THE JOURNAL OF PHYSICAL CHEMISTRY B
A JOURNAL OF THE AMERICAN CHEMICAL SOCIETY

pubs.acs.org/JPCB

Special Issue Preface

Tribute to Xiaoliang Sunney Xie

Published as part of The Journal of Physical Chemistry virtual special issue "Xiaoliang Sunney Xie Festschrift".

Cite This: *J. Phys. Chem. B* 2023, 127, 7797−7799

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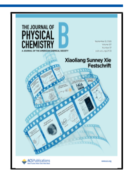
This Festschrift is dedicated to Professor Xiaoliang Sunney Xie, an extraordinarily influential and celebrated biophysical chemist. Throughout his remarkable career, Sunney has contributed to a great number of technological innovations and scientific discoveries. His work in physical chemistry spans four major areas: single-molecule spectroscopy, single-molecule enzymology, single-molecule biology, and coherent Raman spectroscopy. Sunney was among the first scientists to demonstrate single-molecule optical detection at room temperature. His landmark work on applying single-molecule spectroscopy to study protein and enzymatic dynamics led to the birth of single-molecule enzymology and, subsequently, single-molecule biology. In addition, his pioneering developments of coherent Raman microscopy and single-cell genomics have provided scientists with valuable tools to directly observe chemical and biological processes without labeling as well as addressing fundamental questions about life processes, respectively. Over the course of his academic life, he has mentored over a hundred PhD students and postdocs, many of whom have become pillar figures in academics and the biotechnology industry. Sunney's scientific contributions have been recognized by numerous awards, including the Peter Debye Award in Physical Chemistry, the highest award of the American Chemical Society for physical chemists, and the Albany Prize in Medicine and Biomedical Research, one of the largest awards in biomedicine in the United States. In the following tribute, we will review the key stages of his scientific journey.

■ SINGLE-MOLECULE SPECTROSCOPY

Single-molecule spectroscopy and microscopy have become the cornerstones of a large variety of modern technologies. By detecting one individual molecule at a time, therefore removing ensemble averaging, scientists can directly observe the heterogeneity within a sample, which provides important insights into complex systems. In the time domain, single-molecule studies also provide valuable information about kinetics, pathways, and intermediates of those complex dynamical processes. Overall, such an ability to observe and track single molecules offered a widely used tool for chemical and biological sciences.

Although nowadays single-molecule experiments can be carried out in almost any lab that is equipped with the proper instrument, in the early 1990s, the optical detection of a single molecule at room temperature was not thought possible. Sunney was among a pioneering group of scientists working toward this crown jewel achievement. The earlier pioneering efforts of optically detecting single molecules, either via direct absorption by W. E. Moerner or via fluorescence emission by Michel Orrit, were carried out at cryogenic temperature to take advantage of the extremely narrow optical absorption spectra under such conditions. A milestone occurred when Eric Betzig, Sunney Xie,

Published: September 21, 2023



Richard Keller, and colleagues independently demonstrated single-molecule imaging at room temperature using near-field optical microscopy. In these studies, the excitation laser light was funneled through a sharp optical fiber tip that was placed close to the sample at a distance much smaller than the wavelength. By doing so, only a small volume in the immediate vicinity of the fiber tip was excited by the laser. Such confinement of illumination avoided the background luminescence, and the detection of single-molecule emission was achieved.

Successfully carrying out single-molecule spectroscopy at room temperature, as opposed to cryogenic temperature, opened up opportunities for physical chemistry as well as biology. This eventually paved the way for easier and more accessible techniques—researchers around the world subsequently realized that it was also possible to detect single molecules with far-field techniques such as confocal microscopy or total internal reflection microscopy. These techniques soon took off and opened the door to a vastly broad range of applications in biophysics and life science, including super-resolution microscopy.

■ SINGLE-MOLECULE ENZYMOLOGY

Sunney soon realized the great potential of single-molecule spectroscopy in studying complex biological problems. He picked a first-class problem when he adapted the technique to study the dynamics of a fluorescent flavoenzyme: cholesterol oxidase, which contains a flavin adenine dinucleotide (FAD) in its active site and toggles reversibly between its fluorescent form and non-fluorescent form during catalysis. This feature made cholesterol oxidase a great choice to study the dynamics of enzymatic reactions at the single-molecule level. The celebrated Michaelis−Menten mechanism, a guiding law of biochemistry, was visualized at the single-molecule level for the first time. Moreover, a surprising discovery was made on the enzyme dynamics. The rate constant of a single enzyme molecule is not a constant but rather fluctuates in time with a strong memory effect; this phenomenon later turned out to be a universal rule for nearly all enzymes studied. After that, many groups started to apply single-molecule spectroscopy to examine specific mechanisms of enzyme action—a new field was created. Sunney's landmark work in 1998 is widely regarded as birthing the field of single-molecule enzymology.

To further investigate the origin of the rate-constant fluctuation in single enzymatic reactions, Sunney employed electron transfer between the flavin at the active site of flavin reductase and the surrounding tyrosines as a sensitive molecular ruler to probe protein conformation dynamics one molecule at a time. This novel technique revealed that the conformational dynamics of proteins at equilibrium occur on a surprisingly broad range of time scales ranging from milliseconds to minutes, which overlaps with the range of enzyme catalysis rates. Such protein dynamics have a long correlation, similar to the memory effect observed in his 1998 experiment. Hence, Sunney postulated that the underlying conformational dynamics govern the fluctuating rate constant of enzyme catalysis.

In spite of the fluctuating rate constant and conformational dynamics, Sunney later showed the Michaelis−Menten equation still holds at the single-molecule level. Although the rate constant fluctuates in time, the time-averaged behavior still follows fundamental thermodynamic principles. This discovery was unveiled by monitoring the turnover of a single enzyme for hours under different substrate concentrations. The resulting single-molecule Michaelis−Menten equation bridges statistical mechanics to enzyme kinetics. Based on this line of insight, Sunney coined the influential concept of "fluctuating enzymes". Many researchers have followed up on this fluctuating enzyme concept to further understand the connection among conformational dynamics, enzyme catalysis, and kinetics, a topic that is still an area of ongoing research.

■ SINGLE-MOLECULE BIOLOGY

Going beyond his early *in vitro* single-molecule enzymology work, Sunney extended his single-molecule techniques to living cells. This extension of single-molecule techniques from *in vitro* to *in vivo* marked a big leap forward and deeply broadened its application in complex biological systems, just a decade after the first single-molecule fluorescence demonstrations. Nowadays, single-molecule techniques and single-molecule perspectives have been accepted by mainstream biologists.

The central dogma is the most profound axiom in molecular biology, explaining the flow of genetic information from DNA to proteins in transcription and translation. This process presents a single-molecule problem because an individual cell has only one (or two) copy of DNA of a particular gene. After spending more than 5 years on these efforts, his group reported the first real-time observation of translation events one molecule at a time, in individual living cells. In two distinct assays, Sunney found that protein translation happens in bursts, with each burst originating from a stochastically transcribed single messenger RNA molecule. Importantly, the steady-state copy number distribution in a population of cells is related to the burst "size" and "frequency", bridging single-molecule events to the ensemble measurements. These pioneering studies allowed the central dogma of molecular biology to be described in a quantitative manner.

Sunney also discovered that a stochastic single-molecule event (in this case, complete dissociation of the transcription factor from DNA) could trigger phenotype switching of a bacterial cell. He later undertook the study of the other part of the central dogma: transcription, the passing of genetic information from DNA to RNA. Sunney found that transcription also happens in bursts in bacterial cells, similar to translation. This study led to a molecular mechanism attributing the transcriptional bursts to the buildup of DNA supercoiling in a DNA loop containing the transcribed gene.

■ COHERENT RAMAN MICROSCOPY

In parallel to his pioneering single-molecule technological innovations as well as their applications in chemistry and biology, Sunney also developed other unique techniques, taking the vibrational properties of molecules as the imaging contrast. In 1999, he described a novel microscopy technique based on coherent anti-Stokes Raman scattering (CARS). Interestingly, this innovation occurred partially due to an accidental discovery in the lab when two pulsed laser beams were tightly focused onto a piece of glass, generating white light as a result of nonlinear optical processes. For CARS, two synchronized near-infrared beams are focused on the sample to excite certain vibrational modes of the molecules. The nonlinear interaction of lasers with the collective vibrational modes in the excitation volume produces strong coherent radiation at the new anti-Stokes wavelength. Compared to the widely used spontaneous Raman microscopy, the coherent nature of CARS can improve the otherwise slow Raman imaging speed by orders of magnitude and makes possible the high-speed vibrational imaging of

https://doi.org/10.1021/acs.jpcb.3c05596
J. Phys. Chem. B 2023, 127, 7797−7799

biological samples. Ever since the development of CARS microscopy, Sunney has expended considerable time and effort arranging a series of conferences and workshops to advance the technique and facilitate its wider dissemination among users.

However, one major drawback of CARS is the non-resonant background from the electronic response of the sample, which limits both the spectral interpretation and detection sensitivity. To overcome this downside, stimulated Raman scattering (SRS) microscopy was developed by Sunney's group in 2008 as a label-free imaging technique. By detecting the energy exchange between laser fields and molecules, SRS is free from non-resonant background, preserves the Raman spectrum, and exhibits a robust linear concentration dependence. In a later study, high-speed SRS imaging was realized with demonstration on a human volunteer. Working with collaborators, Sunney has pushed SRS microscopy to operating rooms, accurately guiding surgeons in tumorectomy, thanks to its label-free mechanism. The field of SRS has recently exploded with a wide range of innovations spanning instrumentation, chemical probes, and data science.

BEYOND PHYSICAL CHEMISTRY

At the awakening of genomic revolution and next generation sequencing technology, Sunney has also developed novel approaches for single-cell genomics, effecting a profound technological advance for modern biology. Overall, Sunney has applied chemical principles to obtain a more precise and molecular understanding of biological problems. On the technology front, his single-cell sequencing techniques have helped the screening of genetic diseases during the IVF process. So far its medical application has benefited over 4000 families. Sunney's technical developments in single-cell genomics also yielded work of fundamental importance in understanding underpinnings of life processes, for example, the first 3D genomic structure of a single human cell and correlated gene modules. For his seminal contributions to improving human welfare, he was awarded the Albany Prize in Medicine and Biomedical Research, one of the most prestigious prizes in medicine and biomedical research in the United States. To our knowledge, Sunney is the first physical chemist to have received this honor, which speaks to the profound influence of his cross-disciplinary research.

During the COVID-19 pandemic, Sunney quickly responded to this public health crisis by applying high-throughput single-cell sequencing to identify highly potent neutralizing antibodies. His team recently developed a broad-spectrum antibody drug against all existent SARS-CoV-2 variants, which has saved many lives in China.

REMARKS

Sunney is one of the most influential biophysical chemists of our time. His work carries a unique style and signature. Technically, Sunney has been constantly inventing new methods of measurement, pushing the technology into new territories. In this process, many of his techniques have been widely adopted by others in the field. Scientifically, Sunney deeply cares about physical chemistry and is always asking fundamental questions about molecular behavior. His work on fluctuating enzymes and single-molecule and single-cell biology has triggered immense interest in the biophysical chemistry (including theoretical chemistry) community—many leading physical chemists have conducted research on related topics since Sunney's pioneering contributions. In this sense, Sunney is a rare example of someone who has made far-reaching impacts on biophysical chemistry and related fields. We are honored to present this Festschrift issue for his tremendous contributions to physical chemistry. On behalf of all his students, postdocs, friends and collaborators, we wish him many more years of health and happiness, as well as scientific creativity and productivity.

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ASSOCIATED CONTENT

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acs.jpcb.3c05596.

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Notes

Views expressed in this preface are those of the author and not necessarily the views of the ACS. Dr. Zhilun Zhao provided assistance on organizing the information.

https://doi.org/10.1021/acs.jpcb.3c05596
J. Phys. Chem. B 2023, 127, 7797−7799

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