### CHEMICAL HERITAGE FOUNDATION

# JONATHON HOWARD

The Pew Scholars Program in the Biomedical Sciences

Transcript of an Interview Conducted by

Steven J. Novak

at

University of Washington Seattle, Washington

on

23-25 January 1995

From the Original Collection of the University of California, Los Angeles

### ACKNOWLEDGEMENT

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#### **REFORMATTING:**

Marnie Berkowitz, Consultant to the Chemical Heritage Foundation. B.A., Classical Languages and Literatures, University of Minnesota; Ford Foundation Fellowship, Classical Languages and Literatures, University of Chicago.

David J. Caruso, Program Manager, Oral History, Chemical Heritage Foundation. B.A., History of Science, Medicine, and Technology, Johns Hopkins University; PhD., Science and Technology Studies, Cornell University.

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Jonathon Howard (Typed Name) THE REGENTS OF THE UNIVERSITY OF CALIFORNIA

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## JONATHON HOWARD

1957	Born in Sydney, Australia on 15 August
	Education
1979	B.Sc., Australian National University
1983	Ph.D., Australian National University
	Professional Experience
	Australian National University
1983	Postdoctoral Fellow
	University of Bristol, England
1984	Postdoctoral Fellow
	University of California, San Francisco
1985-1987	Visiting Postdoctoral Fellow
1988-1989	Assistant Research Physiologist
	University of Washington
1989-1994	Assistant Professor
1994-present	Associate Professor
	Honors
1976-1978	Australian National Undergraduate Scholarship
1979	Australian Commonwealth Postgraduate Research Scholarship
1981	M. G. F. Fuortes Travelling Scholarship
1988-1990	Fellowship, Fondation pour l'Étude du Système Nerveux Central et Périphérique
1990-1992	Alfred P. Sloan Research Fellowship
1990-1994	Pew Scholar in the Biomedical Sciences

# Selected Publications

Stange, G. and J. Howard, 1979. An ocellar dorsal light response in a dragonfly. *Journal of Experimental Biology*, 83:351-55.Howard, J., 1984. Calcium enables photoreceptor pigment migration in a mutant fly. *Journal* 

of Experimental Biology, 113:471-75.

- Howard, J. and J.F. Ashmore, 1986. Stiffness of sensory hair bundles in a sacculus of the frog. *Hearing Research*, 23:93-104.
- Howard, J. and A.J. Hudspeth, 1987. Mechanical relaxation of the hair bundle mediates adaptation in mechanoelectrical transduction by the bullfrog's saccular hair cell. *Proceedings of the National Academy of Sciences USA*, 84:3064-68.
- Howard, J. et al., 1987. The intracellular pupil mechanism and the maintenance of photoreceptor signal: Noise ratios in the blowfly *Lucilia cuprina*. *Proceedings of the Royal Society of London, Series B*, 231:415-35.
- Nilsson, D.-E. et al., 1987. Optics of the butterfly eye. *Journal of Comparative Physiology, Series A*, 162:341-66.
- Howard, J. and A.J. Hudspeth, 1988. Compliance of the hair bundle associated with the gating of mechanoelectrical transduction channels in the bullfrog's saccular hair cell. *Neuron*, 1:189-99.
- Howard, J. et al., 1988. Mechanoelectrical transduction by hair cells. *Annual Review* of Biophysics and Biophysical Chemistry, 17:99-124.
- Howard, J. et al., 1989. Movement of microtubules by single kinesin molecules. *Nature*, 342:154-58.
- Gittes, F. et al., 1993. The flexural rigidity of microtubules and actin filaments measured from thermal fluctuations in shape. *Journal of Cell Biology*, 120:923-34.
- Ray, S. et al., 1993. Kinesin follows the microtubule's protofilament axis. *Journal of Cell Biology*, 121:1083-93.
- Hunt, A.J. and J. Howard, 1993. Kinesin swivels to permit microtubule movement in any direction. *Proceedings of the National Academy of Sciences USA*, 90:11653-57.
- Hunt, A.J. et al., 1994. The force exerted by a kinesin molecule against a viscous load. *Biophysical Journal*, 67:766-81.
- Meyhöfer, E. and J. Howard, 1995. The force generated by a single kinesin molecule against an elastic load. *Proceedings of the National Academy of Sciences USA*, 92:574-78.
- Howard, J., 1996. The movement of kinesin along microtubules. *Annual Review of Physiology*, 58:703-29.
- Gittes, F. et al., 1996. Directional loading of the kinesin motor molecule as it buckles a microtubule. *Biophysical Journal.* In press.

### ABSTRACT

Jonathon Howard was born in Sydney, Australia. The oldest of four children, he grew up in a suburb of Sydney. He lived near Ku-Ring-Gai National Park, where he loved to hike, camp, and fish. He also played cricket and soccer and surfed. His parents were both architects until his father became a successful landscape architect and his mother a teacher of architecture. None of his siblings finished high school, and Howard disliked school intensely—except for mathematics-playing truant for much of his time there. But along came William Eason, who had been headmaster at Ku-Ring-Gai Chase High School before Howard entered. Eason founded International School, to which Howard transferred and in which he throve. From International School Howard went to Australian National University, obtaining his BSc in mathematics in 1979. He lost interest in mathematics and became interested in physics and neurobiology for graduate work. He obtained his PhD from Australian National University in 1983. He then took a postdoctoral fellowship at the University of Bristol in Bristol, England. Sensing a lack of common interest with co-workers there and not liking the weather, he took a postdoc at the University of California at San Francisco, where he worked in Albert James Hudspeth's lab. He found UCSF's intellectual climate stimulating and exciting. He also met his wife, Karla M. Neugebauer, there. Howard became interested in both vision and hearing, studying first photoreceptors and then hair cells. He accepted an assistant professorship at the University of Washington, which he thought would be a better place to continue his research on kinesin and myosin. He remains there today, attempting to balance his construction of his own tools, his teaching, his thinking, his research, and his life with wife and young daughter. He has won many awards, including the Pew Scholar in the Biomedical Sciences award, and he has many publications to his credit.

#### UCLA INTERVIEW HISTORY

#### **INTERVIEWER:**

Steven J. Novak, Senior Editor, UCLA Oral History Program. B.A., History, University of Colorado; Ph.D., History, University of California, Berkeley; M.B.A., UCLA Graduate School of Management.

#### TIME AND SETTING OF INTERVIEW:

Place: Howard's office, University of Washington.

**Dates, length of sessions:** January 23, 1995 (123 minutes); January 24, 1995 (125) ; January 25, 1995 (130).

#### Total number of recorded hours: 6.3

#### Persons present during interview: Howard and Novak

#### CONDUCT OF INTERVIEW:

This interview is one in a series with Pew scholars in the biomedical sciences conducted by the UCLA Oral History Program in conjunction with the Pew Charitable Trusts's Pew Scholars in the Biomedical Sciences Oral History and Archives Project. The Project has been designed to document the backgrounds, education, and research of biomedical scientists awarded four-year Pew scholarships since 1988. To provide an overall framework for Project interviews, the director of the UCLA Oral History Program and three UCLA faculty consultants developed a topic outline. In preparing for this interview, Novak held a telephone preinterview conversation with Howard to obtain written background information (curriculum vitae, copies of published articles, etc.) and to agree on an interviewing schedule. He also reviewed prior Pew scholars' interviews and the documentation in Howard's file at the Pew Scholars Program office in San Francisco, including his proposal application, letters of recommendation, and reviews by Pew Scholars Program national advisory committee members. For technical background, Novak consulted J.D. Watson et al., *Molecular Biology of the Gene.* 4th ed. Menlo Park, CA: Benjamin/Cummings, 1987 and Bruce Alberts et al., *Molecular Biology of the Cell.* 3d ed. New York: Garland, 1994.

The interview is organized chronologically, beginning with Howard's childhood and education in Sydney, Australia, and continuing through his postdocs at the University of Bristol and the University of California, San Francisco, and his career at the University of Washington. Major topics discussed include the optics of compound eyes, the gating-spring model of ion channels, developing methods of recording from and studying single molecules of kinesin, scientific publishing, and the process of running a lab.

### **ORIGINAL EDITING:**

Kristian T. London, assistant editor, edited the interview. He checked the verbatim transcript of the interview against the original tape recordings, edited for punctuation, paragraphing, and spelling, and verified proper names. Words and phrases inserted by the editor have been bracketed.

Howard reviewed the transcript. He verified proper names and made a number of corrections and additions.

London prepared the table of contents, biographical summary, and interview history.

Kathleen McAlister, editorial assistant, compiled the index.

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