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THERMOREGULATION

Edited by
EVELYN SATINOFF

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SERIES EDITOR'S FOREWORD

It was not too many years ago that virtually all research publications dealing with animal behavior could be housed within the covers of a very few hard-bound volumes that were easily accessible to the few workers in the field. Times have changed! The present-day students of behavior have all they can do to keep abreast of developments within their own area of special interest, let alone in the field as a whole; and of course we have long since given up attempts to maintain more than a superficial awareness of what is happening "in biology," "in psychology," "in sociology," or in any of the broad fields touching upon or encompassing the behavioral sciences.

It was even fewer years ago that those who taught animal behavior courses could easily choose a suitable textbook from among the very few that were available; all "covered" the field, according to the bias of the author. Students working on a special project used *the* text and *the* journal as reference sources, and for the most part successfully covered their assigned topics. Times have changed! The present-day teacher of animal behavior is confronted with a bewildering array of books to choose among, some purported to be all-encompassing, others confessing to strictly delimited coverage, and still others being simply collections of recent and profound writings.

In response to the problem of the steadily increasing and overwhelming volume of informatin in the area, the Benchmark Papers in Behavior was launched as a series of single-topic volumes designed to be some things to some people. Each volume contains a collection of what an expert considers to be *the* significant research papers in a given topic area. Each volume, then, serves several purposes. To teachers, a Benchmark volume serves as a supplement to other written materials assigned to students; it permits in-depth consideration of a particular topic while at the same time confronting students (often for the first time) with original research papers of outstanding quality. To researchers, a Benchmark volume serves to save countless hours digging through the various journals to find *the* basic articles in their area of interest; often the journals are not easily available. To students, a Benchmark volume provides a readily accessible set of original papers on the topic, a set that forms the core of the more extensive bibliography that they are likely to compile;

it also permits them to see at first hand what an "expert" thinks is important in the area, and to react accordingly. Finally, to librarians, a Benchmark volume represents a collection of important papers from many diverse sources, thus making readily available materials that might otherwise not be economically possible to obtain or physically possible to keep in stock.

The choice of topics to be covered in this series is no small matter. Each of us could come up with a long list of possible topics and then search for potential volume editors. Alternatively, we could draw up long lists of recognized and prominent scholars and try to persuade them to do a volume on a topic of their choice. For the most part, we have followed a mix of both approaches: match a distinguished researcher with a desired topic, and the results should be outstanding. So it is with the present volume.

Dr. Evelyn Satinoff is no newcomer to the problem of temperature regulation in warm-blooded animals; she has been publishing in this area for a number of years. More significantly, her recent outstanding reviews (1974, 1978) demonstrate an overall grasp and approach to the topic that is of interest to students and colleagues. Hence, it was singularly appropriate to invite her to serve as editor for this Benchmark volume. We are very pleased that she accepted.

MARTIN W. SCHEIN
STEPHEN W. PORGES

PREFACE

When I was asked to put together a set of papers that were critical in the field of temperature regulation, I was at first delighted. There had never been such a collection of original works in one place, and I had often wished for one to give my students so that they could not only learn about the field but also develop an appreciation of what excellent science is and how one goes about looking for critical problems to work on. Upon reflection, however, I realized that the task would be extremely difficult. Papers on heat and cold adaptation, clinical applications of hypothermia, pharmacological aspects of thermoregulation, hibernation and estivation, bioenergetics, control theory analysis of thermoregulation, and problems in peripheral and central thermodetection could all legitimately be included in a book entitled, "Thermoregulation." However, given the confines of no more than 400 pages, to include papers in all these areas would give the reader only a fragmentary feeling for what is central in the field. Happily, several of these subjects are discussed in Professor Theodor Benzinger's two-volume collection in the Benchmark series in human physiology.*

For me, the question that holds the field together is, "How do animals maintain a relatively constant body temperature in the face of a notoriously inconstant environment?" This question, as it is answered in many of the papers in this volume, may be restated as, "How does the central nervous system integrate an animal's available thermoregulatory responses so as to maintain thermal homeostasis?" The first set of papers defines the concept of thermal homeostasis and illustrates how animals maintain it by using the reflexive and behavioral means available to them.

The second group of papers concerns one of the most exciting stories in neurophysiology—the search for the thermostat. A thermostat implies a master temperature regulating "center" in the brain, and indeed, for many years the concept of centers dominated not only thermoregulation but also work on feeding, drinking, sexual behavior, sleep and wakefulness, and indeed, almost all behaviors that were known to be

*Benzinger, T. H. 1977. *Temperature, Part I: Arts and Concepts; Part II: Thermal Homeostasis*. Benchmark Papers in Human Physiology, vols. 9 and 10. Stroudsburg, Pa.: Dowden, Hutchinson & Ross.

under neural control. The concept is simple and parsimonious, and is therefore a highly attractive way to categorize brain-behavior interactions, but unfortunately, it is almost certainly inadequate. I have included several papers that demonstrate why it is inadequate and the new theoretical direction in which I believe the field is going.

Third, because I believe that the pathology of any system can be tremendously useful in understanding how the normal system operates, I have included several fundamental papers on fever, the most ubiquitous and striking pathology in the thermoregulation (although, as we shall see, it may be inaccurate to describe fever as a pathological condition even though the infection that causes it may be so described). Finally, since the evolution of endothermy, or warm-bloodedness, is a source of endless and fascinating speculation, and must be considered in any theory of thermoregulatory function, I have included two papers on this subject that are highly provocative and may even be true.

This is an idiosyncratic collection. Some of the papers included here are significant because they directed the general course of thermoregulatory research for many years. Others beautifully illustrate important theoretical or experimental points or striking, unexpected findings. Others had great influence over me in the course of my intellectual development. A further analysis of many of the phenomena described in these papers will be extremely fruitful in understanding the basic principles of homeostasis and motivated behavior in general, as well as thermoregulation. The papers have been collected in the hope that some of the people who read this book will be stimulated to investigate the subject further.

EVELYN SATINOFF

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INTRODUCTION

If an animal is to stay alive and healthy, certain basic physiological functions must be held fairly constant. The tissues of the body must receive an adequate but not excessive supply of oxygen. The blood must not become too acidic or too alkaline. Blood glucose levels and body temperature must be maintained within very narrow limits. This is no problem for an organism that lives in a congenial, unvarying environment, like a tapeworm or a fetus. But the rest of us must depend on our own resources to achieve such stability, and the degree to which our resources are automatic determines the time we have to devote to such activities as mating, defending a territory, or reading a book. For instance, if the liver did not store glucose and release it at a controlled rate, we would have to spend most of our time preparing and eating small quantities of food to give us energy to be active. Because of the liver's automatic functions, we are able instead to eat only two or three times a day and spend the rest of our time doing other things. Our bodies do not store and release heat, but we have very efficient behavioral and reflexive mechanisms for maintaining a constant body temperature and so we are largely free from worries about climatic changes. The great French physiologist Claude Bernard (1813–1878) was the first to enunciate this principle. In 1868 he wrote, "The constancy of the internal environment is the condition of a free and independent life" (see Paper 1, this volume). This is the first statement of the principle Walter B. Cannon was later to call "homeostasis" (see Paper 2). *Homeostasis* refers to the state of equilibrium in the body with respect to various functions and chemical composition of fluids and tissues and also to the processes through which such equilibrium is maintained.

Temperature regulation is an outstanding example of a homeostatic process. To understand how this regulation is accomplished, three major questions must be answered: (1) What is the source of the heat that allows endothermic mammals and birds to be warmer than their environment? (2) What responses does an animal use to increase heat production and conservation and to decrease heat loss? (3) How does the central nervous system integrate these responses so that a constant body temperature is maintained? Most of the papers in this collection concern answers to the second and third questions. However, these questions could begin to be studied only after the first problem was resolved. Therefore, for reasons of historical interest and also because I believe that an understanding of the answer to the first question will make it easier to integrate the other two, I will begin with a short history of the inquiry into the source of animal heat. (For much of this history, I am indebted to Goodfield, 1960.)

WHAT IS THE SOURCE OF ANIMAL HEAT?

One of the most obvious differences between living animals and dead ones is that living beings are warm and dead ones are cold. Inquiry into the source of heat in living organisms has been one of the central problems in physiology. The ancient Greeks thought that the heart generated the heat, which was then distributed to the rest of the body through the arteries. The function of the lungs and respiration was primarily to cool the blood. By the end of the eighteenth century, we find several different theories. Some were mechanical, for example, the heat was generated by friction between the blood and the blood vessels. However, such theories were very shortlived. The problem with them was that the blood was fluid and the surfaces of the vessels were so smooth that not enough friction could possibly be generated to provide adequate heat.

Other theories were chemical, for example, that the heat was produced by some sort of fermentation or chemical mixture. In fact, one of these ideas was partially correct in assuming that the decomposition of food eaten was responsible for animal heat. A different, combustion, theory put forward by the Scottish chemist Joseph Black (1728–1799), asserted that animal heat was generated in the lungs which, through respiration, emitted carbon dioxide (or "fixed air"), which was accompanied by heat. (Black did not conceive of heat as a form of energy but rather as a substance that combined with the thing being heated—a sort of physical analog of phlogiston.) Black's theory was correct in equating respiration with combustion, but it was in error in focusing all attention on the lungs. At some point, attention had to be directed to the individual cells in the body.

It remained for the great German organic chemist, Justus von Liebig (1803–1873) to provide an adequate account of the chemical processes involved in the generation of animal heat. He was the first to realize that the carbon dioxide and water breathed out came from the oxidation of the complex foods taken in, and he was able to account for the chemical transformations that took place in the body during this conversion.

> The mutual action between the elements of the food and the oxygen conveyed by the circulation of the blood to every part of the body is the source of animal heat. (von Liebig, quoted by Goodfield, 1960.)

The picture of animal heat we have today is basically unchanged since von Liebig. Oxygen, carried by the lungs through the bloodstream to each cell in the body, combines with the nutrients from the food eaten. This process liberates energy, which is dissipated mainly in the form of heat.

Although von Liebig gave a precise and accurate account of the physicochemical nature of animal heat, he still could not understand how a constant body temperature was maintained—how an animal in contact with the varying external would appeared to be unaffected by it. He invoked the existence of a "vital force," some unique characteristic of living organisms that enabled them to resist the influence of external agents. Here Claude Bernard's great concept of the "milieu interieur" enters, removing the last traces of vitalism from explanations of animal functions, explaining the constancy of body temperature, and establishing physiology as a science in its own right, not subservient to physics and chemistry.

Claude Bernard was a determinist; he believed that all biological phenomena were determined by physical and chemical conditions. But the conditions to which he referred were those of the internal environment of the body, not those of the external world. He was the first to insist that one must look at the whole complex organism—not simply at an isolated organ or biochemical process—and the way in which it interacts with its environment.

> As the organism becomes more and more complex, so this environment becomes more and more isolated from the outside world, and the differences between simpler and more complex creatures are simply differences in this degree of "isolation and protection." (Bernard, quoted by Goodfield, 1960.)

When vital phenomena are looked at in this light, we can see that they are surrounded by their own environment, which has its own regulatory mechanisms. To understand the constancy of body temperature, then, we must understand the regulatory mechanisms of the internal environment, and when they are understood, Bernard said, it will be found that they follow the laws of physics and chemistry.

Thus the animal is not out of touch with or unaffected by the outside world. On the contrary, it is in intimate contact with it, and it is the immediate and successful operation of the animal's buffering systems in response to changes in the external environment that allows for that internal constancy we call *homeostasis.*

HOW IS BODY TEMPERATURE REGULATED?

Body temperature can be regulated only if rates of heat production and heat loss are controlled. This control is exerted by the central nervous system, and it was only after the development of neurophysiological techniques that the nervous control of body temperature could be experimentally investigated. Isaac Ott (1847–1916) (Paper 5) in Philadelphia and Charles Richet (1850–1935) in France first demonstrated that temperature regulation could be deranged by puncturing an area of the brain between the corpus striatum and the optic thalamus. This localization was further supported by observations that, as successive levels of the brainstem were transected, animals were essentially unable to regulate their internal temperature at all unless the hypothalamus remained connected to the rest of the brain below (Bazett and Penfield 1922, Paper 6).

Besides lesions and transections, the technique of thermal stimulation was used to define more accurately the neural area concerned with thermoregulation. Barbour (1912) first showed that heating and cooling the tissue around the corpus striatum in rabbits altered deep body temperature. Magoun, Harrison, Brobeck, and Ranson (1938) then localized the areas more precisely by demonstrating that radio-frequency heating of discrete hypothalamic regions in anesthetized cats evoked the heat-loss responses of increased respiration and panting. These reactions were most marked when the heating electrodes were in the anterior hypothalamus and the preoptic area just rostral to it, but they could still be elicited by more caudal stimulation. These results were confirmed in monkeys (Beaton et al, 1941) and interpreted as identifying a reactive region in the anterior hypothalamus containing elements excited by rising temperature, which in turn activated heat-loss mechanisms.

All these data implied that the hypothalamus is sensitive to its own temperature and to temperature signals from the rest of the brain and body. In 1963 temperature-sensitive units, that is, cells that alter their firing rate in response to changes in their temperature, were identified