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An Introduction to Behavioral Endocrinology

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The cover
A female red deer (*Cervus elaphus*) nurses her fawn. Maternal behavior is mediated by hormones associated with parturition and lactation (Chapter 7). Photograph by Fiona Guinness.

The frontispiece
A red deer stag "roaring" after defeating another male in a fight to secure territory upon which females will graze during the breeding season. The androgenic hormones associated with sperm maturation have been co-opted over evolutionary time to regulate aggressive and mating behaviors (Chapter 10). Photograph by Fiona Guinness.

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To the friends in Berkeley and Austin who have taught me about hormones and behavior: Frank Beach, Howard Bern, Marc Breedlove, Frank Bronson, David Crews, Steve Glickman, Arnold Leiman, Paul Licht, Werner Loher, Carl Nicoll, Lawson Rosenberg, and Irving Zucker.

Preface

Like many professors who write a textbook, my motivation for this task initially arose from my desire to provide a useful heuristic companion to my lectures. I teach a behavioral endocrinology course in a psychology department, but over half of the students in the course are biological science majors. Similar courses with similar students are taught at other institutions by faculty members in biology, zoology, and physiology departments, so a textbook on this topic must integrate material from several disciplines and levels of analysis, and must be accessible to students with a range of scientific backgrounds. As I wrote the text, I had three main goals in mind.

First, I wanted to convey the excitement of a field that has embraced the perspectives and contributions of diverse lines of research. Understanding the interactions between hormones and behavior is truly an interdisciplinary effort which involves the study of phenomena ranging from the molecular to the social level. Because many students taking this course are social science students without substantial training in biology, I have tried to keep the discussions of endocrine physiology and biochemistry to the minimum needed to understand the behavioral concepts being discussed.

Second, I wished to give due credit to those scientists who laid the foundations of the field by presenting current ideas, hypotheses, and theories within the context of their historical origins. Some of the topics described in the text are controversial and may warrant additional discussion; some potential starting points for discussion are offered at the end of each chapter. Also, each chapter ends with a short list of additional readings that provide more detailed information on the material in the chapter.

Third, I attempted to present behavioral endocrinology in a comparative perspective by including examples of hormone–behavior interactions in as many different kinds of animals as possible (although in many areas, all or most of the significant research has been conducted on laboratory rats, so I sometimes necessarily restricted the discussion to this species). The advantage of this comparative approach is that it illuminates the many hormonal and behavioral mechanisms that have evolved in animals to deal with common problems of reproduction and survival.

Toward this end, the adaptive function, as well as the physiological mechanisms, of hormone–behavior interactions are presented throughout the text; I hope that this integrative presentation makes learning about behavioral endocrinology interesting, and provides a useful framework upon which you can arrange the details.

Acknowledgments

I thank the following individuals who read and provided valuable comments on various parts of this book: Elizabeth Adkins-Regan, Greg Ball, Jacques Balthazart, Dan Bernard, Eric Bittman, Elliott Blass, Jeff Blaustein, Sue Carter, Joe Casto, Greg Demas, Courtney DeVries, Don Dewsbury, Paul Gold, David Gubernick, Sabra Klein, Lance Kriegsfeld, Michael Leon, Margaret McCarthy, Martha McClintock, Jim McGaugh, Chris Moffatt, Celia Moore, David Olton, Emilie Rissman, Ed Roy, Ben Sachs, Barbara Sherwin, David Shide, Rae Silver, Cheryl Sisk, Chuck Snowdon, George Wade, John Wingfield, Pauline Yahr, and Irv Zucker.

I am especially grateful to my colleague in the Behavioral Neuroendocrinology Group of the Psychology Department at Hopkins, Greg Ball, who read much of the manuscript, and provided helpful suggestions, references, criticisms, and support during the writing and editing of the book. I also thank Margaret McCarthy, another local expert in behavioral endocrinology, who also provided exceptional assistance and support during the writing. My colleague and wife, Courtney DeVries, provided a tranquil environment in which to read and write, as well as welcome criticism, references, and the amazing patience to cut short a Maine vacation to visit my publisher in Massachusetts. I am grateful to Jon Gerber, Josh Fine, Amy Bennett, Ben Asfaw, Young Kwak, Jack Chiang, Laura Katz, and Courtney DeVries for helping to track down various materials for the book. I am particularly indebted to many other colleagues, who are acknowledged individually in the figure legends, for permission to use graphic and photographic material.

I would also like to thank the team at Sinauer Associates, especially Peter Farley, my demanding, yet ultimately reasonable, editor, who taught me to respect "thoroughness." His incredible attention to detail has greatly improved every aspect of this book. Warm appreciation is also due to Kathaleen Emerson, the project editor, who cheerfully tracked down rights to graphic material around the globe, maintained a veneer of calm and tranquility regardless of extrinsic factors, and kindly asserted that we were "right on schedule" regardless of calendar date. Thanks to Norma Roche for her substantial assistance with copy editing and suggestions for improvements in the style of presentation. This book is much better because of their uncompromising efforts.

Finally, I would like to thank the undergraduate and graduate students in my behavioral endocrinology course at Johns Hopkins, as well as the students in Chuck Snowdon's course at the University of Wisconsin, who provided much welcome feedback and many helpful suggestions on the manuscript. To all of you, thanks a 10^6.

Contents

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The Study of Behavioral Endocrinology

Does anabolic steroid abuse cause violent behavior? Does the sex drive wane with aging? Is the sex drive of women higher or lower than the sex drive of men? Can a woman's mood be affected by her menstrual cycle? Do seasonal cycles of depression occur in people? Why are more men than women in prison for committing violent crimes? Does postpartum depression really exist? Is homosexuality caused by hormone levels that are too low or too high? Is the sexual behavior of women influenced by menopause? Many of us have pondered these questions during informal discussions with friends and family members. Researchers in the field of behavioral endocrinology, the study of the interaction between hormones and behavior, attempt to address these kinds of questions in a formal, scientific manner.

The study of the interaction between hormones and behavior has been truly interdisciplinary: methods and techniques from one scientific discipline have been borrowed and refined by researchers in other fields. Anatomists, psychologists, entomologists, zoologists, physiologists, endocrinologists, and psychiatrists have all contributed to the understanding of hormone–behavior interactions. This exciting commingling of scientific interests and approaches, with its ongoing synthesis of knowledge, has led to the emergence of behavioral endocrinology as a distinct field of study (Beach, 1975).

Historical Roots of Behavioral Endocrinology

Ebbinghaus (1908) stated that psychology has a short history but a long past, and the same can be said of behavioral endocrinology (Beach, 1974a). While

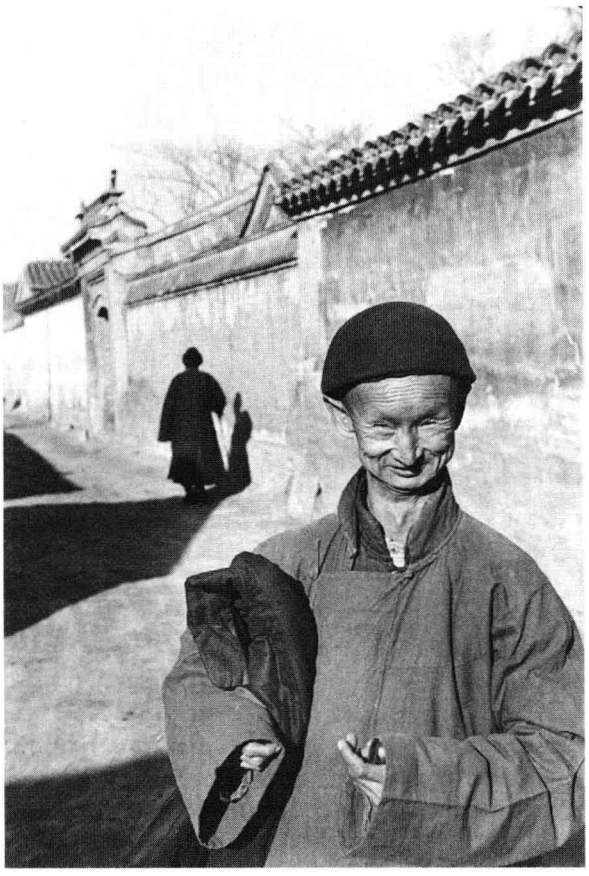
the modern era of the discipline began only about 50 years ago, some effects of hormones on behavior have been implicitly recognized for centuries.

The male sex organs, or testes, produce and secrete a hormone called testosterone, which affects sexual behavior, aggressiveness, territoriality, hibernation, and migration, as well as many other behaviors that differentiate males from females. The testes are usually located outside of the body cavity in mammals and can easily be damaged or removed. Thus, castration, the surgical removal of the testes, has historically been the most common manipulation of the endocrine system. For millenia many species of domestic animals have been castrated to make them better to eat or easier to control, and the behavioral and physical effects of castration have been known since antiquity. Indeed, these effects were known to Aristotle, who described the effects of castration in roosters with great detail and accuracy.

For centuries, royalty employed men castrated before puberty, or eunuchs, to guard women from other men. For example, the Old Testament reports that these emasculated males were used to guard the women's quarters of Hebrew kings and princes (Esther 1:10). Castration in humans often has little or no effect on physical appearance or future sexual behavior when performed after the unfortunate individual attains sexual maturation; however, if human males are castrated before puberty, they will develop a characteristic physical appearance, marked by short stature and long arms (Figure 1.1), and sexual behaviors are unlikely to develop. The typical secondary male sex characters are also affected by removal of the testes. For example, eunuchs never develop beards, and the pubertal change in voice does not occur. Normally during puberty, the vocal cords of males thicken in response to testosterone secreted by the testes. It is the thickened vocal cords that produce the deeper-pitched voice characteristic of males, just as the thick strings of a guitar produce deeper-pitched notes than the thin strings.

You may be surprised to learn that it was once a common practice in Europe and Asia to castrate young boys with exceptional singing voices to prevent the pubertal changes in pitch. These singers became known as *castrati*. Although castrati were prized by church choirs for centuries, their popularity reached a peak in Europe during the 17th and 18th centuries with the development of opera, which made castrati the first superstars of the entertainment world (Heriot, 1974). The first castrato opera star, Baldassare Ferri, died in 1680 at the age of 70 with a fortune worth the equivalent of $3,000,000 today. In hopes of attaining this level of wealth and fame, young boys with musical aptitude were identified early, and poor families offered their sons outright to church leaders, singing teachers, and music academies. Thousands of boys lost their testes but never gained the celebrity or riches of the star castrati.

What did a castrato sound like? Essentially, the castrati had the range of a soprano, but the greater development of the male lungs gave their singing remarkable power. An early critic remarked, "Their timbre is as clear and piercing as that of choirboys and much more powerful; they appear to sing an octave above the natural voice of women. Their voices . . .



1 ***EUNUCH OF THE LAST IMPERIAL COURT,*** photographed in China by Henri Cartier-Bresson in 1949. Note the lack of facial hair and unusually long arms. One eunuch of the Ching Dynasty, Sun Yaoting, still lives in China and is over 90 years old.

are brilliant, light, full of sparkle, very loud, and astound with a very wide range" (Heriot, 1974).

After 200 years, the tastes of the opera-loving public changed. The rise in popularity of the female soprano voice reduced the demand for the castrati, and they soon became an oddity. In 1849, the last great castrato, Giovanni Velluti, retired from opera to his villa in Venice.

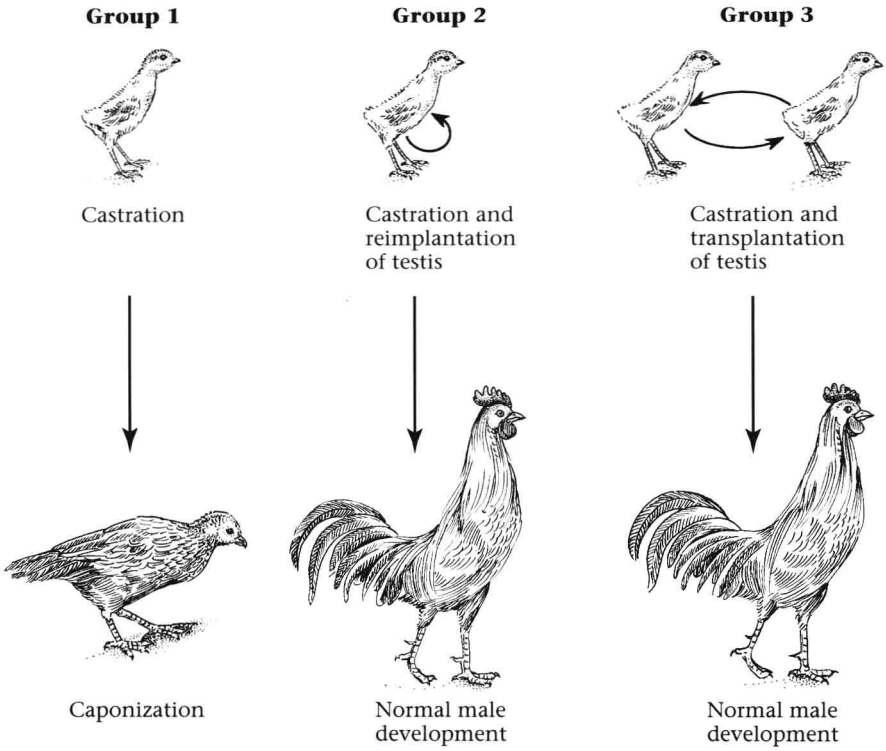
Berthold's Experiment

A useful starting point for understanding research in hormones and behavior is a classic 19th-century experiment that is now considered to be the first formal study of endocrinology. This remarkable experiment conclusively demonstrated that a substance produced by the testes could travel through the bloodstream and eventually affect behavior. Professor Arnold Adolph Berthold, a Swiss–German physician and professor of physiology at the University of Göttingen (Figure 1.2), used chickens in his experiment, and showed that a product of the testes was necessary for a cockerel (an immature male chicken) to develop into a normal adult rooster.

2 ARNOLD ADOLPH BERTHOLD of the University of Göttingen, who in 1849 conducted what is now recognized as the first formal experiment in endocrinology.

As you know, roosters display several characteristic behaviors that are not typically seen among hens or immature chicks of either sex. Roosters mate with hens, they fight with other roosters, and of course, roosters crow. Moreover, roosters are larger than hens and immature birds and have distinctive plumage. On the other hand, capons, male chickens that have been castrated in order to make them more tender to eat, do not show many behavioral and physical characteristics of roosters. They do not attempt to mate with hens and are not very aggressive toward other males. Indeed, they avoid aggressive encounters, and if conditions force them to fight, they do so in a "half-hearted" manner. Finally, capons do not crow like roosters.

The behavioral and physical differences among roosters, hens, capons, and immature chickens were undoubtedly familiar to Berthold when he planned his study, which began on the second day of August, 1848, and lasted for several months (Figure 1.3; Berthold, 1849). He placed six cockerels in three experimental groups, each consisting of two birds. He removed both testes from each of the two cockerels in the first group, and, as expected, these birds eventually developed as capons. They never fought with other males after castration, and they failed to crow; instead, Professor Berthold reported, they developed the "monotone voice of the capon." They avoided females and never exhibited mating behavior. Finally, these birds *looked* different than intact (uncastrated) adult males. Their bodies and heads were small, and their combs and wattles were atrophied and pale in color.



3 BERTHOLD'S EXPERIMENT. The birds in Group 1 were castrated, and, when observed several months later, were smaller than normal roosters and failed to engage in rooster-typical behaviors. The birds in Group 2 were also castrated, but one of each bird's own testes was reimplanted in its abdominal cavity. These birds looked and behaved liked normal roosters when adults. The pair of birds in Group 3 were castrated, and one testis from each bird was transplanted into the abdomen of the other. Several months later, these birds also looked and behaved liked normal roosters. Berthold found that the reimplanted and transplanted testes in Groups 2 and 3 developed vascular connections and generated sperm.

The second pair of cockerels was also castrated, but Berthold reimplanted one testis from each bird in its abdominal cavity after ensuring that all of the original vascular and neural connections had been cut. Interestingly, both birds in this group developed normal rooster behavior. According to Berthold, they "crowed lustily, often engaged in battle with each other and with other cockerels, and showed the usual reactions to hens." Their physical appearance was indistinguishable from that of other young roosters; they grew normally and possessed highly developed combs and wattles that were bright red in color.

The remaining two birds were also castrated, but after the testes were removed, Berthold placed a single testis from each bird in the other's abdominal cavity. Like the cockerels in the second experimental group,

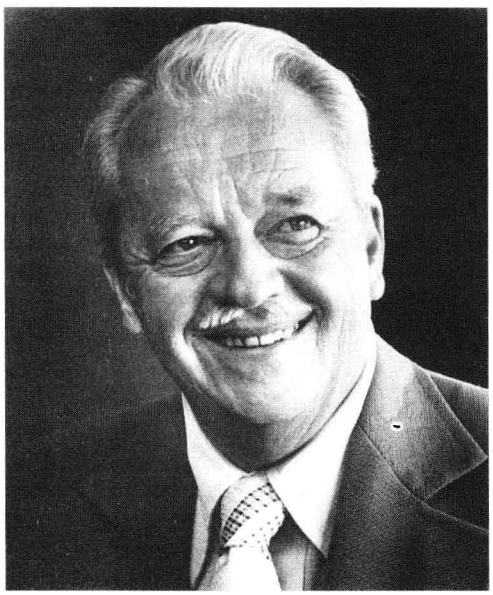
these birds also developed the "voice, sexual urge, belligerence, and growth of combs and wattles" characteristic of intact males.

After observing all six birds for several months, Berthold dissected one of the cockerels from the second group and found that the implanted testis had attached itself to the intestines, developed a vascular supply, and nearly doubled in size. Eventually he examined all the implanted testes under a microscope and noted the presence of sperm.

Based on the results of this experiment, Berthold made three major conclusions: (1) the testes are transplantable organs; (2) transplanted testes can function and create sperm (Berthold drew the analogy to a tree branch that produces its own fruit after having been grafted to another tree); and (3) because the testes functioned normally after all nerves were severed, there could be no specific nerves directing testicular function. To account for these findings, Berthold proposed that a secretory, blood-borne product of the transplanted testes (*productive Verhältniss der Hoden*)

1 FRANK A. BEACH AND THE ORIGINS OF THE MODERN ERA OF BEHAVIORAL ENDOCRINOLOGY

For some time before behavioral endocrinology emerged as a recognized field, its foundations were being laid by researchers in other fields. The anatomists, physiologists, and zoologists who were doing the majority of the work on "internal secretions" prior to 1930 often used behavioral endpoints in their studies. Soon thereafter, psychologists began making important contributions in the study of hormones and behavior. In the early decades of the 20th century, American psychology was undergoing a major change, both in ideology and methodology. Led by John B. Watson, students of the "science of the mind" were casting aside introspection as a method in favor of observation and experimentation. Watson argued that only overt behavior was observable, and psychologists began describing and quantifying all types of overt behavior.



Frank A. Beach (1911–1988)

Karl S. Lashley did his graduate work under Watson at Johns Hopkins University and eventually joined the faculty at the University of Chicago. Lashley investigated the effects of removing parts of rats' brains to discover where in the brain various psychological processes were carried out; he was particularly interested in find-

was responsible for the normal development of the birds in the second and third groups. It is worth noting that three of the four parameters Berthold used to formulate this hypothesis—mating, vocalization, aggression, and distinctive appearance—were behavioral.

In recent years, Berthold's experiment has been credited as the genesis of the field of endocrinology (and of behavioral endocrinology; Box 1.1), but his intriguing demonstration of non-neural control of behavior was apparently not embraced with great enthusiasm by his scientific contemporaries, as his paper does not seem to have been cited for nearly 50 years after its publication. Why, then, did Berthold conduct his study? His experiment was elegant in its simplicity, but unfortunately his report had no introduction, so we cannot know for certain what questions motivated him to conduct the work (Forbes, 1949). We do know that Berthold had previously authored a well-known physiology textbook and had actively conducted research.* A reading of his textbook makes it apparent that

ing where memories were stored. Although he never published any reports on the interaction between hormones and behavior, Lashley was clearly interested in the subject (e.g., Lashley, 1938), and several of Lashley's students became important contributors to behavioral endocrinology, including Calvin P. Stone, Josephine Ball, and Frank A. Beach.

Beach, William C. Young (Box 3.1), and Daniel Lehrman (Box 7.1) were especially influential during the early studies of behavioral endocrinology. Beach's dissertation at Chicago, "The Neural Basis for Innate Behavior," examined the effects of cortical tissue destruction on the maternal behavior of first-time mother rats. In 1937, Beach began working as a curator in the Department of Experimental Biology at the American Museum of Natural History in New York, and began contributing to the museum's tradition of comparative behavioral experimentation. One study completed at the museum which was a logical extension of Beach's dissertation work is of special note: he began investigating the effects of cortical lesions on the mating behavior of male rats. Some brain-damaged rats continued to mate, whereas others failed to do so. Beach was concerned that his lesions were interfering indirectly with the endocrine system, so he injected the nonmating brain-injured rats with testosterone, the primary hormone secreted from the testes. The treatment evoked mating behavior in some of the lesioned rats, and this modification of behavior by hormones prompted Beach to learn more about endocrinology.

Beach audited a course in endocrinology at New York University, but was distressed by the lack of information about the behavioral effects of hormones; the professor responded to Beach's complaint by allowing him to teach one session. While preparing for the lecture, Beach discovered that no comprehensive summary of hormone–behavior interactions existed, and he prepared such a review as a term paper for the endocrinology course. Several years later, Beach expanded his paper into an influential book, *Hormones and Behavior* (Beach, 1948). The publication of this book marked the beginning of the formal study of behavioral endocrinology. Beach is credited with the genesis of this scientific discipline, and he continued to provide intellectual leadership in shaping the field for the next 40 years.

*For example, together with Robert Wilhelm Bunsen, for whom the ubiquitous piece of laboratory equipment was named, he discovered that hydrated oxides of iron can serve as an antidote for arsenic poisoning.