Stanford

Steven Boxer

Camille Dreyfus Professor of Chemistry

Curriculum Vitae available Online

CONTACT INFORMATION

- **Administrative contact**

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Bio

BIO

My laboratory investigates the structure and function of biological systems with a strong physical perspective. We invent experimental methods and develop theory as needed. We are pursuing several interconnected themes:

Excited State Dynamics in GFP & Split GFP

Green Fluorescent Protein (GFP) is widely used as a probe to localize proteins in cells. Our lab was the first to demonstrate that the GFP chromophore exists in two protonation states, interconvertible by ultrafast excited state proton transfer. We and others have since developed this idea to generate novel GFP variants with diverse colors and sensitivities. Current work focuses on split GFP in which structural elements such as entire beta strands are replaced with synthetic ones. We have discovered that some split GFPs can be photodissociated, generating a peptide and a truncated protein; alternatively, in some conditions, light can be used to associate peptides with truncated proteins. Thus these split GFPs are optogenetic elements for manipulations inside cells, and we seek to understand how they work.

Electrostatics and Dynamics in Proteins

We study electrostatics in proteins and how electric fields affect function. Early test systems used mutants of myoglobin, which was first cloned and expressed in our lab. This led to probes whose sensitivity to electric fields can be calibrated by Stark spectroscopy — spectroscopy in electric fields — which we have developed into a broadly applicable method. Vibrational Stark experiments exploit molecular vibrations as local and directional probes to map electrostatic fields in proteins. Current work applies nitrile probes introduced into proteins on inhibitors. These can be used to probe electrostatics and hydration at the active sites of important drug targets. Recent work focuses on carbonyl probes to study enzymatic reactions. By combining the vibrational Stark effect, vibrational solvatochromism and MD simulations, we have developed a general method to measure the absolute field sensed by the carbonyl probe in proteins. This has been used to quantify the electrostatic contribution to the catalytic rate in several enzymes.

Model Membranes

Our group has developed supported lipid bilayers as mimics for cell surfaces and tools in biotechnology. A broad vision is to engineer interfaces between hard surfaces and soft materials, ultimately leading to sophisticated biocompatible interfaces that can be used to control, interrogate or organize complex living systems. We have developed methods to partition and manipulate elements of these unique self-assembled systems; these methods are now used in many laboratories.

Recent work addresses four interrelated areas: 1) characterization of membrane organization, domains and protein associations using a novel type of imaging mass spectrometry; 2) models for membrane fusion and investigations into the fusion of enveloped viruses to their target membrane; 3) development of tethered lipid bilayers as a platform to study membrane domains, junction topology, vesicle fusion and enveloped virus fusion; and 4) a membrane interferometer where a free-standing lipid bilayer is held within a few hundred nm of an atomically flat mirror, with the ultimate goal of measuring protein conformational changes optically with sub-nm precision in parallel with electrical measurements, e.g. in ion channels.

Energy and Electron Transfer in Photosynthesis

Light-driven long-distance electron transfer in photosynthetic reaction centers is one of the fastest known chemical reactions. We study this by femtosecond fluorescence and transient absorption spectroscopy, manipulation in electric fields, site-specific and global mutagenesis and some novel types of Stark spectroscopy. Current work probes alternate pathways of electron transfer in novel bacterial reaction centers that lack normal electron acceptors, and introduces non-canonical amino acids to perturb and probe pathways.

ACADEMIC APPOINTMENTS

- Professor, Chemistry
- Member, Bio-X
- Faculty Fellow, Sarafan ChEM-H
- Member, Wu Tsai Neurosciences Institute

ADMINISTRATIVE APPOINTMENTS

- Chair, Department of Chemistry, Stanford, (2020- present)

HONORS AND AWARDS

- Murray Goodman Memorial Prize, American Chemical Society (2014)
- E. Bright Wilson Award in Spectroscopy, American Chemical Society (2013)
- Elected Fellow, Royal Society of Chemistry (2009)
- Elected Member, National Academy of Sciences (2008)
- Earle K. Plyler Prize for Molecular Spectroscopy, American Physical Society (2008)
- Elected Fellow, Biophysical Society (2007)
- Elected Fellow, American Academy of Arts and Sciences (1997)
- Elected Fellow, American Association for the Advancement of Science (1997)
- Arthur Cope Scholar Award, American Chemical Society (1995)

BOARDS, ADVISORY COMMITTEES, PROFESSIONAL ORGANIZATIONS

- Scientific Advisory Board Member, Quantapore (2015 - present)

- Scientific Advisory Board Member, Apton Biosystems (2014 - present)
- Scientific Advisory Committee Member, Ctr for Laser and Computational Biophysics, State Key Lab Precision Spectroscopy, E China Normal U. (2013 - 2015)
- Consultant, Samsung Advanced Institute of Technology (2005 - 2008)
- Scientific Advisory Board Member, Synamem Corporation (2002 - present)

PROFESSIONAL EDUCATION

- PhD, University of Chicago , Physical and Physical-Organic Chemistry (1976)
- BS with Honors, Tufts University , Chemistry (1969)

LINKS

- Lab Website: https://web.stanford.edu/group/boxer/

Research & Scholarship

CURRENT RESEARCH AND SCHOLARLY INTERESTS

Please visit my website for complete information:

http://www.stanford.edu/group/boxer/

Teaching

STANFORD ADVISEES

Doctoral Dissertation Reader (AC)

Krystal Brodsky, Joshua Sampson, Pengwei Sun, Nancy Zhu

Postdoctoral Faculty Sponsor

Mojgan Asadi, Suman Gunasekaran, Srijit Mukherjee, Bing Xu

Doctoral Dissertation Advisor (AC)

Nahal Bagheri, Steven Fried, Nathalie Hong, My Uyen Ta

GRADUATE AND FELLOWSHIP PROGRAM AFFILIATIONS

- Biophysics (Phd Program)

Publications

PUBLICATIONS

- **A comprehensive test of the AMOEBA force field using spectroscopy, structures, and simulations of nitrile protein environments.** *The Journal of chemical physics*
  Kirsh, J. M., Weaver, J. B., Kozuch, J., Boxer, S. G.
  2026; 164 (15)
- **Magnetic resonance control of spin-correlated radical pair dynamics in vivo.** *Nature*
  Burd, S. C., Bagheri, N., Condon, A. F., Ingaramo, M., Mondal, S., Dowlatshahi, D. P., Summers, J. A., Mukherjee, S., York, A. G., Wakatsuki, S., Boxer, S. G., Kasevich, M.
  2026
- **Covalent Drug Binding in Live Cells Monitored by Mid-Infrared Quantum Cascade Laser Spectroscopy: Photoactive Yellow Protein as a Model System.** *Journal of the American Chemical Society*
  Mukherjee, S., Fried, S. D., Hong, N. Y., Bagheri, N., Kozuch, J., Mathews, I. I., Kirsh, J. M., Boxer, S. G.
  2025

- **Electrostatic atlas of non-covalent interactions built into metal-organic frameworks.** *Nature chemistry*
  Ji, Z., Mukherjee, S., Andreo, J., Sinelshchikova, A., Peccati, F., Jiménez-Osés, G., Wuttke, S., Boxer, S. G.
  2025
- **Covalent Drug Binding in Live Cells Monitored by Mid-IR Quantum Cascade Laser Spectroscopy: Photoactive Yellow Protein as a Model System.** *bioRxiv : the preprint server for biology*
  Mukherjee, S., Fried, S. D., Hong, N. Y., Bagheri, N., Kozuch, J., Mathews, I. I., Kirsh, J. M., Boxer, S. G.
  2025
- **Introduction: Electric Fields in Chemistry and Biology.** *Chemical reviews*
  Boxer, S. G., Head-Gordon, T.
  2025; 125 (15): 6871-6873
- **US must support chemistry research.** *Science (New York, N.Y.)*
  Allen, K., Armentrout, P. B., Berkman, C., Boxer, S. G., Burkart, M., Canary, J. W., Castellano, R. K., Columbus, L., DeRose, V. J., Fairbrother, H., Ferguson, G. S., Foley, J., Haynes, et al
  2025; 388 (6753): 1282-1283
- **Magnetic resonance control of reaction yields through genetically-encoded protein:flavin spin-correlated radicals in a live animal.** *bioRxiv : the preprint server for biology*
  Burd, S. C., Bagheri, N., Ingaramo, M., Condon, A. F., Mondal, S., Dowlatshahi, D. P., Summers, J. A., Mukherjee, S., York, A. G., Wakatsuki, S., Boxer, S. G., Kasevich, M.
  2025
- **Environment- and Conformation-Induced Frequency Shifts of C-D Vibrational Stark Probes in NAD(P)H Cofactors.** *The journal of physical chemistry letters*
  Fried, S. D., Mukherjee, S., Mao, Y., Boxer, S. G.
  2024: 10826-10834
- **Structure-function relationships in pure archaeal bipolar tetraether lipids.** *Chemical science*
  Bhattacharya, A., Falk, I. D., Moss, F. R., Weiss, T. M., Tran, K. N., Burns, N. Z., Boxer, S. G.
  2024
- **A Fluorogenic Pseudoinfection Assay to Probe Transfer and Distribution of Influenza Viral Contents to Target Vesicles.** *Analytical chemistry*
  Bhattacharya, A., Bagheri, N., Boxer, S. G.
  2024
- **Membrane localization accelerates association under conditions relevant to cellular signaling.** *Proceedings of the National Academy of Sciences of the United States of America*
  Huang, W. Y., Boxer, S. G., Ferrell, J. E.
  2024; 121 (10): e2319491121
- **Critical Evaluation of Polarizable and Nonpolarizable Force Fields for Proteins Using Experimentally Derived Nitrile Electric Fields.** *Journal of the American Chemical Society*
  Kirsh, J. M., Weaver, J. B., Boxer, S. G., Kozuch, J.
  2024
- **Secondary Ion Mass Spectrometry of Single Giant Unilamellar Vesicles Reveals Compositional Variability.** *Journal of the American Chemical Society*
  Grusky, D. S., Bhattacharya, A., Boxer, S. G.
  2023
- **Simulation-guided engineering of split GFPs with efficient β-strand photodissociation.** *Nature communications*
  Shamsudin, Y., Walker, A. R., Jones, C. M., Martínez, T. J., Boxer, S. G.
  2023; 14 (1): 7401
- **Autobiography of Steven G. Boxer.** *The journal of physical chemistry. B*
  Boxer, S. G.
  2023; 127 (41): 8711-8716
- **Enhanced active-site electric field accelerates enzyme catalysis.** *Nature chemistry*

Zheng, C., Ji, Z., Mathews, I. I., Boxer, S. G.
2023

- **beta-Lactamases Evolve against Antibiotics by Acquiring Large Active-Site Electric Fields.** *Journal of the American Chemical Society*
  Ji, Z., Boxer, S. G.
  2022
- **Protein Electric Fields Enable Faster and Longer-Lasting Covalent Inhibition of β-Lactamases.** *Journal of the American Chemical Society*
  Ji, Z., Kozuch, J., Mathews, I. I., Diercks, C. S., Shamsudin, Y., Schulz, M. A., Boxer, S. G.
  2022
- **Solvent Organization and Electrostatics Tuned by Solute Electronic Structure: Amide versus Non-Amide Carbonyls.** *The journal of physical chemistry. B*
  Fried, S. D., Zheng, C., Mao, Y., Markland, T. E., Boxer, S. G.
  2022
- **Recombination between 13C and 2H to Form Acetylide (13C22H-) Probes' Nanoscale Interactions in Lipid Bilayers via Dynamic Secondary Ion Mass Spectrometry: Cholesterol and GM1 Clustering.** *Analytical chemistry*
  Grusky, D. S., Moss, F. R., Boxer, S. G.
  2022
- **A two-directional vibrational probe reveals different electric field orientations in solution and an enzyme active site.** *Nature chemistry*
  Zheng, C., Mao, Y., Kozuch, J., Atsango, A. O., Ji, Z., Markland, T. E., Boxer, S. G.
  2022
- **Nitrile Infrared Intensities Characterize Electric Fields and Hydrogen Bonding in Protic, Aprotic, and Protein Environments.** *Journal of the American Chemical Society*
  Weaver, J. B., Kozuch, J., Kirsh, J. M., Boxer, S. G.
  2022
- **Energetic Basis and Design of Enzyme Function Demonstrated Using GFP, an Excited-State Enzyme.** *Journal of the American Chemical Society*
  Lin, C., Romei, M. G., Mathews, I. I., Boxer, S. G.
  2022
- **The Interplay of Electrostatics and Chemical Positioning in the Evolution of Antibiotic Resistance in TEM beta-Lactamases.** *ACS central science*
  Schneider, S. H., Kozuch, J., Boxer, S. G.
  1800; 7 (12): 1996-2008
- **Photosynthetic reaction center variants made via genetic code expansion show Tyr at M210 tunes the initial electron transfer mechanism.** *Proceedings of the National Academy of Sciences of the United States of America*
  Weaver, J. B., Lin, C., Faries, K. M., Mathews, I. I., Russi, S., Holten, D., Kirmaier, C., Boxer, S. G.
  1800; 118 (51)
- **Single-virus content mixing assay reveals cholesterol-enhanced influenza membrane fusion efficiency.** *Biophysical journal*
  Liu, K. N., Boxer, S. G.
  2021
- **Testing the Limitations of MD-Based Local Electric Fields Using the Vibrational Stark Effect in Solution: Penicillin G as a Test Case.** *The journal of physical chemistry. B*
  Kozuch, J., Schneider, S. H., Zheng, C., Ji, Z., Bradshaw, R. T., Boxer, S. G.
  2021
- **Enantioselective Total Synthesis of the Archaeal Lipid Parallel GDGT-0 (Isocaldarchaeol).** *Angewandte Chemie (International ed. in English)*
  Falk, I. D., Gál, B. n., Bhattacharya, A. n., Wei, J. H., Welander, P. V., Boxer, S. G., Burns, N. Z.
  2021
- **Unusual Spectroscopic and Electric Field Sensitivity of Chromophores with Short Hydrogen Bonds: GFP and PYP as Model Systems.** *The journal of physical chemistry. B*
  Lin, C., Boxer, S. G.

2020

- **Mechanism of Color and Photoacidity Tuning for the Protonated Green Fluorescent Protein Chromophore.** *Journal of the American Chemical Society*
  Lin, C., Boxer, S. G.
  2020
- **Membrane-tethered mucin-like polypeptides sterically inhibit binding and slow fusion kinetics of influenza A virus.** *Proceedings of the National Academy of Sciences of the United States of America*
  Delaveris, C. S., Webster, E. R., Banik, S. M., Boxer, S. G., Bertozzi, C. R.
  2020
- **Electrostatic control of photoisomerization pathways in proteins.** *Science (New York, N.Y.)*
  Romei, M. G., Lin, C. Y., Mathews, I. I., Boxer, S. G.
  2020; 367 (6473): 76–79
- **A Preorganized Electric Field Leads to Minimal Geometrical Reorientation in the Catalytic Reaction of Ketosteroid Isomerase.** *Journal of the American Chemical Society*
  Wu, Y. n., Fried, S. D., Boxer, S. G.
  2020
- **Biosynthetic Incorporation of Site-Specific Isotopes in β-Lactam Antibiotics Enables Biophysical Studies.** *ACS chemical biology*
  Kozuch, J. n., Schneider, S. H., Boxer, S. G.
  2020
- **Split Green Fluorescent Proteins: Scope, Limitations, and Outlook.** *Annual review of biophysics*
  Romei, M. G., Boxer, S. G.
  2019
- **Local and Global Electric Field Asymmetry in Photosynthetic Reaction Centers.** *The journal of physical chemistry. B*
  Saggu, M., Fried, S. D., Boxer, S. G.
  2019
- **Structural Evidence of Photoisomerization Pathways in Fluorescent Proteins.** *Journal of the American Chemical Society*
  Chang, J. n., Romei, M. G., Boxer, S. G.
  2019
- **A unified model for photophysical and electro-optical properties of Green Fluorescent Proteins.** *Journal of the American Chemical Society*
  Lin, C. Y., Romei, M. G., Oltrogge, L. M., Mathews, I. I., Boxer, S. G.
  2019
- **pH Dependence of Zika Membrane Fusion Kinetics Reveals an Off-Pathway State** *ACS CENTRAL SCIENCE*
  Rawle, R. J., Webster, E. R., Jelen, M., Kasson, P. M., Boxer, S. G.
  2018; 4 (11): 1503–10
- **pH Dependence of Zika Membrane Fusion Kinetics Reveals an Off-Pathway State.** *ACS central science*
  Rawle, R. J., Webster, E. R., Jelen, M., Kasson, P. M., Boxer, S. G.
  2018; 4 (11): 1503-1510
- **Ladderane phospholipids form a densely packed membrane with normal hydrazine and anomalously low proton/hydroxide permeability.** *Proceedings of the National Academy of Sciences of the United States of America*
  Moss, F. R., Shuken, S. R., Mercer, J. A., Cohen, C. M., Weiss, T. M., Boxer, S. G., Burns, N. Z.
  2018
- **Ladderane phospholipids form dense, low-polarity membranes with low proton/hydroxide permeability**
  Moss, F., Shuken, S., Mercer, J., Cohen, C., Weiss, T., Burns, N., Boxer, S.
  AMER CHEMICAL SOC.2018
- **Genetic Code Expansion in Rhodobacter sphaeroides to Incorporate Noncanonical Amino Acids into Photosynthetic Reaction Centers.** *ACS synthetic biology*
  Weaver, J. B., Boxer, S. G.

2018

- **Structural Insight into the Photochemistry of Split Green Fluorescent Proteins: A Unique Role for a His-Tag** *JOURNAL OF THE AMERICAN CHEMICAL SOCIETY*
  Deng, A., Boxer, S. G.
  2018; 140 (1): 375–81
- **Vesicle Fusion Mediated by Solanesol-Anchored DNA** *BIOPHYSICAL JOURNAL*
  Flavier, K. M., Boxer, S. G.
  2017; 113 (6): 1260–68
- **Atomic Recombination in Dynamic Secondary Ion Mass Spectrometry Probes Distance in Lipid Assemblies: A Nanometer Chemical Ruler** *JOURNAL OF THE AMERICAN CHEMICAL SOCIETY*
  Moss, F. R., Boxer, S. G.
  2016; 138 (51): 16737-16744
- **Vibrational Stark Effects of Carbonyl Probes Applied to Reinterpret IR and Raman Data for Enzyme Inhibitors in Terms of Electric Fields at the Active Site.** *journal of physical chemistry. B*
  Schneider, S. H., Boxer, S. G.
  2016; 120 (36): 9672-9684
- **A Critical Test of the Electrostatic Contribution to Catalysis with Noncanonical Amino Acids in Ketosteroid Isomerase.** *Journal of the American Chemical Society*
  Wu, Y., Boxer, S. G.
  2016; 138 (36): 11890-11895
- **Dynamic Reorganization and Correlation among Lipid Raft Components.** *Journal of the American Chemical Society*
  Lozano, M. M., Hovis, J. S., Moss, F. R., Boxer, S. G.
  2016; 138 (31): 9996-10001
- **Disentangling Viral Membrane Fusion from Receptor Binding Using Synthetic DNA-Lipid Conjugates.** *Biophysical journal*
  Rawle, R. J., Boxer, S. G., Kasson, P. M.
  2016; 111 (1): 123-131
- **Short Hydrogen Bonds and Proton Delocalization in Green Fluorescent Protein (GFP).** *ACS central science*
  Oltrogge, L. M., Boxer, S. G.
  2015; 1 (3): 148-156
- **Measuring Electric Fields and Noncovalent Interactions Using the Vibrational Stark Effect** *ACCOUNTS OF CHEMICAL RESEARCH*
  Fried, S. D., Boxer, S. G.
  2015; 48 (4): 998-1006
- **Quantum delocalization of protons in the hydrogen-bond network of an enzyme active site.** *Proceedings of the National Academy of Sciences of the United States of America*
  Wang, L., Fried, S. D., Boxer, S. G., Markland, T. E.
  2014; 111 (52): 18454-18459
- **Extreme electric fields power catalysis in the active site of ketosteroid isomerase** *SCIENCE*
  Fried, S. D., Bagchi, S., Boxer, S. G.
  2014; 346 (6216): 1510-1514
- **Ground-state proton transfer kinetics in green fluorescent protein.** *Biochemistry*
  Oltrogge, L. M., Wang, Q., Boxer, S. G.
  2014; 53 (37): 5947-5957
- **Putative Hydrogen Bond to Tyrosine M208 in Photosynthetic Reaction Centers from Rhodobacter capsulatus Significantly Slows Primary Charge Separation** *JOURNAL OF PHYSICAL CHEMISTRY B*
  Saggu, M., Carter, B., Zhou, X., Faries, K., Cegelski, L., Holten, D., Boxer, S. G., Kirmaier, C.
  2014; 118 (24): 6721-6732
- **A conserved water-mediated hydrogen bond network defines bosutinib's kinase selectivity.** *Nature chemical biology*

Levinson, N. M., Boxer, S. G.
2014; 10 (2): 127-132

- **Choose your label wisely: water-soluble fluorophores often interact with lipid bilayers.** *PloS one*
  Hughes, L. D., Rawle, R. J., Boxer, S. G.
  2014; 9 (2)
- **Calculations of the electric fields in liquid solutions.** *journal of physical chemistry. B*
  Fried, S. D., Wang, L., Boxer, S. G., Ren, P., Pande, V. S.
  2013; 117 (50): 16236-16248
- **GFP Variants with Alternative beta-Strands and Their Application as Light-driven Protease Sensors: A Tale of Two Tails** *JOURNAL OF THE AMERICAN CHEMICAL SOCIETY*
  Do, K., Boxer, S. G.
  2013; 135 (28): 10226-10229
- **Individual Vesicle Fusion Events Mediated by Lipid-Anchored DNA** *BIOPHYSICAL JOURNAL*
  van Lengerich, B., Rawle, R. J., Bendix, P. M., Boxer, S. G.
  2013; 105 (2): 409-419
- **Colocalization of the Ganglioside G(M1) and Cholesterol Detected by Secondary Ion Mass Spectrometry** *JOURNAL OF THE AMERICAN CHEMICAL SOCIETY*
  Lozano, M. M., Liu, Z., Sunnick, E., Janshoff, A., Kumar, K., Boxer, S. G.
  2013; 135 (15): 5620-5630
- **Electrostatic insights into X-H•••π interactions (X = C, N, O, S) through the vibrational Stark effect**
  Ta, U. M., Fried, S. D. E., Mukherjee, S., Kelly, J., Markland, T., Boxer., S. G.
  CELL PRESS.2026: 341a
- **Who's really in charge? Dissecting directional electric fields in enzyme catalysis**
  Mukherjee, S., Fried, S. D. E., Mathews, I. I., Boxer, S. G.
  CELL PRESS.2026: 50a-51a
- **Interplay of electrostatics and conformational dynamics in dihydrofolate reductase catalysis**
  Fried, S. D. E., Mukherjee, S., Mathews, I. I., Boxer, S. G.
  CELL PRESS.2026: 51a
- **Magnetic-resonance control of spin-correlated radical pair dynamics in a transgenic animal**
  Bagheri, N., Burd, S. C., Condon, A. F., Ingaramo, M., Mondal, S., Dowlatshahi, D. P., Summers, J. A., Mukherjee, S., York, A. G., Wakatsuki, S., Boxer, S. G., Kasevich, M.
  CELL PRESS.2026: 22a
- **Application of Amber Suppression To Study the Role of Tyr M210 in Electron Transfer inRhodobacter sphaeroidesPhotosynthetic Reaction Centers.** *The journal of physical chemistry. B*
  Tran, K. N., Faries, K. M., Magdaong, N. C., Mathews, I. I., Weaver, J. B., Kirsh, J. M., Holten, D., Kirmaier, C., Boxer, S. G.
  2025
- **Detection of covalent drug binding in live cells using a quantum cascade laser and nitrile-labeled amino acids**
  Fried, S. D. E., Mukherjee, S., Bagheri, N., Hong, N. Y., Boxer, S. G.
  CELL PRESS.2025
- **Beyond the Vibrational Stark Effect: Unraveling the Large Redshifts of Alkyne C-H Bond in Solvation Environments.** *Journal of the American Chemical Society*
  Zheng, C., Mao, Y., Markland, T. E., Boxer, S. G.
  2025
- **Optical control of ultrafast structural dynamics in a fluorescent protein.** *Nature chemistry*
  Hutchison, C. D., Baxter, J. M., Fitzpatrick, A., Dorlhiac, G., Fadini, A., Perrett, S., Maghlaoui, K., Lefevre, S. B., Cordon-Preciado, V., Ferreira, J. L., Chukhutsina, V. U., Garratt, D., Barnard, et al
  2023

- **Structural Characterization of Fluorescent Proteins Using Tunable Femtosecond Stimulated Raman Spectroscopy.** *International journal of molecular sciences*
  Chen, C., Henderson, J. N., Ruchkin, D. A., Kirsh, J. M., Baranov, M. S., Bogdanov, A. M., Mills, J. H., Boxer, S. G., Fang, C.
  2023; 24 (15)
- **Serial Femtosecond Crystallography Reveals that Photoactivation in a Fluorescent Protein Proceeds via the Hula Twist Mechanism.** *Journal of the American Chemical Society*
  Fadini, A., Hutchison, C. D., Morozov, D., Chang, J., Maghlaoui, K., Perrett, S., Luo, F., Kho, J. C., Romei, M. G., Morgan, R. M., Orr, C. M., Cordon-Preciado, V., Fujiwara, et al
  2023
- **Carbon-deuterium bonds as reporters of electric fields in solvent and protein environments**
  Fried, S. D. E., Kirsh, J. M., Zheng, C., Mao, Y., Markland, T. E., Boxer, S. G.
  CELL PRESS.2023: 481A
- **A fluorogenic method to directly observe transfer and distribution of influenza viral contents to target vesicles**
  Bhattacharya, A., Boxer, S. G.
  CELL PRESS.2023: 277A
- **Examining compositional variability of giant unilamellar vesicles via secondary ion mass spectrometry**
  Grusky, D. S., Bhattacharya, A., Boxer, S. G.
  CELL PRESS.2023: 81A
- **Application of amber suppression to study the role of Tyr M210 in electron transfer in R. sphaeroides photosynthetic reaction centers**
  Tran, K., Faries, K., Magdaong, N., Kirmaier, C., Holten, D., Boxer, S. G.
  CELL PRESS.2023: 57A
- **A unifying electrostatic basis for designing enzymes faster than natural ones**
  Zheng, C., Ji, Z., Mathews, I. I., Boxer, S. G.
  CELL PRESS.2023: 483A
- **Protein protic and aprotic interactions systematically mapped via IR spectroscopy and polarizable molecular dynamics**
  Kirsh, J. M., Kozuch, J., Weaver, J. B., Boxer, S. G.
  CELL PRESS.2023: 309A
- **Tradeoffs of electrostatics and chemical positioning in the evolution of antibiotic resistance in TEM beta-lactamases**
  Boxer, S. G., Schneider, S. H., Kozuch, J. A.
  CELL PRESS.2022: 346A
- **Nitrile IR intensities directly measure electric fields in protic and non-protic environments**
  Weaver, J. B., Kozuch, J. A., Kirsh, J. M., Boxer, S. G.
  CELL PRESS.2022: 414A
- **A two-directional vibrational probe reveals the distinct electric field orientation at the active site of liver alcohol dehydrogenase**
  Zheng, C., Mao, Y., Kozuch, J. A., Atsango, A. O., Ji, Z., Markland, T. E., Boxer, S. G.
  CELL PRESS.2022: 441A
- **Protein electric fields regulate covalent inhibition of beta-lactamases**
  Ji, Z., Boxer, S. G.
  CELL PRESS.2022: 441A
- **Tuning solvent electrostatic environment of amide carbonyls as prototypical peptide backbones**
  Fried, S. D. E., Zheng, C., Mao, Y., Markland, T. E., Boxer, S. G.
  CELL PRESS.2022: 186A
- **Self-assembly and phase transition properties of pure archaeal tetraether lipids**
  Bhattacharya, A., Falk, I. D., Burns, N. Z., Boxer, S. G.
  CELL PRESS.2022: 290A
- **Modulating the Influenza A Virus-Target Membrane Fusion Interface With Synthetic DNA-Lipid Receptors.** *Langmuir : the ACS journal of surfaces and colloids*

Webster, E. R., Liu, K. N., Rawle, R. J., Boxer, S. G.
2022

- **Halogenation-Dependent Effects of the Chlorosulfolipids of Ochromonas danica on Lipid Bilayers.** *ACS chemical biology*
  Moss Iii, F. R., Cabrera, G. E., McKenna, G. M., Salerno, G. J., Shuken, S. R., Landry, M. L., Weiss, T. M., Burns, N. Z., Boxer, S. G.
  2020
- **Structural and spectroscopic characterization of photoactive yellow protein and photoswitchable fluorescent protein constructs containing heavy atoms.** *Journal of photochemistry and photobiology. A, Chemistry*
  Romei, M. G., Lin, C., Boxer, S. G.
  2020; 401
- **Unified Model for Photophysical and Electro-Optical Properties of Green Fluorescent Proteins**
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