Rheostasis

Homeostasis Reexamined

The concept of homeostasis has become so familiar to biologists today that sometimes they fail to appreciate its splendor, like a fine picture that goes unnoticed because it hangs in the same position on the wall from day to day. But if we pause to look again, we find that the themes that inspired Claude Bernard and Walter Cannon are as universal as ever. Here we are, on this earth, composed of matter that is extraordinarily unstable. It takes only a few minutes of oxygen deprivation before our neurones are irreparably damaged, and a rise in body temperature of only a few degrees centigrade before our proteins begin to denature. Compared with all the cosmic forces that swirl around us, our bodies seem extremely fragile.

What Bernard realized was that the hostile forces outside of us are only part of our environment because we also have an internal environment, the friendly *milieu intérieur.* Numerous physiological reactions maintain stability in this milieu, and we manage to survive despite our mechanical and chemical fragility—and not merely survive, but to survive in a way that enables us to disregard the external environment most of the time. According to Bernard, *"La fixité du milieu intérieur est la condition de la vie libre."* Here *libre* means independent. By maintaining constancy in the internal environment, we free ourselves of constraints from the external environment; we can live in the desert, in the Arctic, even in outer space. Space travel is the ultimate example of homeostasis, because inside the space vehicle, inside the helmet and the space suit, inside the skin, you find the same old *milieu intérieur,* 37°C, 90 mg sugar/dl blood, the same old plasma calcium and potassium concentrations. Much of the technical elaboration that permits space travel has the same purpose as our terrestrial physiologies—to maintain stability in the internal environment. As Bernard (1878) put it, "all the vital mechanisms, however varied they may be, have but one end, that of preserving constancy in the internal environment."

If we go back to Bernard and Cannon, we find a freshness and breadth of vision that are often lacking today. But we too have our strengths. Among the advantages of intense specialization are deepening analysis of the details and the acquisition of major data bases. How do these two approaches fit together?

More specifically, how does the sweeping concept of homeostasis stand up in the light of recent facts? That homeostasis has received so little critical examination attests to its incontestable value in making sense of the facts. Yet at the end of his 1929 paper, Cannon said that errors had probably crept in, that his review was "inadequate and provisional," the start of a process rather than a conclusive statement. "In such a venture . . . crude ideas are sure to be projected which must later be refined." It is a tribute to Cannon rather than a criticism to take up this challenge. And when we look closely again at the magnificent panorama of homeostasis we find that it contains unconvincing passages, erroneous depiction, and some dubious coloring.

Before we consider these inadequacies, it needs to be said that there are several views of homeostasis, with somewhat differing emphasis. There is Bernard's original statement, with constancy of the *milieu intérieur* as its centerpiece. There is Cannon's elaboration, with more emphasis on dynamic equilibria and variability. He picked the word hom*e*ostasis rather than homostasis to indicate similarity, with some variability, rather than sameness. Then comes a newer view: homeostasis is equated with the operation of negative feedback systems. How entrenched this view has become is illustrated by a quotation from a short exposition (Langley, 1965) of homeostasis for undergraduates:

> Cannon's word, *homeostasis* embraces the fixed, or constant, internal environment, but then goes on to suggest dynamic, self-regulating processes that serve to maintain that constancy or to return the internal environment to normal should it get out of whack. This is the concept now referred to as *negative feedback,* that is, if there is a deviation in one direction, there is a reaction in the opposite direction.

Another example comes from Guyton's (1982) textbook.

> The term *homeostasis* is used by physiologists to mean *maintenance of static,* or *constant, conditions in the internal environment.* Essentially all the organs and tissues of the body perform functions that help maintain these constant conditions. . . .
>
> In this mechanism [baroreceptor pressure-regulating mechanism], it is clear that a high pressure causes a series of reactions that promote a lowered pressure, or a low pressure causes a series of reactions that promote an elevated pressure. In both instances these effects are opposite to, or *negative* to, the initiating stimulus, hence the term "negative feedback."
>
> Essentially all other control mechanisms of the body also operate by the process of negative feedback.

There follows here a list of limitations in these various accounts of homeostasis. This list starts with several sections that illustrate why homeostasis should not be equated with negative feedback. It then broadens to consider the lack of evolutionary perspective in early formulations of homeostasis and the failure to encompass changes in defended levels. For many readers these cautions about simplified views of homeostasis will be gratuitous. For those who have not had time to think about the subject they may be helpful.

FEEDFORWARD

It has been realized, especially by McFarland (1970, 1985) that homeostasis does not depend exclusively on feedback; it also involves feedforward. "The term *feedforward* is used for situations in which the feedback consequences of behavior are anticipated and appropriate action is taken to forestall deviations in physiological state" (McFarland, 1985). Although little is known about the actual mechanisms involved, feedforward is not uncommon. For instance, eating usually has osmotic consequences, with salt and other nutrients producing dehydration. Much of a rat's water intake occurs in association with its meals; fine-grain analysis reveals that this prandial drinking takes place mostly before the meal or during the first 30 seconds of the meal, that is too soon for the full osmotic effects of the food to be felt (Kissileff, 1969). Water is also used for evaporative cooling by the thermoregulatory system. Pin-tailed sand grouse, *Pterocles alchata,* in parts of Morocco where air temperatures can reach 50°C, forage for water in the early, cooler parts of the day. This avoids having to fly (and the associated higher metabolic rate) during the intense heat of the middle of the day. Drinking controlled by feedback mechanisms would be more likely to occur during or after the hottest times of day. The early morning flights to water sources seem more likely to be controlled by feedforward mechanisms (Thomas and Robin, 1977).

A good way to appreciate the difference between feedback and feedforward is to note, as in Figure 1–1, that sensors can be made to detect changes in either the regulated variable or in disturbances that affect that variable (Houk, 1980). When the sensors are responsive to the value of the regulated
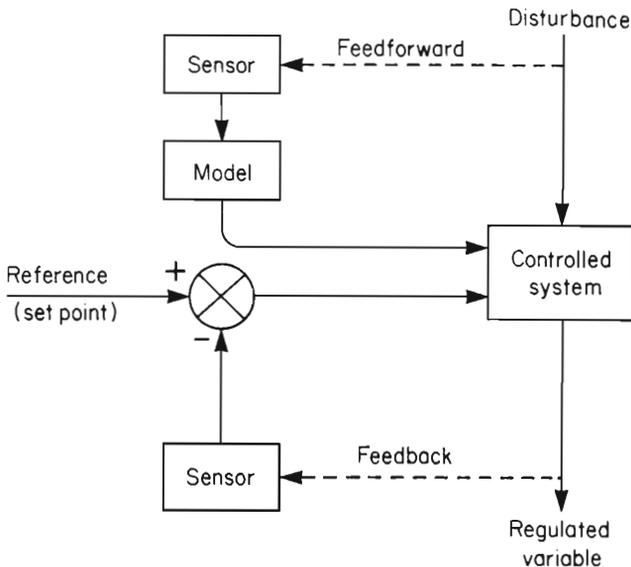

Figure 1–1. A control system having both feedforward and feedback. The feedforward is shown influencing the controlled system, but it might exert its effects at some other point (Houk, 1988). For further explanation, see text.

variable, this is called feedback; when the sensors are responsive to the distur-bances, this is called feedforward. For feedforward to be useful, the system must in essence contain a model of how the regulated variable will respond to disturbance. Such models are probably complex and should be modifiable by learning (Houk, 1980). For instance, the traditional view that tolerance to drugs depends on compensatory feedback mechanisms is being supplemented by the realization that feedforward contributes through the Pavlovian conditioning of responses that oppose and attenuate the effects of the drugs (Siegel et al., 1987). When these anticipatory responses are elicited without the drug itself being given, withdrawal symptoms appear.

Feedforward and feedback are not mutually exclusive: they can operate alongside each other, as an experiment on doves illustrates (Fig. 1–2). When offered water after 48 hours of deprivation the birds started to drink, presum-ably in reaction to feedback signals indicating deficits, but the amounts taken were greater if the birds were put in a warm environment for the test. The doves drank in one draught soon after being given access to water. The greater drink-ing at warm temperatures anticipated the threat of thermally induced dehydra-tion. It is therefore an example of feedforward (Budgell, 1970).

POSITIVE FEEDBACK AND RESPONSE MOMENTUM

A variety of activities are necessary for an animal's well-being. For instance, a rat needs to groom, sleep, eat, drink, find a mate, and build a nest. If behav-iors were initiated as soon as a deficit occurred and terminated as soon as a deficit was abolished, there would be much switching between different activ-ities (de Ruiter and Wiepkema, 1969; McFarland, 1971). A few mouthfuls of food would be enough to eliminate hunger and the animal would then start to do something else. But because it had ingested so little, this other activity would soon be interrupted by another bout of feeding. Such dithering could be energetically wasteful, especially if the food source were far from the home or from the site where other activities occurred. One way to make the rat into a meal eater rather than a nibbler, to maintain response momentum, is positive feedback (Wiepkema, 1971).

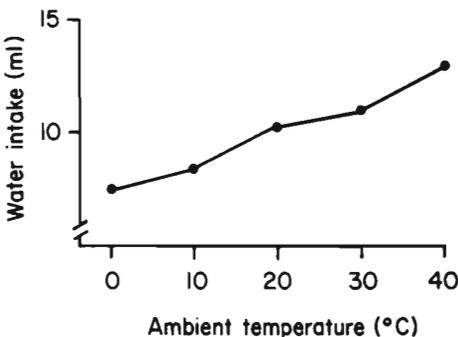The efficacy of appetizers probably depends on positive feedback. The

Figure 1–2. Water intake of doves, after 48 hours without drinking, during short tests conducted at different ambient tem-peratures (adapted from Budgell, 1970).

subject has been well studied in mice (de Ruiter and Wiepkema, 1969; Wiep-kema, 1971). When rodents take a meal, they do not eat continuously but pause between bouts of chewing. In a previously food-deprived mouse these pauses are less frequent and the chewing bouts longer than in an animal at its normal weight. The animal therefore ingests more in a given time. This information about meal structure in a hungry animal helps in interpreting the behavior of a mouse fed *ad libitum*. In the latter the speed of eating increases at the start of a meal. Rather than slowing down and pausing more as more food is taken in, initially the mouse does the opposite and acts as if eating makes it still hungrier. The accelerated ingestion at the start of the meal depends on stimulation from the taste receptors because it is abolished if the food is made unpalatably bitter. Eventually, of course, feeding slackens and stops as the animal becomes fuller, but at first it behaves as if there were a positive feedback. Whether the phe-nomenon actually depends on a positive feedback loop, say some recurrent collaterals coming back to and stimulating their neurones of origin, or on inhi-bition of some other system that normally inhibits eating, is an open question (de Ruiter and Wiepkema, 1969). In either case response momentum is main-tained.

Another example of response momentum that is hard to explain without invoking something in addition to negative feedback occurs after glucopriva-tion. It is possible to make rats eat more than usual by injecting insulin in doses sufficient to lower blood sugar levels to values of about 50 mg/dl. But if rats are prevented from feeding for 6 hours their blood sugar climbs back to the same level measured in saline-injected controls, presumably as a result of glu-coneogenesis from liver glycogen or by other physiological means. Remarka-bly, if food is then offered, the rats eat more than the controls, even though the glucose level is now the same in the two groups (Ritter et al., 1978). Even when plasma glucose levels are raised to just above normal by infusing glucose to-ward the end of the 6 hours without food, the insulin-injected animals eat more than controls that had not been given insulin earlier. Perhaps once the com-mands for defense have been launched there is some obligatory delay before they can be rescinded, or perhaps the feeding is in response to some secondary metabolic change that results from temporary glucoprivation (see also Nona-vinakere and Ritter, 1983). Whatever the underlying mechanism, it is clear that although severe glucoprivation is a way to increase feeding, the glucoprivation does not actually have to be present when the hyperphagia occurs.

A continuing response in the absence of a deficit has also been described in the Pekin duck after challenges with osmotic stimuli (Hammel, 1989). Infu-sions of hypertonic NaCl solutions stimulate the nasal salt gland to become active. However, once triggered, the gland continues to excrete salt at a greater rate than the sodium chloride is infused. This drives the tonicity of the blood down to levels that are actually lower than those needed to trigger the excretory response in the first place. Why does the response outlast the osmotic stress? One possibility that should be considered in such cases is that there is a nega-tive feedback system but with integral rather than proportional control. In in-tegral control the response strength of the effectors depends not only on the discrepancy between the actual and the set value of the defended variable but

also on how long the actual value has been displaced from the set-point (Hardy, 1961). In the case of the Pekin duck, integral control was not supported by experiments in which the rate of infusion was varied. Therefore, a positive feedback loop was suggested as a possible explanation of the continued response.

CRISIS AND NORMAL BEHAVIOR

In discussing the increased speed of ingestion at the start of a meal in the mouse, we assumed that initially there is a deficit and that positive feedback maintains the restorative responses once they have begun. Even this, in some cases, may give too much prominence to deficit correction in the control of behavior. For example, it is not clear that there usually is a deficit when a mouse or rat starts to eat. There is always some food in the stomach of a rat when it has *ad libitum* access to food in the laboratory (Collier et al., 1972; Armstrong et al., 1978), yet it takes a number of discrete meals throughout the course of each day. This number is greatly influenced by the environmental conditions. If the rat must work to obtain a meal, then it takes fewer but larger meals (Collier et al., 1972). The animal adjusts its behavior within a few days each time the work requirement is altered. The strong and relatively rapid influence of environmental conditions suggests that, in a rat at normal body weight, internal energy deficits are relatively unimportant in the control of meal patterns. Before dismissing a depletion–repletion account of feeding in the undeprived animal, there should be a detailed examination of the behavior immediately after schedules are changed, that is before the internal milieu could alter. However, there is already a good case for thinking that the animal acts as an economist would, surveying the distribution of resources in the environment and the costs in obtaining them. It then arranges its patterns of exploitation so that it obtains these resources at the optimum time and rate. Its foraging behavior is not closely governed by any feedback from the *milieu intérieur* (Collier, 1985, 1986).

Of course, meal-taking behavior contributes toward preserving a stable *milieu intérieur* over the long term. Influences from the outside environment on eating patterns do not replace homeostasis. For example, even when the rat has to press a bar 80 times for each meal and takes only a few meals during the day, it still manages to maintain its body weight (Collier et al., 1972). Homeostatic defenses against becoming too fat are also evident despite environmental influences. When a satiated rat is induced to eat more than it ordinarily would at a particular time of day by being presented with a stimulus that has been associated with eating, the animal compensates for the conditioned eating by taking less food later in the day (Weingarten, 1984). Over a 24-hour period, food intake remains relatively constant despite different meal patterns. Environmental constraints on feeding are not, therefore, a negation of homeostasis. They suggest rather that homeostasis is taking a longer-term perspective and the animals are not constantly "riding a roller coaster of energy balance from

the heights of repletion to the depths of depletion" (Weingarten, 1985). In fact, by taking environmental constraints into account, and by eating again before nutrients are emptied from the stomach, the rat is probably able to keep the *milieu intérieur* more stable than would be possible by reactions to signal errors in a simple negative feedback system.

Should some crisis arise, responses to deficits are available, even though they are not normally called upon. More is eaten after glucoprivation, but the blood sugar level must be driven down to near 50 mg/dl to obtain the effect. This is far below the normal levels that occur during intermeal intervals. Moreover, at 50 mg/dl rats become ataxic and show other signs of neurological impairment (Brandes, 1977). It would hardly be adaptive for an animal to start eating only when reduced to this state. It must be said, however, that small drops in blood sugar (about 10%) have been detected just prior to a meal (Louis-Sylvestre and Le Magnen, 1980; Campfield et al., 1985). It is debatable whether these are the primary cause of subsequent eating or the result of hormonal changes (e.g., an anticipatory increase in insulin) that occur once a decision has been taken to initiate a meal shortly. Certainly glucoprivation is not necessary for normal feeding. It has long been recognized that lateral hypothalamic lesions can abolish the feeding response to insulin-induced hypoglycemia but that the lesioned animals still eat meals and respond to food deprivation and changes in environmental temperatures. Glucoprivic control of feeding probably "functions only during emergencies to reverse large and life-threatening decreases in blood sugar" (Epstein et al., 1975).

This discussion of blood sugar and feeding illustrates the general point that behaviors contributing to overall homeostasis need not be driven by discrepancies between actual and set values or by persistent load errors in a negative feedback system. They may result from anticipation, positive feedback, and economic planning over a longer time span in a way that prevents deficits from developing.

In a similar way, breathing is not always driven by rising and falling levels of CO_2 in the blood. During wakefulness some nonchemoreceptor input to the respiratory center keeps CO_2 below levels that stimulate breathing (see Sullivan, 1980). Should the P_{CO_2} rise much above 40 mm Hg—for example during exercise or some emergency—central CO_2-sensitive chemoreceptors in the ventral medulla are ready to boost minute volume (respiratory rate × tidal volume). In more extreme situations peripheral O_2-sensitive chemoreceptors in the carotid and aortic bodies come into action. But chemoreceptors are not essential for breathing to occur. This is evident from a consideration of the affliction known as Ondine's curse, in which minute volume fails to increase in response to elevated P_{CO_2}, in some cases even when P_{CO_2} rises above 60 mm Hg (e.g., Shannon et al., 1976). Yet during the awake state breathing continues in a relatively normal way, driven presumably by some neural input rather than by the chemoreceptors. However, in slow wave sleep breathing fails, the neural input to the respiratory centers evidently being inhibited in this state and the chemoreceptive system remaining deficient (Shannon et al., 1976).

DIFFERENT MECHANISMS FOR CONSTANCY

The existence of behaviors that prevent internal instabilities from developing is only one illustration of the inappropriateness of equating homeostasis with any single type of mechanism. Another is that, even without feedforward, defense of stable levels could be achieved in a variety of ways. One is to compare the value of the feedback against that of a reference signal, or set-point, as shown in the most commonly given type of diagrams (Fig. 1–3). In this case there is a set-point in the strict engineering sense of the word.

It is also possible to generate stability and defense by having two opposing systems balancing each other out at a particular level (Fig. 1–4). For instance, constancy of temperature might arise through inputs from cold and warm detectors activating heat gain and heat loss responses, respectively. The more the heat gain responses were stimulated, the higher the temperature would be driven, but also the more the heat loss responses would be activated. With proportional control, a point of balance would then arise between the opposing systems, the exact level depending on the activation thresholds and proportionality constants for the heat gain and heat loss. A change either in the threshold or in the proportionality constant (slope of the lines in Figure 1–4) would alter the point of balance (Mitchell et al., 1970).

Such a system has no reference signal in the engineering sense, but it still behaves as if there were an engineer's set-point. The term *set-point* may therefore be used in a descriptive way. Houdas and Guieu (1975) have distinguished between descriptive and explanatory models. The former "represent the experimental observations without assuming the structure of the controller." Also Bligh (1975), considering certain temperature changes, concludes, "we can only say that it is *as if* a set-point has been changed." Set-point has also
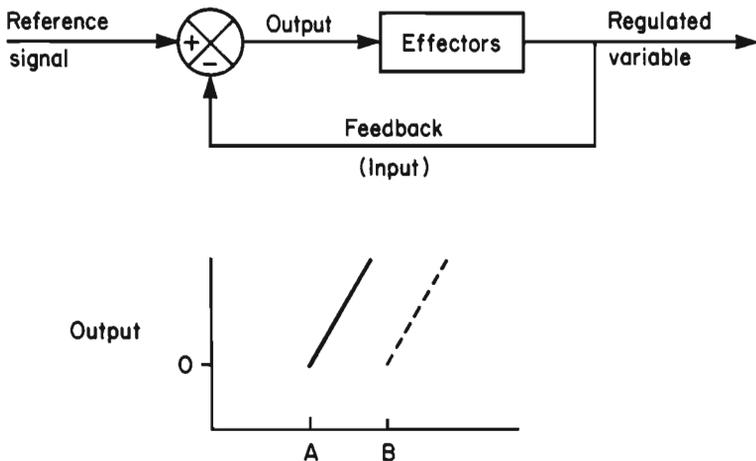

Figure 1–3. Top: control system employing a reference signal/set-point for regulating the level of a variable. Bottom: input–output relationships showing that the regulated level shifts (dotted line) from A to B when the value of the reference signal is raised (adapted from Mitchell et al., 1970).
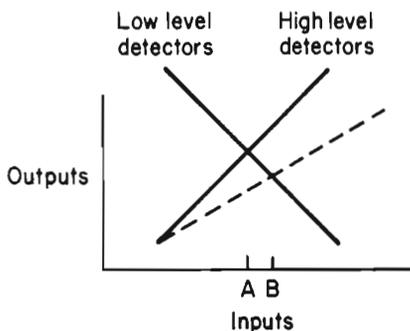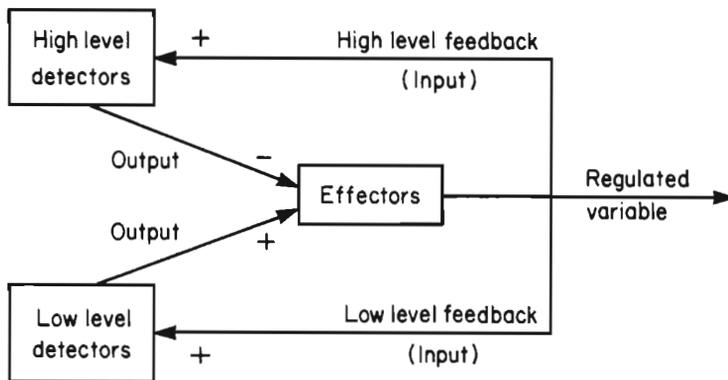
Figure 1–4. Top: a control system for regulating the level of a variable without employing a reference signal/set-point. Bottom: input–output relationships showing that when the gain of the high-level detectors is reduced (dotted line) the regulated level changes from A to B (adapted from Mitchell et al., 1970). In this book changes in the slope of this kind are referred to as changes in responsiveness.

been applied in this way to body weight regulation (Mrosovsky and Powley, 1977). This is the way it will be used in this book, as a convenient descriptive term without implying a particular control system.

It is sometimes possible in particular cases to distinguish experimentally between the control systems shown in Figures 1–3 and 1–4 (Mitchell et al., 1970; Cabanac and Massonnet, 1974; Mrosovsky and Powley, 1977), but it is not especially easy. In many situations the two systems behave in similar ways. All the more reason for emphasizing that homeostasis need not depend on a particular kind of mechanism.

LACK OF EVOLUTIONARY PERSPECTIVE

The fathers of the concept of homeostasis were physiologists. For them, evolution it seems, was linear. Cold-blooded animals were seen as "much less highly organized" (Cannon, 1939), not having attained the controlled internal

environment of birds and mammals. That reptiles could be just as highly specialized for particular niches and for reproducing successfully was foreign to this way of thinking. "All the vital mechanisms," said Bernard, "however varied they may be, have but one end, that of preserving constancy in the internal environment." He did not discuss the possibility that reproductive output might be a higher and overriding end.

Constancy of the internal environment provided independence from the external environment. For Cannon this freedom *from* the external environment implied freedom *for* something else. His remarks when trying to answer the question "freedom for what?" are particularly revealing:

> It is chiefly freedom for the activity of the higher levels of the nervous system and the muscles which they govern. By means of the cerebral cortex we have all our intelligent relations to the world about us. By means of it we analyze experience, we move from place to place, we build airplanes and temples, we paint pictures and write poetry, or we carry on scientific researches and make inventions, we recognize and converse with friends, educate the young, express our sympathy, tell our love—indeed, by means of it we conduct ourselves as human beings. The alternative to this freedom would be either submission to the checks and hindrances which external cold or internal heat or disturbance of any other constants of the fluid matrix would impose upon us; or, on the other hand, such conscious attention to storage of materials and to altering the rate of bodily processes, in order to preserve constancy, that time for other affairs would be lacking. It would be like limiting social activities because of domestic duties. . . ."
>
> Cannon (1939)

Homeostasis was for poetry rather than for producing grandchildren—that would border on the domestic. Why some of the less poetic lower mammals should have equally effective homeostasis is not explained. Views similar to those of Cannon were put forward by Barcroft (1932). He was impressed by the breakdown of his mental abilities—the first to suffer—in experiments that severely challenged his homeostatic systems. From these experiences and other evidence he argued that the CNS, especially its higher functions, were the chief beneficiaries of a constant internal environment. The *vie libre* was, essentially, a matter of intellectual ascendancy.

Lack of modern evolutionary perspective and the absence of terms like *reproductive fitness* do not detract from Bernard's and Cannon's luminous insights into physiology. But their focus on physiological mechanisms for maintaining constancy may help explain their attitudes when confronted with examples in the animal kingdom of variation in the *milieu intérieur*. Those attitudes are outlined in the next section.

CHANGES IN DEFENDED LEVELS

Cannon (1929) appreciated that the fluid matrix was not completely constant but he thought that variations were normally kept within narrow limits. He did not consider the possibility that the internal environment might change but still be homeostatically defended, nor did he cover the topic of biological rhythms.

Bernard talked of *la vie oscillante* but not so much as a description of rhythms as of cases in which the organism's functioning depended greatly on external conditions. Bernard considered mammalian hibernators as examples of *la vie oscillante,* along with plants:

> Tous les végétaux sont dans ce cas. . . . Tous les invertébrés et, parmi les vertébrés, tous les animaux à sang froid, possèdent une vie *oscillante, dépendante* du milieu cosmique. Le froid les engourdit, et si pendant l'hiver ils ne peuvent être soustraits à son influence, la vie s'atténue, la respiration se ralentit, la digestion se suspend, les mouvements deviennent faible ou nuls. Chez les mammifères, cet état est appelé *état d'hibernation*: la marmotte, le loir nous en fournissent des exemples. . . . Il y a absence, chez l'animal à sang froid ou hibernant, d'un mécanisme qui maintienne autour des éléments un milieu constant en dépit des variations atmosphériques.
>
> Bernard (1878)

We now know that when hibernators become torpid it is not because they are overcome by cold, but because they are regulating their temperatures at lower levels. This will be discussed in Chapter 4, along with numerous other examples of changes in defended levels. A change in the defended level of the internal environment is an elaboration, not a contradiction, of homeostasis. It is sufficiently common, however, and it has enough ramifications to merit its own name, rheostasis, the principal topic of this book.

COMPETITION BETWEEN DIFFERENT REGULATORY SYSTEMS

What happens when the demands of different regulatory systems clash? Physiologists working in laboratories usually do not encounter this problem. It may never arise if conditions are standardized and only one variable manipulated at a time. Even when the whole animal is studied, as in Richter's (1943) classic demonstrations of behavior as a way of regulating the internal environment, the experiments usually adhere to a design with a single independent variable. The animal is provided with all its needs except one, the compensatory mechanisms for the deficiency are recorded, and another affirmation of homeostasis is obtained.

Outside the laboratory things may look different. Observations on Merino sheep illustrate the contrast. The body temperature of these animals in the laboratory seldom exceeds 39.5°C; if it does go higher, then shallow panting-type respiration ensues. But when sheep of this breed were fitted with telemetry equipment and allowed loose in a field, body temperatures often rose above 40°C, even above 41°C on occasions; this was in Australia in March (Brown, 1971). Despite these high temperatures, panting was not seen. Outdoors, the upper limits of body temperature were more variable and less well defended than indoors. In this case, it is not obvious why the animals should not maintain stable temperatures when outside.

In other examples the reasons for abandoning stability are evident. Camels *(Camelus dromedarius)* live in an environment that is both dry and hot. They are too large to rely on behavior to keep cool; they cannot burrow into the sand
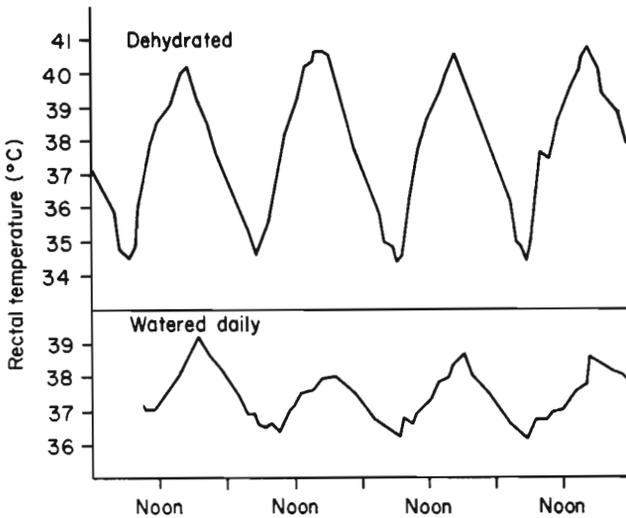
Figure 1–5. Diurnal changes in the rectal temperature of a camel. (Based on Schmidt-Nielsen et al., 1957, adapted from Schmidt-Nielsen, 1964, *Desert Animals: Physiological problems of heat and water.* Oxford University Press.)

or always find shade. The only other means at their disposal is evaporative cooling, but this uses water. The demands of water balance and thermoregulation clash. The camel solves the dilemma by allowing its temperature to rise during the day to levels that would be considered hyperthermic in most mammals (Fig. 1–5). This saves water. The extent of the daily temperature rise depends on the premium placed on water conservation: it is greater if the animal is dehydrated. At night the body temperature falls below mammalian norms, sometimes dropping as low as 34.2°C. This cooling delays the time when dangerously high temperatures will be reached the next day as the camel warms up (Schmidt-Nielsen et al., 1957).

Recently physiologists have been paying more attention to interactions between regulatory systems. For example, a book on thermal physiology (Hales, 1984) devotes a whole section to competition between thermoregulation and other homeostatic systems.

SUMMARY

In a single example, the camel's physiology illustrates many of the principal limitations to the simple concept of homeostasis.

1. Nocturnal hypothermia anticipates the next day's heat; it represents a type of feedforward mechanism.
2. Although temperature is not constant, it is defended (the evidence for this last statement is given in Chapter 5). The animal is not entirely at the mercy of the environment, even though its temperature oscillates with it.

3. The lack of stability in the *milieu intérieur* does not represent a primitive stage in evolution: it is a specialized adaptation.

4. Lack of stability arises out of competition between two regulatory systems, a situation not discussed by Bernard or Cannon.

PREVIEW

Rheostasis of one variable is not the only way of resolving conflicts between the demands of different regulatory systems. Therefore, before describing numerous examples of rheostasis (the core of this book in Chapters 4 and 5), it may be illuminating to consider next (in Chapter 2) what other possibilities exist for conflict resolution. This may help provide some appreciation of the circumstances in which rheostasis is likely to evolve.