SHOP TALK

Norman K. Wessells: A Life in Science

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"In its triple role as locomotory organelle, as a site of deposition of new surface material for the elongating axon, and a source of microspikes (sensory probes), the growth cone becomes the key to axon elongation" Yamada et al. (1971)

Norman K. Wessells' (Fig. 1) colleagues, students, and postdoctoral fellows threw a "retirement" party and symposium in his honor at Stanford University at the end of July 2004. The "Normfest" was hosted by Don Kennedy, President Emeritus of Stanford, and Editor-in-Chief of *Science* magazine. The event was planned and orchestrated by Paul Letourneau, University of Minnesota, who completed his doctoral studies with Norm in 1974; Rae Nishi, University of Vermont, who was an undergraduate researcher in The Wessells Lab in the early 1970s; and Ellen Porzig, Stanford University, who completed her doctoral work with Wessells in 1976.

The party was a bit belated. Norm joined the faculty of the Biology Department at Stanford University in 1962 and left Stanford as emeritus professor and former Dean of Humanities and Sciences in 1988. He then moved to the University of Oregon to become Provost and Vice President for Academic Affairs and Professor of Biology, leaving as emeritus professor in 1999. However, a "retirement" party was certainly too early, because Norm is still actively writing and updating the most broadly based and articulate texts in vertebrate biology available today (see Wessells, 1980a,b, 1988, 1990).

Norm is the author of ten books, including the outstanding texts cited above and the notable and provocative *Tissue Interactions in Development* (1973) and *Tissue Interactions and Development* (1977), and more than 80 scientific papers, including several classic *Scientific American* articles and publications in *PNAS*, *Science*, and *Nature*. What was notable about much of the work of Norm's students was that they were the sole authors cited on the published work that came from their theses and related projects. Norm's reluctance to add his name to their papers reflected his confidence in their work and their independence, as well as his modest assessment of his contribution to the work. This consideration, which essentially more than halved the publication list in his own CV, was much appreciated by his students and postdocs, although all of us were enormously influenced by his contribution to our science.

WESSELLS' IMPACT ON THE FIELD OF DEVELOPMENTAL BIOLOGY

Wessells, the developmental biologist, scholar, and writer, was a pioneer in discovering the roles of the cytoskeleton and growth cone adhesivity in axon guidance and migratory behavior. His own American Cancer Society–sponsored postdoctoral fellowship work with Clifford Grobstein at Stanford had inspired his thinking about the interactions of cells and the substrata over and through which they navigated. In his affectionate and beautifully written tribute for Grobstein, which was published by the National Academy (2000), Norm called Grobstein "the preeminent bridge between classical embryology and late twentieth-century Developmental Biology." He went on to say that, "Grobstein as scientist made the key discoveries that implicated extracellular materials as essential elements during embryonic induction processes. He [Grobstein] made the startling observation that different developing cell populations from embryos could interact across membranous filters that prevented direct cell-to-cell contact. And, he defined the specificity rules for inductive interactions: which combinations of epithelium and mesenchyme (the two kinds of interacting embryonic tissues) would result in morphogenesis or cellular differentiation. Those results, amplified over 40 years by new techniques and molecular biology, have established the importance of the extracellular materials and matrix, cell adhesion molecules, and extracellular enzymes

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DOI 10.1002/dvdy.20560
Published online 8 September 2005 in Wiley InterScience (www.interscience.wiley.com).

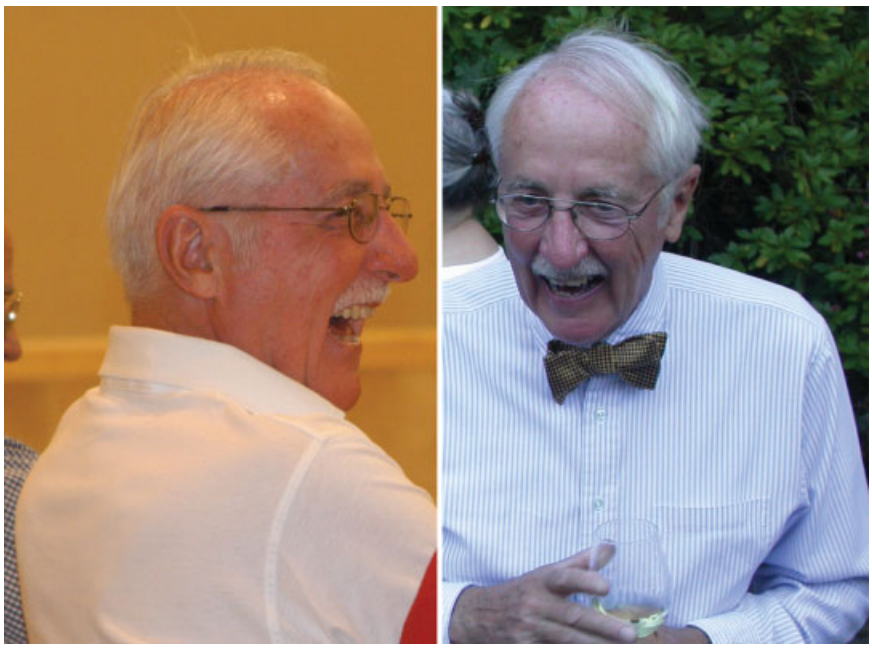

Fig. 1. Two views of Norm at Normfest. Photographs courtesy of Bob Nuttall.

that modify those materials in a variety of normal developmental processes, as well as in cancer metastasis, wound healing, and related biological processes" (Wessells, 2000). In fact, Norm himself had done much of the work in Cliff's lab for which he credited his mentor and Wessells was more of an equal partner in synthesizing the experimental results into theory than he admits in his retrospective of Grobstein's work.

Norm's interests in studying cellular morphogenesis (Spooner and Wessells, 1970a,b; Bernfield and Wessels, 1970; Ash et al., 1973; Goldin and Wessells, 1979; Goldin et al., 1984) and cell motility led him to focus on the role of the cytoskeleton, both in glial cell motility and the motility of the growth cone at the exploratory ends of neurites. He was among the first to watch and to interpret correctly the impact of the ECM on the cell's skeletal elements. In a classic *Journal of Cell Biology* report from 1971, B.S. Spooner, K.M. Yamada, and N.K. Wessells produced the first direct demonstration of a relationship between locomotory behavior in glial cells and cytoplasmic filaments. A year earlier, this highly creative and productive group had studied the role of microfilaments and microtubules in axon growth (Yamada et al., 1970). Spooner, now University Distinguished Professor and Director, Division of Biology at Kansas State University, and his colleagues went on to study mammalian organ development and branching both in terrestrial culture and under conditions of microgravity in spaceflight (Lwigale et al., 2000). K.M. Yamada (M.D. Ph.D. Stanford, 1971, 1972) is one of the most widely cited authors in the United States, editor of *The Journal of Cell Biology*, and currently Chief of the Craniofacial Developmental Biology and Regeneration Branch at the NIH. Yamada is famous for his elegant work begun with Norm (Yamada and Wessells, 1971, 1973) on the interaction of the cytoskeleton with the extracellular matrix (Sakai et al., 2003). His interests are presently focused on determining the structural basis and functional consequences of the interaction of fibronectin domains with different integrin receptors, through both cell and molecular biological approaches involving structural and functional analyses. Another graduate student of Norm's, Kathryn Tosney, has, in iconoclastic fashion, unraveled the mechanics of veil and microspike formation in the growth cone (Stekete et al., 2001; Stekete and Tosney, 2002). In Norm's lab, Tosney conducted her now classic study of neural crest migration (Tosney 1978, 1982; Tosney and Wessell, 1983). The exquisite scanning electron micrographs illustrating this work are found in just about every Developmental Biology text as well as on the walls of many laboratories world-wide the SDB website (Tosney, 1978).

Studies on the role of differential adhesivity in axon guidance were initiated in the Wessells lab in the early 1970s by Norm and Paul Letourneau, whose work on DRG neurons demonstrated the importance of differential adhesivity to the substrate in neurite guidance. Paul laid down grids of substrate materials for which neurites had differential affinities and took exciting time-lapse movies of DRG neurites' navigation through these mazes. He jokes that these were the first scientific PORN (polyornithine substrate) films ever made. Paul and his colleagues have produced a body of work focused on the molecular underpinnings of the dynamics of axon behavior (Gallo et al., 2002a,b; Gallo and Letourneau, 2002; Gehler et al., 2004). Norm's group also studied the directed outgrowth of particular neurons toward their end organs, especially in the seminal work of Michael Coughlin, who has since become a science ethicist at the University of Hamilton, Ontario, Canada and Bob Nuttall's work on axon initiation (Nuttall and Wessells, 1978, 1979).

Thus began an entire subfield of developmental neurobiology, the search for molecules that affect the adhesivity of neurite growth cones, both extracellularly and within the cell, which Letourneau and his colleagues carried on first with Wessells, then in his own lab at Stanford and subsequently at Minnesota in the ensuing years. Letourneau's group has recently demonstrated that the neurotrophin BDNF signals through the actin regulatory protein ADF/Cofilin to regulate filopodial dynamics (Gallo et al., 2002). Paul's take on his time in Norm's lab characterizes the experience of a great many of Norm's students and postdoctoral fellows: "We had the freedom to test our experimental ideas, and through the successes and failures, learn how to do science. Norm respected our ideas, and by acknowledging what was

worthwhile in (most of, some of) them, he stimulated our intellectual growth. His advice was always valuable, including such apposite aphorisms as "Life is too short," "Life is too long," and "Don't rock the boat until you have to." Norm's encouragement of our science and our progress through the academic, medical, or biotech ranks is unstinting and generous.

This may be both a reaction to and appreciation of his own outstanding doctoral mentor, J.P. Trinkaus of Yale, who was something of an *agent provocateur* and a notable eccentric intelligence among developmental biologists. Norm remained at Yale for his Ph.D. after receiving his B.S. magna cum laude in 1954. He completed his Ph.D. at Yale in the Trinkaus lab in 1960. Several of Norm's fellow students from the "Trink" lab went on to adopt Trinkaus' attitude in their own careers, forming a cadre of the "Peck's bad boys" of science, as well known for their stinging wit and ability to deflate a scientifically wobbly idea as for their competitive and excellent science, most notable among them, James A. Weston, who recently retired from the University of Oregon. Norm's wit is just as sharp, but is delivered with a humorous reflection of his real joy and engagement in other people's good ideas.

Trinkaus himself appreciated Norm's creativity and his enormous capacity for work. In his autobiography, he commented on Norm's career. Perry Karfunkel, who was a graduate student of Trinkaus' and a visiting scholar in Norm's lab, commented, "My impression is that Trinkaus thought of Norm as a younger brother, as well as a drinking companion, and clearly he took great pride in Norm's work as well as the other aspects of his career. My suspicion is that Norm also brought out Trinkaus' best characteristics, and I think Trinkaus knew that too. He always spoke of Norm with a certain awe, and he was greatly impressed by the stature that Norm had achieved both within his own department and within the university. Trinkaus' book describes himself as 'the bad boy' he was as a teenager, and that, to no small extent, he continued to take pleasure in being for the rest of his life."

Trinkaus said of Norm, "In all those 40 years in the Biology Department at Yale, before I became Emeritus in 1988, I had many students, postdoctoral, graduate, and undergraduate, a number of whom, to their credit and my joy and pride, did excellent research and went on to distinguished careers. Two of these students were among my earliest and my best, Norman Wessells and Richard Whittaker." Trinkaus goes on to say, "Norman Wessells graduated from Yale College. I first knew him as an outstanding student in Zoo 23, where he developed his interest in embryology. I also knew him as a resident of Branford College [of which Trinkaus was Master beginning in 1966]. After spending two years in the Navy, he returned to Yale to do his graduate work with me. He did a fine piece of work on the differentiation of chick embryo epidermal cells in situ and in chemically defined media, but his best research accomplishments came later at Stanford University where he was a postdoctoral fellow with Clifford Grobstein. There he was soon appointed to the faculty and built a distinguished career for himself. He trained some excellent graduate students, won a prize for excellence in undergraduate teaching, and ultimately became Dean of the Faculty of Humanities and Sciences. With his ever-blossoming research on branching morphogenesis in vertebrate glandular organs and his pioneering work on the role of microfilaments in invagination, he became recognized as a leading embryologist, and was elected President of the American Society for Developmental Biology. The last time I saw Norm was about 10 years ago at the banquet of a zebrafish meeting in Eugene, Oregon, where he was Provost of the University of Oregon. He, Bill Ballard, my old friend and an important role model for me, and I cornered a table behind the screen so that we wouldn't be disturbed by the after-dinner lecture. We had a pleasant, intimate dinner together, with all three of us ultimately becoming lightly and happily inebriated. Bill, though in his eighties, loved his *vin rouge* and Norm and I had always been drinking buddies."

As Steve Helfand, who began his own important work in the Wessells' lab as an undergraduate (Helford et al., 1976, 1978) and who later went on to obtain an MD, said: "the Sperry hypothesis of molecular factors guiding specific axonal connections was now articulated in a physical model. I believe Norm is responsible for having laid down the experimental and intellectual foundation for this overarching theme in developmental neuroscience" (Wessells et al., 1971, 1973, 1974, 1978, 1980). Helfand's work in Norm's lab began the search for and discovery of new "nerve" growth factors beyond NGF, which affected neuronal subtypes other than sensory neurons, including the motoneuron growth factor found in ciliary ganglion neurons ciliary neurotrophic factor (CNTF). CNTF also provided an important focus for Rae Nishi's science, from her undergraduate work in Norm's laboratory, to her doctoral studies of neurotrophic support and cell death in the ciliary ganglion in Darwin Berg's lab at UCSD (Nishi and Berg, 1979, 1981a,b), to studies in her own laboratory, first at OHSU and then at the University of Vermont, where she is Professor of Anatomy and Neurobiology (Lee et al., 2002; Nishi, 2003). Cloning and characterizing CNTF also formed the basis of a scientific "race" between Wessells lab alums Nishi and Frank Collins, who carried on this project in a biotech company setting after having completed his postdoc with Norm. Collins first went to academe after leaving the Wessells lab, then to a series of directorship positions in the industry from which he recently retired. Nishi's work later showed that neuronal cell death and renewal was a constant in ciliary ganglion, rather than occurring in a "wave" as Landmesser and Pilar's classic work (1974a,b) had initially established. Her studies and those of her colleagues identified postmitotic cell sources for neuronal replenishment within the ganglion (Lee et al., 2002).

THE WESSELLS LAB: A COLLECTION OF INDEPENDENT, MUTUALLY INTERACTIVE WORKS IN PROGRESS

Norm Wessells fused together a series of outstanding research groups that were always interactive but never rep-

licative, and sometimes not even directly collaborative. A group of a dozen students and postdocs studying different questions in a variety of model systems with different techniques made an eclectic but vibrant mix in the lab from the early 1970s to the late 1980s (e.g., Grauger et al., 1974; Sidman and Wessells, 1975; Akers et al., 1986). Joan Wrenn, a graduate student from the late 1960s spent much of her scientific career with Norm (Wrenn, 1971; Palmiter and Wrenn, 1971; Spooner et al., 1973; Spudich et al., 1988). Some, including Marilyn (Luduena) Anderson, passed through the lab more than once. Anderson contributed to the early seminal developmental studies of growth cone locomotion as a graduate student (Ludueña and Wessells, 1973) and then returned to the Wessells lab as a visiting scholar in the early 1980s. She then went on to productive studies of spinal cord regeneration with Waxman at the VA in Palo Alto (Anderson and Waxman, 1981,1983, 1985a,b; Anderson et al., 1984a,b, 1985, 1986, 1987; Waxman and Anderson, 1980, 1985) and continued this work in her own laboratory at Colorado State (Anderson, 1993). Her studies on a fish in which spinal cord regeneration was a recurring phenomenon (Anderson and Waxman, 1981, 1983) brought write-ups in the national press, including the *New York Times*.

Through cross-fertilization of ideas fed by endless hours of "shop" talk in the Wessells lab, each person's science was enhanced and honed. Among the many scientific and life lessons that he gave his group was that having such an eclectic mix of scientific problems to work on in one lab is not only possible, but preferable. Norm urged us to discuss and try out new approaches, and invited us to his house to carry on those discussions in a comfortable atmosphere with plenty of food and wine.

Richard Palmiter, who completed his Ph.D. in Norm's lab in 1968, is now a member of the National Academy and an HHMI investigator in the Biochemistry and Genome Sciences departments at the University of Washington. He and his colleagues use genetic techniques to disable neurotransmitter functions in transgenic mice to understand how and where such signaling molecules act in the brain to regulate specific behaviors (Cannon et al., 2004). His lab is also developing mouse models of Parkinson's disease. He began his work on hormonal regulation of tissue function in Norm's lab almost 40 years ago (Palmiter, 1969a–c; Palmiter and Wrenn, 1971) and then moved to Bob Schimke's laboratory at Stanford Medical School as a postdoc where he, Schimke, and colleagues did seminal studies of hormonal regulation of protein synthesis and polyribosome organization in an extraordinarily productive experimental sequence (e.g., Palmiter et al., 1970; Palmiter and Schimke, 1973).

At the "Normfest," Wessells' support of all of us and our science was a constant theme of each speaker. Frank Collins, one of Norm's former postdocs said, "I feel that Norm provided great intellectual freedom within a structured context with high standards and high expectations. This allowed Norm and his students and postdocs to make a number of important contributions beyond what might have been expected from Norm's training and personal interests alone." Two excellent examples of this were Steve Helfand's venture into neurotrophin terra incognita and Randy Johnston's work on neuron outgrowth through new acoustic microscopy techniques with Cal Quate of the Stanford School of Engineering and Norm in the early 1980s (Johnston and Wessells, 1980; Johnston et al., 1979). Norm also encouraged my work on developing new technical approaches to the then novel technique of producing monoclonal antibodies to identify surface markers for neural crest subpopulations and the embryonic neurons they became (Barald, 1982; Barald and Wessells, 1984).

Norm was an intellectual catalyst for an eclectic group of dedicated developmental biologists. Postdocs and visiting scientists who worked in his lab at Stanford and then went on to productive careers in their own laboratories frequently felt free to carry on more than one line of research in their own labs, in imitation of the fruitful mix we found in Wessells' lab. Although the "triple threat" of the professoriate (research, teaching, and service) is seldom realized by contemporary scientists who opt for one aspect of the career over the others, Norm managed to do them all contemporaneously and superbly. Undergraduate students were attracted to his lab by the articulate and synthesizing lectures he gave in his vertebrate and developmental biology courses. Graduate students and postdoctoral fellows were attracted to the Wessells lab by the creativity and quality of the scientific publications and by seminal monographs such as *Tissue Interactions and Development* (1977). This intellectual tour de force of a monograph changed the direction of many people's science and inspired a whole new generation of labs to study fundamental problems in development from a fresh perspective. I swallowed the book at one sitting and then I reread it immediately. It is beautifully reasoned and clearly written, but that doesn't even come close to explaining its power. I wanted to work with the person whose multifaceted synthesizing intelligence enabled him to convey such complex ideas so effortlessly. Many of us have urged Norm to recast that book for a new generation of scientists.

NORM WESSELLS AS MASTER TEACHER

Even as Norm served as the Biology Department chair and then Letters & Sciences Dean at Stanford and throughout his subsequent administrative career at the University of Oregon, he remained devoted to teaching undergraduate classes, at which he was unequalled. Norm's lectures were famous. Several of us took his development course at Stanford more than once. It was different and current each time. Norm could be found in the darkroom early before each 8 AM class making Polaroid slides of material in papers he'd read the night before. By class time, that material was seamlessly integrated into a lecture that kept 200-plus undergraduates awake and interested and most of us on the edge of our seats. No one but Norm is that good a teacher, except perhaps for Ellen Porzig, now Associate Professor (Teaching) in the Stanford Dev. Biol Dept. who also serves as Associate Dean for Graduate Educa-

tion at Stanford Medical School. Ellen remained at Stanford to teach many of the courses Norm had taught, proving by her receipt of the Gores Prize, Stanford's highest accolade for teaching in 1989, that she had learned a trick or two from Norm, himself the winner of the Gores Prize in 1974.

Perry Karfunkel said, "I realized during our time at Stanford last summer that it never occurred to me to explicitly ask Norm, way back thirty years ago, how he actually planned his teaching. It was just assumed in those days that one knew how to teach (or didn't. . .) but the notion that it consisted of learnable skills (beyond the "Elementary Teaching" programs) was beyond us. Only in the last 10 years has Yale had a formal program to train prospective college professors from among its own graduate students; I don't know if Stanford has that to this day."

WESSELLS AS ADMINISTRATOR

At Stanford, Norm served as Department Chair, Associate Dean, and subsequently as Dean of Humanities and Sciences. Wessells was a John Simon Guggenheim Fellow in 1975–1976. Norm was also President of the Society for Developmental Biology, 1978–1979.

Norm's calm and reasoned approach to the issues, some of them inflammatory, that arose at Stanford when he was Dean served as a great example for many of his students and postdocs. Several later took on administrative work as department chairs, program directors, and deans, as well as many Norm lab alums who went on to direct large labs in biotech companies and to serve as highly creative and effective CEOs (Randall Johnston, Matthew Bradley, and Frank Collins among them). Norm demonstrated that keeping one's sense of humor and balance when the process of doing science or academic administration provided obstacles was as important as the intellectual energy and common sense invested in solving the problem.

Norm's ability to treat everyone from undergraduates to senior visiting scientists as colleagues and sources of interesting scientific thought was reflected in the University of Oregon's diversity policies that he crafted with Davison Soper in 1994. An excerpt from that report said, "There is campus-wide agreement that an important goal of liberal education is increased appreciation for unusual ideas, and tolerance of unfamiliar human behavior. This is not a new goal, but the tolerance aspect of it has gained particular urgency because of the increasing cultural diversity of everyday American life.We encourage all members of the University to be accepting of diversity in all areas of our lives together, to be tolerant of differences in race, ethnicity, gender, sexuality, and physical ability, and respectful of variations in political views, religious beliefs, and life styles. The academy cannot prosper and grow without tolerance for the entire range of intellectual approaches and commitment to freedom of expression" (Report authors: Norman K. Wessells and Davison Soper).

NORM AS MENTOR

Over and over again, speakers at the "Normfest" commented on Norm's generous support, his influence on our careers, and his ability to serve as the ideal mentor. As much as his scientific ideas and his facility to express tough concepts in elegant but simple language, his ability to serve as example, teacher, and mentor and his enormous integrity and modesty were recurring themes of his colleagues, his students, and the administrative staff who had worked with him at Stanford and the University of Oregon. He wrote us handwritten letters (not e-mails) of encouragement and congratulations at times of important scientific milestones in our careers and our personal lives and he was famous for his prescient, enthusiastic, and highly personalized letters of recommendation.

When Victor Twitty died, Norm wrote an appreciation of his career (Wessells, 1998). He said "Perhaps Twitty's greatest strength as an investigator lay in an exceptional ability to cut through the complications of a problem or observation and to frame scientific questions in simple terms, which led to straightforward experiments with a minimum of variables and a maximum of interpretable results." It strikes those of us who were lucky enough to have Norm as a mentor that this is exactly his gift, and that although he said it more elegantly of Twitty than we can of him, it is an excellent synopsis of Wessell's own life in science.

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