# LECTURE NOTES IN PHYSICS

H. Linke A. Månsson (Eds.)

# Controlled Nanoscale Motion

**NOBEL SYMPOSIUM 131** 



Heiner Linke Alf Månsson (Eds.)

## Controlled Nanoscale Motion

Nobel Symposium 131





#### **Editors**

Heiner Linke Physics Department University of Oregon Eugene, OR 97403-1274 USA

E-mail: linke@uoregon.edu

Alf Månsson Department of Chemistry and Biomedical Sciences University of Kalmar SE-391 82 Kalmar Sweden

E-mail: alf.mansson@hik.se

H. Linke, A. Månsson (Eds.), Controlled Nanoscale Motion, Lect. Notes Phys. 711 (Springer, Berlin Heidelberg 2007), DOI 10.1007/b11823292

Library of Congress Control Number: 2006938044

ISSN 0075-8450 ISBN-10 3-540-49521-5 Springer Berlin Heidelberg New York ISBN-13 978-3-540-49521-5 Springer Berlin Heidelberg New York

This work is subject to copyright. All rights are reserved, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilm or in any other way, and storage in data banks. Duplication of this publication or parts thereof is permitted only under the provisions of the German Copyright Law of September 9, 1965, in its current version, and permission for use must always be obtained from Springer. Violations are liable for prosecution under the German Copyright Law.

Springer is a part of Springer Science+Business Media springer.com

© Springer-Verlag Berlin Heidelberg 2007

The use of general descriptive names, registered names, trademarks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

Typesetting: by the authors and techbooks using a Springer LATEX macro package Cover design: WMXDesign GmbH, Heidelberg

Printed on acid-free paper SPIN: 11823292 54/techbooks 543210

## **Lecture Notes in Physics**

#### **Editorial Board**

R.	Beig.	Wien.	Austria

W. Beiglböck, Heidelberg, Germany

W. Domcke, Garching, Germany

B.-G. Englert, Singapore

U. Frisch, Nice, France

P. Hänggi, Augsburg, Germany

G. Hasinger, Garching, Germany

K. Hepp, Zürich, Switzerland

W. Hillebrandt, Garching, Germany

D. Imboden, Zürich, Switzerland

R. L. Jaffe, Cambridge, MA, USA

R. Lipowsky, Golm, Germany

H. v. Löhneysen, Karlsruhe, Germany

I. Ojima, Kyoto, Japan

D. Sornette, Zürich, Switzerland

S. Theisen, Golm, Germany

W. Weise, Garching, Germany

J. Wess, München, Germany

J. Zittartz, Köln, Germany

#### The Lecture Notes in Physics

The series Lecture Notes in Physics (LNP), founded in 1969, reports new developments in physics research and teaching – quickly and informally, but with a high quality and the explicit aim to summarize and communicate current knowledge in an accessible way. Books published in this series are conceived as bridging material between advanced graduate textbooks and the forefront of research to serve the following purposes:

- to be a compact and modern up-to-date source of reference on a well-defined topic;
- to serve as an accessible introduction to the field to postgraduate students and nonspecialist researchers from related areas;
- to be a source of advanced teaching material for specialized seminars, courses and schools.

Both monographs and multi-author volumes will be considered for publication. Edited volumes should, however, consist of a very limited number of contributions only. Proceedings will not be considered for LNP.

Volumes published in LNP are disseminated both in print and in electronic formats, the electronic archive is available at springerlink.com. The series content is indexed, abstracted and referenced by many abstracting and information services, bibliographic networks, subscription agencies, library networks, and consortia.

Proposals should be sent to a member of the Editorial Board, or directly to the managing editor at Springer:

Dr. Christian Caron Springer Heidelberg Physics Editorial Department I Tiergartenstrasse 17 69121 Heidelberg/Germany christian.caron@springer.com

#### **Preface**

When the size of a machine approaches the nanometer scale, thermal fluctuations become large compared to the energies that drive the motor. The mechanism and control system for directed nanoscale motion must allow for, or even make use of, this stochastic environment. Controlled motion at the nanoscale therefore requires theoretical descriptions and engineering approaches that are fundamentally different from those that were developed for man-made, macroscopic motors and machines.

Over the past decade, a need to understand and to control directed motion at the nanoscale has arisen in several areas of biology, physics and chemistry. Most notably, the advent of single-molecule techniques in biophysics has given access to detailed information about the performance of molecular motors in biological cells. Combined with a variety of techniques from molecular biology, this information allows conclusions about the physics of biological machines. Even more recently, a variety of approaches including nanofabrication and synthetic chemistry have been used to create artificial nanoscale motors or to control the motion of individual molecules, for example using nanofluidic systems. Many of these approaches were triggered by novel theoretical methods designed to understand how the interplay of stochastic thermal motion and non-equilibrium phenomena can be harnessed to generate an output of useful work.

The present volume is based on selected contributions to the Nobel Symposium 131 on Controlled Nanoscale Motion in Biological and Artificial Systems, held on June 13–17, 2005 at Bäckaskog Slott in Sweden. The peer-reviewed chapters in this book are designed to be tutorial and self-contained and provide insight into the state of the art in the following three areas:

Biophysics of molecular motors and single molecules. Molecular motors are proteins or protein complexes that transduce chemical free energy into work through processes generally believed to involve substantial changes in protein structure. This section describes the physical and biochemical principles of molecular motor function together with an account of some important exper-

imental techniques for their study. The section begins with an overview of the regulation and function of a complex bacterial flagellar motor (Chap. 1). The focus is then shifted towards molecular motors in eukaryotes and the biophysical principles by which they produce force and linear transport. Chapters 2. 3 and 5 consider the mechanisms of operation of members of the myosin motor family, which interact with the actin cytoskeleton, and of kinesins and dyneins, which interact with microtubules. The multitude of biological roles of motors in living cells include tasks of biomedical relevance, such as axonal transport and embryonal development. Chapters 4 and 5 exemplify these functions together with accounts of how such diverse tasks can be achieved by a limited set of motors and cytoskeletal filaments. Chapter 7 describes the role of molecular motors in nanotube dynamics in living cells, including a theoretical treatment of the physics of membrane nanotubes. Chapters 6 and 8, finally, consider nanoscale motion in macromolecules not traditionally counted as molecular motors, including nucleic acid and nucleic acid-binding proteins (Chap. 6) and polysaccharide modifying enzymes (Chap. 8).

Theory of controlled nanoscale motion. Nanoscale motors and machines typically operate far from thermal equilibrium in an environment characterized by substantial thermal motion. In addition, thermal fluctuations of the protein conformational state around a free energy minimum can contribute to the stochastic nature of experimental data. The theory of Brownian motion in and out of thermal equilibrium therefore plays an important guiding role in the design of artificial motors and in the analysis of single-molecule experiments. Chapter 9 describes improved mathematical models of Brownian motion and their use to calibrate optical tweezers. Chapter 10 represents a tutorial introduction to the Jarzynski equation that allows extraction of information about equilibrium processes from data taken under non-equilibrium conditions. Finally, Chap. 11 describes theoretical approaches and methods for the accurate determination of diffusion constants from noisy data.

Controlled motion in nanotechnology. The ability to fabricate and manipulate nanoscale structures offers an impressive array of methods for the control of the motion of nanoscale objects, giving access to a new realm of experimental physics. Chapters 12 and 13 provide tutorial introductions to the physics of nanomechanical and nanofluidic devices for detection and study of single biomolecules. The subsequent three chapters describe two representative approaches to the construction of artificial molecular motors using self-assembly techniques, as well as a synthetic nanopore system that allows control of ion flow similar to a biological ion channel. The final two Chapters (17 and 18) tie together nanotechnology and biological motors by discussing the physics and methods of controlling biological motors using nanofabricated structures.

Nobel Symposium 131, on which this volume is based, was sponsored by the Nobel Foundation through its Nobel Symposium Fund. We thank all speakers and participants for their contributions and the Nobel Foundation for generous financial support.

Kalmar and Eugene January 2007 Alf Månsson Heiner Linke

#### List of Contributors

#### J.-F. Allemand

Laboratoire de Physique Statistique and Dept. Biologie Ecole Normale Superieure France allemand@lps.ens.fr

#### John Allingham

University of Wisconsin Department of Biochemistry USA jallingham@biochem.wisc.edu

#### J.L. Arlett

Division of Physics Mathematics and Astronomy arlett@cco.caltech.edu

#### Robert H. Austin

Department of Physics Princeton University USA austin@princeton.edu

#### D. Bensimon

Laboratoire de Physique Statistique and Dept. Biologie Ecole Normale Superieure France david.bensimon@lps.ens.fr

#### Howard C. Berg

Departments of Molecular and Cellular Biology and of Physics Harvard University USA hberg@mcb.harvard.edu

#### K. Berg-Sørensen

Department of Physics Technical University of Denmark Denmark

#### G. Charvin

Laboratoire de Physique Statistique and Dept. Biologie Ecole Normale Superieure France gilles.charvin@lps.ens.fr

#### Edward C. Cox

Department of Molecular Biology Princeton University USA ecox@princeton.edu

#### H.G. Craighead

Applied and Engineering Physics Cornell University USA hgcl@cornell.edu

#### V. Croquette

Laboratoire de Physique Statistique and Dept. Biologie Ecole Normale Superieure France croquette@lps.ens.fr

#### M.C. Cross

Division of Physics Mathematics and Astronomy California Institute of Technology USA

#### András Czövek

Department of Biological Physics Eötvös University Hungary czigor@angel.elte.hu

#### Gaudenz Danuser

Departments of Cell Biology The Scripps Research Institute USA

#### Imre Derényi

Department of Biological Physics Eötvös University Hungary derenyi@angel.elte.hu

#### Marileen Dogterom

FOM Institute for Atomic and Molecular Physics (AMOLF) The Netherlands dogterom@amolf.nl

#### Martijn M. van Duijn

Department of Bioengineering University of California Berkeley USA

vanduijn@berkeley.edu

#### Henrik Flyvbjerg

Biosystems Department and Danish Polymer Centre Risø National Laboratory Denmark henrik.flyvbjerg@risoe.dk

#### S.E. Fraser

Kavli Nanoscience Institute and Division of Biology and Division of Engineering and Applied Science California Institute of Technology USA

#### Lawrence S.B. Goldstein

Departments of Cellular and Molecular Medicine University of California of San Diego USA lgoldstein@ucsd.edu

#### P.H. Hagedorn

Biosystems Department Risø National Laboratory Denmark peter.hagedorn@risoe.dk

#### Henry Hess

Department of Materials Science and Engineering University of Florida USA hhess@mse.ufl.edu

#### Nobutaka Hirokawa

Department of Cell Biology and Anatomy Graduate School of Medicine University of Tokyo Japan hirokawa@m.u-tokyo.ac.jp

#### Robert D. Horansky

Department of Physics University of Colorado USA

Robert.Horansky@Colorado.edu

#### Christopher Jarzynski

Theoretical Division Los Alamos National Laboratory and Department of Chemistry and Biochecmistry Institute for Physical Science and Technology University of Maryland USA

#### Gerbrand Koster

cjarzyns@umd.edu

Institut Curie France and FOM Institute for Atomic and Molecular Physics (AMOLF) The Netherlands gerbrand.koster@curie.fr

#### N.B. Larsen

Danish Polymer Centre Risø National Laboratory Denmark and Biosystems Department Risø National Laboratory Denmark niels.b.larsen@risoe.dk

#### G. Lia

Harvard University Chemistry and Chemical Biology USA lia@fas.harvard.edu

#### T. Lionnet

Laboratoire de Physique Statistique and Dept. Biologie Ecole Normale Superieure France

#### Thomas F. Magnera

Department of Chemistry and Biochemistry University of Colorado

magnera@eefus.colorado.edu

#### Alf Månsson

School of Pure and Applied Natural Sciences University of Kalmar Sweden alf.mansson@hik.se

#### Dietmar J. Manstein

Institute for Biophysical Chemistry Germany manstein@bpc.mh-hannover.de

#### Charles R. Martin

Department of Chemistry University of Florida USA crmartin@chem.ufl.edu

#### Josef Michl

Department of Chemistry and Biochemistry University of Colorado USA michl@eefus.colorado.edu

#### Lars Montelius

Division of Solid State Physics and The Nanometer Consortium University of Lund Sweden lars.montelius@ftf.lth.se

#### S. Mosler

Danish Polymer Centre Risø National Laboratory Denmark

#### K.C. Neuman

Laboratoire de Physique Statistique and Dept. Biologie Ecole Normale Superieure France

#### XVIII List of Contributors

#### Ian A. Nicholls

School of Pure and Applied Natural Sciences University of Kalmar Sweden

#### Kazuhiro Oiwa

Kobe Advanced CT Center (KARC)
National Institute of Information and Communications Technology (NICT)
Japan
oiwa@nict.go.jp

#### Pär Omling

Division of Solid State Physics and The Nanometer Consortium University of Lund Sweden par.omling@vr.se

#### M.R. Paul

Department of Mechanical Engineering Virginia Polytechnic Institute and State University USA mrp@vt.edu

#### John C. Price

Department of Physics University of Colorado USA john.price@colorado.edu

#### **Jacques Prost**

Institut Curie
France
and
ESPCI
France
jacques.prost@curie.fr

#### Ivan Rayment

Department of Biochemistry University of Wisconsin USA Ivan\_Rayment@biochem.wisc.edu

#### M.L. Roukes

Kavli Nanoscience Institute and Division of Physics Mathematics and Astronomy and Division of Engineering and Applied Science California Institute of Technology USA roukes@caltech.edu

#### O.A. Saleh

Materials Department and Biomolecular Science and Engineering Program University of California USA saleh@engineering.ucsb.edu

#### K.T. Samiee

Applied and Engineering Physics Cornell University USA kts3@cornell.edu

#### E. Schäffer

Center of Biotechnology Technical University Germany

#### D. Selmeczi

Danish Polymer Centre
Risø National Laboratory
Denmark
and
Department of Biological Physics
Eötvös University
Hungary
david.selmeczi@risoe.dk

#### Sameer B. Shah

Department of Bioengineering University of Maryland USA

sameer@umd.edu

#### Zuzanna S. Siwy

Department of Physics and Astronomy University of California USA and Department of Chemistry Silesian University of Technology Poland zsiwy@uci.edu

#### Gudmund Skjåk-Bræk

Department of Biotechnology The Norwegian University of Science and Technology Norway gudmund.skjaax-braek @biotechntnu.no

#### Marit Sletmoen

Biophysics and Medical Technology Department of Physics The Norwegian University of Science and Technology Norway marit.sletmoen@phys.ntnu.no

#### J.E. Solomon

Division of Physics Mathematics and Astronomy California Institute of Technology USA

#### S.M. Stavis

Applied and Engineering Physics Cornell University USA sstavis@gmail.com

#### Bjørn Torger Stokke

Biophysics and Medical Technology Department of Physics The Norwegian University of Science and Technology Norway bjorn.stokke@phys.ntnu.no

#### Sven Tågerud

School of Pure and Applied Natural Sciences University of Kalmar Sweden

sven.tagerud@hik.se

#### Reiko Takemura

Okinaka Memorial Institute for Medical Research Japan

#### S. Tolić-Nørrelykke

Max Planck Institute for the Physics of Complex Systems Germany tolic@nbi.dk

#### Viola Vogel

Department of Materials Swiss Federal Institute of Technology (ETH) Switzerland viola.vogel@mat.ethz.ch

#### Y.M. Wang

Department of Physics Princeton University USA ymwang@wuphys.wustl.edu

#### Ge Yang

Departments of Cell Biology The Scripps Research Institute USA

#### XX List of Contributors

#### H. Yokota

Department of Molecular Physiology The Tokyo Metropolitan Institute of Medical Science Japan hiroaki\_yokota@rinshoken.or.jp Bernard Yurke
Bell Laboratories
USA
yurke@lucent.com

### Lecture Notes in Physics

For information about earlier volumes please contact your bookseller or Springer LNP Online archive: springerlink.com

Vol.665: V. Martinez (Ed.), Data Analysis in Cosmology

Vol.666: D. Britz, Digital Simulation in Electrochemistry

Vol.667: W. D. Heiss (Ed.), Quantum Dots: a Doorway to Nanoscale Physics

Vol.668: H. Ocampo, S. Paycha, A. Vargas (Eds.), Geometric and Topological Methods for Quantum Field Theory

Vol.669: G. Amelino-Camelia, J. Kowalski-Glikman (Eds.), Planck Scale Effects in Astrophysics and Cosmology

Vol.670: A. Dinklage, G. Marx, T. Klinger, L. Schweikhard (Eds.), Plasma Physics

Vol.671: J.-R. Chazottes, B. Fernandez (Eds.), Dynamics of Coupled Map Lattices and of Related Spatially Extended Systems

Vol.672: R. Kh. Zeytounian, Topics in Hyposonic Flow Theory

Vol.673: C. Bona, C. Palenzula-Luque, Elements of Numerical Relativity

Vol.674: A. G. Hunt, Percolation Theory for Flow in Porous Media

Vol.675: M. Kröger, Models for Polymeric and Anisotropic Liquids

Vol.676: I. Galanakis, P. H. Dederichs (Eds.), Half-metallic Alloys

Vol.677: A. Loiseau, P. Launois, P. Petit, S. Roche, J.-P. Salvetat (Eds.), Understanding Carbon Nanotubes

Vol.678: M. Donath, W. Nolting (Eds.), Local-Moment Ferromagnets

Vol.679: A. Das, B. K. Chakrabarti (Eds.), Quantum Annealing and Related Optimization Methods

Vol.68o: G. Cuniberti, G. Fagas, K. Richter (Eds.), Introducing Molecular Electronics

Vol.681: A. Llor, Statistical Hydrodynamic Models for Developed Mixing Instability Flows

Vol.682: J. Souchay (Ed.), Dynamics of Extended Celestial Bodies and Rings

Vol.683: R. Dvorak, F. Freistetter, J. Kurths (Eds.), Chaos and Stability in Planetary Systems

Vol.684: J. Dolinšek, M. Vilfan, S. Žumer (Eds.), Novel NMR and EPR Techniques

Vol.685: C. Klein, O. Richter, Ernst Equation and Riemann Surfaces

Vol.686: A. D. Yaghjian, Relativistic Dynamics of a Charged Sphere

Vol.687: J. W. LaBelle, R. A. Treumann (Eds.), Geospace Electromagnetic Waves and Radiation

Vol.688: M. C. Miguel, J. M. Rubi (Eds.), Jamming, Yielding, and Irreversible Deformation in Condensed Matter

Vol.689: W. Pötz, J. Fabian, U. Hohenester (Eds.), Quantum Coherence

Vol.690: J. Asch, A. Joye (Eds.), Mathematical Physics of Quantum Mechanics

Vol.691: S. S. Abdullaev, Construction of Mappings for Hamiltonian Systems and Their Applications

Vol.692: J. Frauendiener, D. J. W. Giulini, V. Perlick (Eds.), Analytical and Numerical Approaches to Mathematical Relativity

Vol.693: D. Alloin, R. Johnson, P. Lira (Eds.), Physics of Active Galactic Nuclei at all Scales

Vol.694: H. Schwoerer, J. Magill, B. Beleites (Eds.), Lasers and Nuclei

Vol.695: J. Dereziński, H. Siedentop (Eds.), Large Coulomb Systems

Vol.696: K.-S. Choi, J. E. Kim, Quarks and Leptons From Orbifolded Superstring

Vol.697: E. Beaurepaire, H. Bulou, F. Scheurer, J.-P. Kappler (Eds.), Magnetism: A Synchrotron Radiation Approach

Vol.698: S. Bellucci (Ed.), Supersymmetric Mechanics - Vol. 1

Vol.699: J.-P. Rozelot (Ed.), Solar and Heliospheric Origins of Space Weather Phenomena

Vol.700: J. Al-Khalili, E. Roeckl (Eds.), The Euroschool Lectures on Physics with Exotic Beams, Vol. II.

Vol.701: S. Bellucci, S. Ferrara, A. Marrani, Supersymmetric Mechanics – Vol. 2

Vol.702: J. Ehlers, C. Lämmerzahl, Special Relativity

Vol.703: M. Ferrario, G. Ciccotti, K. Binder (Eds.), Computer Simulations in Condensed Matter Systems: From Materials to Chemical Biology Volume 1

Vol.704: M. Ferrario, G. Ciccotti, K. Binder (Eds.), Computer Simulations in Condensed Matter Systems: From Materials to Chemical Biology Volume 2

Vol.705: P. Bhattacharyya, B.K. Chakrabarti (Eds.), Modelling Critical and Catastrophic Phenomena in Geoscience

Vol.706: M.A.L. Marques, C.A. Ullrich, F. Nogueira, A. Rubio, K. Burke, E.K.U. Gross (Eds.), Time-Dependent Density Functional Theory

Vol.707: A.V. Shchepetilov, Calculus and Mechanics on Two-Point Homogenous Riemannian Spaces

Vol.708: F. Iachello, Lie Algebras and Applications

Vol.709: H.-J. Borchers and R.N. Sen, Mathematical Implications of Einstein-Weyl Causality

Vol.710: K. Hutter, A.A.F. van de Ven, A. Ursescu, Electromagnetic Field Matter Interactions in Thermoelastic Solids and Viscous Fluids

Vol.711: H. Linke, A. Månsson (Eds.), Controlled Nanoscale Motion

## Contents

T 1	Navigation on a Micron Scale	
H.	C. Berg	1
Ref	ferences	12
	Myosin Motors: The Chemical Restraints Imposed by ATP	
<i>I. I</i>	Rayment and J. Allingham	15
2.1	Chemistry and Thermodynamics of ATP Hydrolysis	15
2.2	Hydrolysis of MgATP	16
2.3	Kinetic Cycle for Myosin	17
2.4	Structures of Myosin	19
2.5	Active Site of Myosin	24
2.6	Comparison with G-proteins: Molecular Switches	28
2.7	Kinesin Based Motors	31
2.8	Conclusions	36
Ref	rerences	37
3 I	How Linear Motor Proteins Work	
K.	Oiwa and D.J. Manstein	41
3.1	Introduction	41
3.2	Structural Features of Cytoskeletal Motor Proteins	41
3.3	In Vitro Motility Assays: A Link between Physiology	
	and Biochemistry	44
3.4	Structural Features of the Myosin Motor Domain	46
3.5	Amplification of the Working Stroke	
	by a Lever Arm Mechanism	47
3.6	Backwards Directed Movement	50
3.7	Surface-Alignment of Motor Proteins	
	and their Tracks	51
3.8	Controlling the Direction	
	of Protein Filament Movement Using MEMS Techniques	52
3.9	Conclusions and Perspectives	58

Refere	ences	59		
of a	conal Transport: Imaging and Modeling Neuronal Process			
S.B. 4.1	Shah, G. Yang, G. Danuser, and L.S.B. Goldstein	65		
	A Tremendous Transport Challenge	65		
4.2	Meeting the Challenge: Key Players in the Neuronal Transport System	66		
4.3	Unraveling Mechanism: Using Imaging	00		
	and Modeling	68		
4.4	In Vivo Traffic Cameras: Imaging of Vesicles	co		
4.5	in Larval Segmental Nerves  Breaking Down the Film: Vesicle Tracking	68		
1.0		71		
4.6	Understanding the Data: Theoretical Modeling			
4.7	of Axonal Transport	72		
	ences			
E Int	racellular Transport and Kinesin Superfamily Proteins:			
	cture, Function and Dynamics			
	irokawa and R. Takemura	85		
5.1	Introduction			
5.2	Monomeric Motors and Their Functions	88		
5.3	Dendritic Transport and Mechanisms			
	of Cargo Recognition			
5.4	KIF3, Left–Right Determination and Development			
5.5	Monomeric Motor – How Can it Move?			
5.6	KIF2 – Microtubule Depolymerizing Motor	15		
5.7	Conclusions and Future Perspectives			
Refere	ences	19		
6 Stu	idies of DNA-Protein Interactions at the Single Molecule			
Level	l with Magnetic Tweezers			
J.- $F.$	Allemand, D. Bensimon, G. Charvin, V. Croquette, G. Lia,			
T. Lie	onnet, K.C. Neuman, O.A. Saleh, and H. Yokota	23		
6.1	Introduction	23		
6.2	Magnetic Tweezers			
6.3	Stretching and Twisting DNA			
6.4	Protein Induced DNA Looping	28		
6.5	Type II Topoisomerases	30		
6.6	Study of Helicases			
6.7	The Fastest Known DNA Translocase: FtsK	34		
6.8	Conclusion	37		
Refere	References			