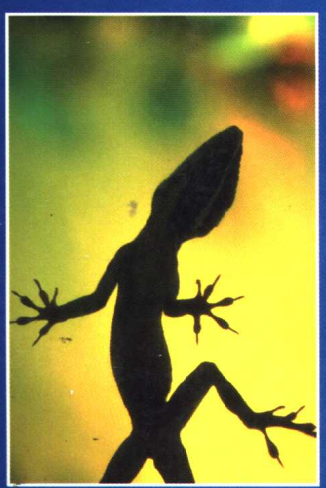
Introduction to ANIMAL PHYSIOLOGY

Ian Kay











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Introduction to ANIMAL PHYSIOLOGY

动物生理学导论

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Preface

This book has been developed from a series of lectures given to first year students at Manchester Metropolitan University, reading for a degree in Biological Sciences. It is intended to provide an easy introduction to the subject of animal physiology at first year university level. At this level, students want to build on and develop the knowledge base they have gained prior to entering university. However, at this stage they do not wish to be inundated and confused with detailed knowledge about the minutia of physiological processes. It is hoped that this book will fall between these two areas and serve as a suitable introductory text.

Many students consider physiology to be the study of mammalian and, in particular, human physiology. This book has deliberately taken a comparative view of physiology. At this stage in their biological careers, students simply require a thorough understanding of the key principles of physiology, and these principles are best learned using examples drawn from a wide range of animals. By understanding these principles, a solid foundation is formed for further physiological studies. The book also serves to reinforce another very important principle: the study of 'simple' animals can provide useful insights into how higher animals (including humans) work. The earliest work on the squid giant axon and the first investigations into the way that neurons work are good examples of this.

Writing this book has been an enjoyable learning experience in itself. Any errors or omissions remain my fault alone and I would be pleased to learn of any. Equally, if you have enjoyed the book I would like to hear from you.

I am grateful to colleagues within the Department of Biological Sciences at Manchester Metropolitan University and former students, who made helpful comments on draft versions of the text. Thanks must also go to the staff at BIOS for their help and advice – in particular, Rachel Offord and Fran Kingston, who have endured so many 'it'll be with you soon' letters, faxes, e-mails and telephone messages! There are

several other people to whom acknowledgement must be made – without them the book would not have been possible. They are my parents, my wife Jan and children Matthew and Amy. I can now get back to being a normal son, husband and dad, free from the shackles of writing.

Ian Kay

Abbreviations

ACTH	adrenocorticotropic hormone
ADH	antidiuretic hormone
ADP	adenosine diphosphate
ANP	atrial naturetic peptide
ATP	adenosine triphosphate
BAT	brown adipose tissue
2,3-BPG	2,3-bisphosphoglycerate
cAMP	cyclic adenosine monophosphate
DAG	diacyl glycerol
ECF	extracellular fluid
EPSP	excitatory postsynaptic potential
FSH	follicle-stimulating hormone
GABA	γ-aminobutyric acid
GDP	guanosine diphosphate
GnRH	gonadotropin-releasing hormone
GTP	guanosine triphosphate
5-HT	5-hydroxytryptamine (serotonin)
ICF	intracellular fluid
IP_3	inositol trisphosphate
IPSP	inhibitory postsynaptic potential
LH	luteinizing hormone
MIH	molt-inhibiting hormone
p	partial pressure
P_i	inorganic phosphate
PIP_2	phosphatidyl inositol bisphosphate
PTTH	prothoracicotropic hormone
RMP	resting membrane potential
STP	standard temperature and pressure
TMAO	trimethylamine oxide
TRH	thyrotropin-releasing hormone
TSH	thyrotropin-stimulating hormone

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Chapter

1

Homeostasis: The central concept in physiology

1.1 An introduction to animal physiology

Physiology is 'the science of normal functions and phenomena of living things'; it concerns itself with how animals work. This science of normal function can be investigated at several different levels, from the cellular level through the functioning of discrete organs to the functioning of the whole animal. Comparative animal physiology looks at the way different animals deal with common problems, such as how oxygen can be delivered to cells to meet their metabolic needs and how animals cope with changes in their immediate external environment; for example, how do estuarine invertebrates deal with the constant changes in salinity to which they are exposed?

The external environment probably presents the biggest challenge that an animal is likely to face. External environments can be divided into two categories: terrestrial and aquatic. It should be remembered that some animals may live in both environments, perhaps at different stages in their development, for example, amphibians which are fully aquatic during their larval stage, but which are semi-terrestrial when adult. Generally, however, an animal's external environment is rarely constant. For example, there will be changes in temperature, water availability, gas concentrations and so on. These changes, which may occur on a daily or seasonal basis, represent a challenge to the normal functioning of the animal. The fact that the external environment is changing means that the body fluids, e.g. **blood plasma**, **hemolymph** and **extracellular fluid**, which constitute the internal environment and which surround the cells of the animal are constantly being challenged. An absolute requirement of animals is that their internal conditions remain constant, or as near constant as possible. This maintenance of a constant internal state is known as **homeostasis**. The fluid that surrounds animal cells in many cases has a composition which is quite different from that of the external environment that surrounds the animal. Obviously, in the case of terrestrial animals, the fluid (which may be either liquid or gaseous) which surrounds them is air. In this

case, comparisons are made between their body fluids and sea water, since this is thought to be where terrestrial animals emerged from during evolution. What animals must strive to do is to maintain their body fluids in a relatively constant state in terms of, for example, ionic composition, pH, dissolved gas concentrations, nutrient levels and so on. Obviously, then, homeostasis is a major theme running through animal physiology. Before looking at the types of mechanisms and processes involved in the maintenance of homeostasis, it is necessary to consider the composition of the fluids which are contained within animals.

1.2 The body fluids of animals

As indicated above, the body fluids of animals must be held relatively constant, in terms of ionic composition, pH, etc., if they are to avoid being at the mercy of their environments. The ability of animals to maintain internal fluids of a relatively constant composition has allowed them to colonize new environments during their evolutionary history, e.g. the transition from aquatic environments to the terrestrial environment. The transition from aquatic to terrestrial environments has only occurred in two groups of animals – the insects and the vertebrates – to any great extent, and in other groups, such as spiders and some molluscs, to a lesser extent. Clearly, the ability to colonize new environments like this opens up all sorts of new possibilities in the evolution of animals. Body fluids are divided into two categories, each of which will now be discussed.

1.2.1 *Extracellular fluids*

The **extracellular fluid (ECF)** is the fluid that surrounds the cells of any particular animal. In the case of the protozoans (considered here as single-cell animals) the ECF is the fluid of their external environment. The ECF of some simple multicellular marine animals is more-or-less identical to the environment in which they live – for example, some jellyfish have a solute composition identical to seawater with the exception that their sulfate concentration is only half that of seawater. The reason for this discrepancy is that the sulfate ion is dense (relative to other ions). This means that alterations to the concentration of sulfate ions in body fluids will have significant effects on the overall density of the animal and, therefore, its buoyancy. Life is thought to have originated in the oceans, so it is not unreasonable that such simple animals should have a similar composition to seawater. However, more advanced marine animals, freshwater and terrestrial animals all maintain an ECF that is quite different in composition from that of seawater. The precise composition of the ECF will vary from animal to animal, but some generalizations may be made. The main extracellular cation is almost always Na^+ and the main extracellular anion is Cl^-. A cation is a positively charged ion, which

moves towards the negative pole (cathode) in an electric field. An anion is a negatively charged ion that will move towards the positive pole (anode) in an electric field. The regulation of body fluid composition in animals is considered in more detail in Chapter 10.

1.2.2 *Intracellular fluids*

As the name implies, **intracellular fluid (ICF)** is the fluid contained within animal cells. By definition, it must have the same total concentration of solutes as the ECF has. Without this the cell would not be in osmotic equilibrium with its surroundings and would be at risk of gaining or losing water and the dangers associated with this. For example, if a cell gains water it will swell, leading to the rupture of the cell membrane and cell death. However, rather like the ECF and external environment, the ECF and ICF need not have identical compositions (indeed this is the case and much metabolic energy is expended in maintaining this difference) as long as solute concentrations are equal. The composition of the ICF will, again, vary from animal to animal, but the major cation in the cell is K^+. In contrast to the ECF, overall electrolyte concentrations are lower and there are large quantities of proteins that are generally associated with negative charges. The pH of the ICF is slightly alkaline. Such conditions are found almost universally in all animals.

1.3 Homeostasis

As described previously, animals must ensure that the ICF and ECF remain as stable as possible – gas concentrations must be held at the correct level, the pH and concentrations of solutes must be constant and so on. This maintenance of a constant internal environment is called homeostasis.

The concept of homeostasis has its origins in nineteenth-century French physiology. It was the French physiologist Claude Bernard who realized the importance of stability in the internal environment. His classic statement of 1857 sums up well this absolute requirement of animals:

> 'It is the fixity of the *milieu interieur* which is the condition of free and independent life, and all the vital mechanisms, however varied they may be, have only one object, that of preserving constant the conditions of life in the internal environment.'

The *milieu interieur* to which Bernard refers is the internal environment of the animal. However, it was several decades later that the term homeostasis was first used. It was coined by the American physiologist Walter Canon in 1929. He stated

> 'This "internal environment" as Claude Bernard called it, has developed as organisms have developed; and with it there have evolved

> remarkable physiologic devices which operate to keep it constant. . . . So long as this personal, individual sack of salty water, in which each one of us lives and moves and has his being, is protected from change, we are freed from serious peril. I have suggested that the stable state of the fluid matrix be given the name homeostasis'.

Homeostasis is the central theme in physiology. There are a huge number of examples of homeostasis, including the maintenance of the correct levels of electrolytes and dissolved gases in body fluids, the maintenance of the optimum pH of body fluids, and so on. Indeed, it is extremely difficult to think of many aspects of animal physiology which do not impinge upon this concept of homeostasis. As animals have become more complicated and specialized during the course of evolution, so homeostasis has become more important to their physiology. Physiology could be viewed, rather teleologically, as the means by which homeostasis is maintained. Accordingly, much of our knowledge of homeostatic mechanisms comes from the higher animals, particularly mammals, and in many of the lower invertebrates homeostasis is less apparent (i.e. fewer aspects of the animal's physiology are controlled and regulated). Many such animals do not maintain an internal environment that is different from their external. Such animals are said to **conform**, and any changes in the external environment are mirrored in the internal environment. However, there are limits to the degree of change that can be tolerated; excessive changes will result in severe disruption and possibly death. This is also the case in animals that maintain an internal environment that differs from the external environment. The internal environment in this case is said to be **regulated**: homeostatic mechanisms maintain this difference and its constancy.

1.4 Homeostatic control systems – feedback

Perhaps the most common homeostatic control system is based around the principle of feedback. Feedback is of two sorts: negative and positive. **Negative feedback** can be defined as the change of a variable that is opposed by responses which tend to reverse this change. For example, in birds and mammals which maintain a constant body temperature, a rise in body temperature produces responses which return body temperature to its original, desired value. Thus, negative feedback leads to stability in physiological systems. This contrasts with **positive feedback** systems where an initial change in a particular variable results in further change. By and large, the role of positive feedback in the maintenance of homeostasis is minimal. One possible example is the process of blood coagulation. This process operates via a positive feedback mechanism and it could be considered to be involved in the maintenance of a constant circulating blood volume. In many other cases, the involvement of positive feedback mechanisms in controlling, or attempting to control the normal physiological

functions of an animal would be disastrous. In the example of temperature control cited above, consider what would happen if this system was under the influence of positive feedback. Suppose body temperature had increased, if this initial disturbance was then subjected to positive feedback the result would be a further increase in body temperature. However, there are other biological examples of positive feedback, for example, the functioning of nerve cells. In this case, the initial influx of Na^+ ions during the early stages of an **action potential** produces a depolarizing response that results in further Na^+ entry. This causes further depolarization and influx of more Na^+ ions. This process will be discussed in more detail in Chapter 2. In general, though, examples of biological processes that are subject to positive feedback are very few.

The components of a feedback system are shown in *Figure 1.1*. There are three principal components: a **receptor**, an integrating center and an **effector** or effectors. The receptor is responsible for detecting change in the environment of the animal, either the external environment in which it lives, or its internal environment (e.g. a change in environmental temperature or intracellular pH). As will be seen later, there are a large number of **receptors**, each monitoring a particular aspect of the environment. The function of the receptor is to convert the detected change in the environment into action potentials which are sent via the afferent division of the nervous system to the integrating center. The integrating center is usually the brain or spinal cord in those animals that possess one. The role of the integrating center is to 'compare' the incoming information about a particular variable with what the variable should be. For example, the **hypothalamic** region of the brain is the integrating center for the control of body temperature in mammals. On the basis of the incoming information, in this case from thermoreceptors, the hypothalamus 'decides' what appropriate responses must be initiated to restore body temperature to its desired value. This response is brought about by the action of effectors, which

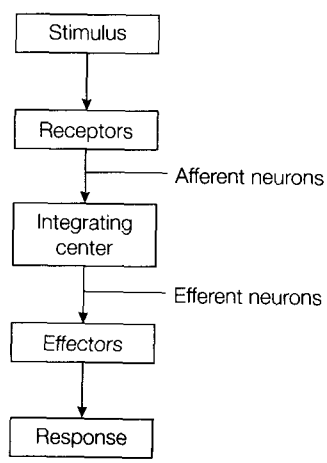


Figure 1.1. The basic components of a feedback system and their arrangement.

are stimulated via efferent (motor) neural pathways. Effector is the general term given to structures which bring about a biological response. Such responses may include muscular, neural or **endocrine** activation. An example of the functioning of a homeostatic control system is shown in *Figure 1.2.*

Clearly, from the above description, the integrating center, whichever organ or tissue it may be, must have a predetermined value for each variable that it controls. This value is known as the set point and it is the value of a particular variable that the animal strives to maintain. In the case of body temperature, for mammals the set point is approximately 37°C. For other animals this value will vary; some birds attempt to maintain a body temperature as high as 42°C, whilst other animals are unable to maintain a constant body temperature. The subject of thermoregulation is considered in Chapter 6. It can be seen from *Figure 1.2* that homeostatic control is really a balance between input and output. In the case of the thermoregulatory system, it is a balance between heat gain and heat loss. The set point is a hypothetical concept; more realistically, there is a range within which the variable is acceptable. In the case of body temperature in humans, the set point is 37°C; however, actual body temperature is acceptable if it lies within ± 1°C of this value. Every other physiological variable will have its own range over which it may vary. For example, plasma (the fluid component of blood) pH is held between 7.35 and 7.45 and plasma K^+ concentration is held between 3 and 5.5 mmol l^{-1}. Since nothing is held at a constant level (albeit the fluctuations around the set point of a particular variable are small), homeostasis is never really achieved in the literal sense of its meaning. The actual range which is permitted will vary for different variables. This introduces the hierarchical nature of homeostasis, by which it is meant that some variables are more

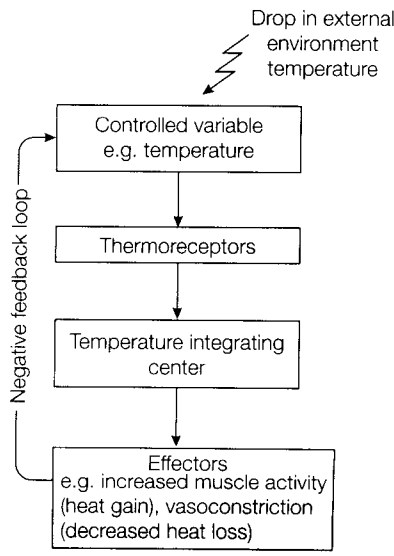


Figure 1.2. The operation of a negative feedback loop regulating body temperature. An initial drop in body temperature is detected by thermoreceptors, which initiate a response that returns temperature to the desired level.

closely controlled than others. This implies that those variables that are most tightly controlled are more important. An example of a variable that is controlled very closely is pH of blood and other body fluids. The reason for this is that even small changes in pH would have severe effects on enzyme (i.e. protein) structure and function. Remember that enzymes are composed of a chain of amino acids whose final structure is maintained by a variety of 'weak' chemical bonds. One such type of 'weak' bond found in enzymes is the ionic interaction between individual amino acids. Changes in pH would alter the ionization status of the chemical groups involved in these ionic interactions, which would lead to disruption of the bonds and, therefore, disruption of the final structure of the enzyme. Obviously, this would have a disastrous effect on the animal's metabolic processes. In contrast, O_2 levels in mammalian blood are less closely controlled – O_2 levels may decrease by 30–40% before any ventilatory effects are noticed (assuming that all other variables remain constant). The fact that control has a hierarchical nature also implies that the various homeostatic control systems work cooperatively, rather than in isolation. For example, consider an animal living in the desert. During the day, there may be times when it is heat-stressed (i.e. in danger of its body temperature rising too high). One way to overcome this would be to lose water by evaporation which would have a cooling effect. However, this now produces a conflict – the need to reduce body temperature versus the need to conserve water. This is discussed in Chapter 9.

1.5 Feedforward

Although negative feedback is an important mechanism for maintaining homeostasis, there are other physiological methods by which control of the internal environment may be achieved. Perhaps the most important of these is the process of feedforward. Feedforward is anticipatory activity – behavior which serves to minimize disruption to physiological systems before it happens. A good example of this is eating and drinking at the same time. Eating has a potentially dehydrating effect; the increased osmolarity of the contents of the gut may promote the loss of water from body fluids to maintain **osmotic equilibrium**. To minimize this disruption to the homeostasis of body fluids, many animals drink at the same time as they eat. There are also other aspects of animal behavior which will contribute to the maintenance of homeostasis. For example, animals can learn to avoid foodstuffs that make them vomit, which has a disruptive effect on homeostasis.

1.6 Non-physiological homeostatic mechanisms

The homeostatic mechanisms described thus far have a basis in the physiology of the animal, requiring some sort of regulatory mechanism (e.g. thermoregulation, pH regulation). However, it is possible to

achieve some sort of control without requiring physiological control mechanisms. This can be demonstrated in many aquatic species, vertebrates as well as invertebrates, living in large bodies of water, the temperature of which changes very little. The body temperature of the animal mirrors that of the water in which it lives, and, assuming that the water temperature changes very little, the animal's body temperature also barely changes. This type of homeostasis is called **equilibrium homeostasis**. In essence, the animals are simply conforming to the temperature of the external environment. Whether this is true homeostasis or not is a debatable issue. This system cannot be employed for all aspects of a particular animal's physiology, with the exception of some of the simplest aquatic invertebrates.

1.7 Acclimatization

So far, homeostasis has been described in terms of physiological variables, each of which has a range within which it must be maintained. Superimposed upon this view of homeostasis is the ability of animals to alter the range over which a particular variable is maintained. This ability to alter the range is called **acclimatization**. It can be considered as a fine tuning of homeostatic control systems, the cause of which is some factor in the environment. In this way, regulation is the product of the basic control system together with environmental influences on a particular variable (an analogy of the situation would be the phenotype of an organism being a product of its genotype and the environment in which it lives). For example, the physiology of animals which live at sea level differs from that of animals of the same species which live at high altitude because of the different amounts of oxygen available at each level. The availability of oxygen decreases with increasing altitude. Thus, humans living at altitude show a variety of physiological (and anatomical) adaptations when compared with their sea level counterparts, such as changes in the sensitivity of the receptors which monitor blood O_2 levels, structural differences in the blood vessels that carry deoxygenated blood back to the lungs, and differences in the number and function of red blood cells.

Further reading

Hardy, R. (1983) *Homeostasis*. Edward Arnold, London.

Langley, L. L. (1973) *Homeostasis – Origins of the Concept*. Dowden, Hutchinson and Ross, Pennsylvania.

Chapter

2

Neurons and nervous systems

2.1 Introduction

The evolution of animals from simple unicellular organisms to complex multicellular organisms allowed the development of specialized, dedicated organs and structures, such as digestive systems and circulatory systems. It released cells from having to be a jack of all trades. However, it also presented these animals with a new problem: it was now necessary to be able to control and coordinate the activities of many different cells. Failure to do so would defeat the advantages of a multicellular way of life. Two systems have evolved to ensure that the activities of any animal are efficiently controlled and coordinated – these are the nervous and endocrine systems. In this chapter, the function and organization of nervous systems will be discussed. The nature of endocrine control will be described in Chapter 4.

2.2 Cellular elements of the nervous system

2.2.1 *Neurons*

The nervous system is made up of two different cell types: neurons and glial cells. **Neurons** are the workhorses of the nervous system. They work by generating and conducting **action potentials**, which are simply changes in the polarity of the potential difference (voltage) that exists across the membrane of a neuron (see Section 2.3.2). Action potentials represent the means by which information is transmitted throughout the nervous system and, therefore, the means by which it achieves control and coordination. The structure of a typical neuron is shown in *Figure 2.1*.

In reality, neurons take on many differing appearances and some examples of the forms they take are shown in *Figure* 2.2. However, irrespective of the actual appearance of an individual neuron, they all share common characteristics. A typical neuron consists of a dendritic