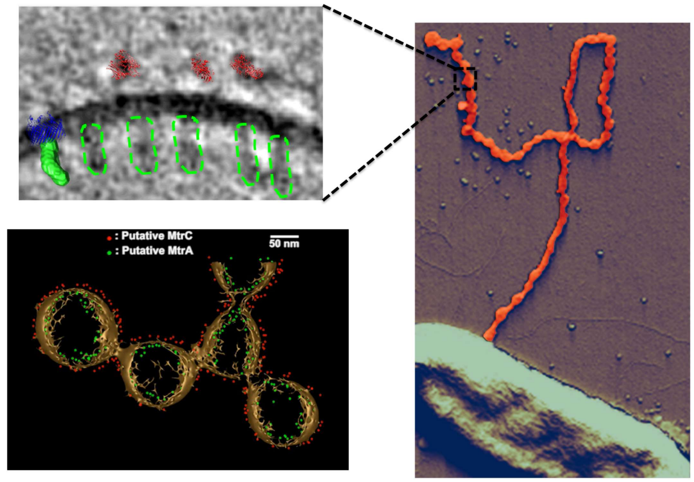

Fig. 4. Advanced imaging techniques allow the nanoscale mapping of microbial electron transfer proteins under native conditions. Left: Overlay of structures of outer membrane decaheme cytochromes MtrC/OmcA (red) and periplasmic decaheme cytochrome MtrA (green) on external and internal electron densities observed during electron cryo-tomography of membrane nanowires. Bottom left shows the reconstruction of the cytochrome network from a complete wire. Right: A wider atomic force microscopy view of a membrane wire extending from a *Shewanella oneidensis* MR-1 cell.

Demonstration of a Cytochrome-Mediated and Thermally-Activated Multi-cell Redox Conduction

Barrozo *et al., Angewandte Chemie*, 57, 6805-6809, 2018

Xu *et al. Journal of the American Chemical Society*, 140, 32, 10085-10089, 2018

In addition to allowing electron transport across the cell wall, our previous measurements had suggested that these electron conduits can facilitate long-distance electron transport laterally along membranes (e.g. bacterial nanowires) and across multiple cells. However, there were no direct demonstrations of this lateral electron transport under physiologically relevant conditions. To address this knowledge gap, we leveraged electrochemical techniques developed as part of this PECASE award, as well as instrumentation acquired from AFOSR through DURIP, to report electrochemical gating measurements of multiple *S. oneidensis* MR-1 cells linking interdigitated electrodes. Critically, we found that the measured thermal activation energy of 0.29 ± 0.03 eV matches electron hopping calculations through the *S. oneidensis* Mtr outer-membrane decaheme cytochromes. AFOSR-supported calculations of the redox landscape in MtrC and MtrF (which allowed us to interpret the temperature-dependent transport simulations) were also published as part of this effort. Our measurements and calculations have implications for understanding and controlling micrometer-scale electron transport in hybrid biotic-abiotic devices that incorporate whole biofilms.

4. National/International Meetings and Invited Seminars by M.Y. El-Naggar

2019	Biomaterial Interfaces **Plenary Speaker** at the AVS National Meeting, Columbus, OH, October 20, 2019
2019	Pittcon 2019 Symposium on Next Generation Analytical Tools for Investigating Waste to Energy Systems **(Invited Speaker)**, Philadelphia, PA, March 2019

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2018	Materials Research Society Symposium on Electronic and coupled transport in biology Boston, MA **(Invited Speaker)**, November 2018
2018	UC Santa Cruz Condensed Matter Physics Seminar, October 19, 2018
2018	Plant & Microbial Biology Department Seminar, UC Berkeley – November 14, 2018
2018	BioMolecular Electronics (BIOMOLECTRO) **(Invited Speaker)**, Madrid, August 30, 2018
2018	Gordon Research Conference on Electron Donor-Acceptor Interactions (Electron Flow: From the Molecular to the Global Scale) **(Invited Speaker)**, Newport, RI, August 5, 2018
2018	Columbia University, Department of Physics, Colloquium, February 26, 2018
2017	Biochemical Society Meeting on Extracellular Electron Transfer, Norwich, UK, August 22, 2017 (**Invited Speaker**)
2017	Blavatnik Science Symposium **(Invited)**, New York, NY, July 17, 2017
2017	Department of Energy's Solar Biochemistry Contractor's Meeting, Gaithersburg, MD, June 5 2017 (**Visiting Keynote Lecture**)
2017	Astrobiology Science Conference (AbSciCon), Mesa, AZ. April 27, 2017
2017	University of Chicago, Institute for Biophysical Dynamics Seminar, March 7, 2017
2017	Duke University, Department of Chemistry Seminar. February 6, 2017
2016	Army Science Planning and Strategy Meeting on Bioenabled Materials Synthesis and Assembly **(Invited Speaker)**, US Army Research Laboratory, Aberdeen Proving Ground, MD, December 1-2, 2016
2016	International Society for Microbial Electrochemistry and Technology, Stanford University **(Keynote Speaker)**. October 5, 2016.
2016	Asilomar Bioelectronics Symposium, Asilomar, CA (**Invited Speaker**). September 5, 2016
2016	American Society for Microbiology, Boston, MA (**Invited Speaker**). June 18, 2016
2015	West Coast Bacterial Physiologists Annual Conference. Invited Speaker: **John Ingraham Lecture in Microbial Physiology**. December 12, 2015
2015	University of California, Berkeley Structural and Quantitative Biology Seminar. November 9, 2015
2015	University of California, Irvine Chemical Engineering and Materials Science Seminar.
2015	**Keynote Lecture** of the 3rd International Workshop on Microbial Life Under Extreme Energy Limitation, Sønderborg, Denmark. September 21, 2015
2015	Gordon Research Conference on Applied & Environmental Microbiology, South Hadley, MA **(Invited Speaker)**. July 14, 2015
2015	Semiconductor Research Corporation Executive Technical Advisory Board Summer Study, Atlanta, GA **(Invited Speaker)**. June 22, 2015
2015	Batsheva de Rothschild Seminar on Molecular Electronics, Jerusalem **(Invited Speaker)**. June 10, 2015

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2015	NSF/NNSC Workshop of US-China Collaborative Research on Microbe-Mineral Interaction: *Microbial Extracellular Electron Transfer with Minerals as Electron Sources and Sinks*. Beijing, China **(Invited Speaker)**. March 23, 2015
2015	2nd Symposium on Functional and Biogenic Materials, Okayama University, Japan **(Invited Speaker)**. March 20, 2015
2014	NASA Astrobiology Institute Director's Seminar
2014	Arizona State University, Department of Chemical Engineering Seminar
2014	Microbial Electron Transfer Symposium, Geoje Island, Korea **(Invited Speaker)**
2014	International Symposium on Microbial Ecology, Seoul, Korea **(Invited Speaker)**
2014	International Society for Microbial Electrochemistry and Technology, State College, PA **(Invited Speaker)**
2014	Meeting on Interface between experimental and theoretical approaches to energy-related enzyme catalysis, University College London **(Invited Speaker)**
2014	1st Symposium on Functional and Biogenic Materials, Okayama University, Japan **(Invited Speaker)**

5. Trainees Impacted by this AFOSR PECASE Project

Postdoctoral Scholars (current position)

2014-present	Shuai 'Matt' Xu, Ph.D. (currently a staff research associate at USC)
2016-2020	Lori Zacharoff, Ph.D. (DARPA Scientific Consultant, *Booz Allen Hamilton*)
2015-2017	Sahand Pirbadian, Ph.D. (Senior Electrochemist, *Cercacor Corporation*)
2011-2014	Kar Man 'Edmond' Leung, Ph.D. (Lecturer, University of Hong Kong)

Graduate Students

2016-present	Grace Chong (current, National Science Foundation Graduate Fellow, Molecular Biology Ph.D. Program)
2016-present	Marko Chavez (current)
2015-2019	Amruta Karbelkar (Chemistry Ph.D, now a Postdoctoral Research Associate, MIT). Dissertation: *Electrochemical Investigations and Imaging Tools for Understanding Extracellular Electron Transfer in Phylogenetically Diverse Bacteria* – defended August 2019
2011-2017	Hye Suk Byun (Process Engineer, *Intel*). Dissertation: *Kinetic Monte Carlo Simulations of Biological Electron Transport: From Single Molecules to Bacterial Redox Networks* – defended March 2017
2011-2016	Yamini Jangir (Postdoctoral Research Associate, Caltech). Dissertation: *Electrochemical studies of subsurface microorganisms* – defended March 2016
2011-2015	Sahand Pirbadian (Senior Electrochemist, Cercacor Corporation). Dissertation: *Bacterial nanowires of Shewanella oneidensis MR-1: composition, structure and mechanism of electron transport* – defended March 2015
2009-2015	Benjamin J. Gross (STEM Instructor, Mirman School). Dissertation: *From fuel cells to single cells: electrochemical measurements of direct electron transfer at microbial-electrode interfaces* – defended April 2015

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