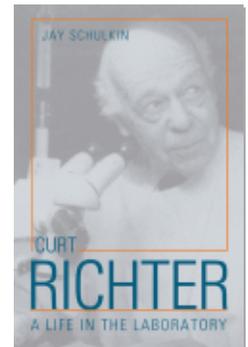# Curt Richter

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CHAPTER 3

Ingestive Behaviors and the Internal Milieu

Self-regulation of the internal milieu was a fundamental scientific subject for Curt Richter. He was not alone in this, but he was a major force in providing interesting and informative contexts in which to consider the biological adaptation required for bodily health. The internal milieu and its maintenance, or the concept of homeostasis (Cannon 1932/1966), was a fundamental category in his scientific lexicon.

Richter's work on the subject was a direct outgrowth of that of Bernard and Cannon. As Richter understood the work: "Both Bernard and Cannon concerned themselves almost entirely with the physiological and chemical regulators of the internal environment. The results of our own experiments have shown that behavior or total organism regulators also contribute to the maintenance of a constant internal environment" (Richter 1942–43, p. 64). Of course, the orientation toward the "total organism" is reminiscent of Adolf Meyer. These are the ideas Richter assumed, the culture of ideas he inherited and combined with a general sense of adaptation.

Another key concept for Richter was the ancient idea of self-preservation. Several hundred years before Darwin, Spinoza (1668/1955), in his great treatise *On the Improvement of the Understanding,* would make self-preservation fundamental to living entities (in long-lived organisms). Darwin (1859/1965) situated the concepts of self-preservation, self-regulation, and self-defense of internal viability within overall biology. Adaptation, speciation, diversity, and sexual dimorphism were all part of both behavior and physiology (Gould 2002).

REGULATION OF THE INTERNAL MILIEU
AND PHYSIOLOGICAL HOMEOSTASIS

Claude Bernard brought an experimental focus to the study of the internal milieu (Olmsted and Olmsted 1952; Holmes 1974). His logic of discovery centered on the functioning of biological tissue during normal conditions and under pathological duress. The body was indeed a "wonderful machine" for Bernard, and he focused his investigations on understanding bodily mechanisms.

Richter was clearly influenced by Bernard. Bernard's mentor, François Magendie, was the founder of experimental physiology and one of the first to use rodents in experimental physiology (Olmsted 1944; Holmes 1974; Wirth 1989). Among other things, Magendie was interested in pancreatic function and bodily responses to toxins. The logic of the experimental method in physiological studies was perhaps clarified by the work of William Harvey and was later expanded on by Magendie, Bernard, and many other investigators (Olmsted and Olmsted 1952; Holmes 1974).

Bernard's work on pancreatic function set the stage for investigations into the "chemistry of digestion" (Bernard 1856/1985, p. 1), which would be integral to understanding the maintenance of the internal milieu. These studies were performed in long-term experimental preparations (e.g., Pavlov 1897/1902; G. P. Smith 2000).[1] The idea of bodily regulation of the internal milieu did not originate with Richter; it was very much in the zeitgeist when he began to study it. Nor did it originate with Cannon, with whom we normally associate the phrase "wisdom of the body," but with a British physiologist, Ernest Starling (1923), in a lecture delivered to the Royal College of Physicians in London.[2]

CANNON AND BODILY REGULATION

Embodied in the concept of the "wisdom of the body" that Cannon inherited from Starling are the ways in which the body adapts to external circumstance and internal needs by generating physiological and behavioral responses. Cannon's experiments were mostly physiological, but he alluded to behavioral regulation, including the ingestion of sodium and calcium in the context of increased bodily needs. Behavioral regulation would figure in Richter's monumental contribution, behavioral homeostasis.

Cannon, in an early book entitled *Bodily Changes in Pain, Hunger, Fear and Rage,* outlined in some detail the physiology of adaptation under various

conditions, including emotional conditions, hunger, and thirst. He criticized James for overassociating emotions with movement and for classifying the emotions as a function of, for example, running away from a bear. We can be afraid and not move. We can move or not—but fear is still there (Cannon 1915/ 1929).

The regulation of the adrenal gland and the enhanced use of glucose during duress figured prominently in Cannon's text. Cannon outlined a peripheralist perspective on thirst and hunger; he saw dry mouth and stomach contractions as the primary antecedents of thirst and hunger, respectively. For thirst, "the first state . . . there is a feeling of dryness in the mouth and throat, accompanied by a craving for liquid" (Cannon 1915/1929, p. 304).

Cannon (1932/1966), in his book *The Wisdom of the Body,* brought together many of his investigations, including research on body fluid homeostasis; thirst and hunger; and homeostatic regulation of salt, sugar, protein, fat, calcium, oxygen, blood, and temperature (Cannon 1932/1966). Each would figure in Richter's inquiry. Perhaps the individual who most influenced Richter's research was Walter Cannon.

In Cannon's words: "The constant conditions which are manifested in the body might be termed equilibria. That word, however, has come to have a fairly exact meaning applied to relatively simple physio-chemical states, in closed systems, where known forces are balanced. The coordinated physiological processes which maintain most of the steady states in the organism are so complex and so peculiar to living beings—involving as they may, the brain and nerves, the heart, lungs, kidneys and spleen, all working cooperatively— that I have suggested a special designation for these states, homeostasis" (Cannon 1932/1966, p. 24). A little later, Cannon said, "It means a condition— a condition which may vary but which is relatively constant" (p. 24). In other words, homeostasis is the key to keeping the internal milieu viable, maintaining levels of glucose, and secreting adrenaline. Cannon's studies in physiology were quite broad and set the stage for Richter. Richter was much influenced by Cannon's perspective on hunger and fluid balance but noted that the brain generates the behavioral adaptations (Richter 1956d).

As noted in chapter 2, Richter found evidence linking patterns of activity and inactivity in rats to stomach contractions. And while he was not wrong to emphasize the stomach, the activation of the stomach is but one peripheral signal among others participating in the regulation of food ingestion (Friedman et al. 1985; G. P. Smith 1997).

Cannon also influenced Richter's work on the biological basis of food choice. After all, on several occasions Cannon noted that behavior serves physiology, that animals are likely to ingest calcium during pregnancy, when the need for calcium is great, and that bone and other tissue suffer the consequences of calcium deficiency. Cannon also suggested that animals might ingest sodium during periods of sodium deficiency (Cannon 1932/1966). Cannon laid the seeds for a view of behavioral regulation of the internal milieu; Richter's contribution was to expand considerably beyond Cannon's physiological perspective and show that behavior serves physiology in this regulation. No one had, or has, demonstrated this in the laboratory as elegantly as Richter. By 1941, Richter, in an essay entitled "Biology of Drives," would assert that "Bernard and Cannon dealt largely with the physiological regulators—responses of individual organs or systems—which serve to maintain a constant internal environment. Several years ago we found that the organism itself, the total organism, may also play an important part" (Richter 1941c, p. 105).

INSTINCT, BEHAVIOR, AND PSYCHOBIOLOGY

Instinct was a fundamental psychobiological category for Richter, and he saw behavior, and in particular the behavioral regulation of the internal milieu, as falling chiefly under this rubric. The concept was understood differently by different investigators.[3] There was no univocal notion of instinct, but it was (and still is) an important concept, one fundamental to Richter's scientific lexicon. Instinctive behaviors explained how animals select the nutrients and minerals needed to maintain physiological viability.

Instinct figured importantly for Darwin (1873). The issue that permeated biology and psychobiology in his day was the relationship between inherited and acquired traits. Darwin was prescient when he said, "I will not attempt any definition of instinct" (Darwin 1859/1965, p. 228). Always the consummate empiricist, Darwin gave examples of what he thought were migratory, sexual, and social instincts. He thought that domestication diminished the effectiveness of instinctive behaviors. For example, through domestication fowls became less "broody," spending less time sitting on their eggs.

Darwin noted that species-specific behavioral and physiological adaptations were richly expressed and perhaps tied to finding sources of energy and to primary motivational systems and their release in suitable environments; this was a precursor to later studies on animal behavior and ethology (Beer 1983; Craig 1918; Tinbergen 1951/1969).

Darwin, like many others, was unclear about "habits" and their link to instincts and about new instincts emerging from domestication. Throughout his writings, Darwin remained a gradualist with regard to evolutionary selection based on the emergence of instincts. He acknowledged that "instincts are not always perfect" (Darwin 1859/1965, p. 256). After all, he understood problem solving as not about perfection but about adaptation. In the *Descent of Man,* he went on to compare our evolution with that of other species and suggested that "the fewness and the comparative simplicity of the instincts in the higher animals are remarkable in contrast with those of the lower animals" (Darwin 1871/1874, p. 65).

The concept of instinct in Darwin's time, and for a hundred years afterward, was rich in multiple and confusing meanings (Beer 1983). Issues about what was heritable and the battle for Lamarckian transmission permeated the debates (Darwin 1859/1965; Morgan 1910; J. L. Gould 2002). Many ideas surround the concept of instinct, but one fundamental feature has always been the dichotomy between the inherited and the learned, or the distinction between innate and learned behaviors. Of course, it need not have been so controversial because learning is part of our innate endowment, as is adaptation to varied environments. The modern question is which behavioral systems are being recruited, and to what degree. For when intelligence is part of adaptation and of instinctive behaviors, distinctions fizzle away; the question is degree, not kind.

James, in an unusually harsh tone, wrote that "the older writing on instinct is an ineffectual waste of words" (James 1887, p. 356). Some consensus centered on the idea that instincts were reflexive responses to characteristic stimuli (cf. James 1887; Watson 1912). James, though somewhat inconsistently, thought that "instinct is usually defined as the faculty of acting in such a way as to produce certain ends without foresight" (James 1890/1952, p. 383; see also Epstein 1982). An instinct reflected sets of impulses and reflexes. One of James's examples of this was the reflexes involved in egg laying.

The sense of being hostage to instinct, blindly performing functions tied to natural selection, is a recurrent theme in the literature about instinct (cf. Epstein 1982; James 1887), as is "the close relation of instinct to reflex action" (James 1887, 1890/1952; Herrnstein 1972). The concept of a reflex became a pivotal part of characterizing instinctive responses (Herrnstein 1972). Reflexes were the way many mechanists understood how to generate a psychology based on science.

As Herrnstein made clear, at some points early in Watson's career his view on instinct was not dissimilar to James's view (Herrnstein 1972; Dewsbury 1992). Though Watson commented that "we have been brought up on James or possibly even on a worse diet" (Watson 1924, p. 110), early on, Watson provided examples of several contexts in which the concept of instinct had validity (Watson 1912; Yerkes 1903). But he also noted the variability of behavioral responses and the effects of altering early environments and minimizing instinctive responses. For example, Watson asserted that the normal fear responses of several species of birds could be suppressed by environmental events. Moreover, he challenged the notion that all behaviors, even those in which there is a biological basis, are adaptive (Watson 1912). Watson may have retained the idea that other animals had instincts, but he was interested only in humans. Therefore, Watson, under the ideological spell of behaviorism, rejected the concept of instinct; as he put it, "There are then for us no instincts. We no longer need the term in psychology" (Watson 1924, p. 94). One behaviorist practice, which would be Skinner's practice, was to apply Occam's razor to the science of behavior; no mental entities have real legitimacy. There was no "inheritance of traits," as Watson would put it; temperament, for example, could not be inherited.

But in a very real sense, instincts are to psychobiology what phrenology is to neurology, and this has resulted in a very long, complicated, and confusing literature. McDougall's (1910) work is but one example. The central questions of this period were: How many instincts can there be? What is the definition of an instinct? What are the constraints for using the concept of instinct?

The fight for legitimacy and coherence of the concept of instinct went back and forth in both North America and Europe. Throughout this fight, there were those who attempted to clarify the concept of instinct and those who primarily rejected it, the latter including Knight Dunlap, the nominal head of Richter's committee in psychology and a close colleague of Watson. Dunlap felt that the concept of instinct should be replaced with a discussion of "instinctive activities" (Dunlap 1919).

Karl Lashley, in his influential article "Experimental Analysis of Instinctive Behavior," noted that he was "well aware that instincts were banished from psychology some years ago, but that purge seems to have failed" (Lashley 1938/1960). The article defended a view of central states in which the brain underlies the periodic behavior that fascinated Richter. In that same paper, Lashley commented on the work of Richter and his colleagues, reminding the

community that stomach contractions are not the primary source of motivation to ingest food. In other words, although the contractions may have been rhythmic and linked to hunger, the instinctive and motivational responses were not. Lashley noted that the problem of motivation was closely linked to that of instinctive behavior and sensory-motor control (Stellar 1954).

Richter assumed that the concept of instinct was fundamental to understanding the specific hungers. And he found a variety of ways in which instinctive behavioral responses serve physiological viability. In other words, Richter understood that behavioral regulation of nutritional choice, the so-called wisdom of the body, and the internal milieu were central to the study of instinctive or innate adaptive responses.

INNATE NUTRITIONAL CHOICE

The intellectual climate Richter inhabited held that nutritional choice and bodily regulation were an apparent piece of biological design. Studies showed that a variety of species could select proteins, carbohydrates, and perhaps even vitamins when they were needed. In 1915, for example, Evvard reported that when swine were offered a set of nine food choices, they displayed adequate growth rates. Osborne and Mendel offered rats diets with balanced or unbalanced amino acid content and reported that the rats selected the balanced diets (Osborne and Mendel 1918).

Anecdotal observations noted in print since the eighteenth century had reported that cattle tended to ingest bone. This was interpreted as possibly reflecting a phosphorus deficiency, representing a specific appetite (Green 1925; Denton 1982). In this biological context, animals approached and avoided objects of specific nutritional value, behaviors that reflected appetitive and consummatory responses (Craig 1918).

Clara Davis studied the choice of nutrients by humans at Children's Memorial Hospital in Chicago (Davis 1928, 1935, 1939). She offered infants from six to eleven months of age, who were recently weaned and had not been exposed to "ordinary foods of adult life" (Davis 1939), a large assortment of nutritional sources. The fresh foods were prepared daily and included sweet milk, peaches, lamb, kidney, wheat, potatoes, peas, beets, and cabbage. The thirty-four food sources were not offered at the same time, but different foods were offered in separate dishes three to four times a day. Davis found that the infants selected a diet that was adequate to maintain bodily viability. She reported that the infants gained body weight and looked healthy over the duration of the test.

One could not imagine doing these experiments today. (Imagine getting by an institutional review board with this research plan.) The rationale was to look at infants at the time they were weaned and determine the adequacy of their early choices. Davis found satisfactory nutrition in most of her subjects, although not all. When four of the infants became undernourished and five appeared to have rickets, these infants were removed from the study. Davis's studies endorsed the concept of the wisdom of the body. Davis suggested that "some innate, automatic mechanism" was operative (1939, p. 260), but because she varied the diet, she also cogently suggested that there was "trial and error sampling." A caveat, however, accompanies what she calls "trial and error methods," namely, the "fallibility of appetite" (1939, p. 261). She then suggests that "there is no instinct pointing blindly to the food." However, what cannot be determined from the Davis experiments are (1) how many combinations or choices would have given a positive result and what was the minimum of choices necessary to accomplish a positive result, and (2) what was the likelihood that offering a random, well-balanced selection of foods would result in a similar outcome.

Richter thought that ingestive behavior reflected innate structure. He stepped into a rich cultural intellectual milieu that was centered around the question of adaptive versus nonadaptive nutritional choice behaviors. An intellectual debate was taking place over issues concerning innate and learned influences on behavior, and Richter would weigh in very heavily on one side. His model of behavioral control was created from the standpoint of a biological engineer. He asked the question, "What structure of behavior ensures an adequate supply of nutrients and minerals for internal viability?" Innate structure figured prominently in this model.

Richter's approach was constant and predictable in retrospect. Remove an organ (often in a surgical tour de force), understand the physiological effects of that removal, and provide opportunities for animals to restore physiological viability through behavior. For example, there was a long and varied context for studying pancreatic function in the use and digestion of foods and fuel sources (e.g., Bernard 1856/1985; Pavlov 1897/1902). Richter and his colleagues added behavioral regulation as a fundamental part of the analysis of adaptation.

McCOLLUM AND THE CORE DIET

The diets for most of Richter's studies were derived from the work of E. V. McCollum, a noted biochemist and nutritionist at Hopkins. Richter looked to

the work of his colleague for instruction in preparing diets. The McCollum diet included, among other foods, graham flour, skim milk powder, casein, butter, calcium carbonate, and salt.

BODY FLUID BALANCE: WATER AND SODIUM REGULATION

Richter thought that the excessive water intake resulting from diabetes insipidus was primarily due to polyuria (Richter 1935). The concept of body fluid regulation arose from the knowledge that water and sodium disturbances were often linked.

In experiments Richter and others observed that damage to the pituitary gland that interfered with vasopressin (ADH) secretion resulted in a compromised capacity to regulate water balance. The normal response, when dehydrated or depleted of extracellular fluid, is to conserve water through the kidney via the secretion of ADH from the pituitary. The rats in Richter's experiments ingested more water than usual. The behavior of water ingestion that normally occurs with dehydration was exaggerated in the animals in which ADH secretion was compromised. Richter concluded that behavior played a large role in maintaining internal viability. Rats drank water as a compensatory response when physiological water regulation became less competent.

Richter selected an important entry to the study of ingestive behavior, the behavioral regulation of sodium. It had been known that adrenalectomy resulted in the depletion of sodium and in potential death and that if sodium levels returned to normal, longevity increased. Cannon and others had suggested, based on anecdotal observations, that "animals travel long distances to salt licks to satisfy their hunger." Cannon added, "The nature of this hunger is quite unknown" (Cannon 1932/1966, p. 96).

Richter's insight was to add sources of sodium to the diets of adrenalectomized rats and study them using the "appetite method," as he liked to call it. When offered a range of choices, rats always ingested sodium of several concentrations in greater amounts than other solutes. Rats were often studied over a considerable period of time, and there was always normative baseline data (in this case, the ingestion of the various solutes by non-adrenalectomized rats) with which to compare the effects of the experimental manipulations (fig. 3.1). In many of the studies, Richter offered sodium solutions individually or with a range of other solutes and plain water.

Richter noted a range of ingestive patterns heavily biased toward sodium solutes when animals were hungry for sodium, as many other investigators
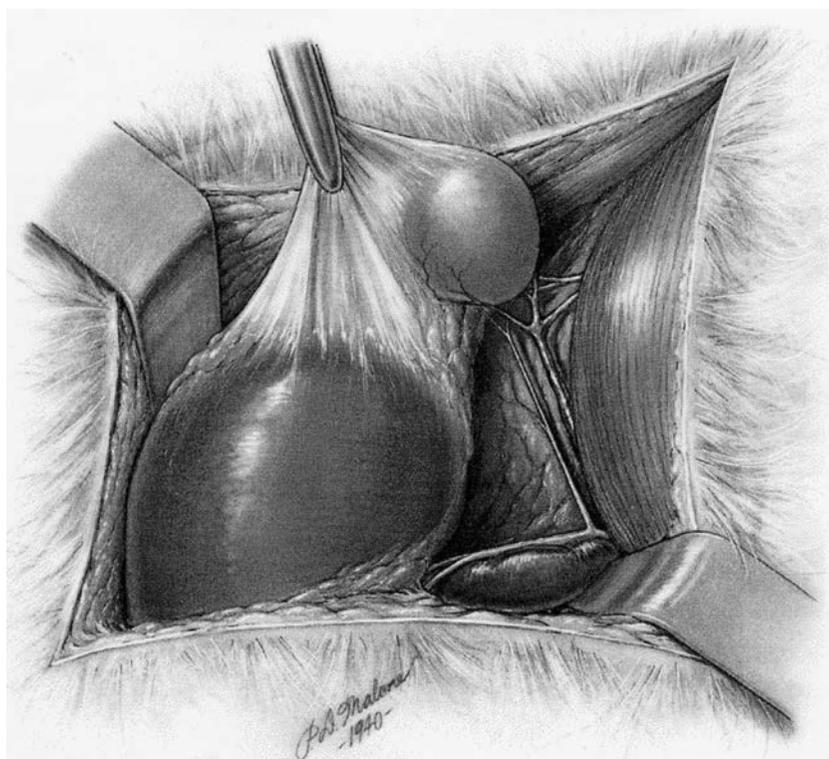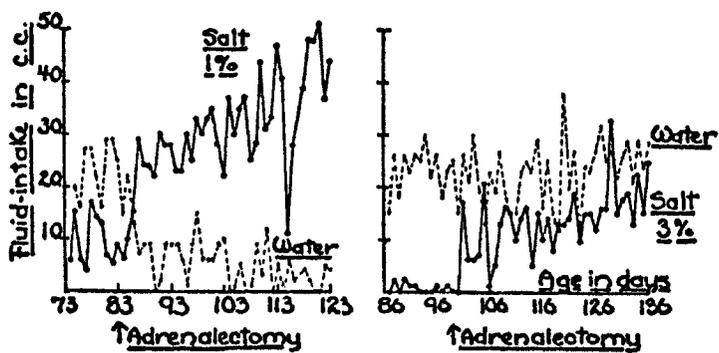
FIG. 3.1. *Top:* Salt (1 percent or 3 percent NaCl) and water intake before and after adrenalectomy. Note the increase in salt intake after adrenalectomy. *Bottom:* The adrenal gland being removed from a rat. *Source:* Richter 1936a, 1941h

have also noted (e.g., Wolf 1969; Schulkin 1991). He also noted that when the adrenal tissue was transplanted, sodium ingestion returned to normal in several of the animals studied because the rats were no longer excreting sodium in excessive amounts.

These experiments, and many others performed by Richter and his colleagues, demonstrated that "the fact that the adrenalectomized rats made advantageous selections from the various chemical solutions offered brings further evidence for the validity of Cannon's concept of the wisdom of the body" (Richter and Eckert 1938).

Richter observed that several of the animals immediately ingested the sodium when it was offered, and he suggested that adrenalectomy-induced sodium loss resulted in an innate specific appetite for sodium, something others would later demonstrate in great detail (e.g., Epstein and Stellar 1955; Wolf 1969; Denton 1982; Schulkin 1991).

Richter noted that salt and water ingestion had an inverse relationship with diabetes and, importantly, that when adrenal tissue was restored the adrenalectomized subjects decreased their intake of sodium, presumably because they could now retain it. When deoxycorticosterone was given to rats with intact adrenal glands, the ingestion of sodium increased over baseline conditions; this suggested that mineralocorticoid regulation was knotted to the behavioral in addition to the physiological regulation of sodium. It was known that water intake increased with injections of deoxycorticosterone, and this was construed as a link to a diabetes insipidus–like syndrome. Katherine Rice and Richter wanted to determine whether water intake decreased when subjects were also given a sodium solution. What were rats really interested in ingesting? Richter alternately varied the content of sodium in the diet and access to water and sodium solutions and found that polydipsia (excessive water drinking) was dependent on sodium and that the appetite for sodium was primary (Rice and Richter 1943).

Indeed, loss of sodium (and elevation of the hormones of sodium homeostasis) trigger an appetite for sodium the very first time sodium salts are encountered (Nachman 1962; Wolf 1969). This was a major tenet of Richter's and has been tested over the last sixty years in many contexts. There are disputes about the degree of specificity, but nearly every investigator agrees that the first time a sodium-hungry animal is exposed to a sodium salt it immediately ingests the salt (Wolf 1969). In such instances, sodium ingestion is relatively specific for sodium salts and occurs too quickly for the consequences

of the ingestion (absorption from the gut) to factor in the rats' immediate ingestion.

Richter described the choices offered in his typical experiments with rats and, of course, the cages in which the diets were provided. In one experiment, the rats were given seventeen choices. They preferred the sodium salt to a considerable degree. They ingested other salts, but not nearly as much as the sodium salts. When salts were offered alone, the ingestion of different concentrations of salt varied depending on the circumstance.

When rendered hungry for sodium by adrenalectomy, the rats ingested more sodium than usual; when the hormone deoxycorticosterone was implanted to the chamber of the eye, the rats' sodium intake normalized because replacing this sodium-retaining hormone halted sodium excretion. Deoxycorticosterone has both mineralocorticoid and glucocorticoid components. Rice and Richter (1943) showed that the mineralocorticoid at higher doses raised the ingestion of sodium salts preferentially over other salt solutions. Years later, others would demonstrate that aldosterone (e.g., Wolf 1964), the naturally occurring mineralocorticoid, had many of the same effects on behavior and physiology that Richter had noted with deoxycorticosterone and that the appetite for sodium is innate (cf. Weisinger and Woods 1971; Schulkin 1978).

Richter suggested that changes in the oral cavity, particularly in the gustatory system, contribute to the search for and ingestion of sodium salts when needed. In other words, the gustatory system plays a major role in the recognition of salt and the release of the consummatory response; an innate recognition or instinctual response underlies this. Richter determined, in both rats and humans, the gustatory thresholds for detecting various salts.

In one experiment, Richter offered adrenalectomized rats different concentrations of sodium salts to determine at what concentration they would prefer the sodium salt over water. Ingestion from the sodium bottle and the water bottle was determined to be about the same before the onset of the experimental manipulation (adrenalectomy). Thereafter, Richter observed the amount of sodium ingested relative to the amount of water ingested from the water and sodium bottles (offered in ascending concentrations). He suggested 0.055 percent NaCl as the concentration at which sodium-hungry rats begin to ingest more sodium salt than water (Richter 1936a, 1939a).

Richter and Alice MacLean would also do experiments in humans on gustatory responses to sodium. They placed different concentrations of NaCl in a dropper, the "drop method" or "swallow method," for normal, non-sodium-

hungry people to taste. They found that the concentration at which subjects noticed the salt taste was close to that at which the sodium-hungry rats demonstrated their sodium-seeking behavior (Richter and MacLean 1939).

Richter suggested that changes in the oral cavity played an important role in sodium regulation. Other investigators would later do more sophisticated taste psychophysics on gustatory detection thresholds in both rats and humans (e.g., Bartoshuk 1974; Spector 2000), but this basic important role of the gustatory system in the regulation of sodium ingestion was accepted. Richter also experimented with cutting all three gustatory nerves in rats and observing compromised salt ingestion (Richter 1942–43, 1956d). Later investigators would show that the chorda tympani nerve is the cranial nerve most linked to the detection of the salt taste (e.g., Pfaffmann 1967; Contreras 1977).

In an article published in 1956, and in a section titled "Salt Appetite as a Regulator of Homeostasis," Richter began, "Bernard and Cannon have shown that mammals are endowed with a number of physiological mechanisms for the maintenance of the constancy of the internal environment. This includes among other things, keeping the composition of the body fluids within exceedingly narrow limits" (Richter 1956d, p. 616). The first sentence in the next paragraph asserted that that "behavioral mechanisms also help to maintain homeostasis is clearly demonstrated by our own experiments" (p. 618). To my mind, this essay is Richter's most elegant statement of his research. In it, Richter remained close to the source of his ideas. He never strayed far, and why should he? The ideas had scientific worth and productivity written into their history.

Always with an eye for the clinical, and to legitimate total self-regulatory behavior, Lawson Wilkins and Richter noted that a three-and-a-half-year-old child with adrenal pathology ingested large amounts of table salts (Wilkins and Richter 1940). This behavior was reported by the parents of the child, who stated that "there was no other one food that he seemed to crave like salt except water." The child showed intense interest in and ingestion of salt. By contrast, he avoided sweet substances. The parents said, tragically, that "even in his sickly condition" the child was very bright and paid attention in detail to the foods offered him at home. When placed on a normal diet in a hospital setting, the child died.

Influenced by the work of Davis, Richter understood this individual case to be an analogue of the adrenalectomized rat's craving for sodium. In other words, Wilkins and Richter interpreted this as another instance of behavior serving physiology in the maintenance of body sodium balance.

CALCIUM HOMEOSTASIS

When Richter turned to the study of calcium homeostasis, he approached the problem in the same manner as he had the study of sodium. First he demonstrated a calcium appetite, and then he suggested that ingestion behavior was organized by an innate capacity to detect calcium salts and triggered by decreased levels of calcium.

Again, the experimental method was the removal of specific tissue that would threaten calcium metabolism and absorption. In this case, Richter removed rats' parathyroid glands. The loss of calcium was life threatening. McCollum, his colleague at Hopkins, had done work on calcium deprivation and the link to rickets and tetany (e.g., McCollum et al. 1922; McCollum 1964). And importantly, Cannon had indicated that, although calcium is needed at all times, there are certain times for a female "when the demand for calcium is especially great. During pregnancy she must provide calcium for the developing fetus and throughout the months of nursing she must provide an even greater amount in the milk" (Cannon 1932/1966, p. 140).

Once again, as he nearly always did, Richter adapted the McCollum low-calcium diet to his own interests. He then offered the parathyroidectomized rats different calcium solutions mixed in water, along with a separate bottle of plain water. In further experiments, he offered them conjointly a range of calcium and other mineral solutions to determine which the rats would ingest. Although he did find that calcium was generally the more consumed mineral product, other solutions were ingested on occasion, including strontium and magnesium, whereas phosphate solutions tended to be avoided (Richter and Eckert 1937b; Richter and Helfrick 1943).

Richter and his colleagues also noted that high calcium content added back to the diet reduced the intake of calcium solutions by the parathyroidectomized rats (Richter and Birmingham 1941) or monkeys (Richter, Honeyman, and Hunter 1940). The method of removing a gland and then reinstating the tissue elsewhere was part of Richter's elegant laboratory expertise and artistry, and he demonstrated that only a small part of the tissue was needed to reinstate function. He reattached parts of the parathyroid to the eye to cause the parathyroid hormone to act as a calcium-retaining hormone. When this was done, the behavior of calcium ingestion was no longer as prevalent (fig. 3.2). When parathyroidectomized rats were injected with parathyroid extracts,
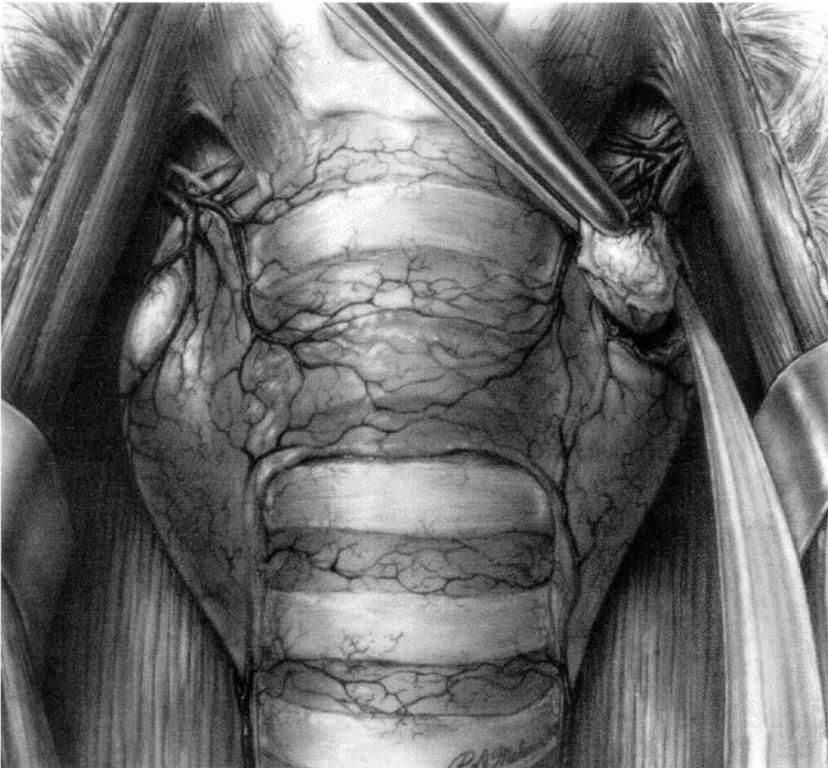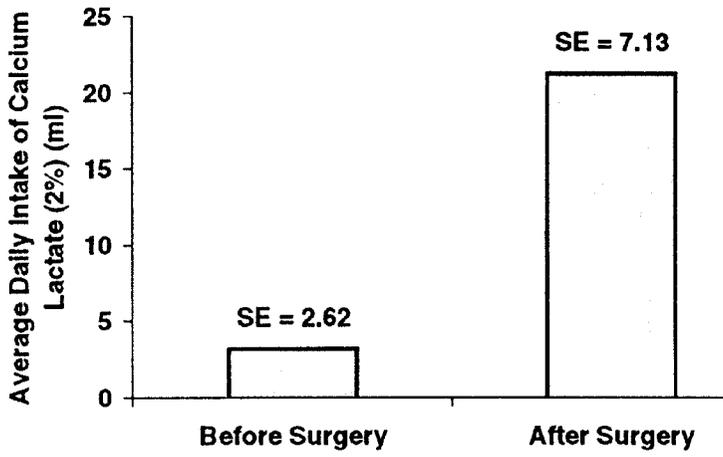
FIG. 3.2. *Top:* Calcium intake before and after parathyroidectomy. Note the change in calcium intake after surgery. *Bottom:* The parathyroid gland being removed from a rat. *Source:* Richter and Birmingham 1941

their calcium intake was also reduced (see also Richter and Birmingham 1941). Since Richter's time, the effects of the parathyroidectomy on calcium ingestion have been confirmed by a number of investigators (e.g., Leshem, Delcancho, and Schulkin 1999; Tordoff 2001).

The degree of specificity in calcium ingestion is still debatable (Leshem, Delcancho, and Schulkin 1999; Tordoff 2001). What is not debatable is that behavior toward calcium salts is altered by the level of calcium in the body, whether that level is reached by ingestion, intubation, or other means. And there is evidence that the appetite for calcium is innate (Leshem, Delcancho, and Schulkin 1999; Tordoff 2001).

PANCREATIC DAMAGE AND EXPERIMENTAL DIABETES

Richter noted that activity patterns were reduced in pancreas-damaged rats and inferred that this might be due to their insufficient capacity to use carbohydrates (Richter and Schmidt 1939, 1941). In several experiments, he and his colleagues ablated rats' pancreases and then determined the long- and short-term choice patterns of the rats. The rats' water intake was elevated by a number of dietary conditions. Richter made two sets of essential observations. One was that the rats avoided carbohydrates. Richter assumed that animals avoided what they could not use and what was health threatening. The elevated level of glucose in their plasma was part of the reason the rats drank more water and, Richter noted, was a result of their diet. The second important phenomenon Richter observed was enhanced oil ingestion by the rats. In further tests with varied diets, Richter and his colleagues expanded their findings of carbohydrate aversion and enhanced oil appetite in the pancreas-ablated rat (Richter, Schmidt, and Malone 1945) (fig. 3.3).

Richter and Schmidt also observed that insulin administration ameliorated the diabetic effects of pancreatic ablation, causing rats to reduce their intake of olive oil and begin ingesting sucrose in greater amounts. Subsequent studies would corroborate and extend Richter's findings by demonstrating that dietary manipulations affect oil and carbohydrate acceptability (Friedman et al. 1985).

Richter, Schmidt, and Malone (1945) described the case of Walter Fleischmann, an investigator and physician from Vienna who worked at the Harriet Lane Home for Invalid Children at Johns Hopkins Hospital. Fleischmann reported that, instead of using insulin, he kept his mild diabetes under control by ingesting lard. Fleischmann, interestingly, was also part of the original group that observed the young boy who ingested salt to compensate for adre-
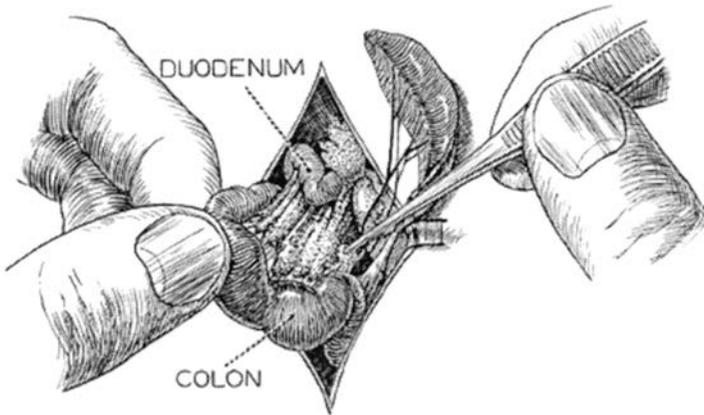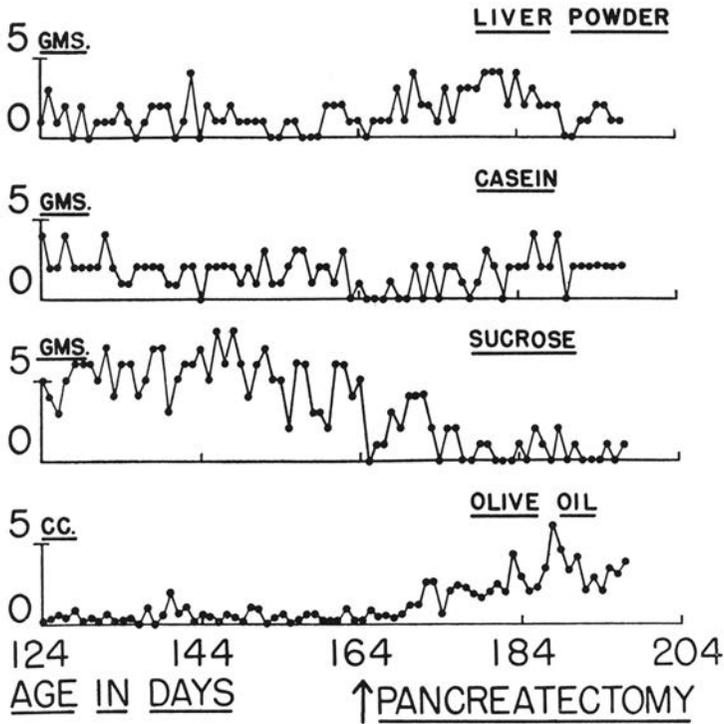
FIG. 3.3. *Top:* Ingestion patterns before and after pancreatectomy. Note the increase in oil intake following surgery. *Bottom:* The pancreas being removed from a rat. *Source:* Richter and Schmidt 1941; Richter, Schmidt, and Malone 1945

nal insufficiency. It is quintessential Richter to make the connection between the adrenal-damaged child ingesting table salt and the use of lard or fat by a mild diabetic.

THIAMINE AND VITAMIN B1 DEFICIENCY

Richter and other investigators (Harris et al. 1933) noted that vitamin B deficiency resulted in behaviors that could ameliorate the need for the vitamin. In Richter's experiment, he offered rats a cafeteria selection of foods and solutions and found that they seized on the source of the vitamin they needed. One method of eliciting a vitamin B deficiency was to eliminate yeast from the diet. The vitamin B–deficient animals decreased their intake of both carbohydrate and protein and increased their fat intake, which was adaptive because fats spare thiamine (Rozin 1976b). In subsequent analyses (Richter, Holt, and Barelare 1937a; Richter and Hawkes 1941), the lack of thiamine was found to be critical for carbohydrate and protein aversion and fat appetite (see also Scott and Verney 1949).

In further experiments, Richter noted that vitamin B–deficient rats ingested all of the solutions available containing B vitamins such as thiamine and riboflavin. Richter noted on several occasions that, although protein was actively ingested by normal rats on a self-selection regimen, vitamin B–deficient rats tended to avoid the protein when the same regimen was offered.

Richter wrote of an essential moment in an experiment with vitamin B: "One vitamin deficient rat drank 11cc or 5,500 international units, in less than half an hour; another rat drank 29cc, or 14,500 international units, in 24 hours" (Rozin 1967). Richter noted that the vitamin B–deficient animal was quite interested in the solutions. "This is shown by the fact that the rats found the bottles at once, even when as many as 12 different other containers filled with different food or solutions were present in the cage at the same time. It was difficult to stop the animals from drinking the substance once they had tasted it" (Richter, Holt, and Barelare 1937a; Rozin 1967, p. 413). Again, Richter, Holt, and Barelare observed that "the animals showed an immediate liking for the vitamin" and, in contrast to Harris and his group (Harris et al. 1933), suggested that the behavior "may not depend entirely on the experiences of a beneficial effect resulting from the ingestion of the vitamin" (Richter, Holt, and Barelare 1937a, p. 355).

Richter and Barelare reported that vitamin B–deficient rats did not ingest protein and sucrose but did ingest oil when it was offered in a self-selection

context. The rats also ingested the thiamin and riboflavin, in addition to other vitamin B components (Richter and Barelare 1939a). Years later, in a letter to Paul Rozin, Richter noted subsequent variability and inconsistency in the vitamin B1–deficient rats' ingestive behavior. In Richter's words, "Let me tell you at once that I have never been able to repeat Barelare and my observations on well over 200 rats. For our original experiments we used natural B1, for all the other experiments we used synthetic preparations. This may in some way account for the discrepancy."

Richter continued, "In a few experiments I believe that we were able to experimentally produce changes in B1 appetite, but in most instances the results showed little consistency." He then noted parenthetically that "some of our best results were obtained—if my memory does not deceive me—from our so called single food choice experiments in which we offered the rats one food source" (personal files of Paul Rozin, University of Pennsylvania, July 11, 1963).

Clear from this line of research, and now well demonstrated, was the adaptive behavior that Richter and others (Barnett 1956; Rozin 1967) observed of ingesting feces as a means of conserving valuable vitamins and other sources of nutrients and minerals. When vitamin B–deficient rats were offered a bowl of feces in addition to other vitamin and nutritional sources, they ingested the feces at a greater rate than did rats that were not B-deficient.

Richter was less certain about the behavioral mechanisms of vitamin B–specific hunger (Harris et al. 1933; Scott 1946; Scott and Verney 1949), and he acknowledged that some form of trial-and-error learning may have been at work (Rozin 1967, 1976b). Investigators building on Richter's insights determined specific behavioral adaptations, such as sampling one food at a time, and then determined the consequences of vitamin B ingestion in the thiamine-deficient rats. Another behavioral mechanism at work was tagging novelty, keeping track of what was new (Rozin 1967, 1976b). The conclusion: there is no innate appetite for thiamine. When thiamine-deficient rats are offered choices of foods they switch to any novel diet rather than continuing to eat the diet that is rendering them ill. The investigators' finding that the rats had learned an aversion to the thiamine-deficient diet would serve as a model for studying other specific hungers (Rozin 1967, 1976b).

SELF-SELECTION OF NUTRIENTS UNDER VARIOUS EXPERIMENTAL CONDITIONS

Richter determined the survival rate of rats that consumed various metabolic fuels. To establish the optimal nutrient sources, he would offer rats a single

item from his array of fats, carbohydrates, and proteins and then determine how long the rats survived on that single item. He then used the superior nutrient sources for his self-selection experiments (Richter, Holt, and Barelare 1937a). His paradigm guaranteed experimental success. This sounds like experimental good sense, except if it turns out the results are artifactual to the design rather than indicative of a real phenomenon (see Rozin and Schulkin 1990; Galef 1991). When Richter embarked on these studies, there existed a history of related experimentation using various animals to describe how appropriate nutritional choices are made (e.g., Evvard 1915).

As Richter understood it, he had already demonstrated successful behavioral adaptation to sodium and calcium deficiency. Now he would demonstrate that rats would select appropriate nutritional sources under general conditions. Rats were adapted to the McCollum diet, their ingestive patterns were determined, and then the diet was switched to a selection of the nutrient sources Richter had found optimal.

Richter used the self-selection apparatus in several metabolic and nutritional contexts (e.g., Richter 1943, 1956d). After determining the survival rate from the ingestion of various metabolic fuels and choosing the fuels with the maximal combination of minerals and vitamins, Richter offered eleven pure substances (casein, sucrose, olive oil, sodium chloride, dibasic sodium phosphate, calcium lactate potassium chloride, dried baker's yeast, cod liver oil, wheat germ oil, and water) in separate containers. Richter found that rats displayed the same normal growth on the self-selection diet that they did on the McCollum standardized diet. He also noted that the self-selection diet had a slightly lower total nutritional content than the McCollum diet, but the data suggested competence and achievement in nutritional intake regardless. Moreover, he demonstrated that one essential behavior was intact: the rats reproduced normally. Richter was not alone in his self-selection observations; disagreement surrounded the findings at that time, but only in terms of the extent to which the behavior was innate or learned.

Richter believed his experiments demonstrated innate organization in response to bodily needs (Richter 1943, 1956d). He asserted that rats have special appetites for a wide range of substances, including sodium, carbohydrates, protein, calcium, and phosphorus, in addition to various vitamins. Some of these assumptions would be challenged (e.g., Rozin, 1976b). How many innate appetites were there? Moreover, in the cafeteria context, did the rats really go into deficiency? If a need state could be considered on a moment-to-moment

basis, could not Richter argue that they were never truly deficient because they were able to select the appropriate nutrients before a deficiency status was reached? Or did they manage to select the appropriate foods because only the optimal nutritional choices were offered? Did this simplify the context enough that, as in the Davis experiments with neonates (1928, 1935, 1939), the experiment was destined for success?

In some similar studies normal growth and adequate self-selection were achieved; in other studies they were not (e.g., Lat 1967). One view expressed by an insightful critic of the self-selection experiments was that it worked best when the diets were maximally nutritious (Galef 1991; see also Davis 1939). Moreover, the environmental context mattered; the way the foods were offered and their nutritional value were important experimental manipulations (Galef 1991). Richter did not vary in great detail the environmental context for self-selection.

Richter next turned his attention to pregnancy and lactation. Figure 3.4 reveals that ingestion of some substances, including sodium chloride and calcium lactate, increased during pregnancy or lactation. Richter noted that water intake was particularly elevated during lactation.

Carbohydrate and sucrose intake did not change during rats' reproductive periods. Moreover, Richter noted that caloric intake started out at 45.3 kcal before mating, rose to 59.8 kcal toward the end of pregnancy, peaked at 160.0 kcal during lactation, and then returned to 52.3 kcal after weaning. This general trend in caloric intake has been documented by others and demonstrated in humans; we also know that this trend varies from species to species and between women in Western and non-Western countries (Prentice 1994).

Richter was confident about the sodium, calcium, and phosphate demands of pregnancy, and the elevated intake of a variety of substances has now been well documented (Denton 1982). It is still not clear, however, to what extent the elevated intake of substances reflects the activation of specific innate regulatory needs rather than general ingestive patterns, such as a tendency to increase ingestion of a variety of (but not all) substances. The magnitude of the effects and the extent to which they have been confirmed have varied in the literature (e.g., Denton 1982; Woodside and Millelire 1987; Thiels, Verbalis, and Stricker 1990).

There is evidence that a number of hormones that are elevated during the reproductive periods, some of which Richter pointed to (mineralocorticoid,
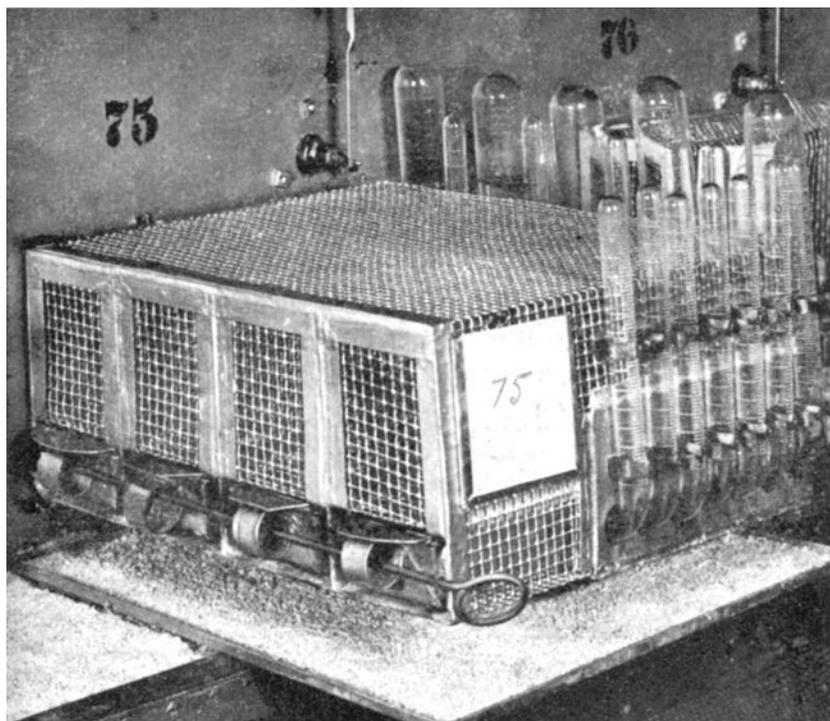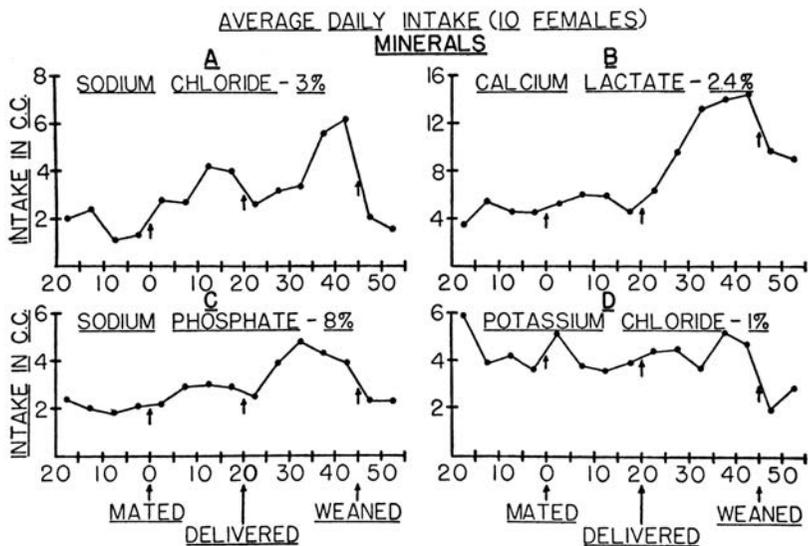
FIG. 3.4. *Top:* Ingestion of salts in pregnant and lactating rats. Note the increase in ingestion of sodium and calcium salts during pregnancy and lactation. *Bottom:* Self-selection cages. *Source:* Richter and Barelare 1938; Richter 1942–43

vitamin D, oxytocin, angiotensin), may also facilitate ingestive patterns (Denton 1982). In other words, hormones that conserve sodium, for example, can also participate in generating the behavioral responses of sodium ingestion (Denton 1982; Fitzsimons 1979).

PERSPECTIVE

Richter helped ignite the study of behavioral regulation of the internal milieu within the context of nutritional choice. There was little of this study within psychology itself, though this changed somewhat later when the phenomenon of taste aversion learning was discovered (see chapter 4). One area of study centered around the questions of which specific hungers were innate and which were learned, how many hungers there were, and how they were demonstrated.

Intellectually, Richter was mostly on the side of innate organization and therefore missed opportunities to investigate the interaction of innate predilection and learning. There were those (e.g., Harris et al. 1933) who argued that learning predominated in the food selections exhibited during the cafeteria experiments and the choosing of vitamin B by vitamin B–deficient rats. Others, like Richter, argued that dietary selection was an instinctive or innate predilection with variation in expression (Dove 1935). The innate conception and organization of behavior had, and still has, traction when the food choice is narrow (e.g., a choice between sodium or water), but when the choices are broad and the sensory signals are not succinct, learning must play a role (Rozin 1976b). This piece of psychobiology was outside of Richter's conceptual framework.

Nutrient search and identification are basic features of biological hardware. The laboratory rats Richter studied revealed several instances of specialized systems for water and sodium, calcium, perhaps phosphate ingestion, and perhaps some aspects of energy balance. The rats' solution was to approach a food source with caution, sample a small amount to determine the physiological outcome, and be wary of novelty (Rozin 1967, 1976b; see Chapter 4). Rats learning to avoid a food source that rendered them viscerally sick led to psychologists' recognition of long-delay learning, a process with rapid and profound lasting effects on behavior (Garcia, Hankins, and Rusiniak 1974; Rozin 1976b; see chapter 4). Visceral learning is a vital aspect of the mechanisms that operate during feeding. Determining what is making one sick is a vital

piece of adaptation that requires distinguishing the novel from the familiar, learning what foods are safe, and limiting choices.

Long-delay learning is a real world event (Rozin and Kalat 1971; Garcia, Hankins, and Rusiniak 1974), and before the mid-1960s long-delay learning was not part of the intellectual arsenal of most behavioral psychologists. An important adaptation that Richter understood is the novel versus familiar dimension of food choice (see chapter 4). Amid the very general adaptive behavioral/physiological systems of the omnivorous rat are specialized systems for nutrient and mineral regulation of sodium, water, and calcium, for example (Rozin and Schulkin 1990).

Richter understood, as would many other investigators, that nutritional choice requires both specialized detector systems (Dethier 1976) and general forms of behavioral adaptation. When confronted with multiple choices, the vitamin-deficient rat may select one food source at a time and determine the outcome in terms of visceral effects (Rozin 1976b). Limiting choice, stabilizing outcomes, and determining consequences is a learning approach that no doubt operates in the success of self-selection.

As I have indicated, perhaps the extreme competence of the rats in Richter's self-selection experiments depended on the palatability of the choices (e.g., Kon 1931; Lat 1967; Galef 1991), how many choices there were, and in what manner the choices were offered (Tordoff 2002). This might explain the variability in replication of the self-selection experiments (e.g., Kon 1931; Harris et al. 1933; Lat 1967; Galef 1991).

Richter posited too many innate behaviors to explain the nutritional choice behaviors. There are limitations or constraints on both the successes and the failures of self-selection. The ability to self-select, when demonstrated, is perhaps less about evolutionary knowledge and more about the test conditions (Galef 1991).

Thus, one limitation of Richter's work was that learning played no role in the lexicon of scientific experimentation. The Psychobiology Laboratory emphasized the innateness of behavior. Another criticism is Richter's own failure to recognize the pervasive ways in which social learning facilitates food selection and avoidance (Galef 1991). Bennett Galef's experiments in a variety of contexts demonstrated that social cues, even for sodium sources, could facilitate food selection. Social context plays a part in alcohol consumption, something Richter studied, but he emphasized, perhaps naively, the adaptive role of alcohol in nutritional regulation.

MEYER, HOMEOSTASIS, ALCOHOL CONSUMPTION, AND NUTRITIONAL REGULATION

I now turn to the context in which Richter investigated homeostatic regulation and alcohol consumption. This line of research, which he began in the 1920s and continued until the 1950s, symbolized a number of interests for Richter. However, Adolf Meyer cautioned Richter that he felt the implications of Richter's research on alcohol might be misleading and worried that it might be misinterpreted and misused in what he referred to as the "alcohol controversies" (Meyer file of letters to Richter, Chesney Archives). Meyer was cautious; he did not want the research to be abused by the general public. It is instructive to look at this work at its outset.

The research began as a follow-up to Richter's dissertation work on spontaneous activity and both the internal and external signals that affect it (chapter 2). Richter did not invent the running wheel as a measure of rat activity, but he simplified and extended its use in the quantification of behavior. Nor was he the first to look at the effects of alcohol consumption on the running activity of the rat (Stewart 1898). Richter found that alcohol did influence spontaneous behaviors in rats (Richter 1926c). In a study that lasted several months, he offered each of several groups of rats, kept in different conditions, different concentrations of alcohol mixed with water. Six animals received 8 percent alcohol, twelve received 10 percent alcohol, and ten received 16 percent alcohol.

Richter noted that food consumption was related to the amount of alcohol ingested. His study suggested that growth patterns remained normal in the developing rats in which the experiments were done. The animals ate less food, however, depending on the concentration of alcohol they ingested. Alcohol, Richter hypothesized, was a source of energy. The animals regulated their energy intake by reducing the amount of regular food they ate (i.e., the McCollum diet) in proportion to the amount of alcohol they ingested.

Richter also conducted these experiments in mature rats and found a precise equilibrium of homeostatic energy. In a study with female rats, the caloric intake averaged over body weight was 167.87 kcal when ingesting 16 percent alcohol, 168.97 kcal when ingesting 10 percent alcohol, and 170.71 kcal when on the diet alone. The amount of food ingested reflected the amount of alcohol consumed, which resulted in homeostatic equilibrium across the three conditions.

Not many control subjects were used, and as usual no statistical analyses were done. Nevertheless, Richter demonstrated that total caloric intake was about the same for the female rats that consumed alcohol and those on the regular diet. He did the same for males, repeating this experiment several times and under different conditions.

Because he drew on both human and animal experiments wherever possible, Richter went on to look at taste psychophysics for alcohol in both rats and humans. The gustatory experiments were designed to characterize thresholds and to determine preferences for different concentrations of alcohol (Richter and Campbell 1940a). At what concentrations would alcohol be preferred over water? At what concentrations would it be clearly distinguishable from water?

In later years, Richter reported differences in rats' ingestion of different kinds of alcoholic beverages, such as wine and beer (Richter 1953). The focus again was on metabolic regulation, eating for calories. Approaching homeostatic regulation from the conceptual framework of a biological engineer, Richter concluded, "All the evidence at hand indicates that rats ingest only as many calories as they can utilize" (Richter 1953a, p. 536). He included the clinical message that "the modern user of alcoholic beverages should be made aware that he will probably do better by eating less food when he takes these beverages; that he will do best when he reduces his food intake in proportion to his caloric intake from the ingested alcohol" (Richter 1953a, p. 538).

Perhaps what made Meyer nervous about these experiments was the suggestion that alcohol could serve as a substitute for food in maintaining metabolic balance (Richter 1941a). Alcohol was seen as dangerous and a seduction. Richter's research was conducted in the conservative ambiance of Hopkins, the institution that ousted Watson for his sexual promiscuity, and under the ever-mindful watch of Meyer, who cautioned about how the results would be understood. Was alcohol a legitimate form of ingestive behavior to serve homeostatic behavior? Richter attempted to prove just that, linking this form of ingestive behavior to the homeostatic regulation of energy balance.

In a memorandum about the summary of Richter's alcohol article, Meyer stated, "I do not like to see contributions from the Clinic touching on questions of a problematic nature published without some safeguards of orientation as to the sense in which the contribution is offered" (Meyer files, Chesney Archives). A little later in the document he stated, "I am anxious to see that there is no temptation furnished to use the results of the study for unintended generaliza-

tion by misquotation." Meyer was anxious that Richter state the limitations of his experiments at the outset. He had little quibble, in the letter, with the behavioral ingestive patterns and their role in metabolic regulation, but warned against getting embroiled in the "alcohol controversies." Interestingly, the paper, entitled "Alcohol as a Food" (Richter 1941a), would be one of the most often cited studies in the Richter corpus of research.

The range and approach of Richter's experimental sensibilities were expressed in these experiments, and despite the warnings of his mentor, Richter pursued this work. Later he would link thyroid activation to both running activity and alcoholic consumption. This research showed three emphases of Richter's work: (1) the fundamental role of biological clocks in behavioral and physiological regulation, (2) the regulation of the internal milieu, and (3) his comparative approach using animals and people.

Although Richter was not isolated, he worked alone. It is not clear what kind of input he received from colleagues. Richter, I think, did not have colleagues who critiqued his work and to whom he made himself vulnerable so much as he had important patrons of his work (G. Smith, pers. comm., November 2002). He assumed the validity of nutritional wisdom, seeing it as a piece of the hardware of bodily adaptation by which behavior serves regulatory physiology to promote viability. This was a prevalent cultural idea, one Richter breathed and assumed to be true. One significant scientist who was a major proponent of this view was Walter Cannon.

CANNON'S SUPPORT: THE NATIONAL RESEARCH COUNCIL

Cannon, as I indicated previously, was an early and important supporter of Richter's research. In correspondence between Cannon and Richter, Cannon alerted Richter to the fact that there are "considerable funds available for research in endocrinology" and asked whether Richter would join a committee of the National Research Council (Cannon Archives, Harvard University, March 16, 1936). This and other funding foundations had begun to play an important role in the rise of biomedical and other forms of research in the United States (Kohler 1991).

In another letter several months later, Cannon alerted Richter to a book on the appetitive behavior of sheep in South Africa (Harvard University Archives). Richter had found himself another patron, but had he found a colleague? Did he talk to Cannon about his experiments on gastric distention? That would have been difficult at that time, near the end of Cannon's life.

In fact, there was almost a decade (mid-1930s to mid-1940s) when Cannon was quite supportive of Richter's work, both in terms of intellectual encouragement and of financial support through the National Research Council, where Cannon chaired the Committee on Research in Endocrinology (see National Academy of Sciences Archives). Cannon was well aware of much of Richter's work on specific hungers and actively supported and promoted the research, as well as Richter's work on cycles. By 1944, however, the support from this source was diminishing. Cannon wrote to Richter, "Let me say personally that I regret that we have not felt justified in continuing our relations with your interesting work" (National Academy of Sciences Archives, April 25, 1944).

The National Research Council played an important role in supporting Richter's research project, and Cannon, sitting at its head, was well aware of Richter's latest findings and of his extension of the concept of homeostasis to a behavioral level of analysis. Cannon embraced Richter's behavioral findings with enthusiasm. They added a whole new dimension to the concept of homeostasis.

CONCLUSION

Richter understood the regulation of the internal milieu in the context of whole-body regulatory activity. He used the activity cage to monitor a broad array of rat behavior, including eating and drinking in the context of other regulatory activities, reflected in the active portion of their activity cycle (G. P. Smith 1997). Richter's contribution to the study of ingestive behavior is phenomenal; he provided real tools and biological explanations for regulatory events.

Richter clearly saw himself as building on the work of other investigators with regard to the selection of dietary requirements. From pigs (Evvard 1915) and rats (Osborne and Mendel 1918) to humans (Davis 1928), ideas about dietary self-selection of needed nutrients were in the intellectual air. "Dietary wisdom," a metaphor Cannon helped to popularize, was seen as a piece of our evolutionary legacy, experimentally expressed in a laboratory context.

Unfortunately, Richter had little intellectual room for the concept of learning and exaggerated the innate component in behavioral regulation of the internal milieu; innate engineering predominated his view of this behavioral adaptation. In this context, instinct means innate structure. Richter inherited this idea from his predecessors' study of self-selection. But there was no restraint placed on what the range of innate structures might be, and no real accounting for the failure of self-selection experiments by some investigators

FIG. 3.5. Playful card depicting Richter ingesting something from what became known as a "Richter tube"

and the failure of animals to thrive when offered various choices in other experiments.

In his essay on the biology of drives, Richter argued that "the reason that human beings often make faulty dietary choices may be explained in part by parental guidance and advertisement" (1941c, p. 109). He suggested that "often when a child expresses a great appetite for certain substances, he is told by his parents that he must not eat them: equally often he is told to eat things which are very distasteful to him. He quickly learns to distrust his own appetite: and . . . comes under the influence of advertisements, he falls prey to them" (p. 109). The suggestion that culture degrades certain parts of our adaptive responses would be a recurrent theme in Richter's work. As noted in chapter 2, Richter mistakenly thought that circadian rhythms were lost in humans as a consequence of culture. Richter believed culture usually masked regulatory competence, although not always, as we will see in chapter 4.

Richter understood, as one commentator noted, "that the central problem for psychology was to discover the determinants of the initiation and termination of bouts of behavior" (Collier and Johnson 1997, p. 159). Richter did not think of behavior in modern ethological terms, in terms of a more modern cost-benefit analysis (Collier and Johnson 1997), or in ecological terms of the

adaptation of species. Nor did he think much in terms of hedonic attraction (Young 1948), social learning (Galef and Whiskin 2001), or other forms of learning in the regulation of the internal milieu. What Richter did do was discover a rich assortment of behavioral and physiological forms of adaptation, suggest interesting routes for further inquiry, and remain close to his own data and the tradition of regulatory whole-body physiology.

Richter understood behavior as reflective of instinctive responses. Instinct was contrasted for years with intelligence and flexibility; then it was associated with the buildup of energy. Instincts were identified with drives, which could be satisfied through behavior—the hydraulic buildup and the depletion and repletion models. In this, Freud (1920/1975) was no different from Hull (1943) or many of the ethologists (Tinbergen 1951/1969); like other investigators of the time, he assumed some form of drive reduction for which behavior was pivotal to reduce excitation and arousal. This conception was common to various behavioral explanations.

Perhaps Richter understood instinct as Donald Hebb, Lashley's student, would: by asserting that "the problem of instinct is the correlative of that of intelligence, or insight, and of learning. It has just been seen that intelligence is not an entity that is quite distinct from learning and we may now see that instinct, also, is not to be cut off sharply from either" (Hebb 1949, p. 165). Instinct is about problem solving. We do not know Richter's views on this because he was not engaged at this level of scientific discourse. He assumed a concept like instinct and then set about demonstrating its validity.

How many innate or instinctive specific appetites are there? Certainly sodium is one, and perhaps calcium. Water seems a likely candidate, and protein remains a possibility. Avoidance of diets that render the animal ill, coupled with a tendency to be cautious of new nutritional options, seems to be operative in food choice, particularly for the omnivorous rat. The ecological adaptations are an essential part of discerning the range of strategies available for an animal to solve its nutritional requirements. Richter's work on nutritional selection was done largely using the rat, an omnivore with several noted specific appetites along with several more general behavioral strategies that serve it in the regulation of the internal milieu. Chapter 4 discusses further one strategy alluded to here, namely, learned taste aversion.

A playful sensibility abounded within the Richter laboratory; science was serious but fun business. Who but a whimsical person would produce a card like that in figure 3.5?