Introduction

At first glance, one might ask what the hunger for sodium has to do with psychology. In fact, most psychology textbooks hardly mention it. By contrast, learning and motivation are typical psychological topics. Hunger and thirst, and the study of stress and the emotions or conceptions of mind, are clearly included under the purview of psychology. What I hope to prove is that the hunger for sodium – or the search for something salty, which is expressed in a variety of different animals – is an ideal behavioral system to study, and is an appropriate topic within psychology.

INTELLECTUAL BACKGROUND

When George Wolf was a graduate student in psychology at Yale in the early 1960s, Neal Miller offered him a choice of topics to study. Miller's interest was primarily in learning and motivation, and in developing simple experimental systems for the study of psychological phenomena. By this time, Miller had embarked, with his students, on the study of how the brain produces motivated innate and learned behaviors, including salt ingestive behavior (see his collected works, 1971*a*, *b*). George was given the choice to work on the problem of visceral learning, or the hunger for sodium. He chose the latter. But, when the time came to defend his thesis, the following question emerged from members of his committee: 'what does the ingestion of salt have to do with psychology?' His defense was that the study of sodium hunger could serve as a system for the study of motivated behaviors and how the brain generates them. To appreciate this, the study of sodium hunger does not begin with George Wolf, but with Curt Richter.

It was Curt Richter who discovered the phenomenon of sodium hunger in 1936. Several years later (1939) he suggested that the hunger for sodium was an innate drive. But, this was left to others to demonstrate. For example, Eliot Stellar, interested in how the brain produces motivated behavior, with his student Alan Epstein, showed that the sodium-deficient rat ingests large quantities of sodium within a short period of time when the rat is exposed to it for the first time (1955). Many others inquirers found similar results (e.g. Denton, 1982; Wolf, 1969*b*).

The fact that the behavior is innate, and easy to study, allowed experimental psychologists to examine what the animal might learn about the location of salt and what it was associated with. That is, rats could demonstrate that they learned something about the significance of the salt when they were not sodium hungry and demonstrate what they learned when they were for the first time (Krieckhaus & Wolf, 1968; Krieckhaus, 1970). The hunger for sodium was therefore used to study how learning interacts with innate prewiring. This is what intrigued Miller & Stellar; here, sodium hunger could be used as a model system in which to study the interaction of learning and homeostatic regulation.

Richter (1941) discovered that hormonal signals also generate a sodium hunger. In fact, hormones essential to the physiological regulation of sodium balance (angiotensin and aldosterone) also generate the behavior of salt ingestion (e.g. Fluharty & Epstein, 1983). The synergy of angiotensin and aldosterone is important to the arousal of sodium hunger (e.g. Epstein, 1984). However, other hormones also generate a sodium hunger. The hormones of female sexual reproduction (prolactin, oxytocin, estrogen), in addition to the hormones that are involved in the adaptation to stress (ACTH and the glucocorticoids), also generate a sodium hunger (Denton, 1982).

It was Richter who also first found that, during reproduction, the female rat's ingestion of salt goes up markedly (Richter, 1956; Denton, 1982). Salt intake is also sexually dimorphic. Females ingest two to five times more salt than male rats under a variety of conditions (Krecek, 1973; Wolf, 1982). Perhaps the greater hunger for sodium in females may have evolved because of the needs of the female during pregnancy and lactation.

A number of behaviors are sexually dimorphic and under hormonal control (Goy & McEwen, 1977). It is more generally known that steroid hormones, during critical periods of development, have profound effects on brain and behavior. Salt ingestion is one of them; virgin female rats typically ingest more salt than male rats, and the elevated salt ingestion, normally seen in adult female rats, is altered by manipulation of gonadal hormones during the neonatal period of development (Krecek *et al.*, 1975).

These steroid effects are manifested because steroid hormones have both organizational and activational effects on both brain and behavior (Goy & McEwen, 1977). Neural circuits are shaped, and behavior is directed, by hormonal influences. Moreover, changes in the structure of the brain that result from steroid hormone actions are not restricted to just critical stages in development (Arnold & Breedlove, 1985). This is also true in the study of sodium hunger since the intake of salt is influenced by the animal's history during adulthood (e.g. Falk, 1965*b*). The hormones of sodium homeostasis, aldosterone and angiotensin, when elevated, also result in the increased responsiveness to salt even when rats no longer hunger for it (Sakai *et al.*, 1987, 1989).

Probably the best-studied hormone-induced behavior is lordosis in female rats. Estrogen and progesterone play an essential role in this female sexual behavior, and the neural circuit that mediates that behavioral effect has been successfully analyzed (e.g. Pfaff, 1980; McEwen *et al.*, 1987). For example, tritium-labeled steroids were mapped to receptor sites in the brain by radioautography and other neuroscientific techniques. The behavior was aroused by the application of the hormone to critical brain regions (ventral–medial hypothalamus), and was suppressed by the inhibition of neurotransmitters being synthesized within this region. The anatomical connectivity of this region of the hypothalamus to other brain regions was worked out, with a resulting analysis of a steroid-induced behavior and its anatomical basis. There are other examples of steroid-induced behaviors whose anatomical bases are now beginning to be understood (see Arnold & Breedlove, 1985). Now we add the study of sodium hunger.

We know something of where the brain hormone receptors that initiate sodium hunger are localized and of their mechanisms of action. In addition, the interaction of peripheral organs (heart, liver, etc), and the brain in the control of salt ingestion, have been outlined. Anatomical tracer studies have allowed for the assemblage of neural circuits that underlie salt ingestion. Thus, one begins to understand how the brain orchestrates the search for something salty by combining behavioral, physiological, anatomical, and biochemical techniques.

While in the search for something salty, animals use gustation to explore their world to select edibles from nonedibles. The question arises as to how the animal recognizes the salty taste, and which parts of the brain are involved. We are now in a position to address this. We know which gustatory (taste) nerves are importantly involved in the recognition of a salty taste, what the mechanisms of sodium transduction are, and at what level of the gustatory neural axis this occurs.

Richter thought that the change in sodium status resulted in an alteration of taste sensitivity and in changes in central states (see 1956 review). When this central state occurs, the animal then searches for, and ingests, the salt. While it is not the change that Richter suggested (increased sensitivity to salty ingesta), the specific need for sodium does, in fact, result in a change in taste sensitivity and in changes in central states.

This change in gustatory sensibility is an arbiter in the control of ingestive behavior. Sodium hunger is guided by specific taste fibers and neurons that are related to the salty taste of sodium. Significantly, the brain controls this behavior.

There is also a hedonic component to salt ingestion. That is what Pfaffmann called the 'pleasures of sensation' (1960), and it is a factor in taste-guided behavior. Richter and others (Nachman, 1962) certainly thought that salt tastes good to the animal that needs it. In fact, there is now strong evidence that gustatory sensibility and nutritional balance, particularly sodium balance, are, indeed, intimately connected, as both Richter and Pfaffmann had thought (e.g. Contreras, 1977).

But, it was P.T. Young (1949) who championed the idea that there is an hedonic factor in ingestive behavior. He did this at a time when such 'mentalistic' talk was sacrilegious, for he did his work in the heyday of American behaviorism. But, Young's criterion for the hedonic was always behavioral (choice and speed of approach), and he made an important distinction between palatability and appetite. Appetite is a response to what is needed – that is, sodium. Palatability responses can be independent of biological requirements.

As you will see, there is a dramatic shift in the oral–facial profile to infusions of hypertonic NaCl (about the concentration of sea water) when rats are sodium hungry. The facial display appears as if they are ingesting something rewarding – like something sweet – when they need the sodium (Berridge *et al.*, 1984). When they do not need sodium, they reject the salt in a characteristic fashion, and the hypertonic NaCl appears aversive. In fact, homeostatic needs like sodium hunger can produce affective changes in the acceptability of NaCl solutions. Similar phenomena have been described in other contexts, e.g. temperature regulation (Cabanac, 1971, 1979) and called 'alliesthesia', or the change in the hedonic response as a function of internal state (Stellar, 1980). In other words, to ensure motivation to ingest substances that normally are somewhat aversive, and to traverse distances and overcome obstacles to obtain the solute, Nature has tied the motivation to reward, and the reward includes pleasure when the salt is obtained.

For Curt Richter, behavior was essential in the regulation of the body's needs: the need for protein, carbohydrates, vitamins, and minerals such as sodium or calcium (see Richter's collected works, 1976; Schulkin, 1989). Richter brought to the study of behavior the idea of the regulation of the internal milieu (Bernard, 1865), and what was called homeostasis and the 'wisdom of the body' (Cannon, 1915, 1932).

The study of sodium hunger, therefore, was, and remains, an optimum place for the 'whole body' physiologist; that is, the physiologists with an interest in behavior were quick to see the importance of sodium hunger. Derek Denton is the outstanding exemplar. No one has studied salt ingestion to the extent and at as many levels as he has over the last 35 years. The experimental scope is vast. It goes from recording rabbits and kangaroos in the wild licking at salt pegs to the thorough analysis of the sodium hunger of sheep and the behavioral, physiological and anatomical mechanisms that control its behavior toward salt. The book he has written on sodium hunger is a classic (Denton, 1982).

The tradition of Denton is medical and physiological, with roots based on the works of Bernard, Cannon, and Richter. Their thesis is that behavior is organized physiologically by messages from the internal milieu to the brain. Perhaps, the messages emanate from sodium reservoirs (Wolf & Stricker, 1967; Stricker & Wolf, 1966), or from the activation of sodium sensors in the brain or liver, or from mechanisms in the heart, adrenals, kidney, and pituitary. The whole body figures in the regulation of body sodium. In other words, the study of sodium hunger allows one to examine the body at large and how it mobilizes itself to maintain sodium balance. One mechanism that it uses is behavior:salt ingestion.

In what follows, we will traverse a range of subjects. This will range from the ecology of salt ingestion to the sodium molecules and the action of various hormones. The emphasis is on experimental and behavioral manipulations of salt ingestion. The first chapter outlines the behavioral expression of salt-seeking behavior; the second, its hormonal regulation; the third is about the gustatory contribution; the fourth is the physiological, molecular, and pathological control or regulation; and the final chapter describes the neural circuits underlying salt ingestion. But, in each chapter, there is discussion of each – behavior, hormones, gustation, physiology, and the brain.

What the reader should walk away with is how a motivational system is organized at a number of levels, e.g. behavioral, physiological, and neurological. Reference is also made, throughout, to other motivations (e.g. hunger, thirst or sex), in addition to the study of affect, innate wiring, learning, and sexually dimorphic behaviors. The work has implications, more generally, beyond the study of sodium hunger.

1 Salt seeking behavior

SODIUM HUNGER: AN OCCURRENCE OF NATURE

The search for food and water which contain proteins, carbohydrates, vitamins and minerals is one of the major activities for most animal species. Evolution selects behavioral strategies that optimize the chances for satisfying bodily homeostatic demands. The behaviors include: 1) arousal; 2) search; 3) recognition; 4) decision to accept or reject; and 5) digestion. There are nutritional and sensory categories that help organize the behaviors (Rozin & Schulkin, 1990). Sodium hunger is, first, a phenomenon of Nature.

Periodically, rainfall depletes the sources of sodium that are being ingested from food by land-dwelling herbivores. This is especially true when the animal is located far from the sea, and probably contributed to the evolution of sodium hunger (Denton, 1982). The selection of a behavioral response to ingest salt is particularly true in females, perhaps because of the demands of reproduction (e.g. pregnancy and lactation – see Chapter 2).

A series of elegant experiments carried out in Australia (Blair-West *et al.*, 1967) demonstrated that, during times when the sources of sodium were low and diluted from rain, and the sodium-retaining hormone, aldosterone, was elevated, rabbits or kangaroos would travel to sodium sources placed by the experimenters to ingest this scarce commodity (Fig. 1.1).

In fact, sodium-deficient animals, particularly ungulates, are known to travel great distances to obtain and ingest salt (Denton, 1982). They are guided, perhaps, by a central gustatory system in addition to other sensory systems (e.g. olfaction and sight) that, like other sensory systems, reaches out to the world (e.g. Gibson, 1966). In this case, they are trying to find sources of sodium. The state of sodium hunger is one of exploration to find the needed sodium.

Thus, there are many instances in the wild of mammals searching for salt. Moose, white-tailed deer, reindeer, caribou, goats, sheep, and even elephants are known to search for salt deposits when sodium is scarce (e.g. Botkin *et al.*, 1973; Belovsky, 1978; Weeks & Kirkpatrick, 1976; Herbert & Cowan, 1971; Cowan & Brink, 1949). Such herbivorous animals tend to display energy maximizing strategies in the search for salt sources (Belovsky, 1978). Sodium in

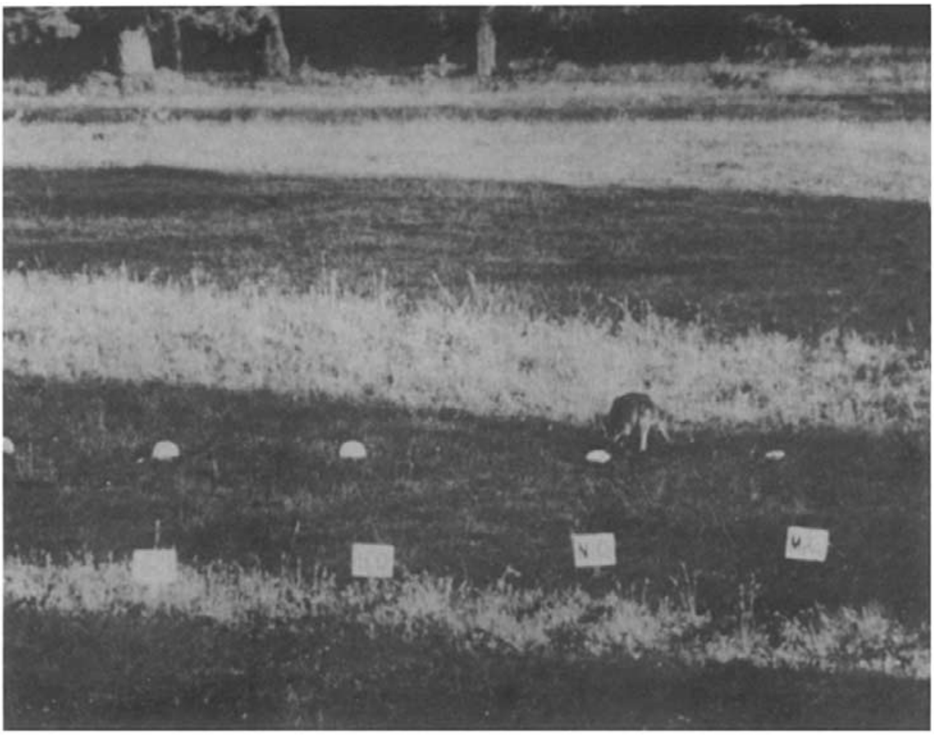

Fig. 1.1. A telescopic lens photograph of a kangaroo at a salt peg (from Denton, 1982).

such contexts is just one of several minerals at the deposit. In fact, gorillas (Schaller, 1963) and chimpanzees (Goodall, 1986) are known to ingest dirt rich in many minerals. Not only do herbivorous and omnivorous animals ingest at such mineral licks when sodium is in short supply, but also, on occasion, carnivores are sighted at such licks (e.g. foxes). These carnivores are probably there to prey on herbivores.

The phenomenon is not limited just to mammals. It is also expressed in birds. For example, the vulture, red crossbill, and gold finch are known to eat at salt licks (Aldrich, 1939; Coleman, Fraser & Pringle, 1985; Peterson, 1942). This is particularly true during the reproductive season, in both birds and mammals, when females are known to be at the lick more often than males (e.g. Dixon, 1958).

In the laboratory, both sodium-hungry sheep (Denton, 1982) and sodium-hungry rats (Fig. 1.2; Arnell *et al.*, unpublished observations) will ingest salt licks. Therefore, sodium hunger is an occurrence of Nature, tied to the demands of evolution, and a phenomenon produced in the laboratory.

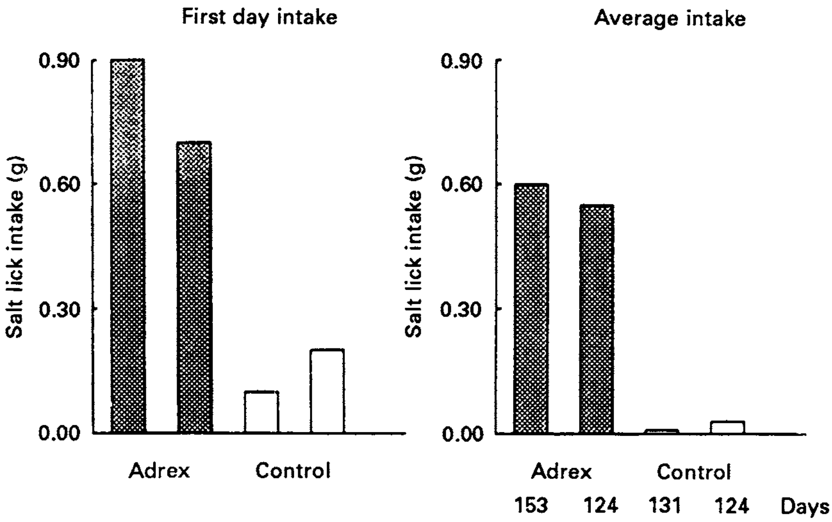

Fig. 1.2. Ingestion of salt lick in control and sodium hungry (adrenalectomized (Adrex)) rats (from Arnell, Schulkin & Stellar, unpublished observations).

INTRODUCTION TO EXPERIMENTAL DEMONSTRATION OF SODIUM HUNGER

What made sodium hunger attractive to study was that a rich set of behaviors were easy to elicit. In this chapter, I will describe some of the laboratory findings regarding the sodium-hungry animal, intermixed with reference to broader psychobiological issues. The animal I will be talking about mainly is the rat, but I will refer to the sheep, and, to a lesser extent, to the pigeon, the hamster, the mouse, the rabbit, and the monkey.

The reader should note, at the outset, that what is unique about sodium hunger, in contrast to vitamin or other mineral regulation, is that it is innate (see Rozin, 1976). That is, the first time rats or sheep are rendered sodium hungry, and then subsequently allowed access to salt, they ingest it within seconds before the body can appreciate the restorative consequences of the ingestion. Almost all vitamin or mineral hungers require some learning. In addition, rats, at least, do not have to be sodium hungry to learn about the significance of salt. In other words, they are prepared to learn where it is found, how to acquire it, and with what it is associated even in the absence of any motivation to consume salt. This should be a common occurrence in Nature; animals do not have to be in the relevant drive state, or in tissue deficit to notice a valued commodity and then return there when they need it (Krieckhaus, 1970).

The sodium-hungry animal is motivated to search for salt. It demonstrates what Wallace Craig (1918), the American naturalist, called both the appetitive and consummatory phases of instinctive behavior. In the appetitive phase, the animal searches for its goal, in this case a salty taste. In the consummatory phase, the animal has reached its goal and consumes the salt. Neither phase requires learning, though learning, no doubt, can influence both events.

Importantly, when an animal is sodium hungry there is a hedonic shift in the perception of salt (see also Chapter 3). In other words, the biological need for sodium is tied to the pleasure or reinforcement associated with salt ingestion. This, no doubt, contributes to the motivation of the animal to search for salt; that is, a hedonic judgment is made by the sodium-hungry rat that results in the salt now being perceived as more rewarding. Like other homeostatic systems, such as general food hunger or thermal regulation, the regulation is tied to hedonic events (Cabanac, 1971; Stellar, 1980).

Psychological, in addition to neurobiological, factors are discussed in this chapter, including: the enhancement of the avidity of the salty taste and its ingestion as a function of having been sodium hungry before, and the use of endogenous circadian clocks in the anticipation of salty commodities.

The picture I would like the reader to consider is the following: when an animal is sodium hungry, a representation of salty taste is activated, which serves to guide the behavior in the search, identification, and ingestion of salt. Innate mechanisms are responsible for the sodium-hungry animal ingesting the salt immediately upon its first exposure, and for noting the significance of the salt when it is not sodium hungry. A hedonic shift in the perception of the salt emerges in sodium hungry animals. The result is a motivated behavior with appetitive and consummatory phases in the search for a salty taste.

THE INNATE HUNGER FOR SODIUM

In the tradition of Cannon (1932), and his doctrine of 'the wisdom of the body', Richter envisioned a variety of innate behavioral capacities in order to select the nutrients and minerals that were needed. Others thought the behaviors were learned (e.g. Harris *et al.*, 1933). Richter was right about sodium hunger; he hypothesized early on that the appetite for salt which results from sodium deficiency is an innate drive (1939; 1956).

Richter's first study on salt appetite, over 50 years ago, used the adrenalectomized rat (1936). Because the adrenal gland had been removed, the animal was without the sodium-retaining hormone aldosterone, and chronically lost sodium. This is a fatal situation if there is no access to salt. With access, the adrenalectomized animal vigorously ingests sodium. The behavioral results are shown in Fig. 1.3. Richter also found that sodium salts were preferentially prefered over nonsodium salts (Fig. 1.4).

Richter did not provide evidence that the appetite is innate, he just hypothesized that it is. The sodium-hungry rat could have learned something

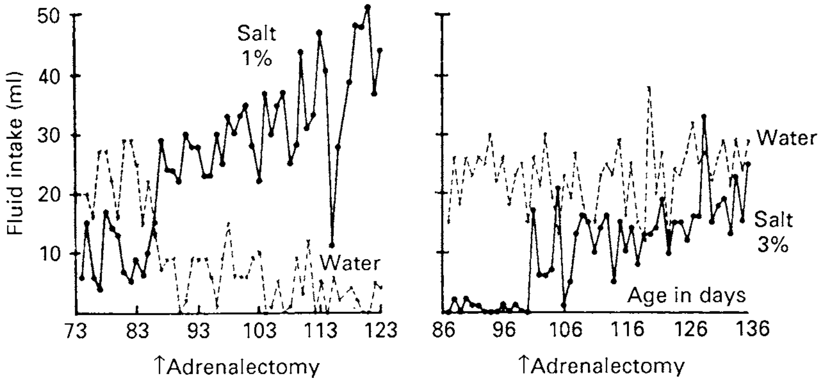

Fig. 1.3. 24-h salt and water intake before and following adrenalectomy (from Richter, 1936).

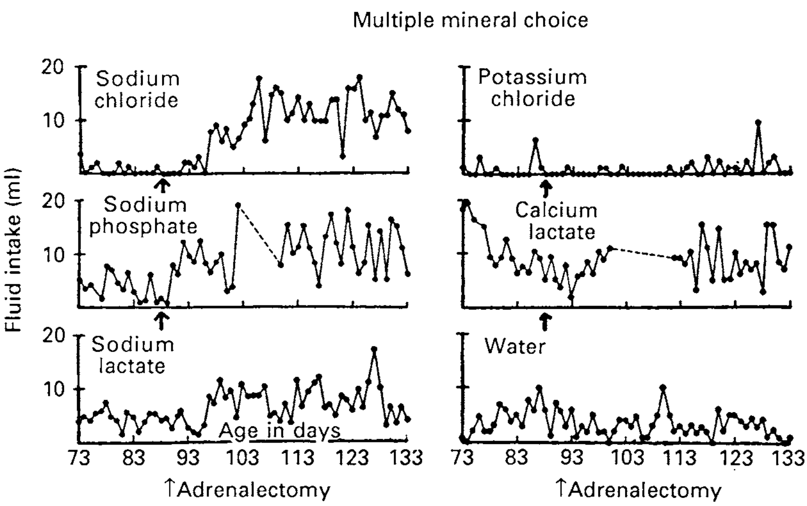

Fig. 1.4. 24-h salt intake before and following adrenalectomy (from Richter & Eckert, 1938).

from the consequences of the salt ingestion, or the exposure to the salt before the adrenalectomy. Bare (1949) also thought the hunger for sodium was innate. He showed that the adrenalectomized rat would ingest sodium within 24 hours. But, this finding does not show that the behavior is innate, since, by 24 hours, the rat may have learned something about the consequences of the salt ingestion. Are the drive and the recognition of the salt taste innate? Answers to these questions awaited further research.