

Curriculum Vitæ

Howard C. Berg

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Education:

California Institute of Technology, Pasadena, California, 1952-1956, B.S. in Chemistry (1956),
undergraduate research with Jerome Vinograd.

Carlsberg Laboratory, Copenhagen, 1956-1957. Fulbright Fellow with Kai Linderstrøm-Lang.

Harvard Medical School, Boston, Massachusetts, 1957-1959, preclinical study as a National Scholar.

Harvard University, Cambridge, Massachusetts, 1959-1964, NIH Predoctoral Fellow. M.A. in Physics
(1960), Ph.D. in Chemical Physics (1964), thesis with Norman Ramsey, "Spin exchange and
surface relaxation in the atomic hydrogen maser".

Honors:

Fulbright Fellow, 1956-1957

National Scholar, Harvard Medical School, 1957-1959

NIH Predoctoral Fellow, 1959-1963

Junior Fellow, Harvard Society of Fellows, 1963-1966

NSF Science Faculty Professional Development Awardee, 1978-1979

Biological Physics Prize of the American Physical Society (with E.M Purcell), 1984

National Academy of Sciences, 1984

American Academy of Arts and Sciences, 1985

Fellow, American Association for the Advancement of Science, 1985

Fellow, American Physical Society, 1990

Fellow, American Academy of Microbiology, 1992

Beams Lecturer, Department of Physics, Univ. of Virginia, 1992

Ida Beam Distinguished Visiting Professor, Department of Microbiology, Univ. of Iowa, 1994

Annual Lecturer, Danish Academy of Technical Sciences, 1998

Guggenheim Fellow, 2000-2001

Chan Memorial Lecturer, Department of Chemistry, Berkeley, 2001

American Philosophical Society, 2002

Carlson Lectureship, Department of Biophysics, Johns Hopkins, 2002

Luria Lecturer, Department of Biology, MIT, 2002

Visiting Fellow Commoner, Trinity College Cambridge, 2005. Sponsor: Colin Hughes

2007 U.S. Genomics Award for Outstanding Investigator in the Field of Single Molecule Biology,
awarded by the Biophysical Society

Doctor of Science *h. c.*, Faculty of Biology and Chemistry, University of Osnabrück, 2007

Overseas Fellow, Churchill College Cambridge, 2012. Sponsor: Ray Goldstein

Sackler Prize in Biophysics 2014

Professional experience

Junior Fellow, Harvard Society of Fellows, 1963-1966.

Guest of Alec Bangham, Institute of Animal Physiology, Babraham, England, summer 1966.

Assistant Professor of Biology and Chairman of the Board of Tutors in Biochemical Sciences, Harvard, 1966-1969.

Associate Professor of Biochemistry and Molecular Biology and Chairman of the Board of Tutors in Biochemical Sciences, Harvard, 1969-1970.

Guest of Julius Adler, University of Wisconsin, Madison, Wisconsin, fall 1970.

Associate Professor of Molecular, Cellular and Developmental Biology, University of Colorado, 1970-1974.

Professor of Molecular, Cellular and Developmental Biology, University of Colorado, 1974-1979, Associate Chairman, 1974-1975, Chairman, 1976-1977.

Sabbatical with Roger Stanier, Pasteur Institute, Paris, and Jorgen Henrichsen, State Serum Institute, Copenhagen, 1978-1979.

Professor of Biology, California Institute of Technology, 1979-1986.

Student, Cold Spring Harbor course in Advanced Bacterial Genetics, summer 1985.

Professor of Molecular & Cellular Biology, Harvard University, 1986-present.

Member, The Rowland Institute for Science, 1986-present.

Professor of Physics, Harvard University, 1997-present.

Lorentz Professor, University of Leiden, spring 2001.

Herchel Smith Professor of Physics, Harvard University, 2003-present

Teaching experience:

Developed courses at Harvard on membrane structure and function, at Colorado on the biology of sensory phenomena, statistical processes in molecular biology, and elements of biophysics, and at Caltech on motile behavior of cells and microorganisms. Since returning to Harvard, have taught an introductory course on cell biology (with D. Branton), developed a Core course, "From DNA to Brain" (with J.E. Dowling), developed courses on statistical processes in cells and on introductory biophysics (the latter with J. Doyle, D. Nelson, and then A. Samuel), taught an upper-level course on statistical mechanics and quantitative biology, and conducted graduate seminars on microbial development and behavior (once with R.M. Losick), motor molecules, gliding motility and swarming. Wrote two books known for their pedagogical value, *Random Walks in Biology* (Princeton 1993) and *E. coli in Motion* (Springer 2004).

Professional societies:

American Academy of Arts and Sciences, American Academy for Microbiology, American Association for the Advancement of Science, American Philosophical Society, American Physical Society (Chairperson, Division of Biological Physics, 1988-1989), American Society for Microbiology, Biophysical Society, National Academy of Sciences.

Committees and editorial boards:

NIH Molecular Biology Study Section, 1974-1977; Biophysical Journal, 1978-1981; Cell Motility, 1980-1990; Modern Cell Biology, 1981-1989; Board on Physics and Astronomy, National Research Council, 1990-1993; American Institute of Physics: Biological Physics Series, 1994-, Advisory Committee on

Physics Today, 1998-2003; Proceedings of the National Academy of Sciences, 2001-2002; Journal of Bacteriology, 2001-2009; NIH Prokaryotic Cell and Molecular Biology Study Section, 2005-2009.

Current research interests:

Motile behavior of bacteria: chemotaxis and flagellar rotation in *Escherichia coli*; flagellar rotation in a motile *Streptococcus*; swimming of a novel cyanobacterium; mechanisms of gliding motility; mechanics of bacterial swarming.

ARTICLES

On problems in atomic physics:

1. Berg, H.C. and Kleppner, D. Storage technique for atomic hydrogen. *Rev. Sci. Instr.* **33**, 248–249 (1962).
2. Berg, H.C. Spin relaxation of atoms in molecular buffer gases. *J. Chem. Phys.* **43**, 1851 (1965).
3. Berg, H.C. Amplitude and decay rate analysis of low level exponentially decaying radio-frequency signals. *Rev. Sci. Instr.* **36**, 330–334 (1965).
4. Berg, H.C. Spin exchange and surface relaxation in the atomic hydrogen maser. *Phys. Rev.* **137**, A1621–A1634 (1965).
5. Kleppner, D., Berg, H.C., Crampton, S.B., Ramsey, N.F., Vessot, R.F.C., Peters, H.E. and Vanier, J. Hydrogen maser principles and techniques. *Phys. Rev.* **138**, A972–A983 (1965).
6. Crampton, S.B., Berg, H.C., Robinson, H.G. and Ramsey, N.F. Determination of the quadrupole coupling constant in the N^{14} atomic ground state. *Phys. Rev. Lett.* **24**, 195–197 (1970).

On the separation of macromolecules according to mass:

7. Berg, H.C. and Purcell, E.M. A method for separating according to mass a mixture of macromolecules or small particles suspended in a fluid, I. Theory. *Proc. Natl. Acad. Sci. USA* **58**, 862–869 (1967).
8. Berg, H.C., Purcell, E.M. and Stewart, W.W. ..., II. Experiments in a gravitational field. *ibid*, pp. 1286–1291.
9. Berg, H.C. and Purcell, E.M. ..., III. Experiments in a centrifugal field. *ibid*, pp. 1821–1828.
10. Purcell, E.M. and Berg, H.C. Particle separator. U.S. Patent 3,523,610 (1970).
11. Barcion, V. and Berg, H.C. Forced axial flow between rotating concentric cylinders. *J. Fluid Mech.* **47**, 469–479 (1971).

On the structure of cell membranes:

12. Berg, H.C., Diamond, J.M. and Marfey, P.S. Erythrocyte membrane: Chemical modification. *Science* **150**, 64–67 (1965).
13. Berg, H.C. Membrane dipole potentials. *Biophys. J.* **8**, 1051–1053 (1968).
14. Berg, H.C. Sulfanilic acid diazonium salt: A label for the outside of the human erythrocyte membrane. *Biochim. Biophys. Acta* **183**, 65–78 (1969).
15. Bender, W.W., Garan, H. and Berg, H.C. Proteins of the human erythrocyte membrane as modified by pronase. *J. Mol. Biol.* **58**, 783–797 (1971).

16. Whiteley, N.M. and Berg, H.C. Amidination of the outer and inner surfaces of the human erythrocyte membrane. *J. Mol. Biol.* **87**, 541–561 (1974).
17. Berg, H.C. and Hirsh, D. Synthesis of diazotized (³⁵S)sulfanilic acid of high specific activity: A label for the outer surface of cell membranes. *Anal. Biochem.* **66**, 629–631 (1975).
18. Wennogle, L.P. and Berg, H.C. Covalent attachment of polydeoxythymidylic acid to human erythrocytes. *J. Mol. Biol.* **123**, 471–483 (1978).
19. Wennogle, L.P. and Berg, H.C. Isolation of cell surface proteins by hybridization. *J. Mol. Biol.* **124**, 689–699 (1978).

On the motile behavior of microorganisms:

20. Berg, H.C. How to track bacteria. *Rev. Sci. Instr.* **42**, 868–871 (1971).
21. Futrelle, R.P. and Berg, H.C. Specification of gradients used for studies of chemotaxis. *Nature* **239**, 517–518 (1972).
22. Berg, H.C. and Brown, D.A. Chemotaxis in *Escherichia coli* analysed by three-dimensional tracking. *Nature* **239**, 500–504 (1972).
23. Berg, H.C. and Anderson, R.A. Bacteria swim by rotating their flagellar filaments. *Nature* **245**, 380–384 (1973).
24. Brown, D.A. and Berg, H.C. Temporal stimulation of chemotaxis in *Escherichia coli*. *Proc. Natl. Acad. Sci. USA* **71**, 1388–1392 (1974).
25. Berg, H.C. Dynamic properties of bacterial flagellar motors. *Nature* **249**, 77–79 (1974).
26. Berg, H.C. and Brown, D.A. Chemotaxis in *Escherichia coli* analyzed by three-dimensional tracking. Addendum. *Antibiotics and Chemotherapy* **19**, 55–78 (1974).
27. Berg, H.C. Flagellar control of bacterial motion. In *Functional Linkage in Biomolecular Systems*, ed. Schmitt, F.O., Schneider, D.M. and Crothers, D.M. (Raven Press, New York, 1975) pp. 290–296.
28. Berg, H.C. Flagellar rotation. Proceedings of the First Intersectional Congress of the IAMS, Vol. 1 (Science Council of Japan, Tokyo) 1975, pp. 665–673.
29. Berg, H.C. Bacterial behaviour. *Nature* **254**, 389–392 (1975).
30. Berg, H.C. Chemotaxis in bacteria. *Ann. Rev. Biophys. Bioeng.* **4**, 119–136 (1975).
31. Berg, H.C. How bacteria swim. *Sci. Am.* **233** (2), 36–44 (1975).
32. Berg, H.C. and Tedesco, P.M. Transient response to chemotactic stimuli in *Escherichia coli*. *Proc. Natl. Acad. Sci., USA* **72**, 3235–3239 (1975).
33. Berg, H.C. Bacterial movement. In *Swimming and Flying in Nature*, Vol. 1, ed. Wu, T.Y.-T., Brokaw, C.J. and Brennen, C. (Plenum, New York, 1975) pp. 1–11.
34. Berg, H.C. How spirochetes may swim. *J. Theor. Biol.* **56**, 269–273 (1976).
35. Berg, H.C. Does the flagellar rotary motor step? In *Cold Spring Harbor Conferences on Cell Proliferation*, Vol. 3: Cell Motility, ed. Goldman, R., Pollard, T. and Rosenbaum, J. (Cold Spring Harbor, 1976) pp. A47–A56.

36. Berg, H.C. Rotary engines in biology. *In* *New Directions in Kinematics Research*, ed. Roth, B. (Proceedings of NSF Workshop, Stanford, August 23, 1976) pp. 101–103.
37. Manson, M.D., Tedesco, P., Berg, H.C., Harold, F.M. and van der Drift, C. A protonmotive force drives bacterial flagella. *Proc. Natl. Acad. Sci. USA* **74**, 3060–3064 (1977).
38. Berg, H.C. and Purcell, E.M. Physics of chemoreception. *Biophys. J.* **20**, 193–219 (1977).
39. Berg, H.C., Bromley, D.B. and Charon, N.W. Leptospiral motility. *Symp. Soc. Gen. Microbiol.* **28**, 285–294 (1978).
40. Berg, H.C. The tracking microscope. *Adv. Opt. Elect. Microsc.* **7**, 1–15 (1978).
41. Berg, H.C. and Turner, L. Movement of microorganisms in viscous environments. *Nature* **278**, 349–351 (1979).
42. Manson, M.D., Tedesco, P.M. and Berg, H.C. Energetics of flagellar rotation in bacteria. *J. Mol. Biol.* **138**, 541–561 (1980).
43. Berg, H.C. Dynamics and energetics of the bacterial rotary motor. *In* *Protein dynamics and energy transduction*, ed. Ishiwata, S.-I. (Taniguchi Foundation, 1980) pp. 312–344.
44. Berg, H.C. Chemotaxis in bacteria: a beginner's guide to the literature. *Lect. Notes Biomath.* **38**, 377–378 (1980).
45. Berg, H.C., Manson, M.D. and Conley, M.P. Dynamics and energetics of flagellar rotation in bacteria. *Symp. Soc. Exp. Biol.* **35**, 1–31 (1982).
46. Segall, J.E., Manson, M.D. and Berg, H.C. Signal processing times in bacterial chemotaxis. *Nature* **296**, 855–857 (1982).
47. Lapidus, I.R. and Berg, H.C. Gliding motility of *Cytophaga* sp. strain U67. *J. Bacteriol.* **151**, 384–398 (1982).
48. Block, S.M., Segall, J.E. and Berg, H.C. Impulse responses in bacterial chemotaxis. *Cell* **31**, 215–226 (1982).
49. Smyth, R.D. and Berg, H.C. Change in flagellar beat frequency of *Chlamydomonas* in response to light. *Cell Motility Suppl.* **1**, 211–215 (1982).
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51. Khan, S. and Berg, H.C. Isotope and thermal effects in chemiosmotic coupling to the membrane ATPase of *Streptococcus*. *J. Biol. Chem.* **258**, 6709–6712 (1983).
52. Block, S.M., Segall, J.E. and Berg, H.C. Adaptation kinetics in bacterial chemotaxis. *J. Bacteriol.* **154**, 312–323 (1983).
53. Berg, H.C. and Khan, S. A model for the flagellar rotary motor. *In* *Mobility and Recognition in Cell Biology*, ed. Sund, H. and Veeger, C. (deGruyter, Berlin, 1983) pp. 485–497.
54. Ishihara, A., Segall, J.E., Block, S.M. and Berg, H.C. Coordination of flagella on filamentous cells of *Escherichia coli*. *J. Bacteriol.* **155**, 228–237 (1983).
55. Block, S.M. and Berg, H.C. Successive incorporation of force-generating units in the bacterial rotary motor. *Nature* **309**, 470–472 (1984).

56. Conley, M.P. and Berg, H.C. Chemical modification of *Streptococcus* flagellar motors. *J. Bacteriol.* **158**, 832–843 (1984).
57. Berg, H.C. and Block, S.M. A miniature flow cell designed for rapid exchange of media under high-power microscope objectives. *J. Gen. Microbiol.* **130**, 2915–2920 (1984).
58. Berg, H.C. Bacterial flagellar rotation and its chemotactic control. *In Information and Energy Transduction in Biological Membranes*, ed. Bolis, C.L., Helmreich, E.J.M. and Passow, H. (Liss, New York, 1984) pp. 215–219.
59. Berg, H.C. Bovine-like rhodopsin in algae. *Nature* **311**, 702 (1984).
60. Segall, J.E., Ishihara, A. and Berg, H.C. Chemotactic signaling in filamentous cells of *Escherichia coli*. *J. Bacteriol.* **161**, 51–59 (1985).
61. Krikos, A., Conley, M.P., Boyd, A., Berg, H.C. and Simon, M.I. Chimeric chemosensory transducers in *Escherichia coli*. *Proc. Natl. Acad. Sci. USA* **82**, 1326–1330 (1985).
62. Berg, H. C. Physics of bacterial chemotaxis. *In Sensory Perception and Transduction in Aneural Organisms*, ed. Colombetti, G., Lenci, F. and Song, P.S. (Plenum, New York, 1985) pp. 19–30.
63. Berg, H.C. Flagellar Motility. *In Roche Seminars on Bacteria: Number 1 in a Series. Properties, Problems and Therapeutic Progress*, ed. Moellering, R.C. (Hoffman-LaRoche, Nutley, N.J., 1985), pp. 1–23.
64. Khan, S. Meister, M. and Berg, H.C. Constraints on flagellar rotation. *J. Mol. Biol.* **184**, 645–656 (1985).
65. Berg, H.C. Chemotaxis gene unveiled. *Nature* **321**, 200–201 (1986).
66. Segall, J.E., Block, S.M. and Berg, H.C. Temporal comparisons in bacterial chemotaxis. *Proc. Natl. Acad. Sci. USA* **83**, 8987–8991 (1986).
67. Lowe, G., Meister, M. and Berg, H.C. Rapid rotation of flagellar bundles in swimming bacteria. *Nature* **325**, 637–640 (1987).
68. Shimada, K. and Berg, H.C. Response of the flagellar rotary motor to abrupt changes in extracellular pH. *J. Mol. Biol.* **193**, 585–589 (1987).
69. Berg, H.C., Block, S.M., Conley, M.P., Nathan, A.R., Power, J.N. and Wolfe, A.J. Computerized video analysis of tethered bacteria. *Rev. Sci. Instr.* **58**, 418–423 (1987).
70. Wolfe, A.J., Conley, M.P., Kramer, T.J. and Berg, H.C. Reconstitution of signaling in bacterial chemotaxis. *J. Bacteriol.* **169**, 1878–1885 (1987).
71. Meister, M., Lowe, G. and Berg, H.C. The proton flux through the bacterial flagellar motor. *Cell* **49**, 643–650 (1987).
72. Meister, M. and Berg, H.C. The stall torque of the bacterial flagellar motor. *Biophys. J.* **52**, 413–419 (1987).
73. Meyer, P.W., Matus, I.J. and Berg, H.C. Avoidance of *Phycomyces* in a controlled environment. *Biophys. J.* **51**, 425–437 (1987).
74. Berg, H.C. A physicist looks at bacterial chemotaxis. *Cold Spring Harbor Symp. Quant. Biol.* **53**, 1–9 (1988).

75. Wolfe, A.J., Conley, M.P. and Berg, H.C. Acetyladenylate plays a role in controlling the direction of flagellar rotation. *Proc. Natl. Acad. Sci. USA* **85**, 6711–6715 (1988).
76. Blair, D.F. and Berg, H.C. Restoration of torque in defective flagellar motors. *Science* **242**, 1678–1681 (1988).
77. Berg, H.C. Biological applications of scanning tunneling microscopy. *Physics Today* **41**(1), S18-S19 (1989).
78. Block, S.M., Blair, D.F. and Berg, H.C. Compliance of bacterial flagella measured with optical tweezers. *Nature* **338**, 514–517 (1989).
79. Meister, M., Caplan, S.R. and Berg, H.C. Dynamics of a tightly coupled mechanism for flagellar rotation. *Biophys. J.* **55**, 905–914 (1989).
80. Conley, M.P., Wolfe, A.J., Blair, D.F. and Berg, H.C. Both CheA and CheW are required for reconstitution of chemotactic signaling in *Escherichia coli*. *J. Bacteriol.* **171**, 5190–5193 (1989).
81. Wolfe, A.J. and Berg, H.C. Migration of bacteria in semisolid agar. *Proc. Natl. Acad. Sci. USA* **86**, 6973–6977 (1989).
82. Blair, D.F. and Berg, H.C. The MotA protein of *Escherichia coli* is a proton-conducting component of the flagellar motor. *Cell* **60**, 439–449 (1990).
83. Berg, H.C. Physical constraints on microbial behavior: How you act if you are very small. *J. Chem. Ecol.* **16**, 119–120 (1990).
84. Berg, H.C. Bacterial microprocessing. *Cold Spring Harbor Symp. Quant. Biol.* **55**, 539–545 (1990).
85. Berg, H.C. and Turner, L. Chemotaxis of bacteria in glass capillary arrays. *Biophys. J.* **58**, 919–930 (1990).
86. Schnitzer, M.J., Block, S.M., Berg, H.C. and Purcell, E.M. Strategies for chemotaxis. *Symp. Soc. Gen. Microbiol.* **46**, 15–34 (1990).
87. Block, S.M., Fahrner, K.A. and Berg, H.C. Visualization of bacterial flagella by video-enhanced light microscopy. *J. Bacteriol.* **173**, 933–936 (1991).
88. Budrene, E.O. and Berg, H.C. Complex patterns formed by motile cells of *Escherichia coli*. *Nature* **349**, 630–633 (1991).
89. Block, S.M., Blair, D.F. and Berg, H.C. Compliance of bacterial polyhooks measured with optical tweezers. *Cytometry* **12**, 492–496 (1991).
90. Blair, D.F. and Berg, H.C. Mutants in the MotA protein of *Escherichia coli* reveal domains critical for proton conduction. *J. Mol. Biol.* **221**, 1433–1442 (1991).
91. Blair, D.F., Kim, D.Y. and Berg, H.C. Mutant MotB proteins in *Escherichia coli*. *J. Bacteriol.* **173**, 4049–4055 (1991).
92. Berg, H.C. Bacterial motility: Handedness and symmetry. *Ciba Found. Symp.* **162**, 58–72 (1991).
93. Budrene, E.O. and Berg, H.C. Pattern formation by bacteria. *Current Biology* **1**, 83 (1991).
94. Stolz, B. and Berg, H.C. Evidence for interactions between MotA and MotB, torque generating elements of the flagellar motor of *Escherichia coli*. *J. Bacteriol.* **173**, 7033–7037 (1991).

95. Berg, H.C. and Turner, L. Selection of motile nonchemotactic mutants of *Escherichia coli* by field-flow fractionation. *Proc. Natl. Acad. Sci. USA* **88**, 8145–8148 (1991).
96. Berg, H.C. Studies of motile bacteria. In *Physics News in 1991*, ed. Schewe, P.F. (American Institute of Physics, New York, 1991).
97. Berg, H.C. Response of *Escherichia coli* to novel gradients. In *Sensory Transduction*, Proc. 45th Symp. Soc. Gen. Physiol., Chpt. 13, pp. 220–223 (Rockefeller Univ. Press, 1992).
98. Dailey, F.E. and Berg, H.C. Mutants in disulfide bond formation that disrupt flagellar assembly. *Proc. Natl. Acad. Sci. USA* **90**, 1043–1047 (1993).
99. Dailey, F.E. and Berg, H.C. Change in direction of flagellar rotation in *Escherichia coli* mediated by acetate kinase. *J. Bacteriol.* **175**, 3236–3239 (1993).
100. Hazelbauer, G.L., Berg, H.C. and Matsumura, P. Bacterial motility and signal transduction. *Cell* **73**, 15–22 (1993).
101. Berg, H.C. and Turner, L. Torque generated by the flagellar motor of *Escherichia coli*. *Biophys. J.* **65**, 2201–2216 (1993).
102. Frauenfelder, H. and Berg, H.C. Physics and Biology. *Physics Today* **47** (2), 20–21 (1994).
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106. Berg, H.C. Torque generation by the flagellar rotary motor. *Biophys. J.* **68**, 163s–167s (1995).
107. Samuel, A.D.T. and Berg, H.C. Fluctuation analysis of rotational speeds of the bacterial flagellar motor. *Proc. Natl. Acad. Sci. USA* **92**, 3502–3506 (1995).
108. Woodward, D.E., Tyson, R., Myerscough, M.R., Murray, J.D., Budrene, E.O. and Berg, H.C. Spatio-temporal patterns generated by *Salmonella typhimurium*. *Biophys. J.* **68**, 2181–2189 (1995).
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112. Budrene, E.O. and Berg, H.C. Dynamics of formation of symmetric patterns by chemotactic bacteria. *Nature* **376**, 49–53 (1995).
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114. Marykwas, D.L., Schmidt, S.A. and Berg, H.C. Interacting components of the flagellar motor of *Escherichia coli* revealed by the two-hybrid system in yeast. *J. Mol. Biol.* **256**, 564–576 (1996).
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119. Berg, H.C. Symmetries in bacterial motility. *Proc. Natl. Acad. Sci. USA* **93**, 14225–14228 (1996).
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121. Berry, R.M. and Berg, H.C. Torque generated by the bacterial flagellar motor close to stall. *Biophys. J.* **71**, 3501–3510 (1996).
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129. Berry, R.M. and Berg, H.C. Torque generated by the flagellar motor of *Escherichia coli* while driven backward. *Biophys. J.* **76**, 580–587 (1999).
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