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2015 Distinguished Career Award: Reflections on a Career in Science

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Abstract

I was very pleased to receive the 2015 Distinguished Career Award from SSIB. This brief manuscript contains reminiscences that might stir up pleasant memories in the older members of SSIB and also some general thoughts that I hope will be of value to the younger investigators who are closer to the beginning of their scientific careers. Although the organization has chosen to honor me with this special award, my own career was shaped by a great many people who have influenced my scientific career and I want to acknowledge them. They include Neal Miller, my doctoral mentor at Yale; Joe Holmes and Alan Epstein, my postdoctoral mentors; George Wolf and Reed Hainsworth, graduate student colleagues; John Brobeck, Paul Rozin, and Phil Teitelbaum, Michael Zigmond, Joe Verbalis, Jim Smith, and Alan Sved, faculty colleagues; Derek Denton, Paul McHugh, and James Fitzsimons, scientific role models; John Bruno, Steve Fluharty, and Linda Rinaman, post-doctoral trainees at Pitt; and Lori Flanagan, Kath Curtis, Michael Bushey, Mike Bykowski, Reza Manesh, Carrie Smith, Jennifer Vaughan, and Myriam Stricker, student trainees at Pitt. I thank them all and also my colleagues in SSIB not only for the honor of this award but for providing an abundant supply of insights and discoveries that have stimulated me throughout my adult life, in addition to being an attentive community in supporting my own work.

Keywords

SSIB; career; food and fluid ingestion

I was very pleased to receive the 2015 Distinguished Career Award from SSIB. I want to thank the committee and its members for selecting me for this honor.

I spent a good many hours in my adult life paying attention to issues of relevance to the brain's control of ingestive behavior. I closed my research lab 7 years ago, and receiving this award and preparing my acceptance talk and this manuscript motivated me to reflect on my career in a way that I had not done recently. In doing so, I had several insights that I wanted to share with the seated audience then and with the reading audience now. This brief manuscript resembles the talk I presented at the SSIB meeting in Denver on 11 July 2015, containing reminiscences that might stir up pleasant memories in the older members of the

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group and also some general thoughts that I hope will be of value to the younger investigators who are closer to the beginning of their scientific careers.

My first such thought is that although the organization has chosen to honor me with this special award, my own career was shaped by a great many people who have influenced my work and I want to acknowledge them. The principle is, *credit should be given where credit is due, and they deserve a lot of credit for what I have done*. Thus, I want to mention who these people are and what I learned from them. The first person I want to acknowledge is my doctoral mentor at Yale, **Neal Miller**. I went to Yale in 1961 to pursue a doctorate in Chemistry, the subject I had studied as an undergraduate student at the University of Chicago. However, at Yale I soon realized that I did not want to have a career in Chemistry so I switched my focus to Psychology. I naively picked Psychology because my older brother had focused his attention on the subject and seemed to enjoy it, which led me to believe that I might enjoy it too. I had to submit a late application for admission into the Department, which I did, and I was accepted even though I had never taken a course in the subject. That's the basis of my second thought. A scientific career can be a long and twisting road, and many academics like to plan and control things every step of the way. I'm one of those people. *Yet some of the most important developments in a career sometime happen less by good planning than by good fortune*. Luckily for me at the time, an incoming graduate student had recently withdrawn from the Psychology Department and thus created an open fellowship; in addition, perhaps my background in Chemistry interested Dr. Miller, whose own work then included studies of chemical brain stimulation. In any case, I had the good fortune to be accepted by the Department, given that scholarship, and invited to join the lab of one of the most prominent psychologists of the 20th century.

I learned a tremendous amount in Dr. Miller's lab, which was especially important since I knew almost nothing when I began. I most recall learning four specific things, for which I have always been grateful. First, Dr. Miller seemed always to be focused on some work-related issue or another rather than engaged in something of casual interest. I had never met anyone like that, and I very much admired his work ethic and adopted it as best I could. Second, he had filled his lab with an unusual assortment of trainees, each pursuing something of great interest to them; it was not always apparent to me that their research was of great interest to Dr. Miller but it was always apparent that the trainee was of great interest to him. I found that element of research training to be admirable, as well. Third, Dr. Miller was wonderfully able to communicate basic elements of experimental design, such as having an adequate number of subjects in each study and the need for control groups. I learned from him these essential features of scientific investigations. Fourth, after a trainee's presentation we always anticipated his question about the significance of our work. His attitude was that *each research project should be worth the time, effort, and resources that were invested in it*. I agreed with that perspective and adopted it as well. In fact, former trainees of mine will recognize that Dr. Miller's question later morphed into the "So what?" question I asked after presentations throughout my own career.

My doctoral thesis concerned the apparent stimulus for thirst caused by a drop in blood volume [1]. Because thirst and vasopressin serve complementary roles in achieving water balance, and hypovolemia already was known to stimulate vasopressin secretion, I guessed

that the same signal might also stimulate thirst, which turned out to be true. Those findings held little or no interest to Dr. Miller but they were of great interest to members of what would become the SSIB community. The success of that research project taught me many useful things. For example, I learned that *an argument by analogy together with the principle of parsimony provide useful insights into organismal function*. I also learned that body fluid homeostasis was the most interesting subject I had ever encountered and was what I wanted to study in the future. Inasmuch as homeostasis was achieved by behavioral and physiological actions, and I did not know enough about either subject, I concluded that I needed postdoctoral training. Such training was not as commonplace then as it is now. I selected for my postdoctoral mentor **Joe Holmes**, who was located in the University of Colorado Medical Center in Denver. Dr. Holmes had been a well-known contributor to the scientific literature on thirst and was a former student of Magnus Gregersen, another prominent scientist who had been perhaps the most successful student of Walter Cannon, who was one of the godfathers of homeostasis. Impressed as much by his pedigree as by his published work, I asked Dr. Holmes if he would accept me as a trainee and he agreed. In retrospect, his decision may have been more an act of kindness than a result of an interest in my work because, unknown to me at the time, he had switched the focus of his research to a different subject. Be that as it may, 50 years ago (i.e., in July 1965) I first came to Denver and joined his lab. I was surprised to discover that no one there was interested in the biological bases of thirst, and in fact my conversations about thirst with Dr. Holmes were very brief and infrequent. Although I was largely left alone, I spent a very productive year in Denver. Each day, virtually 7 days a week, I would go into the lab at 8:30 a.m., inject animals, and from 9 a.m. to 5 p.m. I went to the medical library and read all the articles I could find on body fluid homeostasis. I then returned to the lab, spent an hour collecting data on drinking behavior, and went home. I can tell you that a great many research articles can be read when you spend 8 hours a day doing so for 350+ days.

I believe that if you really want to make progress in a field of research you have to know everything that preceded your work – all the experiments, all the data, and all the ideas. It's a never-ending task, of course, but there is no satisfactory alternative to reading the scientific literature thoroughly. After all, many good people have invested considerable time and thought over the years to the same problems that I wanted to understand, and if ultimately I was going to gain further insight into those issues I recognized that I had to see their published data and read everything they wrote.

At the end of the year in Denver, I felt (mistakenly) that I had read everything that had been published on fluid homeostasis and I wanted to refine my ideas by participating in an academic community of scientists who were interested in ingestive behavior. Therefore, I applied to do a second postdoctoral stint, with **Alan Epstein** at the University of Pennsylvania, who accepted me into his lab. Alan was one of the most prominent scientists in the field of ingestive behaviors and he was my first mentor who seemed to have an interest in my work. Although we disagreed on many issues concerning how the brain worked to control water and food intake, I learned a tremendous amount during the year I spent at Penn from him and from his faculty colleagues there. One of those colleagues was **John Brobeck**, the chair of the Physiology Department, who allowed me to attend the

medical course in physiology and supervise students in the associated laboratory. I recall that I once asked him to sponsor a manuscript for publication in the journal, Proceedings of the Society for Experimental Biology and Medicine, because he was a member of that society and sponsorship by a member was necessary. The manuscript I gave him was covered in red ink when it was returned to me. I thought I had written it well but I learned that there was considerable room for improvement. I apologized for asking John to do so much work but he graciously said that the paper was worth it. It was published later that year [2] but more importantly I learned another lesson: *contrary to popular opinion, data do not speak for themselves. They have to be communicated in well-written manuscripts that are clear and succinct, and hard work is needed to prepare such articles. Put another way, I learned that much more time is spent editing a manuscript than writing an initial draft of it.*

Another significant role model for me at Penn was **Paul Rozin**, then a young assistant professor in the Psychology Department. Coincidentally Paul had been a good friend of my older brother when the two were at college together, and he has been a valued friend to me for almost 50 years. By now he is well-known for his work on human food intake and his ability to think creatively in designing and interpreting his experiments, but I think that the lesson I learned best all those years ago (and since) has been his concern about *the need to teach well in addition to doing research well*. Not surprisingly, Paul has been a legendary teacher at Penn. His concern about teaching resonated with me and led to my conviction that I too would devote my academic career not just to being a scientist but more generally to being an educator, both in the classroom and in the laboratory.

A fourth role model for me at Penn was **Phil Teitelbaum**, already a distinguished professor of Psychology. Phil became another good friend and mentor. He grew particularly interested in my work when it later involved the syndrome of behavioral dysfunctions that resulted from lateral hypothalamic damage (see below). For years we had productive and collegial discussions about whether the syndrome was best analyzed by studying behavior more precisely and thereby having a better basis for inferring the underlying brain function (his view), or whether it was best to study the brain directly (my view). It took us 20 years to realize that these two approaches were complementary, and that his way best suited him and my way best suited me. Ultimately, we co-authored an article making this general point [3], which did not represent a compromise but an overdue recognition that *a full study of ingestive behavior required multidisciplinary approaches and perspectives*. It is wonderful for me to see how this broad and inclusive view now characterizes research in the field and seems to be taken for granted.

I knew much less well several other first-rate investigators at Penn, such as Eliot Stellar, Vince Dethier, and Dick Solomon, but there was one other person there who had a great influence on my scientific development: **Reed Hainsworth**, a doctoral student in Alan Epstein's lab whose thesis work focused on temperature regulation by rats in the heat. Reed introduced me to thermal homeostasis, a phenomenon that I found to be just as interesting as body fluid homeostasis; thus, I recognized that it was homeostasis generally, rather than body fluid homeostasis specifically, that most excited me. Reed was a great scientific colleague to me, providing encouragement and support in addition to insight and perspective -- just as **George Wolf** had done when we were graduate students together at Yale [4] -- and

our interaction led to many research findings that I still consider to be among my best work [5]. It also presaged my scientific collaborations with a series of wonderful colleagues who taught me much about their fields of expertise while providing companionship and support over the years.

One such colleague was **Michael Zigmond**, with whom I worked closely for almost 20 years. His training and expertise was in neuropharmacology, and he was the person who explained to me what Urban Ungerstedt had said when presenting his work at a conference in 1971 regarding the dopamine-depleting effects of lateral hypothalamic (LH) lesions. The following year, Michael and I took our families to Cape Cod for a summer vacation, during which we actually spent 6 hours a day for a month tutoring each other on what we knew best. That is, Michael taught me catecholamine neurochemistry, with an emphasis on brain neurons and the sympathetic nervous system, and I taught him about the LH syndrome: the initial aphagia and adipsia that occurred after LH lesions, the gradual recovery of function despite permanent brain damage, and the residual functional deficits that had suggested loss of specific controls of food and fluid intake. We accomplished a great deal that summer, including the development of a model of synaptic homeostasis that could account for all of the remarkable features of the LH syndrome [6]. We then spent the next 15-plus years testing our model and discovering that almost all of its predicted elements were supported by experimental evidence [7]. Perhaps most striking was the finding that the apparent specific deficits in recovered laterals actually reflected an impaired ability of the brain-damaged rats to respond well to the nonspecific (i.e., stressful) feature of the behavioral tests [8–10].

A second long-time colleague at the University of Pittsburgh was **Joe Verbalis**, an academic physician whose interest and expertise focused on the posterior lobe of the pituitary gland and its secretion of the hormones vasopressin and oxytocin. I had known a lot about vasopressin but Joe knew more, and I had never considered oxytocin other than in the context of lactation and parturition. Among the many things we discovered, perhaps most striking was the inhibition of vasopressin secretion by osmotic dilution during hypovolemia [11], which complemented the inhibition of thirst under the same circumstances [12], and the critical role of oxytocin acting as a neurotransmitter in the brain in inhibiting the intake by rats of solutes, whether in food or saline solution [13–15].

Another close colleague at Pitt and my successor as department chair was **Alan Sved**, a terrific scientist whose expertise was the brain's control of the cardiovascular system – another subject in which I had known a lot but my colleague knew more. Perhaps our most striking finding was that thirst and salt appetite in hypovolemic rats were not disrupted by lesions of the nucleus tractus solitarius in the brainstem [16], which is the projection site of cardiovascular baroreceptors and therefore suggested an important role of angiotensin in mediating the drinking behaviors in the absence of a neural stimulus [17]. Another finding of significance was that arterial baroreceptors did not provide a neural stimulus of thirst during arterial hypotension [18] whereas they did provide a neural stimulus inhibiting thirst during acute arterial hypertension [19, 20]. Yet another intriguing finding was the pronounced and prolonged slowing of heart rate that followed the expected tachycardia in rats with severe hypovolemia in the absence of arterial hypotension. We interpreted these latter results to be an adaptive response to the very viscous blood that remained after 40%

loss of protein-free blood plasma. The underlying mechanism appears to be increased parasympathetic neural activity because the induced bradycardia was blocked by systemic atropine. I mention this study not only because its findings are so interesting but also because it was the last completed scientific project that I was involved in, and I still feel guilty that it was never written up and submitted for publication. I strongly believe that *accepting federal funds to support research creates an obligation by scientists to report to the public all notable and worthwhile findings*. I published close to 300 scientific articles, reviews, and book chapters during my professional career but not this work, at least not yet (although we did report those results at previous scientific meetings [21]).

Another wonderful colleague, though not at Pitt, was **Jim Smith**. Jim is a known expert on gustatory systems but his major contribution to my education came when he introduced me to bout analysis of drinking behavior. I had been pleased with the insights provided by measuring fluid ingestion every hour after treatment rather than simply taking measurements 24 hours later [22], but Jim was able to measure drinking every 6 seconds. Among our most interesting findings was the observation that hypovolemic rats mixed a solution of isotonic saline within a drinking bout rather than in a sequential series of widely spaced and alternating drinking episodes [23], as I had thought. Because the adaptive drinking responses occur much too rapidly for feedback from postgastric or postabsorptive receptors to influence behavior, we concluded that taste likely provides a key sensory input.

I also have learned much from others who I have not yet mentioned. From **Paul McHugh**, for example, a brilliant scientist and clinician in addition to being a great leader as chairman of his department. I had seen other colleagues achieve excellence simultaneously in teaching and research, or in research and clinical work, despite the substantial demands of both pursuits, so I knew that such success was obtainable, but Paul was a role model for including administrative leadership as a third pursuit. Another role model was **Derek Denton**, who was a leading figure in studies of sodium homeostasis – both the stimulation of aldosterone secretion in sheep and the associated stimulation of salt appetite. Those investigations captured the perspective I wanted to bring to my work. In addition, I want to express my gratitude to **James Fitzsimons**, whose careful work on thirst in response to fluid volume depletion and to angiotensin stimulated my own interest in these phenomena for 40-plus years. I have often said that *scientists stand on the shoulders of those who had studied the same issues previously*, and in that regard I have been particularly grateful to James for his pioneering work.

I also want to acknowledge **Steve Woods**, perhaps my closest scientific colleague over the years. Although we never did research together, we shared ideas about a great many things regarding the contributions of ingestive behaviors to homeostasis (captured in a co-authored book chapter [24] and a co-edited Handbook on the subject [25]), as well as life as an academic scientist, teacher, and administrator, and life generally. In addition, I want to mention **John Bruno**, **Steve Fluharty**, and **Linda Rinaman**, three valued scientific colleagues who did postdoctoral training at Pitt [26–28] and whose own careers in research, teaching, and academic administration have been wonderful to follow. Finally, I want to acknowledge my many trainees in the laboratory, who provided the opportunity for me to pass on to others the many valuable lessons I had learned over the years, always a great

satisfaction, while teaching me much that was valuable in return. In particular, **Mark Friedman**, who first introduced me to the physiology of caloric homeostasis and its links to the control of food intake [29]; **Lori Flanagan** and **Kath Curtis**, my last two doctoral students, who did outstanding work in my lab [30, 31] and, more importantly, as academic scientists continue to inspire the next generation of educators (such as Derek Daniels); and the many Master's and undergraduate students who were the main focus of my attention in the laboratory during the six years after I stepped down as department chair and before I closed my research lab, including **Michael Bushey**, **Mike Bykowski**, **Reza Manesh**, **Carrie Smith**, and **Jennifer Vaughan** [32–35], all of whom have completed their medical training by now and have begun careers as physicians and scientists and/or educators, and **Myriam Stricker**, my wife, whose past excellence in the research laboratory [36–38] fully complements her present excellence as First Lady of the Honors College.

In conclusion, I want to thank again my colleagues in SSIB not only for the honor of this award but for providing an abundant supply of insights and discoveries that have stimulated me throughout my adult life, in addition to being an attentive community in supporting my own work. I am mindful of the fact that there are 7.5 billion people in the world and most of them have little interest in the biological bases of food and fluid intake, so I am very grateful for an organization that gathers the few hundred people who have deep interests in these subjects and encourages them to interact productively and collegially in these annual conferences and elsewhere.

Acknowledgments

This brief article does not provide a comprehensive list of all the people who influenced my scientific career and whose collegueship I valued. I apologize for upsetting anyone whose name was omitted.

I also want to acknowledge my gratitude to the federal agencies in Canada (NRC, MRC) and the U.S. (NIMH) that supported my laboratory research continuously for 44 years. In addition, I want to thank the University of Pittsburgh for its general support over the years; for providing me with a series of very stimulating administrative opportunities as Director of the Psychobiology Program (1983–1986), Founding Chair of the Department of Neuroscience (1986–2002), and Dean of the University Honors College (2011 – present); and for attracting a large number of faculty members and students who have been such wonderful colleagues.

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Highlights

- Some developments in a career happen less by good planning than by good fortune.
- Research projects should be worth the time, effort, and resources invested in it.
- To make progress in research you have to know everything that preceded your work.
- Study of ingestive behavior requires multidisciplinary approaches and perspectives.