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Agamemnon Despopoulos
Stefan Silbernagl

Color Atlas of Physiology

生理学彩色图谱

5th edition, completely revised and expanded

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Preface to the Fifth Edition

The base of knowledge in many sectors of physiology has grown considerably in magnitude and in depth since the last edition of this book was published. Many advances, especially the rapid progress in sequencing the human genome and its gene products, have brought completely new insight into cell function and communication. This made it necessary to edit and, in some cases, enlarge many parts of the book, especially the chapter on the fundamentals of cell physiology and the sections on neurotransmission, mechanisms of intracellular signal transmission, immune defense, and the processing of sensory stimuli. A list of physiological reference values and important formulas were added to the appendix for quick reference. The extensive index now also serves as a key to abbreviations used in the text.

Some of the comments explaining the connections between pathophysiological principles and clinical dysfunctions had to be slightly truncated and set in smaller print. However, this base of knowledge has also grown considerably for the reasons mentioned above. To make allowances for this, a similarly designed book, the *Color Atlas of Pathophysiology* (S. Silbernagl and F. Lang, Thieme), has now been introduced to supplement the well-established *Color Atlas of Physiology*.

I am very grateful for the many helpful comments from attentive readers (including my son Jakob) and for the welcome feedback from my peers, especially Prof. H. Antoni, Freiburg, Prof. C. von Campenhausen, Mainz, Dr. M. Fischer, Mainz, Prof. K.H. Plattig, Erlangen, and Dr. C. Walther, Marburg, and from my colleagues and staff at the Institute in Würzburg. It was again a great pleasure to work with Rüdiger Gay and Astried Rothenburger, to whom I am deeply indebted for revising practically all the illustrations in the book and for designing a number of new color plates. Their extraordinary enthusiasm and professionalism played a decisive role in the materialization of this new edition. To them I extend my sincere thanks. I would also like to thank Suzyon O'Neal Wandrey for her outstanding translation. I greatly appreciate her capable and careful work. I am also indebted to the publishing staff, especially Marianne Mauch, an extremely competent and motivated editor, and Gert Krüger for invaluable production assistance. I would also like to thank Katharina Völker for her ever observant and conscientious assistance in preparing the index.

I hope that the 5th Edition of the *Color Atlas of Physiology* will prove to be a valuable tool for helping students better understand physiological correlates, and that it will be a valuable reference for practicing physicians and scientists, to help them recall previously learned information and gain new insights in physiology.

Würzburg, December 2002
*Stefan Silbernagl**

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Preface to the First Edition

In the modern world, visual pathways have outdistanced other avenues for informational input. This book takes advantage of the economy of visual representation to indicate the simultaneity and multiplicity of physiological phenomena. Although some subjects lend themselves more readily than others to this treatment, inclusive rather than selective coverage of the key elements of physiology has been attempted.

Clearly, this book of little more than 300 pages, only half of which are textual, cannot be considered as a primary source for the serious student of physiology. Nevertheless, it does contain most of the basic principles and facts taught in a medical school introductory course. Each unit of text and illustration can serve initially as an overview for introduction to the subject and subsequently as a concise review of the material. The contents are as current as the publishing art permits and include both classical information for the beginning students as well as recent details and trends for the advanced student.

A book of this nature is inevitably derivative, but many of the representations are new and, we hope, innovative. A number of people have contributed directly and indirectly to the completion of this volume, but none more than *Sarah Jones*, who gave much more than editorial assistance. Acknowledgement of helpful criticism and advice is due also to Drs. *R. Greger*, *A. Ratner*, *J. Weiss*, and *S. Wood*, and Prof. *H. Seller*. We are grateful to *Joy Wieser* for her help in checking the proofs. *Wolf-Rüdiger* and *Barbara Gay* are especially recognized, not only for their art work, but for their conceptual contributions as well. The publishers, Georg Thieme Verlag and Deutscher Taschenbuch Verlag, contributed valuable assistance based on extensive experience; an author could wish for no better relationship. Finally, special recognition to Dr. *Walter Kumpmann* for inspiring the project and for his unquestioning confidence in the authors.

Basel and Innsbruck, Summer 1979
Agamemnon Despopoulos
Stefan Silbernagl

From the Preface to the Third Edition

The first German edition of this book was already in press when, on November 2nd, 1979, *Agamennon Despopoulos* and his wife, *Sarah Jones-Despopoulos* put to sea from Bizerta, Tunisia. Their intention was to cross the Atlantic in their sailing boat. This was the last that was ever heard of them and we have had to abandon all hope of seeing them again.

Without the creative enthusiasm of Agamennon Despopoulos, it is doubtful whether this book would have been possible; without his personal support it has not been easy to continue with the project. Whilst keeping in mind our original aims, I have completely revised the book, incorporating the latest advances in the field of physiology as well as the welcome suggestions provided by readers of the earlier edition, to whom I extend my thanks for their active interest.

Würzburg, Fall 1985
Stefan Silbernagl

Dr. Agamemnon Despopoulos

Born 1924 in New York; Professor of Physiology at the University of New Mexico. Albuquerque, USA, until 1971; thereafter scientific adviser to CIBA-GEIGY, Basel.

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At a Glance

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5th edition, completely revised and expanded

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Ruediger Gay and
Astried Rothenburger

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藏书章

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1 Fundamentals and Cell Physiology

"... If we break up a living organism by isolating its different parts, it is only for the sake of ease in analysis and by no means in order to conceive them separately. Indeed, when we wish to ascribe to a physiological quality its value and true significance, we must always refer it to the whole and draw our final conclusions only in relation to its effects on the whole."

Claude Bernard (1865)

The Body: an Open System with an Internal Environment

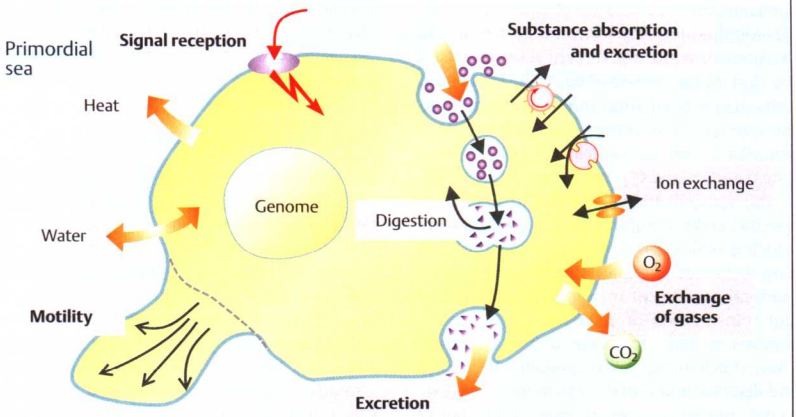
The existence of unicellular organisms is the epitome of life in its simplest form. Even simple protists must meet two basic but essentially conflicting demands in order to survive. A unicellular organism must, on the one hand, isolate itself from the seeming disorder of its inanimate surroundings, yet, as an "open system" (→ p. 40), it is dependent on its environment for the exchange of heat, oxygen, nutrients, waste materials, and information.

"Isolation" is mainly ensured by the cell membrane, the hydrophobic properties of which prevent the potentially fatal mixing of hydrophilic components in watery solutions inside and outside the cell. Protein molecules within the cell membrane ensure the permeability of the membrane barrier. They may exist in the form of *pores* (*channels*) or as more complex transport proteins known as *carriers* (→ p. 26 ff.). Both types are selective for certain substances, and their activity is usually regulated. The cell membrane is relatively well permeable to hydrophobic molecules such as gases. This is useful for the exchange of O_2 and CO_2 and for the uptake of lipophilic signal substances, yet exposes the cell to poisonous gases such as carbon monoxide (CO) and lipophilic noxae such as organic solvents. The cell membrane also contains other proteins—namely, receptors and enzymes. *Receptors* receive signals from the external environment and convey the information to the interior of the cell (signal transduction), and *enzymes* enable the cell to metabolize extracellular substrates.

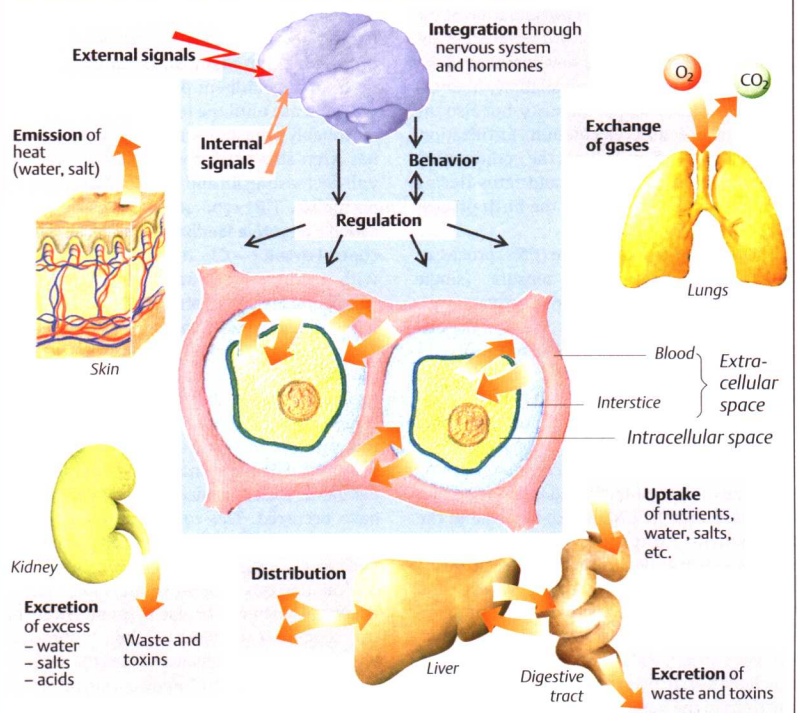
Let us imagine the primordial sea as the external environment of the unicellular organism (→ **A**). This milieu remains more or less constant, although the organism absorbs nutrients from it and excretes waste into it. In spite of its simple structure, the unicellular organism is capable of eliciting motor responses to signals from the environment. This is achieved by moving its pseudopodia or flagella, for example, in response to changes in the food concentration.

The evolution from unicellular organisms to multicellular organisms, the transition from specialized cell groups to organs, the emergence of the two sexes, the coexistence of individuals in social groups, and the transition from water to land have tremendously increased the efficiency, survival, radius of action, and independence of living organisms. This process required the simultaneous development of a complex infrastructure within the organism. Nonetheless, the individual cells of the body still need a milieu like that of the primordial sea for life and survival. Today, the **extracellular fluid** is responsible for providing constant environmental conditions (→ **B**), but the volume of the fluid is no longer infinite. In fact, it is even smaller than the intracellular volume (→ p. 168). Because of their metabolic activity, the cells would quickly deplete the oxygen and nutrient stores within the fluids and flood their surroundings with waste products if organs capable of maintaining a **stable internal environment** had not developed. This is achieved through **homeostasis**, a process by which physiologic self-regulatory mechanisms (see below) maintain steady states in the body through coordinated physiological activity. Specialized organs ensure the continuous absorption of nutrients, electrolytes and water and the excretion of waste products via the urine and feces. The *circulating blood* connects the organs to every inch of the body, and the exchange of materials between the blood and the intercellular spaces (*interstices*) creates a stable environment for the cells. Organs such as the digestive tract and liver absorb nutrients and make them available by processing, metabolizing and distributing

A. Unicellular organism in the constant external environment of the primordial sea



B. Maintenance of a stable internal environment in humans



them throughout the body. The lung is responsible for the exchange of gases (O_2 intake, CO_2 elimination), the liver and kidney for the excretion of waste and foreign substances, and the skin for the release of heat. The kidney and lungs also play an important role in regulating the internal environment, e.g., water content, osmolality, ion concentrations, pH (kidney, lungs) and O_2 and CO_2 pressure (lungs) (→ **B**).

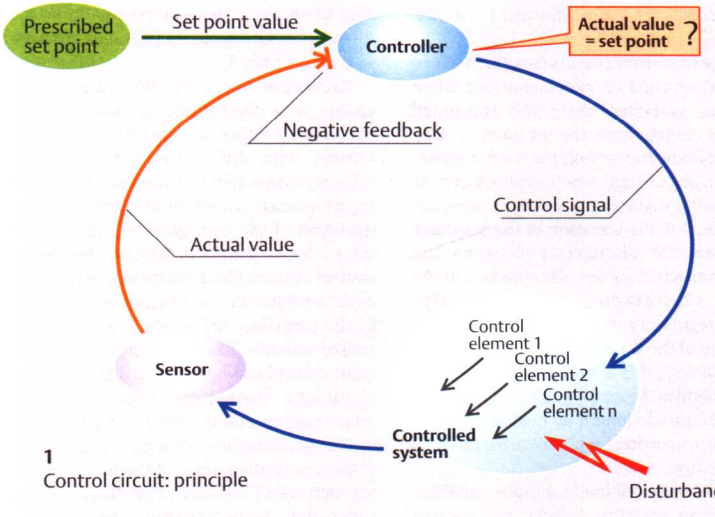
The specialization of cells and organs for specific tasks naturally requires **integration**, which is achieved by convective transport over long distances (circulation, respiratory tract), humoral transfer of information (hormones), and transmission of electrical signals in the nervous system, to name a few examples. These mechanisms are responsible for supply and disposal and thereby maintain a stable internal environment, even under conditions of extremely high demand and stress. Moreover, they control and regulate functions that ensure survival in the sense of **preservation of the species**. Important factors in this process include not only the timely development of reproductive organs and the availability of fertilizable gametes at sexual maturity, but also the control of erection, ejaculation, fertilization, and nidation. Others include the coordination of functions in the mother and fetus during pregnancy and regulation of the birth process and the lactation period.

The **central nervous system** (CNS) processes signals from peripheral sensors (single sensory cells or sensory organs), activates outwardly directed effectors (e.g., **skeletal muscles**), and influences the endocrine **glands**. The CNS is the focus of attention when studying human or animal **behavior**. It helps us to locate food and water and protects us from heat or cold. The central nervous system also plays a role in partner selection, concern for offspring even long after their birth, and integration into social systems. The CNS is also involved in the development, expression, and processing of emotions such as desire, listlessness, curiosity, wishfulness, happiness, anger, wrath, and envy and of traits such as creativeness, inquisitiveness, self-awareness, and responsibility. This goes far beyond the scope of physiology—which in the narrower sense is the study of the functions of the body—and, hence, of this book. Although behavioral science, sociology, and psychology are disciplines that border on physiology, true bridges between them and physiology have been established only in exceptional cases.

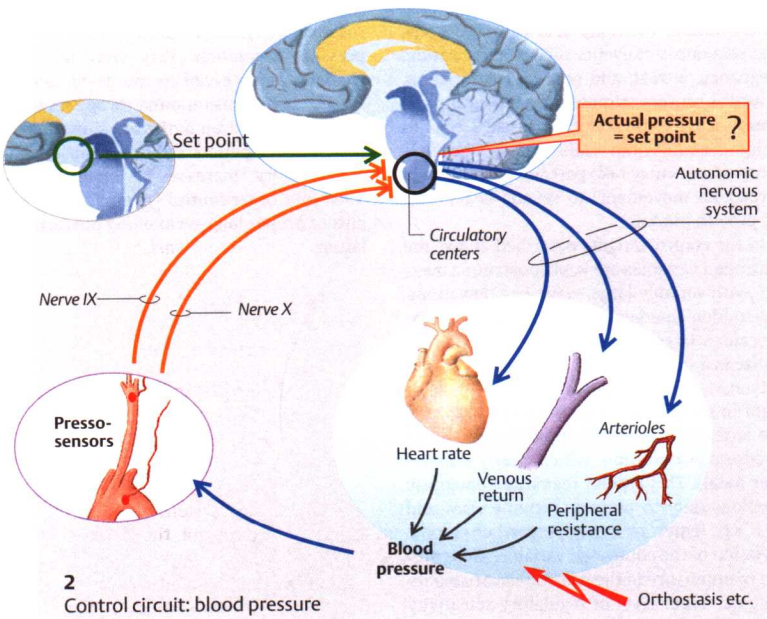
Control and Regulation

In order to have useful cooperation between the specialized organs of the body, their functions must be adjusted to meet specific needs. In other words, the organs must be subject to control and regulation. **Control** implies that a *controlled variable* such as the blood pressure is subject to selective external modification, for example, through alteration of the heart rate (→ p. 218). Because many other factors also affect the blood pressure and heart rate, the controlled variable can only be kept constant by continuously measuring the current blood pressure, comparing it with the reference signal (*set point*), and continuously correcting any deviations. If the blood pressure drops—due, for example, to rapidly standing up from a recumbent position—the heart rate will increase until the blood pressure has been reasonably adjusted. Once the blood pressure has risen above a certain limit, the heart rate will decrease again and the blood pressure will normalize. This type of *closed-loop control* is called a **negative feedback control system** or a **control circuit** (→ **C1**). It consists of a *controller* with a programmed *set-point* value (target value) and *control elements* (*effectors*) that can adjust the *controlled variable* to the set point. The system also includes *sensors* that continuously measure the actual value of the controlled variable of interest and report it (feedback) to the controller, which compares the actual value of the controlled variable with the set-point value and makes the necessary adjustments if disturbance-related discrepancies have occurred. The control system operates either from within the organ itself (*autoregulation*) or via a *superordinate organ* such as the central nervous system or hormone glands. Unlike simple control, the elements of a control circuit can work rather imprecisely without causing a deviation from the set point (at least on average). Moreover, control circuits are capable of responding to unexpected dis-

C. Control circuit



1
Control circuit: principle



2
Control circuit: blood pressure

turbances. In the case of blood pressure regulation (→ **C2**), for example, the system can respond to events such as orthostasis (→ p. 204) or sudden blood loss.

The type of control circuits described above keep the controlled variables constant when **disturbance variables** cause the controlled variable to deviate from the set point (→ **D2**). Within the body, the set point is rarely invariable, but can be "shifted" when requirements of higher priority make such a change necessary. In this case, it is the **variation of the set point** that creates the discrepancy between the nominal and actual values, thus leading to the activation of regulatory elements (→ **D3**). Since the regulatory process is then triggered by variation of the set point (and not by disturbance variables), this is called **servocontrol** or **servomechanism**. Fever (→ p. 224) and the adjustment of muscle length by muscle spindles and γ-motor neurons (→ p. 316) are examples of servocontrol.

In addition to relatively simple variables such as blood pressure, cellular pH, muscle length, body weight and the plasma glucose concentration, the body also regulates complex sequences of events such as fertilization, pregnancy, growth and organ differentiation, as well as sensory stimulus processing and the motor activity of skeletal muscles, e.g., to maintain equilibrium while running. The regulatory process may take parts of a second (e.g., purposeful movement) to several years (e.g., the growth process).

In the control circuits described above, the controlled variables are kept constant on average, with variably large, wave-like deviations. The sudden emergence of a disturbance variable causes larger deviations that quickly normalize in a stable control circuit (→ **E**, test subject no. 1). The **degree of deviation** may be slight in some cases but substantial in others. The latter is true, for example, for the blood glucose concentration, which nearly doubles after meals. This type of regulation obviously functions only to prevent extreme rises and falls (e.g., hyper- or hypoglycemia) or chronic deviation of the controlled variable. More precise maintenance of the controlled variable requires a higher level of regulatory sensitivity (*high amplification factor*). However, this extends the settling time (→ **E**, subject no. 3) and can lead to regulatory instability, i.e., a situation where the actual value oscillates back and forth between extremes (*unstable oscillation*, → **E**, subject no. 4).

Oscillation of a controlled variable in response to a disturbance variable can be *attenuated* by either of two mechanisms. First, sensors with differential characteristics (*D sensors*) ensure that the intensity of the sensor signal increases in proportion with the **rate of deviation** of the controlled variable from the set point (→ p. 312 ff.). Second, **feedforward control** ensures that information regarding the expected intensity of disturbance is reported to the controller *before* the value of the controlled variable has changed at all. Feedforward control can be explained by example of physiologic thermoregulation, a process in which cold receptors on the skin trigger counterregulation before a change in the controlled value (core temperature of the body) has actually occurred (→ p. 224). The disadvantage of having *only* D sensors in the control circuit can be demonstrated by example of arterial pressosensors (= pressoreceptors) in acute blood pressure regulation. Very slow but steady changes, as observed in the development of arterial hypertension, then escape regulation. In fact, a rapid drop in the blood pressure of a hypertensive patient will even cause a counterregulatory increase in blood pressure. Therefore, other control systems are needed to ensure proper long-term blood pressure regulation.

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