BIOLOGICAL HOMEOSTASIS

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Summary

Homeostasis is a fundamental concept in biology because it helps to understand the aims of physiological functions and their behavior, and aids in explaining the mechanisms of regulation during ontogeny. Homeostasis is based on the principle of comparing the actual value of the parameters under control with an intended optimum. In case of discrepancy, the energetic or material input is regulated through a feedback loop conveying the error signal to the effectors. The effectors governing this input may have the nature of a switch or of a pump; in the latter case, the fatigue, or the défaillance, of the pump is controlled in its turn. This additional control is particularly important for the regulation of stores, because it primes a search program that directs motile organisms towards a food source that enables the restoration of optimum conditions. With few exceptions, homeostasis follows the strategy of 'negative feedback'. Homeorrhesis, i.e., the control of trajectories in space, can be schematized in the same way as homeostasis, but the feedback loop that conveys the error signal acts on

the vector(s) of the system, causing its steering toward the goal. Homeorrhesis usually follows the strategy of 'positive feedback'. The control of trajectories in time (e.g., in embryogenesis) works in the same way, by utilizing the information from internal and external sensors to regulate the flux of information stored in a memory (e.g., in the genome). The many homeostats that operate even in the simplest cell work according to hierarchical rules, which may be empirically understood only in the simpler cases. Homeostasis is the chapter of cybernetics that better allows an understanding of the reliability and economy of the functioning of living beings.

1. Introduction

Biological homeostasis was conceived by the French physiologist Claude Bernard for the purpose of understanding the stability of the inner milieu and self-control in animals. Also Alfred Russell Wallace, in his famous paper on evolution, spoke of self-regulation, although in a less cogent manner: to account for the balance observed in the body structure of animals, he referred to the fly-ball governor, the only homeostatic device then in use. However, the scientific interpretation of the self-control of internal parameters in organisms begins with a lucid work by Wilhelm Ostwald, entitled *Die Energie* (1908). In this work, the renowned chemist introduces the concept of 'steady state', defined as the condition of a system which maintains the uniformity of its structural and functional characters through the control of the flux of incoming matter or energy.

Self-control in animals received its soundest formulation in 1929 when the American physiologist W. B. Cannon described the logical and functional bases of homeostasis, i.e., the process that achieves the steady state of a given parameter, and assigned the name of homeostat to the corresponding device.

Soon after Cannon, homeostasis became a conceptual tool of great relevance both in the field of engineering (1936) and in physiology, and in the field of comparative behavior.

In biology, the comprehension of the mechanisms enabling self-control in living beings allows us to rationally define the aims of physiological functions and purposive behavior in ethology without making concessions to vitalistic or finalistic interpretations, and to rationally understand ontogenetic and morphogenetic processes without resorting to entelechy or to arcane virtues.

2. Stabilization

In technological treatises as well as in some biological textbooks, the chapters dedicated to regulatory systems deal with both stabilizers and homeostats. A stabilizer opposes random fluctuations directly by exploiting the principle of mass action, whereas a homeostat proper controls the parameters of a system through a feedback effect on its own supply channels. The properties of the stabilizers can be formalized in a simple algebraic form, whereas in the case of homeostats such formalization can be useful when designing the apparatus, but not so when describing its properties. The latter aim can be better achieved by using block diagrams, the method we adopt here.

Stabilization devices act directly on the static or dynamic conditions of a system, by buffering, deadening, or suppressing the fluctuations that disturb its dynamic or chemical adjustment. Well-known dynamic stabilizers are the vertical and horizontal empennages of airplanes, the rigid fins of sharks, the dorsal fins of cetaceans, and so on.

Devices that oppose turbulence can also be classified among stabilizers. Such for instance is the bastard wing (or *alula*) of birds, which impedes or limits the detachment of fluid fillets from the dorsal surface of the wing, thus avoiding stall. Another example is the hydrodynamic outline and the skin texture of cetaceans, which reduces or suppresses the turbulence of the water in which these animals move. Anti-turbulence devices reduce the energy expense of locomotion and reduce the risk of sighting by predators.

Whereas the function of mechanical stabilizers is easily understood, what is less obvious is the role of chemical buffers, which also function according to the law of mass action and resist changes in concentration of hydrogen ions according to the reaction $[HX] \Leftrightarrow [H+] + [X-]$, where HX is a weak acid.

4. Homeostasis

4.1. Logic and Structure of the Homeostat

First of all, it must be noted that the logic of homeostatic control is circular and thus does not allow the usual distinction between cause and effect.

The underlying principle of homeostatic devices is simple: comparing the actual state of the parameters under control with a threshold (or intended optimum, or ideal state), and in case of discrepancies (deviations), regulating the supply channels through a feedback loop so as to readjust the value of the parameter in question.

Two strategies can be adopted: (1) with negative feedback, which implies that when the actual value exceeds the threshold, the delivery of the item must be stopped, or that when it is below the threshold, the delivery must be enhanced; (2) with positive feedback, which implies that when the actual value is below the threshold, the delivery must be stopped (vanishing to nought), or that when the actual value exceeds the threshold, delivery must be increased (rising to infinity).

In most cases physiological homeostats utilizes the strategy of negative feedback. Positive feedback in physiological functions reveals a pathological condition. Only the homeostats controlling the digestion of food or the attack of parasites use positive feedback with vanishing to naught. In such cases, the strategy adopted can be summarized as follows: in the presence of something self-incompatible, digest it.

The operative scheme of a homeostat controlling a system (Figure 1) comprises: (1) the analyzer (i.e., the measuring unit, or comparator) endowed with two inputs and an output carrying the 'error signal'; (2) a feedback loop; (3) one or more effectors (controllers); (4) the channels supplying the system.

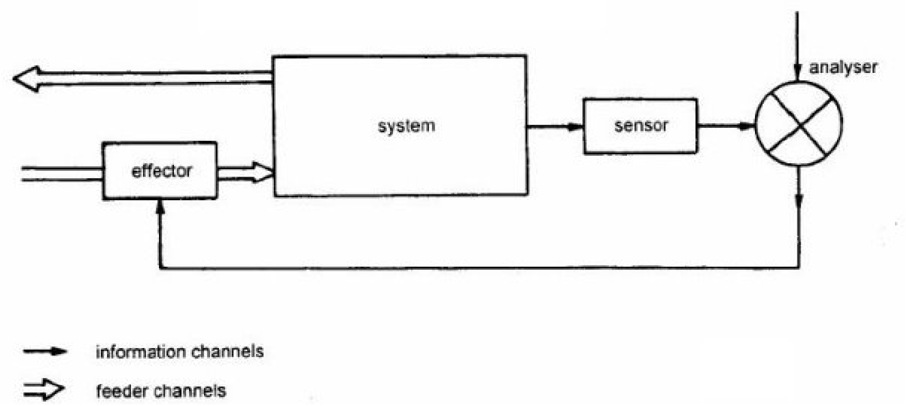

Figure 1. General block diagram of a homeostat. This graph differs from those utilized in technology, as the information channels are indicated separately from the feeder channels.

4.2. The Components of the Homeostat: the Measuring Unit

The analyzer works as the key of the homeostat, because it detects the discrepancies between the threshold and the actual value of a parameter of the system (e.g., the cytoplasmic electrolyte content, the body temperature). To accomplish the required comparison, the analyzer receives two inputs, one coming from internal sensors and informing on the system status, the other carrying the threshold value for the given parameter. The threshold usually consists of a genetically established constant value; sometimes, however, it is produced by another control device that establishes it according to some variable environmental condition (e.g., the time of day, temperature, etc.).

To understand the working of the analyzer, it is of the highest importance to consider the properties of biological sensors. These are either energy transducers or detectors of organic molecules, which means, more properly, that they either transduce some energy form into signal energy, or recognize, by virtue of complementary van der Waals' surfaces, some species of organic molecule and consequently set the signal going. Therefore, because of their nature, biological sensors are incompetent to provide information on physical entities which do not have the dimensions of energy, like temperature, length, time lapse, and so on. The sensors may, however, give indirect measures of these entities by measuring some energy flux that is algebraically associated with them. For instance, a thermal sensor can measure the temperature from the heat flux that is brought about by temperature variations, provided that other parameters involved, such as conductivity, remain steady. A length sensor can measure the elongation of the cell flagellum from the exertion required to wave it in a medium of constant viscosity. A time lapse may be measured through the consumption of a fixed quantity of substrate, provided that the metabolic rate remains uniform, and so on.

Such a method of measuring physical parameters does not differ from the one employed in various technological fields, and its precise knowledge helps understand many aspects of physiological control and particularly of morphogenetic regulation.

As said above, a homeostat whose sensor gives an indirect measure of the parameters under control works properly as long as other physical factors remain steady. Yet, whenever one of them varies, the adjustment of the item will be regulated at a different level. Considering the quoted examples from this point of view, some anomalies of the control may become more understandable. In the case of thermal regulation of higher vertebrates, it happens that the heat transfer from the hypothalamic receptors (a heat source!) is inversely proportional to the blood temperature and directly proportional to the conductivity of the medium, and thus to the velocity of the hemal flux and even to the receptors' thermogenesis. Consequently, an adjustment of the body temperature to a different level will correspond to any variation of these parameters. In the case of the flagellum length of a protozoon, which is controlled through the amount of work required to move the cell, it may be foreseen that when the viscosity of the external medium increases, the flagellum length will decrease.

During embryonic development, length, surface and mass of the various parts are indirectly controlled through the effort required to move them in a milieu having fixed characteristics. Thus, it becomes quite clear why morphogenesis gets distorted by any experimental treatment that inhibits the motility of the embryonic structures or modifies the characteristics of the milieu in which the morphogenetic processes take place.

A signal of discrepancy between the actual and ideal state, or 'error signal', is the output of the comparator. The signal travels along the feedback channel to the effector(s) situated on the feeder of the system.

3.5 The Components of the Homeostat: The Effector

The effector (controller) may have either the characteristics of a switch or of a pump. The switch consumes a negligible amount of energy, so that sometimes the signal energy itself suffices to bring it into action; the pump, on the contrary, consumes much more energy and requires an autonomous power supply. If the flux running through the system proceeds along a gradient, a switch suffices. If the flux proceeds against a gradient, regulation requires a pump. Referring to household appliances, we find an example of an automatic switch in the flat-iron thermostat, and an example of a pump in the refrigerator thermostat which gives out heat in an environment having a higher temperature. Referring to biological systems, we find that the amount of fluid flowing from the roots to the leaves of a plant is regulated by the opening and closing of the stomata, whereas the blood flux in vertebrates is regulated by a powerful muscle, the heart. When the effector is a pump, potency is of relevance and so is the range within which the control remains effective.

In technology, potency is proportional to the standard working conditions of the apparatus: the air-conditioning unit of a building is calibrated so as to be able to face the harsh periods of the local climate, not any imaginable conditions. This also applies to living beings: different populations are capable, by hereditary and physiological acclimatization, to resist a range of hard conditions, not to the hardest possible. It is a matter of economy. Most mammal species living in temperate climates regulate their internal body temperature to about 37°C, to cope with environmental variations comprised between -15° and 45°C.

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Biographical Sketch

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