

Terminology and Definitions

RHEOSTASIS OR HOMEORHEUSIS?

In this book the term *rheostasis* is used to describe regulation around shifting set-points. In 1977 Nicolaïdis, recognizing that such phenomena were widespread and needed designating, constructed the word *homeorheusis*. The *stasis* in Cannon's homeostasis was replaced with *rheusis* to convey something flowing rather than static. However, Cannon (1929) did not use *stasis* to imply something static but to convey the idea of a condition or general state. He was explicit about this.

Objection might be offered to the use of the term *stasis*, as implying something set and immobile, a stagnation. *Stasis* means, however, not only that, but also a condition; it is in this sense that the term is employed. *Homeo*, the abbreviated form of *homoio*, is prefixed instead of *homo*, because the former indicates "like" or "similar" and admits some variation, whereas the latter, meaning the "same," indicates a fixed and rigid constancy. As in the branch of mechanics called "statics," the central concept is that of a steady state produced by the action of forces; *homeostatics* might therefore be regarded as preferable to homeostasis. The factors which operate in the body to maintain uniformity are often so peculiarly physiological that any hint of immediate explanation in terms or relatively simple mechanics seems misleading. For these various reasons the term homeostasis was selected.

(Cannon, 1929)

Whether or not Cannon's use of Greek words was too liberal is debatable. The fact is, the term *homeostasis* has become part of the English scientific vocabulary. I therefore prefer to replace the *homeo* with *rheo* to describe a condition that is regulated at changing rather than similar levels or values, and to accept Cannon's point that the condition is a product of dynamic processes, rather than being something that remains the same merely through stagnation. Another advantage of the term *rheostasis* is that it triggers association with the

word *rheostat*; a rheostat precisely and vividly exemplifies a device whose setting may easily be adjusted.

A further reason for not taking up Nicolaïdis' (1977) use of the term *homeorheusis* is that 20 years earlier Waddington (1957) employed "homeorhesis" as an alternative to "canalization." Waddington's terminology, such as "homeorhetic cross-section" in the "epigenetic landscape," is related to a particular way of visualizing some of the features of development. Moreover, the term is limited to development; it refers to the tendency to return after perturbation to specified paths or developmental trajectories rather than to fixed states. As such, it is not broad enough to cover the full range of circumstances in which alterations in regulated levels occur—e.g., temporary alterations in response to pathogens.

RHEOSTASIS

Rheostasis refers to a condition or state in which, at any one instant, homeostatic defenses are still present but over a span of time there is a change in the regulated level. Therefore rheostasis includes a change in set-point, both when the term is used descriptively without specifying a mechanism (Chapter 1) and when it is used to indicate a mechanism comprising negative feedback with a reference signal.

Change of a variable that is normally defended is not in itself proof of rheostasis. When changes take place with great regularity or repeatability, they may constitute highly circumstantial evidence for rheostasis, just as stability constitutes highly circumstantial evidence for regulation around a constant level. Stronger evidence for rheostasis is a demonstration of defense of different values of a variable at different times or in different circumstances.

SLOW AND SUDDEN CHANGES

Rheostasis may apply to both gradual and sudden changes. Whether something is rapid or gradual depends on the frame of reference, and whether something changes in a continuous manner or in one step depends on the resolving power of experimental methods; something that appears continuous may in fact be composed of rapid discrete steps. If set-points remain the same for only short periods, it may be difficult to study responses to challenges before set-points have altered.

Terms like *sliding set-point* or *climbing set-point* are not informative about the precise mechanisms of change. They may, nevertheless, be used to describe cases in which changes continue for a time long enough for it to be feasible to test whether different set-points are operative at different stages in the adjustment process. It is possible that, during cycles, set-points may change continuously and that stable values are never reached. Rheostasis does not imply that new stable levels are reached, only that there is a change in regulated levels.

PROGRAMMED AND REACTIVE RHEOSTASIS

Two circumstances in which rheostasis occurs can be distinguished. Changes in defended levels may be obligatory at certain phases of the life cycle and may occur regardless of conditions. These will be referred to as examples of programmed rheostasis. *Programmed rheostasis* is often cyclical, though it need not be so. There may also be developmental, once-in-a-lifetime examples of rheostasis. *Reactive rheostasis* occurs in response to stimuli, stimuli that may or may not be encountered.

This distinction between programmed and reactive rheostasis, as that between slow and sudden changes, is not always clear cut. Rheostasis during pregnancy and lactation may be considered to be part of the reproductive program, once pregnancy is initiated, but it also may be considered reactive in that pregnancy is not inevitable. In this book rheostasis in association with reproduction will be included in the programmed category because reproduction is a common part of life cycles. Really there is a continuum between programmed and reactive rheostasis, with interactions between the two being possible. It is still useful to distinguish the ends of a continuum. The temperature changes in camels again provide an instructive example (Fig. 1-5). The daily warming is programmed in that it happens whether the animal has access to water or not. But the extent of the temperature rise is greater if the camel lacks water. This part of the change is reactive because it depends on the immediate situation. It is something separable that occurs in addition to the obligatory change. The reactive and the programmed changes work together in this case; they are not mutually exclusive.

OTHER REJECTED TERMINOLOGY: PREDICTIVE HOMEOSTASIS

Moore-Ede introduced the term *predictive homeostasis* (1986) for "corrective responses initiated in anticipation of a predictably timed challenge." Used in this way only, predictive homeostasis is equivalent to anticipation or feed-forward, which others have recognized as an important part of homeostatic mechanisms (Chapter 1). In fact, Moore-Ede applies his term to various different aspects of homeostasis and rhythmic processes. In places, rhythmic changes in set-points are included as examples of predictive homeostasis. Mostly, however, Moore-Ede talks about "predictive homeostatic responses." For example in man, the response to infusions of potassium (K^+) varies according to the time of day, urinary excretion of K^+ being much less at night. These are called *predictive circadian modulations*, in that usually at night people eat little and so there is little need to excrete excess electrolyte. The poorer excretory response at this phase of the cycle needs to be distinguished from any changes in regulated levels of K^+ . Another example relates to an animal pressing a lever in anticipation of receiving food: this is also called *predictive*. When the animal presses the lever to obtain food that is actually available, this is called *reactive*. There is no implication that set-points are different; in both cases the bar pressing corrects or attempts to correct energy deficits.

Even when predictive homeostasis is applied to a set-point change, it is not always transparent that Moore-Ede's definition is met. For instance it is not obvious that a lower body temperature set-point in man during the early hours of the morning is a corrective response initiated in anticipation of a predictably timed challenge. It might just as plausibly be perceived as a way of avoiding having to make corrective responses at that time. Similarly, the higher regulated temperatures of rats during the night might be seen as a way of reducing the need to initiate heat loss responses.

These various points show that the term *predictive homeostasis* is being used too loosely and generally to be helpful in the present discussion. The term *rheostasis* is retained as applying specifically to changes in regulated levels. Whether or not effector systems also change is an interesting but separable question. *Programmed rheostasis* covers circadian changes but also encompasses changes in set-points occurring during ontogeny. *Reactive rheostasis* is clearly different from Moore-Ede's reactive homeostasis. The latter is simply part of usual homeostasis and carries no implication of a change in defended levels, whereas such a change is the essence of reactive rheostasis.

Nevertheless, one may agree with Moore-Ede (1986) that the relationship between homeostasis, biological rhythmicity, and predictability is fundamental. It can profitably be reconsidered and illustrated with contemporary examples (Moore-Ede, 1986). As Aschoff (1964) put it:

Homeostasis is a shielding against the environment, one might say, a turning away from it. For a long time, this phenomenon has been taken as the prime objective for an overall organization in physiology; and it evidently has great survival value. But there is another general possibility in coping with the varying situations in the environment: it is, instead of shielding, "to turn toward it"; instead of keeping the "milieu interne" stable, to establish a mirror of the changing outside world in the internal organization. This has one clear prerequisite: the events in the environment must be predictable, which, of course, is the case when they change periodically.

The essential additional point that rhythmic changes do not involve a contradiction of homeostasis was cogently put long ago by Halberg (1953; see also Aschoff, 1970; and Mrosovsky, 1976, for further discussion):

The conception suggested here resembles Cannon's principle of homeostasis with the important difference that the base-line about which variations are held to occur is not the straight line (and its range of "common variation") which has been postulated since Claude Bernard developed the concept of the constancy of our internal environment. The "base-line" is rather the *curve* of a 24-hour cycle . . . data are interpreted as variations from a 24-hour curve rather than from an assumed horizontal line.

SUMMARY

1. *Rheostasis* is defined as a condition in which, at any one instant, homeostatic defenses are present but over a span of time, there is a change in the level that is defended.

2. The term *rheostasis* is preferred over the term *homeorheusis* as being more in accord with Cannon's use of the word *stasis* and his recognition that steady states are a product of dynamic processes.
3. Rheostasis implies change in regulated level, whereas the phrase *predictive homeostasis* has also been applied to changes in effector systems and is therefore insufficiently precise.
4. *Programmed rheostasis* refers to changes that are obligatory at certain phases of the life cycle. *Reactive rheostasis* occurs in response to stimuli that may or may not be encountered. It is emphasized that the distinction between programmed and reactive rheostasis is not always clear cut. These subcategories are used partly as a matter of convenience and to indicate the range of circumstances in which rheostasis occurs.

PREVIEW

It would be pointless to fuss over definitions if rheostasis were not common and biologically important. The next three chapters provide numerous examples and candidate examples of rheostasis.

