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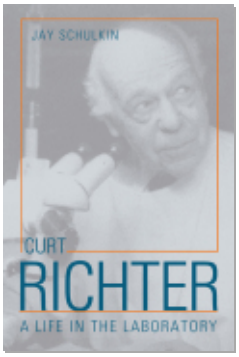
Curt Richter



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CHAPTER 4

A Psychobiological Perspective on the Domesticated and the Wild

BIOLOGICAL AND CULTURAL CONTEXT

Richter was born in the century of Darwin's discoveries. Darwin often wrote about domestication and evolutionary change. During his first trip to the Galapagos Islands, as he recounted in *The Origin of Species,* Darwin was awed by the great variation in species (Darwin 1859/1965). His observations would eventually lead to his theory of natural selection and the idea that speciation developed through the selective pressures of geographical and ecological constraints. Ideas about adaptation, secondary sexual characteristic expression, and functional fit guided Darwin's thinking. To understand physiological and behavioral expression he looked to the niche, the organic conditions in which an animal had to live. In this adaptationist framework—an engineering, ecological context—Richter and many other students of animal behavior would feel very comfortable.

Darwin revolutionized the study of behavior by giving it a biological context. This was quickly adopted by those in the emerging field of psychology, and psychobiology was soon understood within the evolutionary context of adaptation. But Darwin held a Lamarckian perspective on certain hereditary changes, including use and disuse and intergenerational effects (S. J. Gould 2002). Use and disuse, instinct and habits, and the effects of domestication were dominant intellectual themes for Richter's predecessors and for Richter himself throughout his career; these categories figured in almost all of his investigations.

Darwin was worried by the price of domestication. He wanted "to estimate the amount of structural differences" that occurred as a result of cultural

imposition (Darwin 1859/1965, p. 38). The other concern that came to dominate his thinking was the inheritance component: instincts were seen as guiding regulatory mechanisms in the organization of behavior. Richter was not theoretical in general about the concept of instinct, but this concept was at the root of his biological inquiry. The issue of biological predisposition, whether rigid (as instinct was thought to be) or more malleable, was understood in terms of behavioral and physiological adaptation. The Psychobiology Laboratory was centrally involved in this arena.

DOMESTICATION

In a number of his reviews on domestication, Richter pointed out that the rat was an ideal animal to study. The animal was championed by Claude Bernard's teacher, François Magendie (see also Holmes 1974, 2004) and, as I have indicated, was introduced in this country as a laboratory animal by Adolf Meyer in the early 1890s. Henry H. Donaldson expanded on the use of rats as experimental subjects. Richter noted the experimental advantages of the rat, including its diet, its similar physiology to humans, the ease with which it reproduces under domestic conditions, its resistance to infection, and its inclination toward domestication and resultant willingness to be handled.

One feature of rats noted early on was temperamental variance; some rats were more aggressive than others. Yerkes, in a 1913 study, investigated the heredity of savageness and wildness in rats. Within a few years, Richter would be introduced to Yerkes at Harvard. Richter was greatly interested in measuring the impact of experimental manipulations, not only on behavior but also on physiology. The rat proved a convenient tool in this regard. Richter studied the adrenal gland, among other end-organ systems, to observe the effects of domestication in the laboratory. The glandular structure of the inbred, domesticated strains of rat differed from that of the wild hybrid, as did their less aggressive nature (King and Donaldson 1929; King 1930). Darwin was right: domestication altered both the internal physiology and the behavior of species.

Henry H. Donaldson was an important figure for Richter, as he had been for Watson (Boakes 1984). Richter visited him often and knew him well. Donaldson, as noted earlier, was a teacher of Watson and the author of the book *The Rat Data and Reference Tables for the Albino and the Norway Rat* (Donaldson 1915).[1] In this book, Donaldson described the "history of the rat since it arrived in Western Europe" (Donaldson 1915, p. 111), the animals' life charts, their behaviors, and the significant effects of domestication on their end-organ

systems, including the brain, which is smaller in the domesticated variant of rat. Interestingly, many decades later, enriched environments were shown to produce improvements in domesticated rats' neuronal structure and learning (Rosenzweig and Bennett 1996). Wild rats must be embedded in a much richer social context than domesticated rats.

EXPERIMENTAL CONTEXT

Before Richter and his colleagues embarked on their investigation, a body of evidence had already been gathered on the effects of domestication on rat behavior and physiology. For example, the adrenal gland had been demonstrated to be larger in the wild gray rat than in "the tame albino rat" (Donaldson 1915).

Richter's study revealed seasonal changes in the wild rats' adrenal size. Wild rats caught in the summer months had smaller adrenal glands than rats caught in the winter. Rogers and Richter (1948) noted that the effect was larger in males and that seasonal change in females was negligible (fig. 4.1). Of course, they gave only descriptive statistics (percentages, averages, etc.) in their paper, consistent with Richter's usual method. They mentioned seasonal differences only parenthetically, but did so with insight into the functional implications of size changes of the adrenal gland. Rogers and Richter (1948) cited conditions under which adrenal activities increased, including adaptation to colder temperatures and various forms of duress (Selye 1946). In addition to

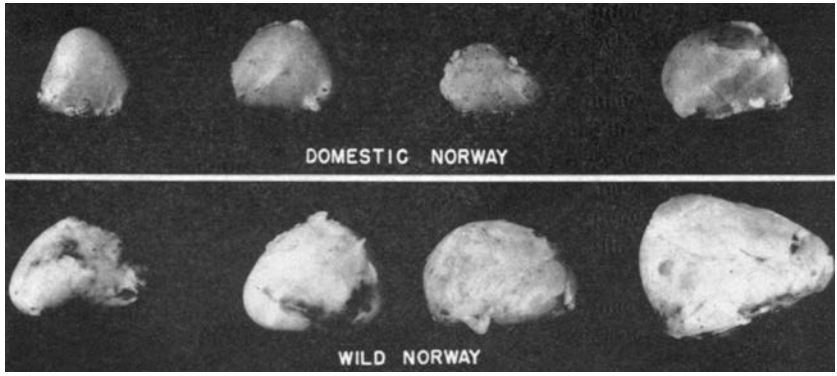

FIG. 4.1. Adrenal glands of the domestic and wild Norway rat. Note the apparent size difference in the wild and the domestic rat, matched by body weight of the animal. *Source:* Rogers and Richter 1948

several anatomical differences, they described the adrenal gland; the fasciculata and reticularis regions were thicker in undomesticated rats.

FAILURE TO EXPRESS THE BEHAVIORAL REGULATION OF SODIUM IN WILD RATS

Richter always returned to the phenomenon he took to be paradigmatic of a specific innate behavior: sodium ingestion following sodium loss or sodium need. For rats, domestication did have advantages, including the regulation of body sodium. Adrenalectomized domesticated rats, Richter discovered, survived quite well as long as they ingested sodium. Would wild rats also compensate for adrenalectomy and ingest sodium as a behavioral adaptation?

In a series of studies, Richter, Rogers, and Hall demonstrated that wild rat strains, captured in the streets of Baltimore, showed differences in sodium regulation from the domesticated variant. Both groups were adrenalectomized by the method that Richter had perfected in 1936 and 1941. As usual, both male and female rats were used. Using diets either rich or low in sodium, Richter and his colleagues looked at the regulation of sodium in food and in water. The rats always had water. Not surprisingly, both wild and domesticated strains died without access to sodium if the entire adrenal gland was removed (Richter, Rogers, and Hall 1950). Richter surmised that if partial tissue were left, the animals could survive without sodium, and he demonstrated that fact in the laboratory.

In experiments with what Richter called "salt therapy," he gave the rats a 3 percent NaCl solution. Richter noted a lot of variation in sodium intake in the wild strain of rat. The domesticated rats ingested the sodium more than the wild rats and had much higher survival rates. The study stated that the rate of survival was about 2 percent in the wild strain and 87 percent in the domestic strain (Richter, Rogers, and Hall 1950). Richter noted repeatedly that even the individual wild rats that increased their salt intake often died. This was not the case for the domestic variant.

Richter always emphasized "the high degree of suspiciousness of all new foods" in wild rats (Richter 1950c). Richter, Rogers, and Hall speculated that the wild rats' failure to increase their salt intake rested "chiefly on a psychological rather than a physiological basis" (1950, p. 239). They suggested that an exaggerated neophobia (suspicion of new food) in the wild strain impeded their regulatory competence in the confines of the safe laboratory. The wild rats died of a reluctance to sample and experience the beneficial effects of the

sodium. Surprisingly, adjusting the concentration and forcing ingestion still resulted in fatality in the wild rats. Salt therapy, the researchers concluded, was not beneficial. To my knowledge, this experiment was never examined again. Subsequent studies have demonstrated both differences between strains and individual variation in sodium intake (e.g., Denton 1982; Roland and Fregly 1988).

Administering deoxycorticosterone to wild rats in addition to salt replacement still often resulted in death and in some instances caused sudden death. The wild variant was just less adaptive to changes in body sodium. Mosier and Richter reported that the adrenal glands of the domesticated rats were much more responsive to reductions in dietary salt concentration than were those of wild rats. On the low-sodium diet, the glomerulosa layer of the adrenal gland increased more in the domestic rat than in the wild rat (Mosier and Richter 1958). When placed on a high-sodium diet, both strains showed a reduction in adrenal size. Domestic rats increased their water intake to a greater extent than did wild rats. Of course, in both cases it is possible that changes could be observed more readily in domestic rats because their smaller baseline adrenal size made the effects of the switch to the low-sodium diet more noticeable. The wild rats, with their larger adrenal glands, presumably had more aldosterone and corticosterone in systemic circulation. Nonetheless, Mosier and Richter reported an anatomical difference in the domesticated and wild strains at the level of the zona glomerulosa (Mosier and Richter 1958).

That the wild variant did not demonstrate a sodium appetite in response to a sodium need, or to hormonal signals associated with sodium need, left many questions. Were the wild rats less adaptive than the domesticated rats? Was the experience of being trapped and transported traumatic, elevating levels of corticosterone enough to compromise wild rats' behaviors? What did this say about salt appetite, and was this phenomenon genetic or developmental? How long would a rat need to be domesticated to develop a salt appetite?

RATS, TASTE AVERSION, VISCERAL DISTRESS, AND POISONS

Richter's interest in self-selection paid off in his investigations of what rats ingest and what they avoid. He noted "in 1937, while studying the relation between the taste of substances and their nutritive or toxic values, I found that my laboratory rats have a remarkable ability to select nutritive substances and to avoid poisonous ones" (Richter 1948c, p. 255). Rats avoided certain kinds of tastes as if they could tell ingesting the substances would make them sick. For

example, they avoided the toxin alpha-naphthylthiourea (ANTU). Richter studied this as part of his larger experimental interest in "bait shyness," the exaggerated neophobic response to possibly dangerous sources of foods or other objects.

GUSTATORY STUDIES: RATS AND PEOPLE

Richter designed psychophysical and taste avoidance tasks with several toxic substances. Building on his salt and sucrose psychophysical taste studies and comparing rats and people (Richter 1939a), he embarked on a study to determine taste thresholds for a number of toxic substances (Richter and Clisby 1941b). He knew that this taste had an innate genetic component, and he also wanted to contrast its study with previous studies of sucrose and salt taste. He presented human subjects with two glasses, one containing distilled water and the other containing the toxic compound. He wanted to determine the point at which the two substances could be distinguished. When subjects noted a definite bitter taste, this was considered the detection threshold.

Richter and Kathryn Clisby stated that "we know now that rats and human beings have almost identical taste thresholds for common sugar, salt, and phenylthiocarbamide" (Richter and Clisby 1941b, p. 163). This point can be disputed. Conducting the rat study, they added the toxic compound to a dextrose solution to facilitate its ingestion. Half the rats died within twelve hours, and the rest survived because they did not ingest significant amounts.

Some years later, Richter tested ten toxic compounds on basic gustatory psychophysical measures, using the same method that he had used earlier. He initially took the rats' rejection of toxic solutions to indicate a taste threshold. He saw their continued ingestion of both distilled water and a toxic compound as evidence that the rats had not reached their taste threshold for the toxin. Reduced ingestion indicated arrival at a threshold measure. But Richter also looked at what he called "a toxic symptom threshold," the concentration at which animals became sick (Richter 1950c).

The ten compounds included thallium sulfate, sodium fluoroacetate, thiosemicarbazide, arsenic trioxide, and ANTU. Richter noted that the gustatory properties of a toxic compound were linked to its solubility. Some of the toxins appeared to have no distinct taste, and he rightly asserted that a "tasteless toxic substance could not have existed widespread in nature in readily available forms at any time in evolutionary history, since in the absence of a taste warning every animal or man that ingested it would have perished" (Richter 1950c, p. 370). He noted that all of the tasteless compounds were not

found in nature but made by humans. Though probably an exaggerated claim, this smacks of evolutionary common sense.

POISONING WILD RATS

In the 1940s, the U.S. military was interested in various kinds of poison warfare and thus supported Richter's research (Richter Archives, National Academy of Sciences). In collaboration with chemists from Dupont, Richter and his colleagues worked to generate a toxic substance that would be ingested by wild rats (Andrus et al. 1948).

First, though, he had to catch the rats. Richter and John Emlen modified a rabbit trap for use in capturing the wild rats of Baltimore, working with the city's Bureau of Street Cleaning.[2] The day before the traps were set, the areas where they were to be used were cleaned of debris. Using 265 traps, the researchers caught 70 rats on the first night and a total of 225 rats over a thirteen-day period for their initial study (Richter and Emlen 1945). Richter had noted in several places that, "owing to their high degree of suspiciousness, the wild rats are far more difficult to poison than are the domesticated rats" (Richter 1949a, p. 38).

In an interesting paper for the *Journal of the American Medical Association* on the incidence of rat bites, Richter wrote that "wild rats, even more than any domesticated animals, enjoy a very intimate living arrangement with man. They can live in the same house, share the same beds, eat the same foods, carry the same internal and external parasites, and suffer from the same diseases and plagues" (Richter 1945c, p. 324). He noted the incidence of rats biting people in Baltimore, specified where in the city the bites occurred, and even indicated what part of the body was bitten in each case (table 4.1).

Mentioning that the bites occurred while the victims were asleep and that twenty-some victims received multiple bites, Richter suggested that "a strong craving for blood might explain why, once having bitten a person, the rats apparently are apt to bite another." He then offered blood to several wild rats and noted that they ingested it. As always, Richter's interest in regulatory and cyclic phenomena and his medical focus (in this case, transmission of disease from rat to human) were at the heart of his research.

In a subsequent study on ANTU, Richter and his colleagues determined the effects of ANTU on pulmonary edema and changes in fluid balance in rats. They surmised that the toxic compound worked by causing pulmonary edema (a buildup of fluid in the lungs). They attempted to determine the extent to

TABLE 4.1. Parts of Body Bitten by Rats

Location	No. of Persons with Bites
Arms	
Hands and fingers	41
Forearm	5
Shoulder	2
Head	
Cheek, lips	11
Ear, eyebrow	5
Top of head	4
Legs	
Feet	19

Source: Richter 1945

which this occurred when rats were exposed to different amounts of the toxin (Dieke and Richter 1945; Richter and Emlen 1946; Richter 1952b). Richter was never squeamish experimentally, and in one study he bled rats to death so there would be no bleeding when their chests were opened.

Pulmonary edema began in the first hour after toxin ingestion. The lungs were full before the effusion of fluid into the pleural cavities. Lung weight was enhanced considerably by the administration of the toxic compound. Having observed pulmonary edema in these animals, Richter documented other physiological changes, including immunological changes. He concluded that the toxic poisoning shifted large amounts of extracellular fluid to the lungs. Later he would report species variation in this response (Dieke and Richter 1945; unpublished results cited in Dieke and Richter 1946a).

In one study, Sally Dieke and Richter looked at variation in rats' responses to poison across strain, age, and gender. They injected ANTU intraperitoneally or administered it by intragastric intubation, varying the dose by body weight. They found fewer fatalities in the youngest rats. Suckling rats and young rats weighing less than 200 grams were six times more resistant to the poisoning. They reported no difference with gender (Dieke and Richter 1946a).

Richter also noted that removal of various endocrine tissues—the thyroid, parathyroid, and gonads—did not alter the rats' response to the toxin. He thought that perhaps the weight of a rat's adrenal glands might contribute to its vulnerability to toxicity. In other experiments, he mixed different amounts of the toxin into the stock McCollum diet and gave the rats water ad libitum (Richter 1946a). He wanted to determine the rats' tolerance of and survival rates after ingestion or noningestion of the diet.

Richter was also interested in further determining the gustatory and visceral mechanisms of the tongue and other organs of the alimentary tract that may contribute to the vulnerability of domestic and wild rats to toxins. Richter and his colleagues first determined the structure of the tongue of the domestic rat (Fish, Malone, and Richter 1944) and then expanded their investigations to the wild rat (Fish and Richter 1946). They noted that the tongue of the domestic rat was smaller than that of the wild rat by about 17 percent. In another study, Richter and Emmett Hall looked at intestinal length in wild and domestic rats and found that the wild rats had longer intestines, which they speculated contributed to the differences in vulnerability to the toxins (Richter and Hall 1947).

Richter described some unique characteristics of the wild rats in context of these poisoning experiments. These included what he described as "psychotic behavior," which he speculated was induced by an exaggerated fear of food poisoning. Richter summarized the core finding of the poisoning experiments as follows: if the rats survived the poisoning, they learned to avoid the food source. He also described the doses that resulted in avoidance or fatality: the concentration at which rats learned food avoidance was within a small range of 0.03 to 0.09 percent; doses higher than this killed rats straight away, and lower doses did not make them ill at first exposure. Those wild Norway rats that became ill but survived the poisoning, however, displayed what Richter described as "psychotic" behavior (though just "bizarre" might have been more accurate). The rat, during both the light and dark periods, would hold itself erect at the back of the cage, standing on its hind legs and holding onto the top of the cage (fig. 4.2). One of Richter's assistants called the phenomenon "straphanging." Richter then noted that "often one foot was held in the air in a manner reminiscent of the postures seen in catatonic patients." The normally escape-prone wild rats remained frozen in this posture. Richter inferred that the poisoning experiences induced "abnormal" behaviors (Richter 1950b).

BAIT SHYNESS

The self-described "reluctant rat-catcher" (Richter 1968b) caught many rats in the wilds of Baltimore city over a ten-year period. He tackled this part of his research, which consisted of scanning a rough environment for wild rats on which to test modern substances that might be linked to genetic taste functions. The landscape of alleys and yards was a long way away from his Colorado youth, but, drawn to the Norway rat and its study, Richter quickly

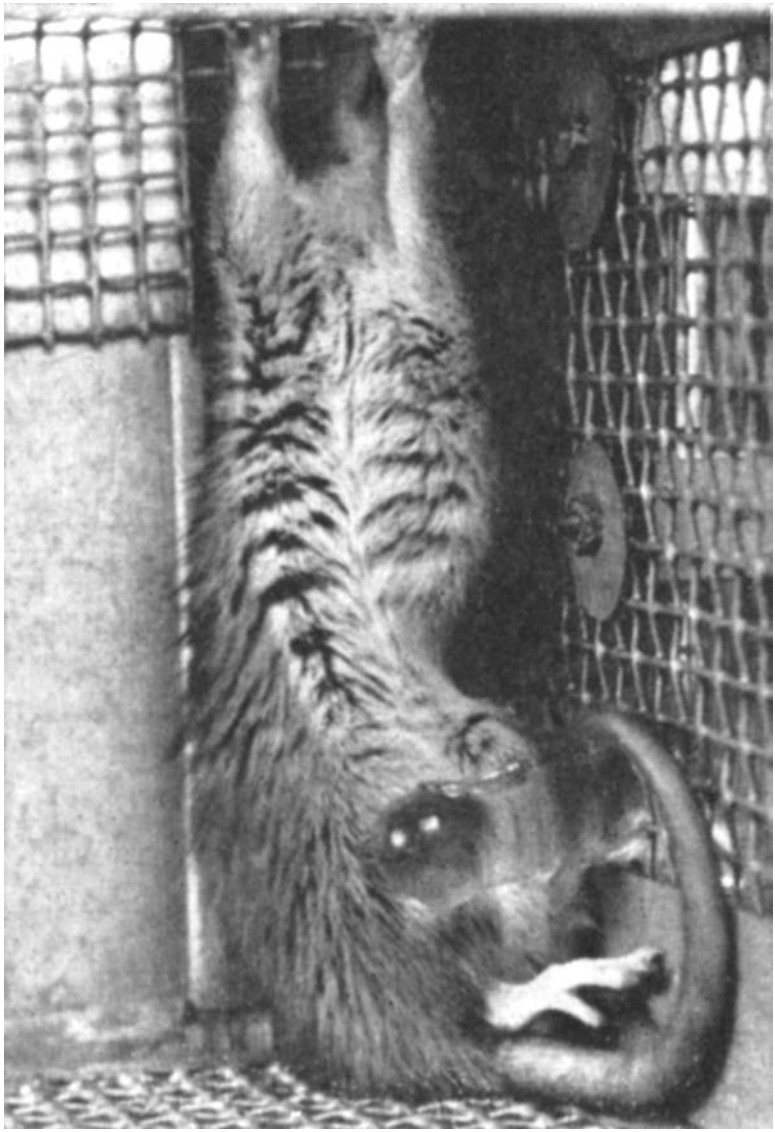

FIG. 4.2. Abnormal prolonged "straphanging" posture of a rat exposed to a toxic compound. *Source:* Richter 1950b

became fascinated by the whole phenomenon. Chasing down the rats was almost an urban version of his early hunting days in Colorado.[3]

Of course, bait shyness and the difficulty of poisoning rats had been known for ages and documented in several investigations, including Richter's. Wild

rats' reluctance to ingest unfamiliar foods is a special behavioral adaptation that serves them well in tagging food sources and, most importantly, in linking specific food ingestion with visceral distress in animals in which taste and olfaction are essentially tied to food regulation (Rozin 1976b; Garcia, Hankins, and Rusiniak 1974).

Richter was close to suggesting something like a form of taste aversion with his emphasis on "bait shyness," food avoidance, and visceral distress from poisoning. Noticing the relationship between the concentrations of toxins and rats' avoidance of them, he found that rats stopped eating poisoned food after it "made them sick" (Richter 1946a, p. 366) (fig. 4.3). Richter acknowledged that the mechanism of this response "has not been determined. It could depend on association of ill effects with the taste of ANTU or smell" (Richter 1946a, p. 370).

Of course, being close and nailing it are quite different. Richter was also looking at the development of tolerance to toxins by small exposures to them. Perhaps he missed the boat on taste aversion learning because he ignored the learning part of behavior, remaining instead outside the intellectual battles of psychology.

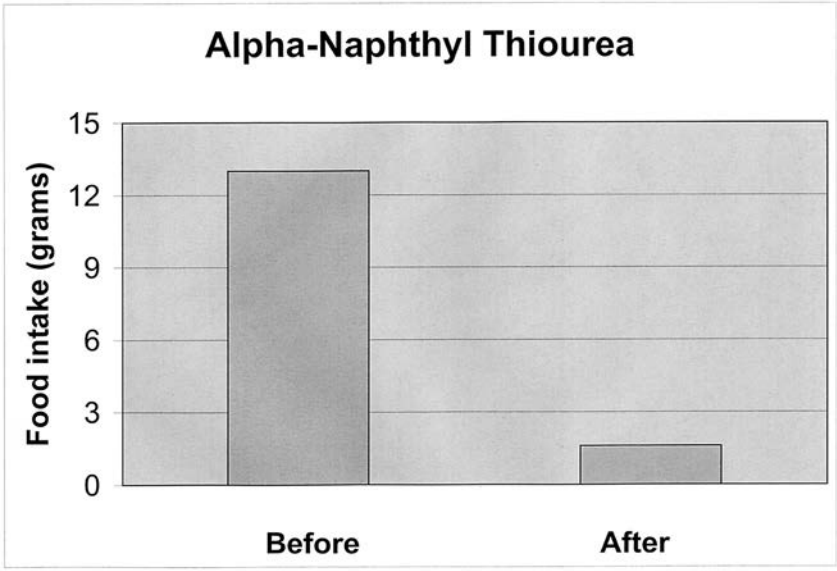

FIG. 4.3. Ingestion of food sources before and after exposure to a toxic compound. *Source:* Data from Richter 1946a

Taste aversion learning became a special case: a very specific biological form of learning (Garcia, Hankins, and Rusiniak 1974). A variety of animals associated the ingestion of a food source with visceral illness. This is a specialized form of learning outside of the immediate realm of associative learning (see Rozin 1976b). The learning of an association can take hours; there are constraints on learning because stimuli are not all equal in their associative potential. For Richter's rats, gustatory stimuli took precedence over visual stimuli; the converse held for birds, in which visual acuity is more evolved than it is in rats (Shettleworth 1972; Rozin 1976b).

Richter did not lose track of real-world events such as light/dark cycles, thirst, fear, and food ingestion the way many psychologists in North America tended to during the dominance of learning theory across academic psychology.[4] Richter probably understood bait shyness, what later became known as "taste aversion learning," in terms of adaptive specialization. Of course, if he had been more oriented toward a theoretical approach that included learning, he might have discovered that some stimuli were more closely linked to gastric distress than others.

Richter continued to write and think about his experiments and experiences as a "reluctant rat-catcher" for some time after the work in the late 1930s and 1940s. In a late article (Richter 1968b), he described the poisoning experiments, catching wild rats, being bitten, and his respect for this hardy animal. At the time of this publication, the work on taste aversion was about to be understood within psychology and psychobiology. The article makes no mention of the emerging work on taste aversion learning. This work would have a profound effect on psychology (Rozin and Kalat 1971; Garcia, Hankins, and Rusiniak 1974).

TEMPERAMENTAL FEATURES OF THE WILD AND THE DOMESTICATED RAT

Though bait shyness is part of the normal wariness of most wild rats (e.g., Barnett 1956, 1963), social wariness is sometimes linked to temperament; in groups of rats, some individuals are more wary of unusual objects than are others (e.g., Hall 1941).

Darwin described shyness as behavior toward something socially unfamiliar (Darwin 1872/1998). But evidence of strain and individual differences pervades the animal literature, which recognizes an animal's temperament as a factor in shyness. Differences between individuals of a species reflect tem-

peramental characteristics, for example, the degree of reluctance to sample a food source or of aggression or tameness. Individual differences are also often linked to differences in problem-solving abilities.

Fear of unfamiliar objects is a basic, broad-based biological predisposition for a wide range of animals, including humans (Hebb 1949; Kagan 1989). This fear has long been noted by investigators (Sadovnikova-Koltzova 1926) and was central to Richter's work on bait shyness, strain differences, and the effects of domestication. But some animals are, by their biological predisposition, more or less likely to approach or avoid a food source.

Richter had found it much easier to poison domesticated rats than their wild counterparts, and had concluded that the price of civilization is the reduction of biological wariness of new, unfamiliar objects. But we still do not know what role temperament played in the poisoning experiment. What if the particular group of wild rats Richter caught happened to be unusually shy, or his group of domesticated rats was especially unwary by temperament? If domestication is a factor in wariness, how long do rats have to be domesticated before they become less wary?

HOPELESSNESS AND VOODOO DEATH

Richter was always intellectually close to Cannon. Both scientists were rooted in regulatory physiology and the maintenance of bodily viability. Cannon, in an influential though speculative paper for *American Anthropologist,* theorized that individuals frightened to despair were vulnerable to "sudden death" (Cannon 1942). Superstitious fear was linked to this sudden death—sometimes called voodoo death. In what were commonly referred to at that time as "primitive" cultures, voodoo death occurred when a person was literally frightened to death by an experience imposed on him or her by a shaman or other individual.

Cannon had long been interested in what William James called "the energies of men" (James 1907/1968), the range of energy required to sustain action (Benison, Barger, and Wolfe 1987). As Benison, Barger, and Wolfe noted, "Cannon found the idea [of voodoo death] provocative and at once took steps to exploit its similarities to some of his own experimental observations" (Benison, Barger, and Wolfe, 1987, pp. 316–17). Cannon believed a feeling of hopelessness was endemic to the state preceding voodoo death and rendered an individual vulnerable to pathology and the breakdown of bodily adaptation and the energies of humans.

Referring to anecdotal evidence of human voodoo death, Cannon asked whether "those who have testified to the reality of voodoo death have exercised good critical judgment" (Cannon 1942, p. 171). He cited William James's comments on the profound vulnerability of socially isolated individuals, cut off from their peers and their community, to voodoo death. Voodoo death often occurred in individuals who were ostracized from the community. Noting that persistent fear without relief can cause a harmful chronic activation of the sympathetic and adrenal systems, Cannon concluded that "voodoo death may be real, that it may be explained as due to shocking emotional stress" (Cannon 1942, p. 180).

In his essay on sudden death, Richter picked up the Cannon theme of a "state of shock" and then went on to state that "as so often happens, this phenomenon was discovered during the course of other experiments" (Richter 1957f, p. 193). Richter and his colleague Gordon Kennedy were studying sodium metabolism and trimmed rats' whiskers so that sodium trapped on them would not contaminate other food sources. Richter then moved on to an experiment in which he measured endurance and survival times of domesticated and wild rats forced to swim in water. This was somewhat analogous to survival times after prolonged ingestion of only one nutrient (fat, protein, etc.). He began the studies with domesticated rats. Richter observed that survival time was related to water temperature. Of interest was that "at all temperatures a small number of rats died within 5–10 minutes after immersion." Then emerged a Richter moment: "Would a rat swimming without whiskers show the peculiar behavior of the rat in the metabolism cage?" (Richter 1957f, p. 194). He observed that about one-third of the twelve domesticated rats with clipped whiskers that he tested died rapidly.

Richter then turned his attention to hybrid wild and domesticated rats, and found that five of the six hybrid rats died within a brief five- to ten-minute period. When Richter looked at the effects of clipped whiskers on wild rats, he found that all thirty-four of the wild rats with clipped whiskers died rapidly when placed in the water. Richter noted that these rats were newly trapped and that, as part of the whisker-cutting procedure, the rats had been transported in a black bag from a holding facility. The rats had been immobilized for a time because, as Richter noted, "held in this way, the rats can neither bite nor escape" (1957f, p. 196).

Richter concluded that the wild rats had lost "all hope of escape." He observed that some of the wild rats died simply from being held in the black

bag. Richter noted that the situation was "one of hopelessness: whether they are restrained in the hand or confined in the swimming jar, the rats are in a situation against which they have no defense. This reaction of hopelessness is shown by some wild rats very soon after being grasped in the hand and prevented from moving: they seem literally to give up" (Richter 1957f). Richter noted that the wild rats were more susceptible to this sudden death. So, while whisker clipping was incidental to avoiding food contamination and animal restraint was incidental to whisker clipping, it appeared that perhaps both of these events were instrumental in provoking hopelessness and even death.

A phenomenon called "learned helplessness" (Seligman 1972) would be understood sometime later and would become an important part of academic psychology. In one example of learned helplessness, rats and dogs were placed in an uncontrollable aversive context; they were unable to avoid electric shock. When later given an opportunity to avoid the shock, they were less likely to do so as a function of the prior experience. They had presumably learned that their avoidance behaviors were ineffective, and they tended to give up.

Some of Richter's results, though not all, were replicated by other investigators (cf. Grifiths 1960; Hughes and Lynch 1978). Hughes and Lynch noted that hopelessness might not be the best explanation; it was still not clear why the wild rats tended to drown to a much greater degree than did the domesticated rats after their vibrissae had been shaved and they had been held for a period of time. The reasons for this reaction, which was particularly common in wild rats, remain unexplained (Boice 1973; Hughes and Lynch 1978). Hughes and Lynch could only conclude that wild rats were much more vulnerable to drowning than the domestic rats (Hughes and Lynch 1978).

Neil Miller, the experimental psychologist, commented, "If you give these rats a chance to escape just once from this situation, when you later expose them again they will keep swimming for a long time" (Miller 1979, p. 44). But this concept of learning and expectation was not the sort of thing that Richter would go after with experimental gusto.

What Richter observed in the wild rat was a failure of behavioral adaptation. In the wild, a physiological response to an external event leads to a behavioral response, such as flight or biting, which in turn leads quickly to either success or failure. In the laboratory, however, such behavior was prevented. Adaptation was degraded, making the wild rats more vulnerable to a broad array of behavioral failures.

THE PROBLEM OF DOMESTICATION: BACK TO CANNON

Richter depicted voodoo death as not just a feature of "primitive" cultures, describing instances in our culture of deaths from excessive fear in war. Richter observed, "A phenomenon of sudden death has been described that occurs in man, rats, and many other animals, apparently as a result of hopelessness: this seems to involve overactivity primarily of the parasympathetic systems. In this instance as in many others, the ideas of Walter Cannon opened up a new area of interesting, exciting research" (Richter 1957f; Blass 1976, p. 329). Wolfe, Barger, and Benison recognized Richter's relationship to Cannon's work, commenting that "fifteen years later 'voodoo death' was reprinted in an issue of *Psychosomatic Medicine* that contained papers presented at a meeting of the American Psychosomatic Society held in 1957 to memorialize Cannon. Among the contributions was one by Curt P. Richter of Johns Hopkins, which followed up Cannon's article" (Wolfe, Barger, and Benison 2000, p. 479).

W. H. Gantt, Richter's colleague at the Phipps Clinic at Hopkins and translator and disciple of Pavlov, held a conference celebrating the twenty-fifth anniversary of the Pavlovian Laboratory at Hopkins. The proceedings of the conference were published as a book, *Physiological Bases of Psychiatry* (Richter 1958e).

In his presentation at this conference, Richter made no mention of Pavlov. The research he discussed was rooted not in Pavlov but in Cannon (Richter 1958e). Richter noted that it was Philip Bard, his colleague at Hopkins and a student of Cannon, who called his attention to the phenomenon of sudden death. He commented that "the reading of Cannon's paper stimulated me to start a search on a wider basis for an explanation of the sudden unexplained death in our rats. This search has led me to many new and unexplained fields" (Richter 1958e, p. 117).

Extending what I described above, Richter made the point that he noticed sudden death primarily in the wild rats, which he knew had larger adrenal glands. The rat felt trapped and unable to cope or to remove itself from the aversive situation. In Richter's own research, when rats were forced to swim for a long period, few of the rats that were not held died, whereas many of those that were held died. In other words, when Richter held rats for a period of time, he noted, "such a reaction of apparent hopelessness is shown by some

wild rats very soon after being grasped in the hand and prevented from moving. They seemed literally to give up" (Richter 1958, p. 120).

DOMESTICATION, SCIENCE, AND CIVILIZATION

Richter extended experimentally Darwin's concept of domestication, which had been discussed in the literature for more than fifty years (e.g., Yerkes 1913), applying his laboratory state of mind to the problem. He noted that since the publication of Darwin's book on domestication (Darwin 1868/1892), one species—the Norway rat—had been domesticated for a specific purpose (Richter 1949b). This animal was used "not as a source of food or clothing, not as a pet, but as an animal for scientific research in all branches of biology and medicine" (Richter 1949b, p. 379).

Darwin noted that "in all parts of the world, man has subjected many animals and plants to domestication or culture" (1868/1892, 1:2). He also observed the morphological effects of domestication in a wide variety of species. This was the background against which Richter embarked on his own studies on domestication. Some systems, such as reproduction, were enhanced by domestication. In Darwin's words, "our domesticated animals, which have been long habituated to a regular and copious supply of food, without the labor of searching for it, are more fertile than corresponding wild animals. It is notorious how frequently cats and dogs breed, and how many young they produce at birth" (Darwin 1868/1892, 2:89).

Of human evolution, Richter wrote that "primitive man lived in an environment in which physical strength, endurance and aggressiveness were at a premium" (Richter 1952a, p. 273). He said about what he assumed was the "growth of community life" that the more aggressive forms of behavior of the "primitive state" became less important as civilization developed (p. 273). Of course, this explanation of our behavioral biology is now outdated; we know that cooperation, deception, and cunning were just as important to our biological legacy as overt aggressiveness.

Richter asserted that "the wild Norway rat, like primitive man, lives in an environment in which it must constantly be on the alert and often has to fight for its very existence" (Richter 1952a, p. 275). Of course, we modern humans also fight for existence, and perhaps the reduction of adrenal capacity (assuming a phenomenon observed in animals whose food options are less predictable and less easily accessible also applies to us) is an important adaptation as we

shift our metabolic and cognitive resources elsewhere. Richter, following his intellectual predecessor Cannon, focused on the adrenals because of their vital function in adapting to duress.

Richter, always mining his data, recalled that spontaneous running occurred less in domesticated rats than in wild rats. Fasting produced much greater activity in wild rats than in domestic rats (Richter and Rice 1954). Richter and Uhlenhuth noted that no such difference in running activity was found in the wild variant when compared with the domestic variant after gonadectomy. The article suggests that the reduction in adrenal gland activation is compensated for by a greater dependence on gonadal secretion. This is nice evolutionary physiology hand waving. The reasons for the larger pituitary gland in the domestic strain of rat began to look confusing, and Richter acknowledged some of the confusion but did not really engage the issue. He used biology just enough to open discussion (table 4.2).

In "Domestication of the Norway Rat and Its Implications for the Problem of Stress," Richter asserted that "the use of the captive wild rat" represented "the completely wild animal in its free state" (Richter 1949a, p. 42). He also suggested that cultural selection tended to favor the tamer rats, the ones that were more easily handled by humans. Richter then suggested that "the diseases of adaptation" (Selye 1946) were a feature of domestication. Richter focused in these studies on how the effects of civilization both aid us (increasing our ability to solve problems of self-selection) and diminish our physiology (making our adrenal glands less robust).

TABLE 4.2. Comparison of Weights of Organs of Domestic and Wild Norway Rats

Larger in Wild Norway Rats	Larger in Domestic Norway Rats	Same Size
Adrenals	Pituitary	Lungs
Brain	Thymus	Ovaries
Heart	Uterus	Testes
Kidney		
Liver		
Pancreas		
Preputials		
Prostate		
Seminal vesicles		
Spleen		
Thyroid		

Source: Richter 1949b

As Richter understood it, the effects of domestication interacted with an individual's temperament and personal features, and particularly with individual variation of activity and inactivity (see also Kagan 1989). Richter suggested that some individuals had "richer" systems and expressed more "pep" (Richter 1932). He saw clock mechanisms at work in activity and inactivity (Richter 1932).

CONCLUSION

Richter's roving experimental eye brought him to taste aversion learning, a phenomenon that would later have a profound effect on American psychology and the understanding of learning. Richter, rooted in biological considerations, simply understood that a normal reluctance to ingest unfamiliar foods made wild rats difficult to trap, and that gustation was a primary sensory modality and part of the alimentary canal that included gastrointestinal functions. This phenomenon would play an important role in the coming battles about the biological basis of learning. But the ideological battles were not Richter's concern. It was the phenomenon itself that interested him.

Richter inherited the problem of domestication's influence on behavior and physiology and certainly made important contributions to this area of inquiry. The effects of domestication on a variety of behavioral and end-organ systems are now fairly well known (e.g., Price 1984, 2002).

Richter always maintained a practical, clinical focus on the effects of domestication by culture. A good deal of this research was done during World War II and was supported because of a prevailing emphasis on what was called military research, or military medicine. Richter suggested that the study of the wild rat could help in the war effort (Study of Wild Rats, Richter Archives, National Academy of Sciences).

The Committee on Medical Research supported Richter's research on bait shyness and food aversion learning, the ANTU ingestion research (Ormsbee 1948). In an article written for *Advances in Military Medicine,* Ormsbee cited Richter's work on "rodent control," describing how "ANTU was shown to be a valuable weapon in the control of the common Norway rat" (Ormsbee 1948, p. 654). Richter housed his research in real-world events; practical implications were always in close proximity.

Richter assumed a whole set of cultural ideas, some of which emerged from biology, others from the social sciences. He never argued for his ideas; he made assumptions and then sought their demonstration. He invented instruments,

developed experimental methods, and examined data. Richter began his investigations with an adaptationist conception of evolution (see S. J. Gould 2002 for limitations of this view) and the use and disuse of morphological and behavioral expression.

Richter expanded on a problem of domestication that began with Darwin. Both the work of Donaldson on domestication and the speculations of Cannon on voodoo death figured importantly in Richter's investigations. Richter mentioned that he visited Donaldson often (Richter 1985); one assumes this was to discuss the interesting findings Richter discovered in his laboratory.

Richter was one of a number of individuals looking at the effects of domestication on end-organ systems (King and Donaldson 1929), work that would continue over a long period (e.g., Price 2002). Domestication and temperament influence a wide variety of behavioral and physiological events, including rats' activity patterns and escape behaviors (Price 2002), and Richter's work fits nicely within a tradition of exploring these phenomena.

Richter referred to "captive wild rats as validly representing the completely wild animal in its free state" (Richter 1949a, p. 42). But what is a free state? Typically it is conceived of as the opportunity to succeed or fail in the attempt to survive and reproduce. In Richter's rats, the effects of domestication were reduced suspiciousness and ferocity due to lower levels of adrenal secretion, but better reproductive ability due to larger gonads. If Richter was entirely consistent he would have noted that domestication had great benefit, namely reproductive fitness. In other words, perhaps one advantage of domestication was an ability to easily express a sodium appetite (and a corresponding increase in longevity) and a greater ability to reproduce, thanks to higher levels of estrogen and lower levels of cortisol. These events, Richter suggested, parallel our own evolution, in which better adjusted but physically weaker individuals emerged: us moderns. Richter wondered whether the "diseases of adaptation" Hans Selye (1946) described (e.g., adrenal atrophy) were a reflection of domestication, writing, "In summary, the experiment started 100 years ago with the domestication of the Norway rat may help throw some light on trends of development of animals that live in a controlled environment and of the factors involved in the production of these trends. It may also give us data that will help to study the effects that the controlling of the environment may have had on man" (Richter 1949a, p. 45).

In a commentary at the end of this article, Selye noted, "I have followed Dr. Richter's work for many years and I so heartily agree with his conclusions

FIG. 4.4. Cartoon about Richter's work which appeared in a Baltimore newspaper. *Source:* © 1944, the *Baltimore Sun*. Reprinted with permission.

that I think I am the wrong man to discuss the paper. I feel that the interpretation of his data which he has given is very well supported" (Selye 1946, p. 45).

Richter noted three types of selection: selection in the wild, cultural selection by humans in an uncontrolled environment, and selection in a "controlled environment" (Richter 1949a, p. 45). This version of social Darwinism sought to explain the "production of the so-called weaker, the milder, better-adjusted individual" (Richter 1952a, p. 283). Richter wrote that the human "resembles . . . our domesticated Norway rat—happily living out its caged existence" (Richter 1952a, p. 283). This is a long way from the freedom of Colorado and the West where Richter grew up. He was clearly worried about the effects of domestication and the controlled environment on human physiology and human heredities.

A glorified conception of freedom and our restrained wild nature guided Richter (1953f) and manifested itself in this inquiry, as well as in his suspicion of what he called "designed research." He was wary of the consequences

of the controlled environment on human freedom, expression, and physiology. Of course, this notion is romantic, seductive, and can be misguided.

It is not clear to what extent Richter understood the possible limitations of the work and of his point of view. He was best at embarking on interesting empirical investigations. Though the details or the mechanisms remain unclear, the science was, I submit, endlessly interesting.

Richter's work did not go unnoticed by the local newspaper in Baltimore (fig. 4.4).