

Homer Wheelon, M.D., Gastrointestinal Physiologist and Artist:

Origins of the Decorative Tailpieces

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ABSTRACT

The attractive drawings used as tailpieces at the ends of articles in *The American Journal of Physiology* and *The Journal of Applied Physiology* since the 1950s come from an illustrated poem, "Rabbit No. 202." The artist and poet, Charles Homer Wheelon, M.D., conducted meritorious research in gastrointestinal physiology and became a respected internist. This is the story of how he became a physiologist, how and why he combined his interests and talents in this poem, and how his drawings came to be used in those journals.

PROLOGUE

The tailpieces that adorn the papers in *The American Journal of Physiology* and *The Journal of Applied Physiology* have attracted the attention of most physiologists at one time or another (Fig. 1).



Fig. 1. Animals, Conduits, for the Passage of Food, from Homer Wheelon's epic poem, *Rabbit No. 202*. The poem was both written and illustrated by Wheelon, the illustrations being drawn in pen-and-ink in the style of woodcuts. The American Physiological Society later adopted many of the illustrations (including this one) as the tailpieces that follow articles in *The American Journal of Physiology* and *The Journal of Applied Physiology*.

In 1983, a casual inquiry into the source of these drawings suggested that their origin might be uncommonly interesting. The artist, Homer Wheelon, was a physiologist and, later, an internist. The path to his admirable physiological and artistic accomplishments was neither easy nor straightforward. This paper describes that path, through the artist's struggles to choose a career, his erratic education, his success as a practicing physiologist and internist, and the culmination of his scientific, cultural, and artistic interests in his creation of the illustrations that served as the impetus for our research.

On Saturday, April 15, 1933, Homer Wheelon, M.D., entered the laboratory of his colleague, Dr. John Lingenfelter, a young reproductive endocrinologist and obstetrician.¹ Lingenfelter was conducting a Friedman test² to determine whether one of his patients was, in fact, pregnant. The ovaries of a virgin, female rabbit, which had previously been injected with the patient's urine, lay dissected on Lingenfelter's bench. Lingenfelter searched the ovaries for corpora hemorrhagica, an almost certain indication that the rabbit had ovulated in response to hormones (at that time, unidentified) in the pregnant patient's urine.

Wheelon was an internist and a physiologist. Early in his career, he had decided that cultural endeavors, especially art, would be an important part of his life, whatever other profession he chose. To this erudite man, Lingenfelter's test was a revelation. Here was a rabbit—not only one of our meekest animals, but also a symbol of fecundity, a symbol of the rebirth of spring, a symbol of Easter—being used to test for pregnancy in a human. Nearly every spare minute of the next seven years was consumed in the writing and illustrating of a 322-page poem, *Rabbit No. 202*. All that remains of this enormous endeavor and of this unusual man, for most of us, are the haunting pen-and-ink illustrations, reduced to postage-stamp size, in *The American Journal of Physiology* and *The Journal of Applied Physiology*.

IMPOVERISHED AND ROOTLESS CHILDHOOD

George Washington Wheelon and Minerva Clark Wheelon, impoverished Free Methodist preachers, had their second son, Charles Homer Wheelon, on June 29, 1888, in Santa Clara, California.³ When “Homer”, as he was known throughout his life,⁴ was five years old, his parents moved to Salt Lake City, Utah, in an abortive attempt to establish a congregation. Over the next ten years, the family endured hardship, life-threatening accidents, and privation. Worshippers brought fruit and vegetables for the collection basket, but the preachers' family often went hungry as they moved from one cramped, dirt-floored adobe house to another. The family took their ministry from Salt Lake City to Ogden, Utah, and on to Shelburn, Oregon, in search of more secure means of support.

Perhaps the foundations for Homer's interests in biology and medicine were laid in Shelburn, for it was there that he carefully penned his name in *The human body and its health*,⁵ a relatively sophisticated textbook of anatomy and physiology for grade school. Homer's mother had attended the Iowa State Normal School, where she developed a love of (and minor talent for) poetry. Disappointed with her children's education,⁶ Mrs. Wheelon insisted on moving to Seattle, Washington. She wanted her children to be educated in the academic and spiritual environment of a Methodist school, the Seattle Seminary.⁷

When Wheelon entered the Seattle Seminary in the eighth grade, he was one to two years older, and probably much more experienced, than most of his peers. He earned good grades in his college preparatory curriculum. He was particularly active in the debating club, and its members were his closest friends.

As a teenager, Wheelon developed a consuming fixation on an artistic career. Camp meetings, sometimes conducted by his parents, became opportunities to caricature his fellow "worshippers." Family outings became sketching or painting opportunities. Wheelon became an avid and skillful photographer, experimenting with films and processing techniques. However, his enthusiasm for art provoked disputes between him and his strict ministerial parents. To them, the life of the artist seemed full of disorder, temptation, and danger. Wheelon's mother was apprehensive that her son's training as an artist might require that he draw nudes.

By the fall of 1905, dissension over his career had reached such proportions that it seemed best for Wheelon to spend his junior year visiting relatives in Palo Alto, California.⁸ Wheelon later said that his principal reason for this sojourn was to study art.⁹ Indeed, he was artistically active that year, producing a number of studies in pencil, pen-and-ink, and watercolor.

Upon his return to the Seattle Seminary, Wheelon continued his strong academic performance, and he was chosen to give one of four senior orations at his commencement in 1907. His emotional but poorly focused speech, *The Price of Freedom*, was a heartfelt hodgepodge of anthropology, history, politics, and religion that probably confused and dismayed his pious audience. Indeed, shortly after graduation, a young woman who had shared the honor of Senior Orator dismissed Wheelon as "an infidel."¹⁰ Homer Wheelon was, if not an infidel, at least an unusually widely read generalist for a nineteen-year-old.

Proudly independent and fiercely nonconformist, Wheelon probably rejoiced in his fellow orator's opinion. The opinion of Miss Lula Meacham, however, was another matter. Lula was the beautiful, bright, high-spirited, and demanding daughter of a sometime farmer, sometime Free Methodist minister, and sometime real estate agent. She was two years behind Wheelon at the Seattle Seminary. Lula and Homer had met many years earlier through their parents' activities in the Free Methodist Church, but Homer's brashness had frightened Lula, and as a young girl she wanted to have nothing to do with him.¹¹ During adolescence, however, her attitude changed. She flirted with Homer and teased him. Little more than a year after Wheelon's high school graduation, he had proposed to Lula Meacham,¹² and their engagement would last for seven trying years.

ARTIST TO BIOLOGIST

Homer was the first in his family to seek a bachelor's degree, studying liberal arts at the University of Washington. His grades were good, and he took part in The Biological Club, The Philosophical Club, and the Lincoln Literary Society. He also acted in the sophomore play. Photographs taken in his freshman year clearly show that Homer had artistic talent and aspirations (Fig. 2), talent and aspirations that his parents hoped would be relegated to the status of a hobby. Homer seemed to acquiesce to his parents' wishes at the University because his course selection changed, subtly at first and then more dramatically. In his freshman year, he took no courses in the biological

sciences. However, in his junior year, he took three courses in zoology and one in bacteriology.¹³

BIOLOGIST TO PREMEDICAL STUDENT

Early in his tenure at the University of Washington, Homer met Trevor Kincaid, the first of many mentors whose advice and example would shape his career. Wheelon must have found particular encouragement in his association with Kincaid, Professor of Zoology and Director of the University's Puget Sound Marine Station.¹⁴ In addition to his scientific profession, Kincaid was also a bibliophile with broad cultural interests.¹⁵ Wheelon and Kincaid spent many hours discussing art and literature.¹⁶



Fig. 2. Wheelon, a freshman in college, posing as "The artist as a young man." Some of the works shown are by Wheelon. He was torn between his strong artistic interests, with questionable financial promise, and a scientific career, that would provide greater financial security and be acceptable to both his and his fiancée's parents.

Through Kincaid's example, Wheelon was convinced that a career in science did not preclude a major commitment to art. With few lapses, Wheelon maintained that conviction throughout his life.

Wheelon spent two summers as Kincaid's assistant at the Puget Sound Marine Station. His duties included helping set up the campsites where both students and

faculty lived, gathering and photographing specimens, tending the workboats, and helping maintain the laboratories. In addition, he attended courses. The Station was both a research and a teaching institution that attracted an outstanding international faculty and student body. This was Wheelon's first taste of professional science of this quality, a seminal experience for him.

Wheelon was already practicing his synthesis of science and art. A good student and a hard worker, he had ample spare time. Characteristically, he filled this time with art. He recorded every facet—scientific, social, and aesthetic—of his two summers' activities at the Station, photographing, painting, and sketching scenes from several of the San Juan Islands. He drew portraits of fellow ferry passengers and silhouettes of many of the students, faculty, and staff, and gathered their signatures and addresses.

Wheelon bound this material, over 500 illustrations on 125 pages, into a 2-inch-thick book, *Memoirs of The Puget Sound Marine Station, 1910-1911*.¹⁷ This document demonstrated to himself and his family that if art could not be his vocation, it would certainly be a serious avocation. *Memoirs* was the first manifestation of Wheelon's proclivity for compendia, which would eventually include review articles, lists of diseases, catalogs of personal effects, and detailed logs of vacation trips.

During Wheelon's senior year, he began to have doubts about a career in science. At the Marine Station, he saw basic research that eventually could lead to discoveries and publications, but those accomplishments seemed distant and vague. Further, he had begun to recognize that, although Kincaid's enthusiasm for science was infectious, his research was unfocused and unproductive. He was further discouraged by the meager financial rewards a zoology professor could expect. During Wheelon's senior year, Kincaid appeared to have sensed this unrest and he suggested that Wheelon apply to medical school.¹⁸

Medicine may have promised a resolution to some of Wheelon's conflicts. As a physician, he would have a measure of financial security, and neither his family nor that of Lula Meacham would disparage his profession¹⁹. In addition, medicine might provide him with the leisure to pursue his artistic interests. To convince himself that he could reconcile his newly chosen career with his love for art, Wheelon began to experiment with medical illustration. His immediate accomplishments were several awkward drawings of dissections of the human neck and shoulders.²⁰ Unpromising as these illustrations were, they provided training for what would later be an important source of income and self-esteem. Wheelon almost certainly did not perceive that, in making this career change, he was heading for a profession that, despite its potentially unlimited challenges, might not, in its practice, satisfy his expansive nature.

Thus, based on his own misgivings and Kincaid's advice, Wheelon finished his career at the University of Washington convinced that he should become a physician. However, he lacked several prerequisites. His second mentor, John Freeman Bovard, provided a solution to this deficiency. Bovard had just completed his Ph.D. at Berkeley and had accepted a position at the University of Oregon. He met Wheelon at the

Marine Station the summer before assuming those responsibilities. Bovard, like Wheelon, was a generalist. His interests encompassed not only marine biology but also ornithology, paleontology, neurophysiology, and exercise physiology. He and Wheelon were comfortable together, and Bovard offered Homer a teaching and research assistantship at the University of Oregon. Homer accepted happily. There, he would be paid to teach while completing his prerequisites.

At Eugene, Homer taught histology, organized a physiology laboratory, took physics and organic chemistry to prepare for medical school, and conducted research toward a Master's degree under Bovard. Despite his many responsibilities, Wheelon continued to test his ability to practice art while furthering his path in medicine. Succumbing to a penchant for yearbook illustration,²¹ he had scarcely been on campus a month before he volunteered to make drawings for that year's edition of the University's yearbook.²² He contributed nine drawings, ranging from dramatic full-page illustrations, introducing each of the classes, to small tailpieces and filler material. In one case, Wheelon asked Lula Meacham²³ to return a drawing he had made of her so that he could adapt it for the introductory plate for Women's Sports (Fig.3). Wheelon and Lula Meacham had, by now, been engaged for three years.

However, Wheelon's sojourn at University of Oregon was their first separation of a significant distance. Although both had access to telephones, that form of communication was prohibitively expensive. However, both the Wheelon and Meacham families had strong writing traditions: they were correspondents, diarists, and amateur poets.²⁴ Homer and Lula solved the problem of their loneliness by maintaining that tradition. Between his arrival in Eugene and his marriage approximately four years later, Homer wrote to Lula more than 300 fact-filled but longing and romantic letters. Although he sometimes complained that his letters were not reciprocated, Lula wrote nearly 250 letters to him in the same period.²⁵



Fig. 3. Wheelon's drawing introducing the women's sports section of the 1912 University of Oregon yearbook. The drawing was a portrait of, Wheelon's fiancée, Lula Meacham. At his request, she returned it for use in the yearbook.

There is little information about Wheelon's research at Eugene. Bovard suggested that he study the anatomy of the innervation of the liver, but we know nothing about the motivation for the study, what aspect of that anatomy he was investigating, nor even with what animal he worked. Wheelon's brief descriptions of his efforts suggest that he received little assistance from Bovard. Nevertheless, he made some progress on the project, and he completed a number of drawings and drafts of chapters for a dissertation.²⁶ Near the end of year, Homer wrote to Lula about finishing his dissertation the following fall while taking chemistry, anthropology, the second semester of physics, and teaching comparative anatomy. In a premonition of his future research, he stated that he would like to "devise a means of using the X-rays for physiological purposes."²⁷

At the end of the semester, however, Homer made one of the abrupt transitions that characterized his education. He decided to apply to medical school that fall, without finishing his Masters degree and without completing his prerequisites. Through his links to Seattle's Methodist community, he may have learned that conditions were to his advantage at the medical school of strongly Methodist Northwestern University.

In 1911, Northwestern increased its prerequisite requirement for medical school from one to two years of undergraduate study. As a result, enrollment dropped by nearly 50 percent.²⁸ The medical school faced dire financial straits and recruited heavily. Wheelon easily convinced Northwestern's interviewer in Seattle that, despite his single semester of physics and mediocre postgraduate grades at Oregon, he would be a good risk. He was accepted summarily.

Wheelon arrived in Chicago in September, 1912. Having exhausted his savings on his train fare, he lacked money for rent, board, and tuition. He earned his rent and obtained his meals by waiting tables three meals a day in a café.²⁹ He worked off his tuition as an assistant to yet another scientist with broad interests, Winfield Scott Hall, Chairman of the Department of Physiology.

Earlier in his career, Hall had written physiology and nutrition textbooks. By the time Wheelon arrived at Northwestern, Hall, a devout Methodist, was beginning to write moralistic sex education texts for boys, girls, parents, and high school teachers.³⁰ Wheelon's duties were to conduct literature searches for two new texts, one on the male reproductive organs and the other on eugenics. In addition, he was to paint illustrations of the reproductive organs and draw charts and figures for the eugenics text.³¹ In his "remaining time," Wheelon was to help Hall conduct his laboratory research.^{32 33} Once again Wheelon had found a mentor whose enthusiasm engendered excitement for research, but whose academic activities were poorly focused.

Medical school did not challenge Homer, and he complained to Lula that he was required to repeat courses that he had already taken at Washington or Oregon.³⁴ Worse, the intellectual standards of some of his professors disappointed him. On the other hand, he found solace in painting illustrations for Hall's textbook. Indeed,

Wheelon's artistic abilities attracted the attention of other faculty members, including Steven Ranson, Chairman of Anatomy, who told Wheelon that he would be glad to have him illustrate his work, as well. Wheelon was proud that his artistic talent was able, at least partially, to support his medical career. He must have seen in this accomplishment some vindication of his artistic aspirations.³⁵

MEDICAL STUDENT TO GRADUATE STUDENT

As was his custom, Hall spent the summer after Homer's first year of medical school in Europe. To Wheelon's consternation, Hall's return was delayed, leaving Homer without a source of tuition for his classes. The stage was set for a major event in Wheelon's career—his introduction to Roy Hoskins. Although scientific in its nature, this was an event that would have reverberations even forty years later, when it played a role in the decision to use Wheelon's art in journals of the American Physiological Society.

Roy G. Hoskins assumed an associate professorship in the Department of Physiology at the beginning of Wheelon's second year of medical school. Hoskins had been the first doctoral student of Harvard's Walter Cannon, soon to become the dean of American physiologists. As an undergraduate at the University of Kansas, Hoskins had worked with the noted insect endocrinologist C.E. McClung. Hoskins was a determined man, and he had decided to conduct his Ph.D. research in endocrinology. He balked at Cannon's suggestion that he engage in the work for which Cannon was famous, gastrointestinal physiology. Indeed, Hoskins' refusal has been credited with the impetus for Cannon's famous research on the adrenal medulla.³⁶ Wheelon's first conversation with Hoskins was a revelation.³⁷

Hoskins, not yet an M.D.,³⁸ suggested that Wheelon might serve himself better, and humanity just as well, as a medical scientist rather than as a physician. Of course, Wheelon had already considered and rejected a career in basic science. By this time, however, his letters to Lula indicate that he was weary of waiting on tables. Hoskins offered Homer a research assistantship in exchange for his medical school tuition for the current year, an Instructorship in Physiology with an excellent salary the following year, and a true collaborative role, including co-authorship in their research. Homer happily agreed.

The research interests of Wheelon's mentors to date had been broad and unfocused, poor training for a career in twentieth century physiology. When Wheelon was considering a career in medicine, the nature of his research experience may not have been of primary importance. Now, when he was once again planning to be a scientist, participation in a sharply focused research program would have been beneficial. Arriving at Northwestern, Hoskins' research aims appeared to meet that criterion. Earlier, after studying the relationships between the thyroid gland and several other endocrine organs in Cannon's laboratory, Hoskins had taken a position at the Starling Ohio Medical School.³⁹ There, at Cannon's suggestion, he had begun to study

the role of the adrenal gland in circulatory regulation, and he quickly accomplished some of his better research.⁴⁰

A contemporary hypothesis held that the constant secretion of epinephrine by the adrenal glands was necessary to maintain normal arterial pressure.⁴¹ Hoskins showed that infusions of epinephrine that were too small to substantially alter arterial pressure were already so large that they completely inhibited intestinal motility. He reasoned that adrenal secretions could not possibly support arterial pressure on a minute-to-minute basis if, in doing so, they disrupted digestive function. It was likely that this endocrinological research that attracted Hall's attention to Hoskins.

At Northwestern, Hoskins planned to continue his studies of the circulatory role of the adrenal gland. Rather than study the effects of epinephrine itself, however, he chose to study the effects of removing all adrenal secretions on the activity of the sympathetic nervous system. Therefore, although the research he would share with Wheelon was "focused" on the sympathoadrenal regulation of the circulation, that research topic, by its nature, was already extremely broad.

The first experiments conducted by Hoskins and Wheelon were meant to validate methods which they would use in future studies of the role of the adrenal in circulatory regulation. Those studies would require repeated measurement of arterial pressure and heart rate in the same dog over periods of hours to days. Hoskins and Wheelon could find little information in the literature on the variability of arterial pressure over long periods of time, and they decided to obtain these data first-hand. Racing to obtain results for a winter meeting of the American Physiological Society, they had conducted eighteen experiments by mid-December of 1913; eight or ten more would be finished before Christmas. Wheelon certainly had never experienced research done at this pace, and he was elated.

The first of the Hoskins and Wheelon publications (which, despite his having had three mentors, was Wheelon's first publication) described their early winter's observations on serial measurements of arterial pressures in dogs.⁴² They were satisfied that intra-animal variations in pressures and responses were small enough that stable baselines for their ensuing studies could be obtained.

Having completed their control studies, they were ready to advance towards their major goal. Hoskins' earlier demonstration that a direct effect of adrenalin on the vasculature was not necessary for the maintenance of normal arterial pressure, clear as it was, left open an alternative role for the adrenal medulla. Perhaps very small amounts of circulating adrenalin (less than might be necessary to raise arterial pressure directly) were necessary to maintain the tonus of the sympathetic nervous system by acting either centrally, at the sympathetic ganglion, or at the junction between postganglionic sympathetic axons and blood vessels.

In the early twentieth century, many thought that the lethal effects of adrenalectomy could be attributed, not to the loss of adrenocortical secretion, but to the loss of this adrenalin-related tonus. Contemporary understanding of the role of the adrenal cortex

lagged behind that of the adrenal medulla.⁴³ In 1910, Biedl had described studies in fish, where such maneuvers were possible, in which he had separately removed analogs of adrenal "cortical" and "medullary" tissue. He had demonstrated that, in these animals, it was the "cortical" tissue that was necessary for life.⁴⁴ Nevertheless, it would not be until 1917 that it was clearly demonstrated in a mammal that the adrenal cortex could sustain life in the absence of the adrenal medulla.⁴⁵ Given this state of knowledge, then, the goals of Hoskins' proposed experiments were both important and interesting.

In theory, the rationale for their experiments was straightforward. As discussed below, in practice the experiments left much to conjecture. Sympathetic excitability at central, ganglionic, and peripheral sites was measured before (or at the time of) ligation of all of the adrenal vessels. Excitability was assessed periodically as the dogs' conditions deteriorated over subsequent hours. The excitability of the blood vessels themselves was assayed by measuring the magnitude of increases in arterial pressure elicited by intravenously administered adrenalin. The excitability of postganglionic sympathetic neurons was assayed by measuring the magnitude of the arterial pressure increase elicited when these neurons were excited by intravenously administered nicotine,^{46 47} presumably accounting for the increases elicited by adrenalin. Finally, central nervous system excitability was estimated from the size of the arterial pressure increase elicited by afferent peripheral nerve stimulation, again presumably taking into consideration the responses to the first two stimuli.

Hoskins and Wheelon were unable to demonstrate any effect of adrenal ligation on sympathetic transmission at central, ganglionic, or peripheral sites.⁴⁸ They concluded that a deficit in adrenomedullary secretions was not responsible for the circulatory collapse after adrenalectomy, nor could the presence of these secretions be credited with the maintenance of normal pressure in the intact animal. They further concluded, with little evidence, that adrenal deficiency caused a more general metabolic disability, probably due to a loss of adrenal cortical secretion. This disability, they suggested, weakened cardiac muscle, but not smooth muscle, eventually leading to circulatory collapse.

Although addressing an important question and requiring difficult experiments, these experiments suffer from several deficiencies from a present perspective. First, Hoskins and Wheelon lacked important controls in their methods paper. They made serial measurements of pressures and pressor responses over intervals of days to weeks, probably anticipating future experiments (described below) in chronically prepared animals. However, they conducted no experiments to control for the serial anesthetization and measurements made on the same dog on the same day. They did not control for the laparotomy required for the adrenal ligations, nor for the morphine with which they sedated their dogs during inter-experimental periods.

Second, the quantification of the magnitudes of pressor responses elicited by the various procedures in each dog was questionable. Presumably, responses were measured between baseline pressures and maximal response pressures. However, Hoskins' and Wheelon's figures often do not show stable baseline pressures. Hoskins

and Wheelon would have recognized only dramatic changes in the amplitudes of pressor responses. Thus, significant changes in the excitability of segments of the sympathetic nervous system might have escaped observation.

Third, the use of changes in arterial pressure as their sole indicators of the efficacy of sympathetic transmission was inadequate. The many factors that contribute to arterial pressure changes (which Wheelon would address in detail six years later)⁴⁹ again probably confounded the data to a degree that only very large alterations in transmission could have been detected. Finally, the paper does not describe the order in which nerve stimulation, nicotine, and adrenalin were delivered, nor whether this order was the same in all dogs or randomized.

In defense of Hoskins' and Wheelon's experiments, they represent one of the first attempts to quantify transmission in individual segments of the sympathetic nervous system in the same animals, a challenge even with today's techniques, and many contemporary endocrinological studies suffered from deficiencies similar to those sketched above. Furthermore, when Hoskins failed to corroborate all of the results of these experiments in the following year, he was quick to point out this discrepancy and to try to account for it.⁵⁰

Typical of the intensity of effort in Hoskins' laboratory, the experiments described in their first two papers were conducted and submitted for publication within six months of Hoskins' arrival at Northwestern. Suddenly, however, it became clear that the apparently sharp focus of Hoskins' research was illusory. With only the weakest of rationales, Hoskins and Wheelon quickly moved on to study the (presumed) effects on sympathetic transmission of parathyroid deficiency,⁵¹ and ovariectomy.⁵² Experiments were also conducted (and published two years later) on the effects of injections of pancreatic and salivary gland extracts.⁵³ Given Wheelon's previous research exposure, it is unlikely that he was concerned by this lack of focus. Even if he were, he was now committed to Hoskins' laboratory. Anxious to obtain his Ph.D. as quickly as possible, Wheelon began his dissertation research in February of 1914.⁵⁴

Using the methods that he and Hoskins had developed, Wheelon planned to measure the effects of removal of the testes on the excitability of the sympathetic nervous system. Technically, this project could have been a simple extension of his work to date with Hoskins. However, Wheelon's wide range of interests and, perhaps, the poor example set by his previous mentors led to a substantially broader design. Wheelon included, in addition to cardiovascular studies, behavioral observations; he predicted, not surprisingly, that castrated dogs would be less active and aggressive. If sympathetic transmission were compromised at any site, perhaps that reduced transmission could account for the behavioral changes. Therefore, "Fully developed, aggressive animals were chosen in order that any depressive changes might be followed more easily during the period of observation."⁵⁵

Using techniques identical to those developed by him and Hoskins, Wheelon found that the pressor response to adrenalin was not much changed. However, the response

to nicotine was substantially reduced, and he attributed this reduction to a castration-induced decrease in the excitability of the sympathetic postganglionic neurons.

Five of Wheelon's dogs exhibited decreases in aggressiveness which he conceded might have been caused by prolonged confinement but which he preferred to attribute to their castration. He did not speculate on a mechanism for the reduced sympathetic excitability. Instead, without additional data, he sought to relate the reduced excitability to the reduced aggression. To this end, he invoked the currently-popular, James-Lange hypothesis of emotion.⁵⁶

This hypothesis held that emotions are generated in response to the peripheral actions of the autonomic nervous system. For instance, fear would be considered a response to the elevated heart rate and other manifestations of the perception of danger. Wheelon reasoned that any reduction in sympathetic transmission that reduced sympathetic activity would reduce emotional expression. He suggested that, according to this hypothesis, the reduced range of emotions manifested by castrated animals, such as geldings and steers, could be explained by diminished sympathetic excitability.

Although he did not recognize any contribution from him, W.S. Hall would certainly have welcomed Wheelon's conclusions. In his future textbooks, Hall would argue strenuously against masturbation for its depletion of what "we know to be a far more vital fluid than the same volume of blood."⁵⁷ Hall probably would have equated castration with chronic masturbation, a behavior to which he attributed "flabbiness of muscle, shiftiness of eyes, clamminess of hands, and a disinclination to enter into any physical contests." As interpreted by the James-Lange hypothesis of emotion, Wheelon's observations of decreased sympathetic excitability could account for Hall's alleged behavioral observations.

Neither Hall nor Hoskins played any role in writing the paper reporting the results of castration, for by the time Wheelon began the manuscript, Hoskins had left for his summer vacation and Hall had traveled to Germany to rescue his family as World War I loomed.⁵⁸ Although Wheelon acknowledged Hoskins' encouragement and suggestions, citing this work as a continuation of their collaboration, it is notable that Hoskins was not included as an author. It is likely that, as a physiologist, Hoskins wanted to distance himself from Wheelon's behavioral conclusions. Hoskins was still in close communication with Walter Cannon, and he almost certainly knew that Cannon had, just five months earlier, strongly refuted the James-Lange hypothesis.⁵⁹

If, by the end of his second year at Northwestern, Wheelon's academic and professional progress appeared to be satisfactory, his financial position had not improved. His instructorship at Northwestern would not begin until the fall of 1914 because Hoskins was not active in the laboratory during the summer. In the meantime, Wheelon had to earn a living. He contacted A.J. Carlson, Chairman of Physiology at the University of Chicago. Carlson appointed Wheelon to an Assistantship in Physiology⁶⁰ for the summer. Thus, he could earn his living by teaching and working in Carlson's laboratory rather than by waiting tables. During the course of the summer,

Carlson recommended Wheelon to Don R. Joseph, the recently appointed Chairman of Physiology at St. Louis University⁶¹. Joseph was building his department and needed staff.

Joseph offered Wheelon an Instructorship at a salary of \$1200 per year, more than twice his anticipated salary at Northwestern.^{62 63} If Wheelon were willing to abandon his productive collaboration with Hoskins, he would still be able to conduct his own research with excellent facilities. As Wheelon wrote ecstatically to Lula Meacham about his new position at St. Louis University, the higher salary would enable him finally to marry her.⁶⁴

Another benefit of Wheelon's instructorship was that, for the first time, he was assigned a research assistant. With some fanfare, Joseph led Homer into the laboratory to make introductions. Wheelon could hardly believe his eyes. His new assistant was J. Earl Thomas, a junior (but superb) member of the debating club during Wheelon's tenure at the Seattle Seminary. Thomas had just arrived at St. Louis University to obtain his B.S. and M.D. degrees.⁶⁵ Reunited, Wheelon and Thomas were not only mentor and student, they became colleagues for the next six years.

PHYSIOLOGY INSTRUCTOR TO MEDICAL STUDENT AND PHYSIOLOGIST

Married for a year, living in St. Louis, and anxiously awaiting signs of a child,⁶⁶ Wheelon began to have second thoughts about his chances for professional development on a medical faculty without an M.D.⁶⁷ In his two years at St. Louis University he had failed to find a research preceptor for his doctoral dissertation. Instead, he had met several clinicians who were able to maintain both medical practices and research programs. With the enthusiastic encouragement of Hall,⁶⁸ Wheelon veered again and decided to complete his medical degree while continuing his research.

Wheelon conducted four kinds of research at St. Louis University: endocrinological, circulatory, hematological, and gastrointestinal. The gastrointestinal research that he conducted with Earl Thomas was exceptional, and we will describe it in some detail below. However, his other research was reminiscent of his work with Hoskins: although in some cases it represented considerable effort and creativity, it was poorly focused.

Wheelon's sole endocrinological study from St. Louis University, conducted with a friend, John Shipley, completed observations that Wheelon made previously on the effects of testicular transplants in reversing the cardiovascular sequelae of castration. These experiments confirmed Wheelon's previous, preliminary observation that testicular transplants partially restored sympathetic function after castration.⁶⁹

Wheelon's cardiovascular research at St. Louis University was more extensive, if even less focused. He was one of the few contemporary physiologists who had made serial measurements of arterial pressure in the same animals over periods ranging from hours to weeks. He and Hoskins had noticed substantial variations in serially measured pressure, even over short periods, and these variations fascinated him. Wheelon

savored the role of the iconoclast. Therefore, it is not surprising that his cardiovascular research was aimed at dispelling no less a myth than the constancy of arterial pressure.

It was Wheelon's opinion that physicians attached altogether too much significance to single measurements of arterial pressure, and much of the paper is a polemic against this perceived inadequacy. His cardiovascular research, most of which appears to have been conducted on medical students, was published in a single, rambling paper several years after the research was conducted. The title of this paper indicates its scope, *The Interpretation of Blood Pressure Variations: With Observations on Normal Pressure Variations and the Relation of the Adrenals and the Autonomic Nervous System to the Production of Blood Pressure.*⁷⁰

Wheelon's third line of research in St. Louis was conducted with Charles Neilson, a physician and scientist. Indirect evidence suggests that Wheelon's motives for working with Neilson were financial and professional rather than scientific. Neilson, Chairman of Medicine, was something of a gadfly. He had little time to conduct research himself, but he was willing to pay others to conduct it for him. Wheelon probably received either tuition benefits or a stipend for working with Nielson. In addition, Nielson liked Homer and Lula, and they were occasional dinner guests. Although Wheelon later declined the offer, Nielson offered him a partnership in his practice upon completion of his residency.

Nielson wanted to study red blood cells' resistance to lysis in different diseases and to develop an index whereby this sensitivity could be quantitatively measured. Blood samples were taken from a finger wound. Aliquots of these samples were mixed with solutions containing graded concentrations of saponin. Their assumption was that the higher the concentration of saponin that the red blood cells could withstand without lysing, the more resistant the cells were to hemolysis in general. The resistance to hemolysis of blood from 99 healthy subjects was compared with that of 86 determinations that Wheelon did on his own blood to determine the variability of the assay. Without reference to any previous source, the authors stated the hypothesis that plasma levels of cholesterol are directly related to the resistance of the red blood cells to hemolysis; they conducted a "cross-over" experiment using red blood cells from one donor and plasma from the same and other donors to demonstrate that resistance to hemolysis was conferred by the plasma and was not a property of the cells.⁷¹

In their subsequent papers,^{72 73} Nielson and Wheelon applied their technique to the blood of pregnant women and patients with malaria, tuberculosis, typhoid fever, syphilis, lead poisoning, jaundice, anemia, cardio-renal disturbances, and malignancies, and they continued to argue for a relationship between plasma cholesterol concentration and resistance to lysis. These studies differed from Wheelon's earlier work in an important respect: they were his first truly focused experiments. Only one or two techniques were required, and although Neilson and Wheelon analyzed blood from patients with many diseases, the intellectual scope of their project was narrow. The experiments exhibited little of the expansiveness of design, and the writing exhibited none of the interest in physiological interactions that characterized all of Wheelon's previous work. Thus, it is very likely that Nielson played a major role, not only in

directing the research but also in helping write the papers. This research was completed and drafts of the papers were written before the Wheelon and Thomas' research was begun. Wheelon had learned important skills, both in research and in writing from his experience with Nielson, and these are reflected in his subsequent work.

Wheelon's fourth line of research in St. Louis, the research for which he is best remembered, consisted of gastrointestinal studies that he conducted with Thomas. This research produced nine articles between 1920 and 1923 and an additional article in 1926. What accounts for Wheelon's abrupt transition from endocrinology and cardiovascular physiology to gastrointestinal physiology? Among his earlier mentors and benefactors, only A.J. Carlson worked in gastrointestinal physiology. Although Wheelon was briefly Carlson's research assistant, no contributions from him are acknowledged in any of Carlson's publications. The factors that account for the change in Wheelon's area of research are important not only for understanding Wheelon's motivations but Thomas' motivations as well. It was Thomas, after all, who became a leader in gastrointestinal physiology, publishing approximately two hundred papers in the field.⁷⁴

In fact, Wheelon and Thomas' research in gastrointestinal physiology derived from a variety of forces, both internal and external. Wheelon may initially have been predisposed to gastrointestinal physiology by his interest in x-rays. Walter Cannon had revolutionized gastrointestinal physiology through the use of x-ray observations of the gastrointestinal tract.^{75 76} Wheelon almost certainly was aware of those discoveries, and, on two occasions, expressed interest in incorporating x-rays in physiological research. The first of these occasions was shortly after publication of Cannon's landmark study, *The Mechanical Factors of Digestion*,⁷⁷ while Wheelon was still an assistant to Bovard at the University of Oregon.⁷⁸ The second was a year later, while working as Hall's laboratory assistant.⁷⁹ One year after receiving his M.D., in addition to being a Resident, Wheelon was also Chief of the Department of Roentgenology at St. Louis University's Bethesda Hospital,⁸⁰ with excellent access to x-ray equipment.

In addition, Wheelon and Thomas probably received (but did not acknowledge) suggestions from senior faculty at St. Louis University. Charles Neilson had studied factors that affected gastric emptying⁸¹. Albert Kuntz, who had sponsored Wheelon in an internship at Woods Hole in 1914⁸² and with whom Thomas would later publish experiments on the autonomic regulation of gastrointestinal motility,⁸³ had a long-standing interest in the gastrointestinal tract.⁸⁴

Most important, however, especially for an understanding of Thomas' later career, was Don Joseph's experience in Meltzer's laboratory at The Rockefeller Institute. Shortly before assuming the Chair in Physiology at St. Louis University, Joseph conducted two studies at Rockefeller in which he used methods very similar to those adopted by and elaborated upon by Wheelon and Thomas.^{85 86} In those experiments, Joseph used multiple balloons, connected *via* multiple catheters to kymograph tambours, in order to record the simultaneous motilities (pressures) of the stomach and duodenum. The hallmarks of Wheelon and Thomas' research, and of Thomas'

research for many years following, were the high-quality recordings (Fig. 4) of gastrointestinal activity, obtained with ingenious intragastric and intrainestinal transducers of Thomas' design and manufacture.

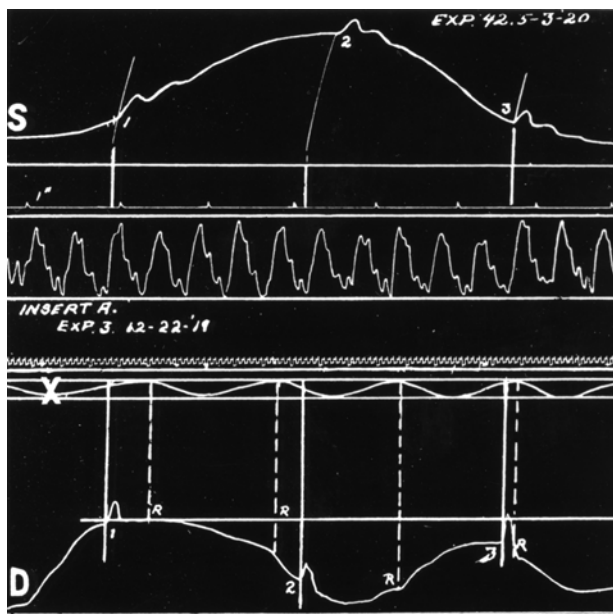


Fig. 4. High-quality kymograph records from Wheelon and Thomas' report on the relationship between the motilities of the duodenum and the pylorus.⁸⁷

The first of Wheelon and Thomas' papers is best characterized as a review, embellished with fragments of their own data. In its breadth and style, it was strongly reminiscent of Wheelon's past, unfocused work. The subject was broad: *The autonomic nervous system and disorders of the stomach*. Factors ranging from cellular processes to the effects of stress and other psychological conditions were considered.⁸⁸ The paper included an elegant summary diagram by Wheelon that illustrated interactions between these levels of organization.⁸⁹

Then, in an abrupt change of focus and style, Wheelon and Thomas concentrated on factors that regulate gastric emptying, with little reference to extrinsic neural and endocrine factors. Pavlov had received the Nobel Prize for his work on digestive secretion in 1904,⁹⁰ and Walter Cannon had published his influential monograph on gastric motility in 1911.⁹¹ But then, both Pavlov and Cannon had transferred their interest from studies of the digestive tract to studies of neural and endocrine systems. Thus, it became politically safer to criticize their gastrointestinal conclusions.⁹² Whether by chance or by design, Wheelon and Thomas' gastric emptying research put them in direct conflict with one of Walter Cannon's more strongly held tenets, that acid regulated the emptying of the stomach by controlling the opening of the pyloric sphincter.

Cannon's observations had led him to a characteristically clear description of gastric emptying through the pyloric sphincter.⁹³ According to Cannon, the pyloric sphincter

was normally contracted during much of digestion and relaxed and opened when exposed to sufficiently high concentrations of acid. In turn, acid in the chyme stimulated secretion of digestive juices by the duodenum, and these juices, in turn, neutralized the acid in the duodenum. The resulting decrease in acidity permitted the pyloric sphincter to return to its closed state. Thus, the sphincter aperiodically opened and closed, depending on the concentration of acid in its vicinity.

Cannon amassed a significant body of evidence and opinion in support of this model.⁹⁴ To succeeding physiologists, this model was potentially vulnerable on two fronts: 1. was the pyloric sphincter, in fact, normally contracted, relaxing and opening infrequently to pass chyme to the duodenum, and 2. was acid the stimulus for the opening of the pyloric sphincter? Wheelon and Thomas attacked the first of these issues, and used their observations to suggest an answer to the second.

Wheelon and Thomas used x-rays to observe gastrointestinal motility, as Cannon had done, and they also made simultaneous measurements of the pressure in the antrum and of the contraction of the pyloric sphincter. Soon after, they added simultaneous measurements of pressure in the duodenum. The accomplishment of this research depended on Wheelon's ability to make x-ray images of gastric emptying in dogs and Thomas' skill in designing and building the apparatus for studying gastrointestinal motility.

By using this combination of methods, Wheelon and Thomas observed that the antrum, pyloric sphincter, and duodenum appeared to move in a closely coupled manner. The pyloric sphincter did not represent a barrier to the passage of chyme into the duodenum. Instead, its contractions were related to those of the antrum and duodenum in a coordinated, albeit complex, pattern. As a wave of activity moved across the antrum, pylorus, and duodenum, the pyloric sphincter relaxed, permitting the chyme to open the sphincter as it traversed the pressure gradient from the antrum to the duodenum. During subsequent contraction of the duodenum, regurgitation of chyme into the antrum was prevented by contraction of the pyloric sphincter. Wheelon and Thomas concluded that, because the movements of the stomach, pyloric sphincter, and duodenum were so tightly coordinated, a local action of acid on the sphincter could not be responsible for the sphincter's relaxation.^{95 96 97}

Wheelon and Thomas's gastrointestinal research was well received. It was considered to be on the cutting edge. In fact, the renowned gastrointestinal physiologist Walter Alvarez candidly admitted in one of his papers⁹⁸ that:

Just as we were about to send off our report on the subject there appeared an article by Wheelon and Thomas which described many of the phenomena which we had been studying...As there were a few differences between our observations and conclusions and those of Wheelon and Thomas, we have spent several months more on experimental work and have rewritten our paper.

Even Walter Cannon, whose interpretations were sometimes questioned in the Wheelon and Thomas papers, responded positively to work from the same period on which Wheelon was the sole author.⁹⁹ For instance, Cannon wrote to Wheelon:

I was especially pleased to read your discussion of the relation of the gastric content to the secretory and motor functions of the stomach. I have long felt that there is a good deal of unproved assumption in the claims made for gastric analysis and the evidence that you offer is most pertinent on that point.¹⁰⁰

Wheelon and Thomas's gastrointestinal research was reviewed favorably in the textbooks of gastrointestinal physiology written by Alvarez¹⁰¹ and by Bockus.¹⁰² It was frequently cited throughout the 1920s,¹⁰³ and it has been cited as recently as 1987.¹⁰⁴

Wheelon and Thomas, in addition to being compatible as friends, were well matched as colleagues. Each brought important skills to their research. Thomas was an accomplished machinist, capable of making the delicate instruments used to record gastric, pyloric, and duodenal motility.¹⁰⁵ Wheelon provided both the skills and the X-ray equipment necessary to directly observe gastrointestinal motility in both humans and dogs.

Perhaps as important to Wheelon and Thomas's collaboration were their respective intellectual attributes. Wheelon was not only more experienced in research than was Thomas, he also had a more comprehensive understanding of physiology. Wheelon's experience and training had predisposed him to an expansive view of his research, as manifested, for instance, by his work in humans on the relationship between gastric content and the motor and secretory functions of the stomach.¹⁰⁶ Thomas, on the other hand, was a more intellectually focused individual. Even as a debater at the Seattle Seminary, he had a reputation for carefully crafted and orderly presentations.^{107 108} As a scientist, he spent the majority of his career studying the regulation of gastric emptying, using extremely precise equipment and techniques of his own design.¹⁰⁹ It is likely that Thomas, while profiting from Wheelon's perspective, was the steady hand in conducting these experiments and analyzing the data.¹¹⁰

Throughout their stay in St. Louis, the Wheelons wrote home longingly about returning to the Northwest. Not only did they miss their families, they hated the climate extremes of St. Louis. Indecision had marked each stage in Wheelon's career; to be an artist or a scientist; to be a scientist or a physician; to remain a medical student or obtain a Ph.D.; to continue graduate school or return to medical school. However, by 1918, seven years after graduating from college, his career path was set. Wheelon had decided that, after receiving his M.D. in June, he would take an internship and a residency in St. Louis. Then, he and Lula would escape St. Louis' harsh climate and return to the Northwest. His and Lula's families enthusiastically supported this plan.¹¹¹

However, leaving St. Louis would have disadvantages. Wheelon appeared to enjoy his research more than his clinical activities, and he and Thomas had learned to exploit their mutual talents. Lula recalled Homer and Earl returning to their apartment long

after she had gone to bed, working the rest of the night to analyze the data from that day's experiment.¹¹² Nevertheless, in 1920 and early 1921, several factors precipitated the Wheelons' return to Seattle.

Wheelon's father died during the autumn of 1920, and his mother begged Homer and Lula to return. Then, in the spring of 1921, Earl Thomas, disappointed at his prospects at St. Louis University, accepted a position at the University of West Virginia School of Medicine. Without his collaborator and friend, research in St. Louis was far less attractive to Wheelon. In the spring of 1921, he traveled to Seattle and negotiated a partnership agreement with H.J. Davidson, director of a group practice that would eventually become the Polyclinic.

Because Wheelon would not be able to pursue basic research in Seattle, he was faced with the task of completing what Lula called his "overripe" publications before moving. Day after day, he wrote and Lula typed. As moving day approached, Lula took charge of all the packing and disposal of their furniture. Finally, in July of 1921, the Wheelons moved to Seattle, keeping the exact date of their arrival secret so that they might have a vacation before Homer was expected to begin practice.¹¹³

INTERNIST AND ARTIST

Although his return to Seattle was to mark the end of Wheelon's academic career, he was unwilling to relinquish that role. He was a frequent guest lecturer at the University of Washington.¹¹⁴ He may have taught Abnormal Psychology during the academic year 1923-24, and he was appointed briefly to the position of Lecturer in Psychology.¹¹⁵ He conducted clinical research.¹¹⁶ He reworked lectures and publications from his days at St. Louis University and presented them to local medical societies,¹¹⁷ and, over the next twenty years, he published nine clinical studies and two textbook chapters, usually related to endocrinology or endocrinological disorders.

Since his youth, Wheelon had tried to find ways either to incorporate art into his professional life or to practice art as a parallel activity. Until he reached St. Louis, he had been successful in this objective. Then, for almost seven years his artistic output had been limited largely to technical illustrations in his scientific publications. One reason that Wheelon joined a group medical practice was that he would have the freedom to engage in other activities.¹¹⁸ Now, for the first time, he could indulge his cultural interests in both the financial and social safety of his medical profession.

Returning to the city in which his artistic talent had first blossomed, Wheelon resembled a freed prisoner. He painted and photographed, exhibiting his work in regional salons and exhibitions. He worked in a broad range of media—pen-and-ink, pencil, watercolor, oil, and even woodcut (Fig. 5).



Fig. 5. Examples of Wheelon's artwork during the 1920s. (A) Untitled pencil drawing of trees. He drew many versions of this scene, some of which are delicately tinted. (B) Untitled oil of ferns and flowers. (C) "Prometheus," painted in the early 1920s. This oil painting portrays his own hands in a rendering of the Greek myth of the god who stole fire from the other gods and delivered it to humans. Unlike the Greek god, Wheelon's Prometheus is bound only by himself.

His styles were equally varied. During the 1920s, they ranged from realistic, pastoral landscapes, through surrealistic, metaphorical paintings, to pure designs. Both his realistic work and his abstractions drew praise from critics.¹¹⁹ Although many of his realistic works, mostly landscapes, were gentle and unchallenging, his abstractions could be dark and even threatening.

Always an eclectic bibliophile, Wheelon read and collected books with increasing avidity. His catalog of approximately 600 titles reveals his extraordinary breadth of interests: physical and biological sciences, clinical medicine, art, philosophy, religion, poetry, theater, fiction, history, biography, music, anthropology, archaeology, and geology. Above all, however, there was William Blake. Wheelon was fascinated by Blake's marriage of poetry and art, and he collected fine, hand-colored editions of Blake facsimiles, eventually accumulating one of the largest private collections of these works in the West.

Nor were art and reading Wheelon's only activities. He passionately researched his own genealogy. He made a detailed study of American Indian mythology. He studied the incidence of endocrine disorders in local counties.¹²⁰ The energy with which he

pursued his avocations belied the calm, almost ascetic physician whom his patients and fellow clinicians knew. During these years, his activities encompassed an ever-enlarging intellectual scope while becoming increasingly compulsive.

By 1933, Wheelon was in a period of crisis. He found aspects of his medical practice tedious.¹²¹ At home, his life was in disarray because of dissension between him, Lula, and their restive, adopted, teenage son.¹²² Wheelon spent many hours in his basement study, immersed in mythology, philosophy, and Blake.¹²³ It was in this condition that Wheelon happened upon John Lingenfelter and his rabbit as described in the Prologue to this paper.

Inspired by this experience, Wheelon spent innumerable hours writing and illustrating *Rabbit No. 202*. Wheelon wrote the first 121 pages of *Rabbit No. 202* between the spring of 1933 and autumn of 1934.¹²⁴ It took him approximately six more years to finish the remaining 201 pages. In his first year of writing, whenever he was not at the Polyclinic he lived an almost-solitary existence, working alone in his study. Never having required much sleep, he worked until nearly morning, even during the week. On many weekends, he worked from Friday night to Monday morning, emerging only for occasional naps and meals.¹²⁵ He was a man possessed.

In this long, rambling poem, Wheelon found a way to bring together his disparate cultural, scientific, and medical interests. Perhaps Wheelon was emulating his mentors, all of whom had lived full cultural lives. Indeed, Hoskins had just published *The Tides of Life*, an endocrinology text written for a lay readership.¹²⁶ Whatever Wheelon's motivations, it is no surprise that, in writing a long, illustrated poem, he emulated his hero, William Blake.

In the middle and late 1930s, Wheelon spent less and less time working on *Rabbit No. 202*. In addition to his clinical duties, he was elected several times as President of the Polyclinic, a position that carried administrative duties. He also held the position of Medical Director of the Columbus Hospital. In the 1940s, Wheelon had a large practice of internal medicine with many loyal patients. He was particularly popular among the faculty at the University of Washington.¹²⁷ His Presidency of the Polyclinic continued to add distinction to that group. When the Columbus Hospital became the St. Cabrini Hospital, he became its first Chief of Staff. Throughout this period, however, sometimes intensely and sometimes casually, Wheelon continued to work on his poem.

RABBIT NO. 202

The format of *Rabbit No. 202* is its most easily described feature. Its 322 pages are divided into 12 chapters. Each chapter is preceded by a short prologue that summarizes the succeeding material (see below). Each of the poem's 38 illustrations has a short title, in all but one case a line from the poem. Some of the illustrations interpret the poem. Others are either loosely related to the poem or, in a few cases, apparently unrelated. Nearly all of the illustrations were rendered in pen-and-ink, drawn to

resemble woodcuts (Figs. 6-9). Some of the illustrations were original to the poem; in keeping with artists' frequent usage, however, many were illustrations that Wheelon had previously drawn, such as Christmas cards, and then modified.¹²⁸

Although the rabbit was the inspiration for Wheelon's poem, it provides only the most tenuous organizing principle. Very much like his senior oration in high school and some of his early publications, the poem rambles over an extraordinary range of topics. Consider the chapter titles: "Rabbit No. 202, Myths, Magic, Life, Science, Symbols, Theory, Confusions, Realities, Reflections, Projections, Ways." The prologue to Symbols demonstrates the breadth of material covered in just a single section of this poem.

Herein are recorded many facts as established by the "scientific process"—conclusions derived from logically arranged data collected by means of the experimental method—critical challenge of nature. Conclusions as facts, hypotheses, theories, and ultimately laws (convenient abstractions compounded from the stuff, observed phenomena). Conveniences derived through impartial observations and cold reason; abstractions symbolizing meaning...Symbols, the conclusions of inquisitive and believing man...and perchance, errors of man, i.e., acceptance of symbols as such instead of that which is symbolized—knowledge without experience.

Herein also, are set down various characteristics of man and many of the results of his doings; especially those having to do with man's conclusions relative to his position in the stream designated by him as process, his discoveries (experiences) and the use he has made of them—culture. Man laboring to solve the problem—man; gathering facts for his theories...Facts and theories of man.

The poem contains material ranging from a taxonomical categorization of Homo sapiens, and a complete short-course in reproductive endocrinology, to a gentle love poem to Lula. This is not to say that there are no organizing principles. Wheelon used both typographical and thematic schemes to unify the poem.



Fig. 6. Winter of disbelief, from *Rabbit No. 202*, illustrates a portion of the poem in which Wheelon is describing the origins of rites of spring, relying heavily on Frazer's *The Golden Bough*.¹²⁹ The figure symbolizes the loss of faith in the early goddesses of spring, such as Eastre, as well as the annual disbelief that spring would always follow winter. The illustration is an evocation of the barrenness of both doubt and winter.

Structurally, Wheelon dealt with the broad range of material in the poem by using an outline form. Beginning with a central topic near the left margin, he successively indented subtopics until he had exhausted the central topic. Then, he would return to the left margin and declare another central topic. A section from Part 2¹³⁰ of the poem demonstrates this principle.

Man,
Alleys, life, and destiny,
 Conjectures of man—
Dinosaurs went in for mass,
 Tons of mass and armor plate;
 Flourished in the Jurassic age;
 Swarmed down the alley mass;
 Finished up as fossils.
 Tons of mass and armor plate—
 Dinosaurs wrote the history of mass in fossils...
 Small heads and large bellies for a day:
 Life projected through mass reduced to fossils,
 Dinosaurs and their day.
 Out of the fogs of morning,
 Into the blaze of day,

Through the doors of night,
 Life entered,
 Unfolded,
 Then passed that way—
 Out of the fog into the night.
 Dinosaurs passed that way—
 Alleys?

Homo sapiens, naked biped, went in for brains,
 Efficient brains and opposed thumbs;
 Hunted the woolly mastodon;
 Turned environment down the alley of brains;
 Made his own fossils.
 Efficient brains and opposed thumbs—
 Homo sapiens writing the history of brains on paper...
 Large heads and small bellies of today:
 Life projected through brains reduced to marks on paper...
 Man and his day—
 Life trying alleys?

Wheelon also repeated short motifs to link portions of the poem. For example, he used the lines "Running sap in trees/Urgency in seed" in discussions of spring, descriptions of the rabbit, references to female fertility and the menstrual cycle, and Christ's death and resurrection.

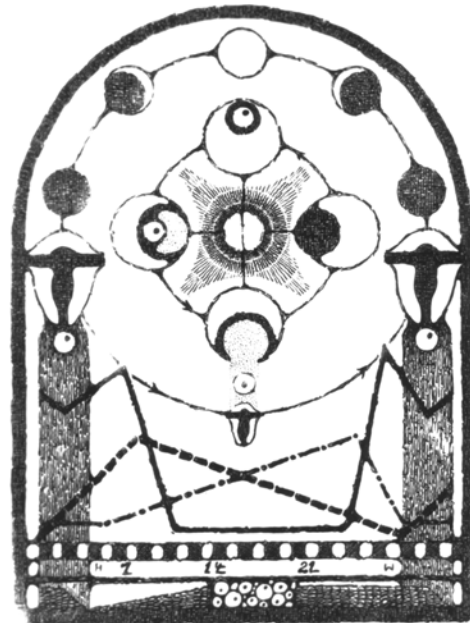


Fig. 7. Tides of Menses, one of the least polished of the figures in *Rabbit No. 202*, illustrates a portion of the poem that constitutes a summary of reproductive physiology, as understood both in primitive times and in the 1930s. The cycles of the moon, at the

top, are linked to the cycles of the ovary, in the center. The lower portion of the diagram is a chart of hormone levels throughout a twenty-eight-day cycle.

Perhaps the poem's most pervasive theme is the relationship between human models and symbols (including, of course, art) and the reality that these models and symbols profess to describe. A second theme is the relationship between what humans are convinced is fact, and what they are willing to admit is illusion. A third theme is humans' plunder of the rest of the natural world and their rationalizations for this.

The tone of the poem is often, but not always, critical. Wheelon was generally suspicious of human institutions and human intellectual constructs, and this skepticism pervades *Rabbit No. 202*. At the same time, his overall view of humans as *individuals* was optimistic. He valued the ability of humans to relate to one another when those relationships were positive and non-exploitative. Indeed, he considered companionship to be the species' highest attainment.



Fig. 8. Slow Ascent—Man, from *Rabbit No. 202*, illustrates one of several portions of the poem that describe the evolution of humans. Most simply, it can be seen as a depiction of human evolution from the sea, represented by the swirls at the lower left. However, in the context of the entire poem, it almost certainly represents the slow, uncertain evolution of human culture. Nevertheless, Wheelon's optimism is manifested by the path that goes through the confines of the drawing's frame to freedom.

The heterogeneity of *Rabbit No. 202* fits the pattern of Wheelon's early scientific writing. He was, after all, a "compiler." He had thoroughly documented his summers at Friday Harbor in his "Memoirs of the Puget Sound Marine Station." He had conducted exhaustive literature searches for Winfield Scott Hall, and when Hall did not use them, Wheelon did, as material for his own reviews and textbook chapters.^{131 132 133 134} He compiled long lists of patients with similar diagnoses, searching for common etiological features. Until 1940, he kept an elaborate bibliography of every endocrinological article he read. His personal papers contain lists of his works of art and their locations, lists of his previous addresses, lists of illnesses, and lists of books and phonograph records.¹³⁵

Perhaps another reason for the poem's heterogeneity is that Wheelon used *Rabbit No. 202* to record his thinking and to consolidate his reading during its seven years of creation. Although the event that inspired the poem, the observation of a pregnancy test, could have had such significance only for a person of Wheelon's erudition, the writing of the poem, once begun, motivated even more reading, more research, and more learning. On occasion, this research appears in the poem surprisingly undigested. For instance, major portions of Part One's Chapter 2, Myths, are a poetic transliteration of a portion of Frazer's *The Golden Bough*,¹³⁶ a work that Wheelon cited in a verse of his poem.

The poem was constructed and eventually published in two parts. A study of the poem's manuscripts suggests that the first and second parts were conceived separately. Two complete manuscripts of Part 1 exist.¹³⁷ One, apparently typed in the mid-1930s is single-spaced. The other, which was marked for publication, was double-spaced. The presence of these two manuscripts suggests that Wheelon originally conceived of Part 1 as a complete entity. Indeed, it concludes with an epilogue:

Leaves

Weary, frost-tinted leaves
Red, yellow, and brown—faded greens,
 Answering the call of breezes—
 Falling in the lap of breezes—
 Leaves rustling in corners,
 Ghosts of Spring.
 Farewell—
 Gentle spring,
 Warm summer,
 Harvest moon.
Weary leaves piled in corners—
 Hopes grown in Spring,
 Mulch for the sprouts of Spring—
 Dead leaves.



Fig. 9. Symbols Given Meaning, from *Rabbit No. 202*, illustrates a discourse on symbols and their uses by humans, both in science and art. It combines a wide range of symbols from music, science, and religion.

The manuscript for Part 2 of the poem contains a long (eventually unprinted) introduction that contains no mention of the rabbit, nor does it promise that the themes of Part 1 will be continued. It concludes:

In a word, the immediate purpose of this second part of *Rabbit No. 202* is to bring together and present various of the meanings of man through his words, words illustrative of his ever-changing thoughts about himself and the universe as known to him. His words, symbols of his thoughts, projections of himself, wings with which to soar, or fetters to imprison!

The poem's heterogeneity is augmented by the insertion of verses that may have been written previously and, like many of the illustrations, adapted to *Rabbit No. 202*:¹³⁸

...Fifty yards astern follows a gull
 With the even stride of pulsing turbines
 In the hold of the ship—
 Spread wings gliding down the wind.
 In the wake of passing memories
 Stalks a ghost's noiseless stride
 In rhythm to a bursting heart,
 Noiseless feet pacing the course of time.
 Spread wings gliding down the wind,
 Ghosts of yesterday,
 Memories.
 Stars in the crimson of approaching night,
 Stars and shadows in pools of moonlight,
 Yesterday united with today,
 Reflections,
 Memories
 Silent as the flow of time on wings of tomorrow;
 The mirrored flight of birds in pools;
 The birth of a thin crescent moon in the sunset;
 The twinkling of stars in the wilderness of space;
 The form of clouds at dawn;
 Silent as the glow of love in a maiden's eyes;
 The grinding hurt of a broken heart;
 The aching depths of longing;
 And the ashes of hope—
 Silent as a memory.
 Yesterday united with today,
 Memories...

THE PUBLICATION OF *RABBIT NO. 202*

Six years after he had begun writing it, Wheelon began to plan for the publication of his poem. He knew that this would be a difficult task, and he discussed his concerns with a fellow scientist and poet, Chauncy Leake.¹³⁹ Both were long-time members of the Phi Beta Pi Medical Fraternity, and Leake was the editor of the fraternity's *Quarterly*. Having read a portion of the manuscript, and unaware of the scale of Wheelon's epic, Leake suggested that the *Quarterly* might publish *Rabbit No. 202*.¹⁴⁰ Wheelon was delighted. The *Quarterly* would stand the cost of setting the type, and Wheelon could purchase reprints at a nominal cost.

The correspondence between Leake and Wheelon concerning the publication of *Rabbit No. 202* reveals much about both men. Wheelon was honored that Leake had taken on the publication of the poem. At the same time, he was insistent that his aesthetic principles not be compromised by Leake's concerns for war-time paper rationing or by the costs that might be incurred by the fraternity in publishing so large a work. For Leake's part, he considered his securing the poem for the *Quarterly* a coup,

and he accommodated many of Wheelon's requests. At the same time, he did not hesitate to reject drawings that he thought were weak or superfluous, or to ask Wheelon to redraw, in pen-and-ink, woodcuts or pencil drawings that he felt would not reproduce well.

One extraordinary letter from Leake to Wheelon reveals the nature of their relationship.¹⁴¹ Apparently, Wheelon had just returned the proofs for what Leake had assumed was most of the poem. With the proofs, Wheelon sent "some" additional material. In a somewhat stiff postscript to a letter in which a number of publication details had been cordially discussed, Leake said,

It now dawns on me that the material you sent, after your original manuscript was in the printer (sic) hands, contains a vast section (pages 169-372) comprising part 3, Realities of Chapter 6, Symbols. This material exceeds the original manuscript as submitted by fifty per cent. It alone takes up 204 pages whereas the original manuscript was only 173 pages. I am sorry that it was not clear to me at all that you were submitting additional material. I thought you were sending only corrected material and in order not to confuse the printer or delay the work I didn't send it on. Your corrected manuscript would more than double the space allotment which was made available originally. I see no way by which we can take care of the matter at the presnt (sic) time since the manuscript as originally submitted is already set up in type...

In effect, Wheelon had submitted a "note added in proof" which was longer than the original manuscript. The problem of the additional material was amicably resolved by its subsequent publication in two additional numbers of the *Quarterly*, with Wheelon paying much of the additional cost.¹⁴²

Wheelon mailed most of the 500 reprints of the first volume of *Rabbit No. 202* to friends, colleagues, libraries, and famous physiologists around the world. The recipients of these gifts responded with hundreds of letters of praise and thanks. Others who saw the poem requested copies for themselves. Unfortunately, by the time the



Fig. 10. Man Assumed the Burden of Fire, a smoky drawing with an ironic title, illustrates perhaps the most productive and destructive uses by humans of fire. Wheelon was obsessed with legends concerning the origins of fire. In the 1920s, he created one of his most striking oils, "Prometheus." Both Greek and Native American legends describing the origins of fire are recounted in the poem.

reprints of the balance of the poem appeared, the United States was deeply engaged in World War II, and postal restrictions, combined with Wheelon's heavy, war-time workload, precluded a similarly ambitious mailing of the second volume.¹⁴³

The Second World War was difficult for Wheelon, both emotionally and physically. His correspondence indicates that he took the events of the war, especially the attack on Pearl Harbor, very hard.^{144 145} At the Polyclinic, he was left with the exhausting task of treating not only his own patients but also those of the younger doctors who had entered the military. Wheelon wanted, desperately, to be actively involved in the war effort. However, he had to be content with a limited contribution through appointment to the Medical Advisory Board of the Civilian War Commission.¹⁴⁶

After the war, Wheelon resumed his life of broad cultural concerns. The Wheelons were important patrons of experimental theater in Seattle, and Homer continued to build his collection of works by William Blake. He took a strong interest in—and experimented with—Chinese poetry¹⁴⁷. Although there is no evidence that he painted or drew, he experimented with photography.¹⁴⁸ Proud of his earlier artistic accomplishments, he submitted works, many of which dated from the 1920s and 1930s, to exhibitions of the American Physicians' Art Association. In 1947, that Association invited him to submit a work to its international competition in Buenos Aires.¹⁴⁹ His surrealistic work, "Brains and Clouds," was awarded the gold medal for paintings.¹⁵⁰

THE AMERICAN PHYSIOLOGICAL SOCIETY DISCOVERS *RABBIT NO. 202*

It is not immediately obvious how, in the 1950s, the illustrations from *Rabbit No. 202* came to be used as tailpieces in the *American Journal of Physiology* and the *Journal of Applied Physiology*. Although Wheelon remained a member of the American Physiological Society until his death in 1960, he published his last article in the *American Journal of Physiology* in 1922. However, a likely scenario can be constructed.

After receiving his M.D. at the Johns Hopkins University School of Medicine in 1921, Roy Hoskins had assumed the Chair of Physiology at the Ohio State University School of Medicine.¹⁵¹ His first postdoctoral fellow had been Milton O. Lee, who worked in Hoskins' laboratory and served as Hoskins' editor until after World War II. Mrs. Lee had been Hoskins' secretary. Lee was on the publication board of the journal *Endocrinology* in 1936 when that journal made major changes in the format of its volume 20. Among these changes was the use of ornamental tailpieces to occupy space at the ends of articles.

By 1953, Milton Lee was the managing editor of the American Physiological Society's journals. That year, the *American Journal of Physiology* changed from a one- to a two-column format, leaving awkward spaces at the ends of some articles. From his experience with *Endocrinology*, Lee knew that he could solve this aesthetic problem by using tailpieces to occupy the blank space, but what could he use?

Lee knew Homer Wheelon through his long association with Roy Hoskins. Indeed, Lee had requested and received a copy of Part 1 of *Rabbit No. 202* from Wheelon in July of 1941.¹⁵² Lee greatly admired both Wheelon's writing and his art, and he felt that there could be no better source for the tailpieces than the illustrations from *Rabbit No. 202*.¹⁵³ Although enthusiasm was mixed among members of the Board of Publication Trustees, the use of the illustrations was approved.¹⁵⁴

The tailpieces first appeared in Volume 174 of the *American Journal of Physiology*¹⁵⁵ with a brief attribution:

Illustrations used for tailpieces are reproduced from *Rabbit No. 202* (Seattle, 1940), through the courtesy of the author-artist, Homer Wheelon.

At its meeting in November of 1953, the Society's Board of Publication Trustees commented favorably on the use of the illustrations.¹⁵⁶ In fact, it suggested a more complete (if inaccurate) attribution:

Illustrations used for tailpieces are reproduced from *Rabbit No. 202* (Seattle, 1940), through the courtesy of the author-artist, Homer Wheelson (sic), Professor of Medicine at the University of Washington,¹⁵⁷ and member of the American Physiological Society since 1919.

The original attribution was used in one more volume of the *American Journal of Physiology*. The illustrations were first used two years later in Volume 8 of the *Journal of Applied Physiology* without attribution. Wheelon's images have continued to adorn these journals to the present day, but without even periodic attribution.

SUMMATION

It is a measure of our mortality that, only 50 years after his death, Homer Wheelon is relatively unknown, although he accomplished much in his life. Wheelon contributed 32 publications to the physiological literature, and he trained J. Earl Thomas, an important twentieth century gastrointestinal physiologist. However, the scholar studying Wheelon and Thomas's burst of gastrointestinal studies from the early 1920s might wonder what became of the senior author.

Wheelon practiced medicine in Seattle for 40 years, but the only traces of his labors are a few of his paintings hanging in hospital corridors. Wheelon's paintings and drawings occasionally appear in shops in the Northwest. In 2003, the abstract painting that hung in the Wheelons' front hall for many years was offered for sale on the Internet. His notable eye for design and sometimes startling worldview must raise questions in the mind of the library browser who discovers a copy of *Rabbit No. 202*. Readers of the *American Journal of Physiology* and the *Journal of Applied Physiology* are fortunate to see some of his images, but they must puzzle about their source and relevance.

We have sought to describe the background for the physiological and artistic accomplishments of Homer Wheelon, to trace how his disparate interests coalesced in a lengthy, illustrated poem, and to discover how images from that poem have remained in publication for half a century. Our purposes will have been served if we have captured Homer Wheelon's memory, satisfied the curiosity of some of our readers, and provoked others to study the tailpieces in the *American Journal of Physiology* and the *Journal of Applied Physiology* more closely.

ACKNOWLEDGEMENT

Mrs. Lula Wheelon, Homer Wheelon's widow, provided access to her private correspondence and other papers and artifacts, and she spent many hours relating events in her life and Homer Wheelon's life.

Ms. Lucy Lawrence, as a young woman, typed the original manuscripts of *Rabbit No. 202* from Homer Wheelon's almost impossibly illegible script. Forty-five years later, she spent hours helping the author with early drafts of this manuscript.

Dr. F. Wilson Jackson III, M.D. served an internship with L. Schramm before entering medical school. His sharp eye and sensitivity to poetry led to most of the interpretations of *Rabbit No. 202* used in this paper.

Wayne Hayward, one of Lula Wheelon's "house boys" while he attended the University of Washington, and John and Dorothy Conway, close friends of the Wheelons, provided valuable insight into the daily lives of the Wheelons.

Toby Apel shared minutes of the American Physiological Society's committee meetings.

Dr. John Wiegenstein, M.D., Wheelon's colleague at the Polyclinic introduced L. Schramm to Lula Wheelon and provided important insights into Wheelon's final years at the Polyclinic.

Horace Davenport provided important criticism of an earlier draft of this manuscript as well as insight into the history of physiology. His encouragement is very much appreciated.

Karyl Winn of the Manuscripts and University Archives Division of the University of Washington provided invaluable assistance in moving the collection of the Wheelon and Meacham family papers to the University of Washington Library.

Finally, and perhaps most importantly, Diana Schramm has lived for twenty years with her husband's compulsion to understand Homer Wheelon. She has provided invaluable criticism, editorial assistance, and moral support.

ENDNOTES

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- ¹ Dr. John Lingenfelter confirmed this account of the inspiration for Rabbit No. 202 in interviews in 1985 and 1987.
 - ² Friedman, M.H. and M.E. Lapham. A simple, rapid procedure for the laboratory diagnosis of early pregnancies. *American J. Ob. and Gyn.* 21: 405-410, 1931. The Friedman test was published just two years before Lingenfelter used it in Seattle. Its accuracy in the early determination of pregnancy was one of the great triumphs of 20th century medicine.
 - ³ Accounts of Wheelon's early life are drawn from descriptions written by him in middle age and transcribed by his wife, Mrs. Lula Wheelon. These written accounts were supplemented by second-hand accounts provided by Mrs. Wheelon during interviews. Unless otherwise stated, all written material on which this paper is based resides in the Manuscripts and University Archives Division (hereafter, MUAD) of the University of Washington, Seattle, Washington. This material is cataloged as *Wheelon and Meacham Families*, Accession Numbers 3954 and 3954-2.
 - ⁴ Wheelon's middle name, Homer, was clearly his and his parents' favorite. The name was derived from that of Homer Horatio Seerley, Wheelon's mother's favorite professor at the Iowa State Normal School. Wheelon signed his drawings and paintings "Charles Homer Wheelon" or "C. Homer Wheelon" until adolescence, at which time he dropped the "Charles" completely, even on many official documents.
 - ⁵ Smith, W.T., *The Human Body and Its Health*. New York, American Book Company, 1884.

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- ⁶ It is not certain that Wheelon attended schools only in Shelburn. In fact, his report cards from this period are from the Albany, Oregon, school system. Albany would have been only a short train ride from Shelburn.
- ⁷ The Seattle Seminary survives as the Seattle Pacific University.
- ⁸ While Homer was in Palo Alto, a cousin of the Best family lived with his parents while working as a teacher in Seattle. It is not clear whether there was any connection between these two events. Best went on to become a well-known inventor.
- ⁹ Wheelon, L.M., personal communication.
- ¹⁰ Meacham, L.M., diary, January 10, 1908.
- ¹¹ Wheelon, L.M., personal communication. Mrs. Wheelon described her first meeting with Homer as follows. The Wheelons and the Meachams were at a camp meeting. The children and some of the adults went swimming at a nearby beach. Although almost everyone else splashed in the water, Homer occupied himself on the shore with a toy cannon, appearing to take pleasure in the anxiety elicited in the other children by its loud reports.
- ¹² Meacham, L.M., diary, August 22, 1909.
- ¹³ Transcripts for Homer Wheelon, University of Washington.
- ¹⁴ This is now the University of Washington's Friday Harbor Station, San Juan Island, Washington.
- ¹⁵ Gaberlet, M. L. *The Windows on his World: the Story of Trevor Kincaid*. Palo Alto, California, Pacific Books, 1975.
- ¹⁶ Wheelon, H. to Lula Meacham, letter #25, undated, but probably 1911. L.M. Wheelon confirmed these conversations.
- ¹⁷ MUAD, accession number 3954-2, see endnote #4.
- ¹⁸ Wheelon, L.M., personal communication.
- ¹⁹ Lula's mother invoked as an example of the artist's sordid life the recent sensational murder of Stanford White. In 1906, White, one of America's leading turn-of-the-century architects, was shot by Harry K. Thaw, the husband of White's alleged mistress, Evelyn Thaw. The sensational case came to trial in January, 1907, approximately one year before Mrs. Meacham's reference. Newspaper articles on the anniversary of the trial may have brought it to mind.
- ²⁰ Gift to Lawrence Schramm from L. Wheelon.
- ²¹ Wheelon contributed drawings to a number of high school and college yearbooks, among them the yearbook for the Sunnyside High School in 1910 and *The Cascade* of the Seattle Seminary in 1911.
- ²² Wheelon drew nine of the illustrations for the 1913 *The Oregana*, published in 1912. The reason for the discrepancy in the dates is that the yearbook was officially a project of the *Junior* class.
- ²³ Wheelon, H. to L. Meacham, October 9, 1911.
- ²⁴ MUAD, Accession Number 3954, Box 3
- ²⁵ MUAD, Accession Number 3954, Boxes 5A and 5B. These letters provide a valuable source of information on graduate, medical, and nursing student life in the early twentieth century.
- ²⁶ Wheelon, H. to L. Meacham, January 3, 1912 and February 22, 1912.

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- ²⁷ Wheelon may have just read Walter Cannon's recently published monograph describing his use of X-rays to study the motility of the gastrointestinal tract. Cannon, W.F. *The Mechanical Factors of Digestion*. New York, Longmans, Green and Co., 1911.
- ²⁸ Williamson, H.F. and P. S. Wild. *Northwestern University: A history 1850-1975*. Evanston, Northwestern University, 1976, pp. 113-123. In 1911-12, the first year that the medical school required two years of college for matriculation enrollment dropped from 533 to 259. In Wheelon's first year, 1912-13, enrollment dropped further to 200, and in 1913-14, it reached a low point, 181. In addition, the entire university was suffering financially as it tried to expand programs and facilities in the face of strong pressures not to incur debt.
- ²⁹ Wheelon had to miss some classes in order to work, and, for this reason, he nearly forfeited a grade in chemistry.
- ³⁰ See, for instance Hall, W.S., *Youth and Its Problems*. Philadelphia, The John C. Winston Company, 1918.
- ³¹ This book was never published. However, one of the completed illustrations and several sketches survive.
- ³² Wheelon, H. to L. Meacham, March 15, 1913 and May 9, 1913.
- ³³ The paper that was to result from this research, Hall, W.S., "A problem in embryonic nutrition," was scheduled for the section on Pathology and Physiology of the American Medical Association's annual meeting in Minneapolis, Wednesday, June 18, at 2:00 P.M. (See program in *J. Amer. Med. Assoc.* 60: 1452, 1913.) However, because Hall subsequently went to Europe, the paper was not given, and the abstract did not appear in the proceedings in *J. Amer. Med. Assoc.* 61: 32, 1913).
- ³⁴ Wheelon, H. to L. Meacham, October 20, 1913.
- ³⁵ Wheelon, H. to L. Meacham, October 20, 1913.
- ³⁶ Bennison, S. A.C. Barger, and E.L. Wolfe. *Walter B. Cannon, The Life and Times of a Young Scientist*. Cambridge, Massachusetts, Harvard University Press, 1987, p. 257.
- ³⁷ Wheelon, H. to L. Meacham, October 12, 1913.
- ³⁸ Hoskins would eventually earn an M.D. at The Johns Hopkins University School of Medicine.
- ³⁹ Later to become the Medical School of The Ohio State University.
- ⁴⁰ Hoskins, R.G. and C.W. McClure. The adrenal glands and blood pressure. *Arch. Int. Med.* 10:343-356, 1912.
- ⁴¹ Elliot, T.R. On the action of adrenalin. *J. Physiol.* 31: xx-xxi, 1904.
- ⁴² Hoskins, R.G. and H. Wheelon. The variability of blood pressure and of vasomotor irritability in the anesthetized dog. *Am. J. Physiol.* 34: 81-88, 1914.
- ⁴³ Gaunt, R. History of the adrenal cortex. In Greep, R.O. and E.B. Astwood (eds). *Handbook of Physiology*, Section 7: Endocrinology. Washington, D.C., American Physiological Society, 1975, pp1-12.

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- ⁴⁴ Biedl, A. *Innere Sekretion*. Berlin, Urban & Schwarzenberg, 1910. In this same work, Biedl extensively reviews the history of adrenalectomy and concludes that, most likely, it is the adrenal cortex, not the adrenal medulla, that is necessary for life. However, he does not strongly support any of the then current hypotheses on the role of the adrenal cortex. An excellent translation of this monograph is: Biedl, A. *The Internal Secretory Organs: Their Physiology and Pathology*. London, John Bale, Sons & Danielsson, Ltd., 1913.
- ⁴⁵ Wheeler, T.D. and S. Vincent. The question as to the relative importance to life of cortex and medulla of the adrenal bodies. *Trans. Roy. Soc. Can.* 11: 125-127, 1917.
- ⁴⁶ Elliot, T.R. On the action of adrenalin. *J. Physiol.* 31: xx-xxi, 1904.
- ⁴⁷ Langley, J.N. and W.L. Dickinson. Pituri and nicotine. *J. Physiol.* 11: 19-306, 1890, pp.297.
- ⁴⁸ Hoskins, R.G. and H. Wheelon. Adrenal deficiency and the sympathetic nervous system. *Am J. Physiol.* 34: 172-185, 1914.
- ⁴⁹ Wheelon, H. The interpretation of blood pressure variations. *New York Medical Journal* 6: 505-513, 1921. Some portion of this work was read before the St. Louis Medical Society, February 15, 1921. The occasion was a symposium on hypertension and renal disease. Although the program lists ten minutes as the time allotted to the paper, the published version in the *New York Medical Journal* fills nine, large-format, double-column pages.
- ⁵⁰ Hoskins was unable to replicate all of these results in subsequent experiments (Hoskins, R.G. The effect of partial adrenal deficiency upon sympathetic irritability. *Am. J. Physiol.* 36: 423-429, 1915.) In this paper, he described a *decrease* in sympathetic excitability due to chronic, *partial* destruction of adrenal tissue. He could not explain the discrepancy between the studies, but he suggested that the extra stress due to the laparotomy (which was acute in the earlier experiments) caused other systems to fail before the sympathetic nervous system failed. He did not recognize the debilitating effects of the multiple ether anesthetizations required by the earlier paradigm.
- ⁵¹ Hoskins, R.G. and H. Wheelon. Parathyroid deficiency and sympathetic irritability. *Am. J. Physiol.* 34: 263-270, 1914.
- ⁵² Hoskins, R.G. and H. Wheelon. Ovarian extirpation and vasomotor irritability. *Am. J. Physiol.* 35: 119-123, 1914.
- ⁵³ Beifeld, A.F., H. Wheelon, and C.R. Lovellete. The influence of hypotensive gland extracts of vasomotor irritability. *Am. J. Physiol.* 40: 360-365, 1916.
- ⁵⁴ Wheelon, H. to L. Meacham, March 3, 1914.
- ⁵⁵ Wheelon, H. Extirpation of the testes and vasomotor irritability. *Am. J. Physiol.* 35: 283-291, 1914.
- ⁵⁶ James, W. *Psychology*, New York, H. Holt and company, 1982.
- ⁵⁷ Hall, W. S., *Youth and its Problems: The Sex Life of a Man*. Philadelphia, The John C. Winston Company, 1919.
- ⁵⁸ Hall, W.S., II. Personal communication.
- ⁵⁹ Cannon, W.B. The interrelations of emotions as suggested by recent physiological research. *Am. J. Psychol.* 25: 256-282, 1914.
- ⁶⁰ Wheelon taught (or taught in) the summer physiology course.

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- ⁶¹ From Wheelon's list of positions, transcribed by Lula Wheelon: "Dr. A.J. Carlson recommended me to Dr. Don Joseph as an Assistant in the Department of Physiology at the St. Louis University." Actually, the position was probably a Lectureship.
- ⁶² Wheelon, H. to L. Meacham, October 19, 1914.
- ⁶³ Wheelon, H. to L. Meacham, October 9, 1914.
- ⁶⁴ Wheelon, H. to L. Meacham. August 16 and September 20, 1914.
- ⁶⁵ Code, C.F. Presentation of the Julius Friedenwald Medal to Jacob Earl Thomas. *Gastroenterology* 63: 725-727, 1972.
- ⁶⁶ Lula Wheelon had had a "kitchen table" appendectomy as a girl. The Wheelons learned several years later that adhesions from that operation had left her unable to have children. See, for instance, Wheelon, L. to Esther Meacham, January 7, 1921.
- ⁶⁷ Wheelon, L.M., personal communication.
- ⁶⁸ Hall, W.S. to H. Wheelon, December 21, 1916.
- ⁶⁹ Wheelon, H. and J.U.L. Shipley. The effects of testicular transplants upon vasomotor irritability. *Am. J. Physiol.* 39: 394-400, 1916. This paper represents a low point in Wheelon's writing. It does not have a proper introduction; the experiments are superficially described; it contains no discussion.
- ⁷⁰ Wheelon, H. The interpretation of blood pressure variations. *New York Medical Journal* 6:505-513, 1921. Some portion of this work was read before the St. Louis Medical Society, February 15, 1921. The occasion was a symposium on hypertension and renal disease. Although the program lists ten minutes as the time allotted to the paper, the published version in the *New York Medical Journal* fills nine, large-format, double-column pages.
- ⁷¹ Neilson, C.H. and H. Wheelon. Studies on the resistance of the red blood cells. I. Resistance of the red blood cells in health to the hemolytic action of sapotoxin. *J. Lab. Clin. Med.* 6: 454-462, 1920-21.
- ⁷² Neilson, C.H. and H. Wheelon. Studies on the resistance of the red blood cells. II. The resistance of the red blood cells in disease to the hemolytic action of sapotoxin. *J. Lab. Clin. Med.* 6: 487-504, 1920-21.
- ⁷³ Neilson, C.H. and H. Wheelon. Studies on the resistance of the red blood cells. III. The relation of cholesterol to the resistance of the red blood cells to the hemolytic action of sapotoxin. *J. Lab. Clin. Med.* 6: 568-578, 1920-21.
- ⁷⁴ Code, C.F. Presentation of the Julius Friedenwald Medal to Jacob Earl Thomas. *Gastroenterology* 63: 725-727, 1972.
- ⁷⁵ Wheelon, H. to L. Meacham, May 9, 1913.
- ⁷⁶ Cannon, W.B. *The Mechanical Factors of Digestion*. New York. Longmans, Green, 1911.
- ⁷⁷ Cannon, W.F. *The Mechanical Factors of Digestion*. New York, Longmans, Green and Co., 1911.
- ⁷⁸ Wheelon, H. to L. Meacham, January 30, 1912.
- ⁷⁹ Arey, L.B. *Northwestern University Medical School, 1859-1959*, Northwestern University, Evanston, 1959, p. 194. A senior course in roentgenology was introduced at Northwestern in 1912.

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- ⁸⁰ Directory of the Bethesda Hospital, Published in the Bethesda Herald, Thirteenth Annual Report, Vol. 29, Number 3, July and August 1919.
- ⁸¹ Neilson, C.H. and S.T. Lipsitz. The effect of various procedures on the passage of liquids from the stomach. *J. Amer. Med. Assoc.* 64: 1052-1058, 1915.
- ⁸² Wheelon, H., telegram to L. Meacham, June 18, 1915 and letter, June 21, 1915.
- ⁸³ Kuntz, A. and J.E. Thomas. On the nature of the rhythmic contractions in the stomach and intestines. *Proc. Soc. Exp. Biol. and Med.* 20: 256-258, 1922.
- ⁸⁴ Kuntz, A. The distribution of sympathetic neurones in the myenteric and submucous plexuses in the small intestine of the cat. *Anat. Record* 14: 42, 1918.
- ⁸⁵ Joseph, D.R. and S.J. Meltzer. A demonstration of the inhibitory effect of magnesium upon normal and artificial peristalsis of the stomach and duodenum. *Proc. Soc. Exptl. Biol. and Med.* 7: 95-96, 1909-1910.
- ⁸⁶ Joseph, D.R. and S.J. Meltzer. Simultaneous graphic registration of gastric and duodenal peristalsis in rabbits: a demonstration. *Proc. Soc. Exptl. Biol. Med.* 8: 15-16, 1910-1911.
- ⁸⁷ Wheelon, H. and J.E. Thomas. Observations on the motility of the duodenum and the relation of duodenal activity to that of the pars pylorica. *Am. J. Physiol.* 59: 72-96, 1922.
- ⁸⁸ Wheelon, H. and J.E. Thomas. The autonomic nervous system and disorders of the stomach. *Modern Medicine* 2: 283-290, 1920.
- ⁸⁹ Wheelon, H. and J.E. Thomas. The autonomic nervous system and disorders of the stomach. *Modern Medicine* 2: 283-290, 1920, figure V, p 298.
- ⁹⁰ For an excellent, modern description of Pavlov's research on the stomach and the events leading up to the Nobel Prize, the reader is referred to Todes, D.P., *Pavlov's Physiology Factory*. The Johns Hopkins University Press. Baltimore, 2002.
- ⁹¹ Cannon, W.B. *The Mechanical Factors of Digestion*. New York. Longmans, Green, 1911.
- ⁹² In Pavlov's case, the most damaging criticism came from the English physiologists, Bayliss and Starling, whose research diminished the importance of neural pathways in controlling digestive processes. Bayliss, W.M. and E.H. Starling. The mechanism of pancreatic secretion. *J. Physiol.* 28: 325-353, 1902. In Cannon's case, the most damaging evidence against the control of gastric emptying by acid was provided by the work of Wheelon and Thomas. Davenport, *op cit.*, p 35ff.
- ⁹³ Cannon, W.B. The acid control of the pylorus. *Am. J. Physiol.* 20: 283-322, 1907.
- ⁹⁴ Davenport, *op cit.* pp 33-34.
- ⁹⁵ Wheelon, H. and J.E. Thomas. Observations on the motility of the antrum and the relation of rhythmic activity of the pyloric sphincter to that of the antrum. *J. Lab. Clin. Med.* 6: 124-143, 1920.
- ⁹⁶ Wheelon, H. and J.E. Thomas. Observations on the motility of the duodenum and the relation of duodenal activity to that of the pars pylorica. *Am. J. Physiol.* 59: 72-96, 1922.
- ⁹⁷ Wheelon, H. and J.E. Thomas. Rhythmicity of the pyloric sphincter. *Am. J. Physiol.* 54: 460-473, 1921.
- ⁹⁸ Alvarez, W.C. and L.J. Mahoney. The relations between gastric and duodenal peristalsis. *Am. J. Physiol.* 63: 371-386, 1923.

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- ⁹⁹ Wheelon, H. Relation of the gastric content to the secretory and motor functions of the stomach. *Arch. Int. Med.* 28: 613-631, 1921.
- ¹⁰⁰ Cannon, W.B. to H. Wheelon, March 13, 1922.
- ¹⁰¹ Alvarez, W. C. *The Mechanics of the Digestive Tract.* New York, Paul B. Hoeber, Inc. 1928.
- ¹⁰² Bockus, H.L. *Gastro-enterology.* Philadelphia, W.B. Saunders Company, 1943.
- ¹⁰³ Based on a survey of citations in the *American Journal of Physiology* and the *Journal of Clinical Investigation* from 1920 to 1930.
- ¹⁰⁴ Gaffney, P.R., J.W. Hall, and M.P. Brady. The manometric findings at the human pylorus. The evidence against the presence of a tonic sphincter. *Sc. J. Gastr.* 22: 525-533, 1987.
- ¹⁰⁵ Friedman, M.H.F., In Memoriam—J. Earl Thomas, M.D., D.Sc. *Proceedings of the Thomas (J. Earl) Memorial Symposium.* Baltimore, University Park Press, 1975, pp. ix-xi.
- ¹⁰⁶ Wheelon, H. Relation of the gastric content to the secretory and motor functions of the stomach. *Arch. Int. Med.* 28: 613-631, 1921.
- ¹⁰⁷ Code, C.F. Presentation of the Julius Friedenwald Medal to Jacob Earl Thomas. *Gastroenterology* 63: 725-727, 1972.
- ¹⁰⁸ Wheelon, L.M., personal communication.
- ¹⁰⁹ An excellent historical account of the controversy over the role of the pylorus in regulating the emptying of the stomach can be found in Davenport, H.W., *Gastrointestinal physiology, 1895-1975: motility.* In Wood, J.D., *Handbook of Physiology*, Section 6: *The Gastrointestinal System*, Bethesda, American Physiological Society, 1989, pp 35-36.
- ¹¹⁰ In an interesting unpublished manuscript which Wheelon and Thomas worked on in 1926 (currently in the possession of M.H.F. Friedman), Thomas's criticisms in the margins suggest that Wheelon was over interpreting data and drawing unjustified conclusions. By this time, Thomas played the role of the senior scientist cautioning a student.
- ¹¹¹ Wheelon, L.M. to H. Wheelon, April 24, 1918.
- ¹¹² Wheelon, L.M., personal communication.
- ¹¹³ Wheelon, L.M. to Esther Meacham (by then divorced from Edward Stillwell) July 4, 1921.
- ¹¹⁴ Wheelon, L.M., personal communication
- ¹¹⁵ The University of Washington Catalog for 1923-24, p. 23, lists Wheelon as Instructor in Psychology. For some reason, he is not listed with the other instructors on page 13. In his notes, Wheelon identified Abnormal Psychology as the course he taught. Page 264 of the Catalog lists "Guthrie" as the teacher of Abnormal Psychology. Perhaps Guthrie was on leave.
- ¹¹⁶ Wheelon, H. Duodenal motility: Radiographic observations following the direct injection of barium into the human duodenum. *J. Amer. Med. Assoc.* 80: 615-620, 1923.
- ¹¹⁷ See, for instance, the note on blood pressure variations recorded in the *Bulletin of the King County Medical Society* 6: 16-22, 1927.
- ¹¹⁸ Lula Wheelon, personal communication.

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- ¹¹⁹ See, for instance, "Annual Art Exhibit Opens," *Seattle Times*, April 27, 1924; Pollard, L. "Why is Modernistic Art? Critic Replies." *Seattle Post-Intelligencer*, April 6, 1928. That Wheelon's artistic efforts were not so well known 9 years later is indicated by the notice in the *Seattle Times* for September 30, 1937, that the exhibition of his surrealist work, *Brains and Clouds*, was "a surprise to Dr. Wheelon's many friends."
- ¹²⁰ Wheelon, H. The incidence of endocrinopathies in the Puget Sound basin. *Endocrinology* 7: 689-698, 1923.
- ¹²¹ Conway, J, personal communication.
- ¹²² Having discovered that Lula would not be able to have children, the Wheelons desperately and hurriedly adopted a five-year-old son, "Kay," from eastern Washington in 1924. Shortly after he arrived, Kay was diagnosed with tuberculosis. The Wheelons had not learned that his mother had died of the disease. Kay was quarantined, and when he returned to the Wheelons, he failed to become acculturated to the household. In 1934, Kay left to live with relatives in eastern Washington.
- ¹²³ Hayward, W., personal communication.
- ¹²⁴ Wheelon, H. to L.M. Wheelon, summer, 1934.
- ¹²⁵ Accounts of Wheelon's work habits were related by L.M. Wheelon and corroborated by Dr. W. Hayward.
- ¹²⁶ Hoskins, R.G. *The Tides of Life: The endocrine glands in bodily adjustment*. New York, W.W. Norton & Company, Inc., 1933.
- ¹²⁷ Wiegenstein, J. personal communication.
- ¹²⁸ Several of these cards exist in MUAD, see endnote #4.
- ¹²⁹ Compare this portion of the poem with Frazer, J.G., *The Golden Bough: A Study in Magic and Religion*. New York, The MacMillan Company, 1960 (abridged edition), Chapters XXIX through XLII.
- ¹³⁰ Wheelon, H. *Rabbit No. 202*, Part 2, p. 161.
- ¹³¹ Wheelon, H. The internal secretion of the testes (Collective Abstract). *Interstate Medical Journal* 24: 1089-1099, 1917.
- ¹³² Wheelon, H. The testicular hormone. *Endocrinology* 3: 16-28, 1919.
- ¹³³ Wheelon, H. Physiology, physiological chemistry and experimental pathology of the testis. In *Endocrinology and Metabolism*, Barker, L.F. (Ed). New York, D. Appleton and Company, 1922, pp. 430-470.
- ¹³⁴ Wheelon, H. Incretory functions of the testis. In *The Cyclopedia of Medicine*. Piersol, G.M. (Ed). Philadelphia, F.A. Davis Company, 1932, pp. 217-264.
- ¹³⁵ MUAD, accession number 3954, Box 13.
- ¹³⁶ Compare this portion of the poem with Frazer, J.G., *The Golden Bough: A Study in Magic and Religion*. New York, The MacMillan Company, 1960 (abridged edition), Chapters XXIX through XLII.
- ¹³⁷ MUAD, accession number 3954, Box 1
- ¹³⁸ Wheelon, H. *Rabbit No. 202*, p. 123.
- ¹³⁹ John Lingenfelter, the endocrinologist whose performance of the Friedman pregnancy test had inspired *Rabbit No. 202*, had introduced Leake and Wheelon several years earlier.

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- ¹⁴⁰ Leake, C.D. to H. Wheelon, July 29, 1940. "...We'll do a good job for you in the *Quarterly*. You can at least have the intellectual satisfaction and joy of being able to distribute attractively prepared copies of it to your friends. These will be put out as though they were privately printed and will contain no reference to the *Quarterly*."
- ¹⁴¹ Leake, C.D. to H. Wheelon, October 14, 1940.
The reprints consisted of two volumes. Part 1 constituted the first volume. Parts 2 and 3 constituted the second volume.
- ¹⁴³ At this writing, approximately 400 copies of Part 2 exist.
- ¹⁴⁴ Wheelon, H. to R. G. Miller, February 20, 1942.
- ¹⁴⁵ Wheelon, H. to C.D. Leake, January 12, 1942.
- ¹⁴⁶ Thompson, M. to H. Wheelon., October 31, 1940.
- ¹⁴⁷ For instance, Wheelon, H., *A Face Cut in Jade*.
- ¹⁴⁸ This work is represented by hundreds of negatives in MUAD, see endnote #4.
- ¹⁴⁹ Wheelon, H. to F. H. Redewill, Secretary of the American Physicians Art Association, September 29, 1947.
- ¹⁵⁰ Rose, A.L. to H. Wheelon. March 15, 1948.
- ¹⁵¹ Hoskins had been at this same school, after leaving Cannon's laboratory, when it had been the Starling Ohio Medical School.
- ¹⁵² Himwich, W.A. to Wheelon, H., July 12, 1950; Lee, M.O. to H. Wheelon, August 4, 1941; Lee, M.O. to H. Wheelon, September 30, 1941.
- ¹⁵³ Leslie, S. personal communication.
- ¹⁵⁴ Davenport, H.W., personal communication. Apparently, the objections owed more to the animosity between some members of the Trustees and Milton Lee than to dissatisfaction with Wheelon's drawings *per se*.
- ¹⁵⁵ This was the second volume of the journal to use the new two-column format.
- ¹⁵⁶ Draft and summary minutes of the Publications Trustees of the American Physiological Society for November 15, 1953. Notes kindly provided by Dr. Toby Appel.
- ¹⁵⁷ In fact, Wheelon was not on the staff of the Medical School.