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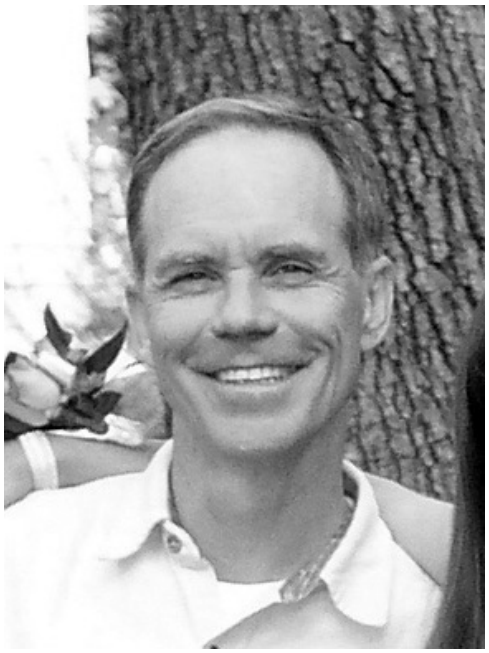
IN MEMORIAM

Grant Wood Balkema



July 1, 1951–November 24, 2004

One clear, crisp November day, Grant returned to the lab after attending a high school sports event with his family. An hour later an arrhythmia stopped his heart. Those who knew Grant knew of his devotion to his family, his science, and soccer. Few of us knew how many lives he touched until over 1200 people gathered in the early afternoon of November 29, 2004 to remember their husband, father, brother, nephew, friend, colleague, coach, and mentor.

Grant was a true son of Grand Rapids, Michigan; his father was a banker and his uncle an optometrist—both were important models that instilled the young Grant with an ethic for hard work and thrift. It is not clear whether it was his love of things electrical or thrift that drove an early experiment in communications. Grant's close friend, Paul Lombroso of Yale University recounted this story: "When [Grant] was 13 years old, he decided his neighborhood needed some improved services. He went out and wired all the surrounding houses into one communal party phone system. Worked like a charm. . .until it rained one day. The entire phone service in the neighborhood went out. The service men who arrived on the scene followed the wires back to Grant's house . . . and they took him downtown. No . . . not to the police station, but to the phone company to show him how the phone system really worked. And then told the budding scientist to come back and work for them when he finished school [that summer]."

Grant traveled from Grand Rapids to West Lafayette, IN where he matriculated at Purdue University; first as a Physics major and then completing a Biology degree. At Purdue, Grant developed a lifelong interest in Physiology—which would become the hallmark of his career. He enrolled in Purdue's graduate Physiology program and joined the laboratory of Larry Pinto, which had embarked on a genetic dissection of the mouse visual system by using naturally occurring mutants from the Jackson Laboratory. Together with Ursula Dräger, they showed that the response properties of neurons in the superior colliculus and visual cortex in the mutant *pearl*, were radically altered—a great deal more stimulus luminance was required to evoke responses than from wild-type mice.

Realizing that recordings from retinal ganglion cells were needed to define the mechanism, Grant developed the first method for recording from mouse ganglion cells. This was a challenging task, there were no reports of mouse ganglion cell properties, no assured method for maintaining the mammalian retina *in vitro*, and no sterotaxic atlases! Undaunted, Grant developed the technically challenging route of recording from the mouse optic nerve. He used the preparation to characterize the receptive-field properties of mouse retinal ganglion cells, demonstrated spectral shifts in their action spectra, confirming the contemporaneous discovery of cones in the mouse retina by Carter-Dawson and LaVail. Moreover, he demonstrated that the visual defect in *pearl* mutants lie within the retina, the sensitivity of the ganglion cells was abnormal. In some respects, this work was 15 to 20 years ahead of its time, as Grant and his co-workers proved for the first time the power of mouse genetics in dissecting the retina, and the importance of rigorous physiological testing of phenotypes.

In a landmark *Science* paper, Grant, Nancy Mangini, and Larry Pinto demonstrated a year or so later that the response properties of ganglion cells recorded in the isolated, wild-type mouse retina accurately reflect the properties recorded from the intact animal; in contrast, isolation and superfusion of the retina restored visual sensitivity in the *pearl* mutant retinas, apparently correcting the genetic defect. Together, they extended their screening to show that other hypopigmented mutants had similar visual sensitivity defects. The mechanism of these hypopigmentation defects occupied him, in part, for the rest of his career.

After completing his graduate work, Grant sought training in anatomical methods to compliment his training as a physiologist. He left Purdue to do postdoctoral work with Ann Milam at the University of Washington in Seattle; there he developed a solid

foundation and interest in the photoreceptor. In Seattle, Grant also met the woman he married—Marilee Ogren.

For a second *post-doc*, Grant returned to work with Ursula Dräger, this time at Harvard University. Together, they developed an impressive panel of reagents; the first of these were a series of antibodies that recognized functionally different states of the visual pigment. In a startling cover article in *Nature*—Grant and Ursula identified light-activated photoreceptors with an antibody to phosphorylated rhodopsin. Grant and Ursula lit up the retina, and that year's ARVO meeting with the words FIAT LUX "etched" into photoreceptors. The same screen produced the first antibody that selectively labeled the unique specialization in the photoreceptor terminal, the ribbon. This "B16" antibody led to a series of papers on the development of the ribbon and presaged the era of bassoon, ribeye, and other ribbon-associated proteins.

After his success at Harvard, Grant took his first faculty position at Boston College (BC). He was tenured in a startlingly fast four years! The twin interests: synaptic structure and the mechanism of hypopigmentation defects led to a series of papers: Grant identified the source of ganglion cells that give rise to the ispilateral projection in the mouse, their aberrant routing in hypopigmented mice; the developmental sequence of ribbon formation. He published 18 papers from his own laboratory and several others will be published posthumously; including one with his eldest daughter, Natalie. Grant's largest NSF award in his career arrived just months before his death. His current work, on photoreceptor genesis and protection, is among his best work ever.

Research was not the sole product of Grant's activity at BC; teaching and mentoring students was equally important to him. He mentored countless students both in the laboratory and the classroom, training a large number of both graduate and undergraduate researchers. His BC faculty colleague Tony Annunziato said: "Grant worked unceasingly to make the Biology Department a better place for research and instruction, though many of his contributions were made behind the scenes. . . . He labored tirelessly as Chair of the Graduate Admissions Committee to attract and retain the best possible student applicants. He worked hard to obtain NSF funding for Biology's *Davis Laboratory of Computational Biology*. . . . Virtually single-handedly, Grant established two sections of a remarkable, hands-on Physiology lab for undergraduates, which he himself taught. . . . But perhaps his most lasting contribution to our Department and to this University lay in his Herculean efforts in the area of Information Technology." Grant helped to modernize BC's computer infrastructure; bringing in NSF funds to support high-speed internet access in the early-1990s, followed by a high-speed wireless network less than ten years later. Was this what he had in mind when he rewired the phone system in his hometown at age 13?

Shortly after Sanford Palay retired from Harvard Medical School, Grant and Marilee collaborated in bringing Sandy to BC as emeritus professor of Biology. There, Sandy was an invaluable mentor for Grant and all the other neuroscience faculty but importantly, Grant and Sandy developed a History of Neuroscience course together. In the later years, as Sandy's health failed—knowing both how important the students were to Sandy and Sandy to the students—Grant regularly drove a group of BC graduate and undergraduate students to Sandy's home in Concord so Sandy could continue to teach. This practice continued until the semester before Sandy died in 2002.

Boston College encourages its faculty to become involved in the larger community. At this task, Grant excelled. Many of his scientific colleagues knew of Grant's interest in soccer and his many years of coaching, but not the extent of it, nor that he was an accomplished soccer referee, until Paul Levy, the President of Beth Israel Deaconess Medical Center, spoke at his memorial. Levy, fighting back his emotions, spoke of Grant's devotion to Newton Girls Soccer and said of Grant as he was walking off a soccer field after having refereed a game: "He is *always* smiling. He *loved* to referee. He never took himself too seriously, and he always did what he could to help make the game fun . . . he understood that the *best* game was the one in which people *forgot* that there was a referee on the field." Paul Levy also spoke of a high point in Grant's coaching career, when exuberance and pride in his players overtook him: "Lo and behold, [with Grant coaching] this underdog team of high school girls made their way to the State Championship, where they came in second place. . . . At the awards ceremony, a passer-by watching Grant hand out the awards to the girls [would have thought] . . . Newton had *won* the tournament. . .". In recognition of the contributions to the soccer community, Newton Girls Soccer has endowed a scholarship in his name for a youth referee. The first winner of that Scholarship is Grant's second daughter, Julia.

Hard work was not all that drove Grant, he enjoyed to tinker and to play. His laboratory was filled with contraptions of all types (many from his own hand as there was nothing he could not do with a muffin fan). His students all speak of the many mischievous games Grant would play on them and his fellow colleagues. A recent addition to his play was a radio controlled light-air balloon; this he navigated around the newly renovated five storey atrium of the Biology Building—to the amusement of his students but most especially his eight-year-old son, who inherits Grant's name as well as his inventiveness.

In summary, we borrow again from Paul Lombroso: "[Grant] was a natural scientist imbued with those qualities that make a good scientist: curiosity about how things worked and an innate sense that there was nothing he couldn't do." Grant's greatest joy, mentoring, shone bright in his smile, that enigmatic and joyful simile that signaled the everlasting boy in him. As Annunziato said: "his wit brightened our lives, and his intelligence illuminated our science—Fiat Lux, indeed."

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