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Historical Review

# Ethology and the origins of behavioral endocrinology

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**Abstract**

The neurosciences embrace many disciplines, some long established, others of more recent origin. Behavioral endocrinology has only recently been fully acknowledged as a branch of neuroscience, distinctive for the determination of some of its exponents to remain integrative in the face of the many pressures towards reductionism that so dominate modern biology. One of its most characteristic features is a commitment to research at the whole-animal level on the physiological basis of complex behaviors, with a particular but by no means exclusive focus on reproductive behavior in all its aspects. The search for rigorously defined principles of behavioral organization that apply across species and the hormonal and neural mechanisms that sustain them underlies much of the research. Their aims are much like those put forth in the classical ethology of Lorenz and Tinbergen, one of the roots from which behavioral endocrinology has sprung. But there are others that can be traced back a century or more. Antecedents can be found in the work of such pioneers as Jakob von Uexküll, Jacques Loeb, Herbert Spencer Jennings, and particularly Charles Otis Whitman who launched a tradition that culminated in the classical contributions of Robert Hinde and Daniel Lehrman. William C. Young was another pioneer. His studies revolutionized thinking about the physiological mechanisms by which hormones influence behavior. An earlier potent influence was Karl Lashley who helped to shape the career of Frank Ambrose Beach who, more than anyone, has played a leading role in launching this new field.


*Keywords:* Behavioral endocrinology; Ethology; Complex behavior; Historical antecedents

A dire prediction about the future of behavioral biology was published by E.O. Wilson (1929–present) in his 1975 book on sociobiology. Ethology would shortly be cannibalized and disappear, with sociobiology and behavioral ecology taking its place on one flank, and integrative neurophysiology on the other. The prospects for behavioral endocrinology were also regarded as dim, "since it is concerned with the cruder tuning devices of nervous activity" (Wilson, 1975, p. 6), a judgment that has elicited some trenchant responses (e.g., Beach, 1978b). What actually happened is that ethology came of age, and behavioral endocrinology thrived, becoming something of an inheritor of the ethological tradition. Wilson failed to appreciate that, at its heart, classical ethology was essentially a mechanistic, physiologically oriented discipline. Although Tinbergen (1907–1988) eventually became engrossed with questions of function and adaptation, the primary thrust was always very different from that of behavioral ecology and evolutionary biology. It was focused rather on the mechanisms responsible for the conduct of behavior and for managing the sensory and motor interactions between organisms and their physical and social environments. As I view the sequence of events, ethology morphed smoothly, naturally, and highly productively, in two slightly different directions. One led to neuroethology, which then became increasingly inclined over the years towards reductionism, and the other to behavioral endocrinology, which inherited much of ethology's vitality and breadth. It has also strived to maintain ethology's primary focus on behavior at the level of the whole organism, and this has proved to be one of

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behavioral endocrinology's most distinctive and valuable attributes.

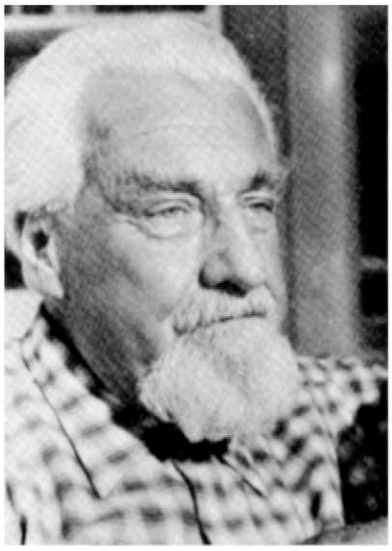
## Benders and ethologists

Having said that, many questions arise about the nature of the inheritance from ethology. Whose ethology do we have in mind? Is it the classical ethology of the 40s and 50s (see Figs. 1A–E), of Baerends (1916–1999), Lorenz (1903–1989), Tinbergen (1907–1988), Thorpe (1902–1986), and Hinde (1923–present), or should we go further back in time? Was ethology the only taproot, or should we regard behavioral endocrinology as polyphyletic, actually springing from several sources? Using 'benders' as my provisional shorthand for behavioral endocrinologists, where did they find the courage to resist the reductionistic fervor that so dominates biology today?

How can we begin to think about the factors that influence the emergence of a science over time? One way is to look for the advent of a new technique, with sufficient impact to wreak a sea change. This happened with work on the ethology of birdsong with the invention of the sound spectrograph in World War II. It became a basic descriptive tool for the discipline, used by Thorpe to launch the biology of birdsong as a new and ultimately highly productive research domain (Marler, 2004; Zeigler and Marler, 2004). Rosalyn S. Yalow's (1921–present) Nobel prize-winning invention of radioimmunoassay techniques had a revolutionary impact on benders, and on all other endocrinologists. I well recall when John Wingfield brought the methods developed with Donald Farner into action, with his own refinements, in my Millbrook laboratory, laying the groundwork for future adventures in field endocrinology (Wingfield and Farner, 1975; Wingfield and Moore, 1987; Wingfield et al., 1990). Even autoradiography, now largely superceded by developments in immunocytochemistry, first made it possible to locate hormone receptors in the songbird brain (Arnold and Saltiel, 1979; Arnold et al., 1976). But although technical progress is enormously important (Nelson, 2000), to get at the kind of questions I have in mind, the key issue is how were they used, what kinds of problems were being addressed? Many benders stand out for their determination to use the new methods to grapple with integrative questions about complex behaviors, striving to analyze their physiological basis, rather than, say exploring the mysteries of fertilization or embryonic development. Also it is not always productive when grappling with these larger issues to look at who first conducted some of the classical experiments, like castrating a cockerel, or implanting a crystal of hormone in the brain, important though these were at the time. I am convinced that in searching for historical clues about where the passion for understanding the behavior of whole animals came from, in all of its complexities, we need to go back to the very origins of behavioral science, a century or more ago.

## The birth of psychology

If we explore this period, around 1900, a time when we can witness the birth of the behavioral sciences, we might find some genealogical clues about the origins of the distinctive attitude towards research that benders typically display. The post-Darwinian period was an extraordinary time for the emergence of psychology and comparative study of the human mind (Glickman, 1985). On the one hand you have Wilhelm Wundt (1832–1920; Fig. 1F) and William James (1842–1910; Fig. 2A) making their separate contributions, with many others, to create the new discipline of psychology (James, 1890; Wundt, 1874, 1902). Their major focus was on the experimental psychology of humans, or of animals as human surrogates. As in many aspects of science at this time, German researchers played a leading role and many American students went to study psychology there, returning well read in the German literature and ready to help launch the new science in America. Sixteen students from Canada and the United States received their degrees in Germany from Wundt (Hothersall, 1984), who had been preaching his version of experimental psychology for 25 years or more before the first book was translated into English in 1900. The predominant focus in much of this early work was on the human mind, and those working on the animal side had a similar preoccupation with mental processes. Rereading Lloyd Morgan (1852–1936), a famous zoologist studying animal behavior at this time, I found I had forgotten that he also identified himself as a psychologist, as did George Romanes (1848–1894), a contemporary of Charles Darwin, before him (Morgan, 1896; Romanes, 1884, 1889). Rather than focusing on the particulars of the natural behavior, or as Darwin and many others called it, the instinctive behavior of animals, and characterizing it in terms that might invite physiological study, Morgan organized his thinking around chapter titles like "the criteria of mind", with little in the way of a truly comparative emphasis. Even the anti-reductionistic invertebrate zoologist Jakob von Uexküll (1864–1944; Fig. 2B), whose book on the "*Umwelt und Innenwelt der Tiere*" (von Uexküll, 1909) conveys something of his fascination with the comparative study of sensory worlds, was more prone to veer in a psychological direction than towards physiology. He was even inclined, late in his career, towards a kind of vitalism, a term defined by the second edition of Webster's dictionary as 'the doctrine that the life in living organisms is caused and sustained by a vital principle that is distinct from all physical and chemical forces and that life is, in part, self-determining and self-evolving'. Webster's adds the interesting codicil, as 'opposed to mechanism'. Von Uexküll did however place strong emphasis on the need to resist the blandishments of anthropomorphism, and he always preached the need for strictly objective methods of observation. This determination is epitomized in an unusual 1899 paper, written jointly with two pioneering invertebrate physiologists, Beer and

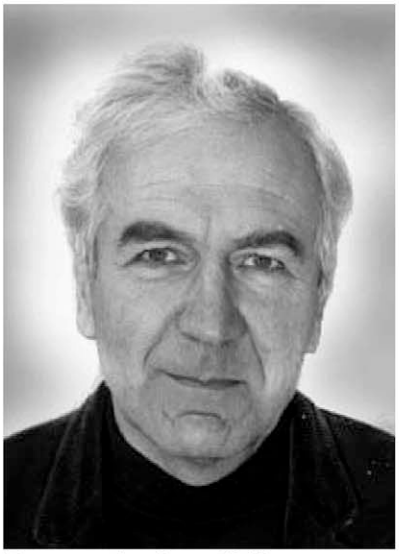


A Konrad Lorenz (1903-1989)

B Nikolaas Tinbergen (1907-1988)

C William H. Thorpe (1902-1986)

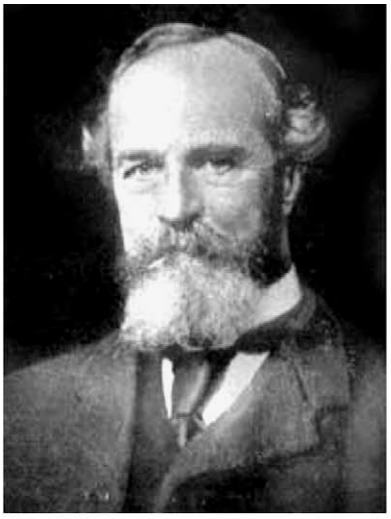
D Gerardus P. Baerends (1916-1999)



E Robert A. Hinde (1923-present)

F Wilhelm Wundt (1832-1920)

Fig. 1.



A William James (1842-1910)

B Jakob von Uexküll (1864-1944)

C Jacques Loeb (1859-1924)

D J.B. Watson (1878-1958)

E Herbert Spencer Jennings (1868-1947)

F Karl Lashley (1890-1958)

Fig. 2.

Bethe called "A proposal for an objective nomenclature in the physiology of the nervous system" (Beer et al., 1899). Von Uexküll's schema for characterizing the relationship between the inner and outer worlds of an organism bears remarkable similarities to later concepts of Konrad Lorenz. And his reflections on the dynamics of perception as an organism moves through its environment are uncannily reminiscent of the thinking of J.J. Gibson (1904–1979) more than a generation later. There is more than a hint of correspondence between von Uexküll's *Umwelt* and Gibson's concept of affordances (Gibson, 1966). But von Uexküll was such an idiosyncratic thinker, especially later in his life, that his concepts never crystallized into a formal system that might have given rise to classical ethology; the potential link to behavioral endocrinology is even more tenuous, although his influence on Lorenz is clear. Similarly, none of the psychologists from this period seems to qualify as a founding father of either classical ethology or behavioral endocrinology.

## The physiology of behavior

Despite the lead initiated by Charles Darwin in broaching the question of physiological substrates for behavior in *The Expression of the Emotions in Man and Animals* (Darwin, 1872) there are many signs of reluctance at this time, especially among those who were psychologically inclined, to look favorably on physiological approaches to behavior. This reluctance was made explicit by William James, perhaps as a carry-over from Cartesian philosophy, and the presumed separation of mind and body, even though the famous James-Lange theory of emotional behavior does have a Darwinian flavor. The universal importance of reflexes was not denied, and James' *Principles* has an early chapter on the brain, but the emphasis quickly shifts to thinking and intelligence, and remains the primary focus. Yet, we find a strikingly different attitude prevailing among biologists of the time. To appreciate the extent of the contrast, consider the almost simultaneous publication of Charles Sherrington's (1857–1952) *Integrative Action of the Nervous System* (Sherrington, 1906). It is worth noting however that Sherrington himself was cautious about the prospect at that time of carrying the integrative theme forward. Even 40 years after publication of the first edition of the 1906 book, we find Sherrington admitting that "in comparison with the great field of behavior in general, pure reflex action of itself cannot be seen to cover such extensive ground as do the instincts actuated by 'urges' and 'drives'. But the mechanism of these has hardly been analyzed sufficiently for laboratory treatment" (Sherrington, 1906, second edition 1947, p. xiv). As neurophysiology unfolded the Sherringtonian inheritance gradually became more and more reductionistic, under the influence of people like Edgar D. Adrian (1889–1977). Before long oscillographic techniques were the method of choice, with the neuron as the primary focus. It was a long time before integrative forces became dominant again with the emergence of cognitive neuroscience (Gazzaniga, 1995).

In this search for historical clues, the prospects might seem better with Jacques Loeb (1859–1924; Fig. 2C), given his fixation, even obsession, with strict objectivity. However, Loeb was also by nature a reductionist, and in time his highly mechanistic tropistic approach to behavior became almost biophysical in nature as you can see if you compare Loeb's two books published 18 years apart (Loeb, 1900, 1918). Nevertheless, in the midst of the synergistic hotbed of activity at Chicago and Johns Hopkins at that time, Loeb's objectivism struck a chord with many, helping to launch J.B. Watson (1878–1958; Fig. 2D) on his path to behaviorism. Also participating in this intellectual turmoil was another biologist of note, Herbert Spencer Jennings (1868–1947; Fig. 2E), and here there is more promise of an ancestral link with ethology and behavioral endocrinology. Even though his main subjects of study at this time were protozoa and coelenterates, Jennings was led to generalizations about the organization of natural behavior that we see echoed in Lorenzian ethology much later (Jennings, 1906). Like Loeb, Jennings was another teacher of J.B. Watson, as well as a source of inspiration for Karl Lashley (1890–1958; Fig. 2F): all three, Jennings, Lashley, and Watson, joined forces in a remarkable series of field investigations of the social and homing behavior of Noddy Terns in the Dry Tortugas (Lashley, 1915; Watson and Lashley, 1915). Picturing in our mind's eye this close-knit group of researchers at work we can perhaps begin to discern a merger of three critical components; a focus on objective natural history, a fascination with principles of behavioral organization that are generalizable across species, and the conviction that these principles can be approached physiologically. For the first time we see a combination of methodological convictions and philosophical preoccupations that might have been transmuted over time into something like a bender mindset. Unfortunately Watson soon relinquished the comparative approach, and Jennings turned to genetics and in so doing, becoming a controversial advocate of eugenics, no longer especially interested in animal behavior.

## The role of Charles Otis Whitman

There is yet another biologist from this amazingly fertile period whose efforts favored holistic approaches to the analysis of behavior, while at the same time acknowledging the value of physiological approaches to the underlying mechanisms. In the search for the roots of behavioral endocrinology, with Charles Otis Whitman (1842–1910; Fig. 3A) we strike gold. He had an unusual history as a scientist. Having pursued a PhD in Germany as a cell biologist, learning the new cytological techniques of the time and bringing them back to America, he took a series of positions before migrating from Clark University to become a professor at the newly minted University of Chicago;

A Charles O. Whitman (1842-1910)

B William C. Young (1899-1965)

C Oscar Riddle (1877-1968)

D Daniel Lehrman (1919-1972)

E Frank A. Beach (1911-1988)

F Gladwyn K. Noble (1894-1940)

Fig. 3.

among others, he joined W.C. Allee on the faculty there. He took with him as junior colleagues Jacques Loeb, William Morton Wheeler (1865–1937) of ant fame, and Frank Lillie (1870–1947), destined to become a leading endocrinologist. Dempsey (1968) has drawn attention to the parallels between the research plans Lillie laid out for the famous

and influential National Research Council Committee for Research in Problems of Sex and those developed later by another graduate of the Zoology department at the University of Chicago, William C. Young (1899–1965; Fig. 3B), destined to become a pioneer in the emergence of behavioral endocrinology. Whitman was Chair of Zoology at Chicago, a cofounder of the Journal of Morphology, and Director of the Marine Biological Laboratory at Woods Hole. In all of these roles he was immensely influential in shaping biology as an academic discipline.

Most germane to our present purpose is his intense preoccupation, especially in later life, with the behavior of doves and pigeons. He kept hundreds of them, apparently not in the laboratory but at home, where he seems to have done most of the bird care himself. We are told that for years his house resonated with the cooing of doves, much as I experienced years later visiting the Institute of Animal Behavior at Rutgers in the reign of Daniel Lehrman (1919–1972). Comparative studies fascinated Whitman. At one stage he had 500 birds of 30 different species, breeding many hybrids and keeping copious notes on their morphology and behavior. When he died in 1910 he left a mountain of unpublished material, much of it never made properly available. In an extraordinary labor of love, two of his many devoted students, Wallace Craig (1876–1954) and Oscar Riddle (1877–1968; Fig. 3C), worked for several years with special funding to salvage what they could. Much of it remained fragmentary, but what survived was quite prophetic and, with Wallace Craig's help, pointed the way towards aspects of classical ethology, as Lorenz acknowledged in his Nobel address. I am firmly convinced that, like ethologists, benders are also in Whitman's historical debt, especially those in the line of intellectual descent we associate with Daniel Lehrman (Fig. 3D).

Whitman had 44 graduate students while in Chicago; seven of them used pigeons for their studies, researching topics like spermatogenesis, fertilization, and embryological development. W.C. Allee (1885–1955) used some of Whitman's doves in his classical studies of dominance, and one of his students, Nicholas Collias, subsequently made seminal contributions to the emerging synthesis of behavioral and hormonal studies (Collias, 1950). Reproductive physiology was the specialty of Oscar Riddle, as it was of Frank Lillie, who succeeded Whitman as chair at Chicago. This is where avian reproductive endocrinology was born. Whitman strived to add behavior to this mix but, coming so late in his career, his innovations were stillborn. Except for Wallace Craig's valiant efforts, they remained dormant, until they burst forth, phoenix-like, in ethology, and the integrative research programs of people like Hinde and Lehrman. You can reasonably regard Lehrman's magisterial 1961 review of parental behavior in W.C. Young's "*Sex and Internal Secretions*", the bible of the time, as the culmination of a scientific progression that began as much as a century before, in the pigeon lofts of Charles Otis Whitman (Lehrman, 1961; Young, 1961).

## Beach and Young: another clade of benders

There are of course several bender lineages or clades as evolutionists call them, and not all of the lines of descent stem obviously from Whitman, or for that matter from classical ethology. As Beach pointed out the role of hormones in the control of behavior was barely mentioned by ethologists until Hinde published his masterly synthesis of ethology and comparative psychology (Beach, 1981; Hinde, 1966). It goes without saying that any list of the founders of behavioral endocrinology must obviously include the names of Frank Ambrose Beach (1911–1988) and William Caldwell Young (1899–1965), and neither of them really fits the pattern I have described. Although nominated by Beach as a founder of the field, the focus of Young's own work was primarily neuroanatomical and physiological, though often with significant behavioral relevance: Young seems to have been especially responsible for sustaining a firm focus on linkages between hormones and behavioral mechanisms and for maintaining a solid biological foundation for the new discipline (Diamond, 1968). The studies he and others conducted on the behavioral consequences of pre- and perinatal exposure of the embryos of guinea pigs, rats, and monkeys to sex steroids following upon Pfeiffer's earlier work (Pfeiffer, 1936) were crucially important in establishing the distinction between organizational and activational effects of hormones on the central nervous system (Feder and Whalen, 1965; Harris, 1964; Harris and Levine, 1965; Phoenix et al., 1959; Young, 1965; Young et al., 1964).

During this same period dramatic progress in neuroendocrinology had profound implications for understanding the physiology of behavior (Scharrer and Scharrer, 1963), exploring functional linkages between hormones and the brain and spinal cord (Hart, 1967), especially the intimate, reciprocal interactions between steroid hormones, the hypothalamus, and the pituitary gland (Harris, 1955, 1964; Harris and Michael, 1964). One important step forward was the creation of the International Society for Psychoneuroendocrinology in 1969.

In something of a contrast with these physiological and neuroanatomical pioneers, Frank Beach (Fig. 3E) always had a primary focus on behavior. In the course of his career he became an enthusiastic supporter of ethology, and the flavor of animal behavior while he worked in the Department of Experimental Physiology at the American Museum of Natural History, first as assistant curator and later as director of the renamed Department of Animal Behavior, had many ethological overtones. But I suspect that to understand how he became a bender we have to search earlier in his career, as Hinde suggests in his foreword to an important volume to which many of Beach's students contributed (Hinde, 1978, in McGill et al., 1978, p. viii). As Beach describes it, he seems to have become distracted by sexual behavior at an early age, and he blames that for his poor grades as an undergraduate. His father bundled him

off to Ohio, where Frank says he proved that the girls there were much like those in Kansas. But then lightning struck. After completing a PhD under Harvey Carr (1873–1954) on a brain lesion-learning project on rats he came under the influence of Karl Lashley, first at Chicago and later on as a postdoc at Harvard. Lashley kindled in him what was to become a life-long passion for the comparative study of behavior. He was deeply impressed by the breadth of Lashley's interests, and by his commitment to rigorous, objective description of whole-organism behavior, leaving an imprint on Frank that in turn characterizes the whole field to this day.

Beach's sojourn in New York, in his first job in the department of Gladwyn Kingsley Noble (1894–1940; Fig. 3F), may have had more influence on his future in behavioral endocrinology than is usually acknowledged. Noble had built up an impressive facility for experimental physiology at the American Museum of Natural History. It was generously supported by the Museum to discourage him from pursuing two other offers, from Columbia, to replace T. H. Morgan (1866–1945) as Professor of Experimental Zoology, and from Cornell as a Professor of Microscopical Anatomy; as a facility for the study of behavior it was said to be matched only by that of Karl von Frisch (1886–1982) in Germany. Noble was unusually well versed in comparative anatomy, endocrinology, and neurology and eager to expand into behavior; it seems probable that Beach benefited considerably from the contact, though Noble's abrasive personality may have led his students and associates to acknowledge the debt with only muted enthusiasm. Yet Beach speaks with pride of publishing 16 papers over 9 years at the museum, on the relations between hormones and behavior, on subjects ranging from cotton and rice rats, to cats, pigeons, lizards, and one small alligator (Beach, 1978a). As a formative experience this seems to have predated his exposure to classical ethology and may well have had even more impact, even though he himself describes it disparagingly as 'hunt-and-peck' experimentation. Tinbergen visited the Museum in 1938 but Beach does not mention meeting him. Frank Beach went on to become the leading integrative scholar in the field, with a host of brilliant and influential students at Yale and subsequently in Berkeley where I had the pleasure of joining forces with him and anthropologist Sherwood Washburn to create a field station for the study of animal behavior. I served on the thesis committees of many students who were a constant source of Beach-inspired ideas and erudition in the many seminars we participated in together. Beach was the leader of his generation in creating a kind of hybrid undertaking. He had no patience with the myopia of many comparative psychologists of his generation (Beach, 1950). The wide-ranging conferences he organized in 1961 and 1962 on sex and behavior, and the book it gave rise to (Beach, 1965) lent powerful support to the coherence of the new discipline as a truly comparative enterprise, along with the many other thoughtful, brilliant, and amazingly comprehensive syntheses he published over the years (Beach, 1948, 1975, 1981). In his version of the classical interdisciplinary experience he describes how "psychologists regarded me as an endocrinologist, endocrinologists thought I was a psychologist, and specialists in each discipline forgave me for ignorance in their own area on the assumption that I must be an expert in the other" (Beach, 1978a, p. 30).

## The role of Karl Lashley

Looking back over this minihistory, I am fascinated by how often Lashley's name surfaces, and I find myself wondering, as others have done, whether he might not have anticipated much of classical ethology, had he chosen to try. His 1938 masterpiece on "the experimental analysis of instinctive behavior" could easily have served as an ethological manifesto (Lashley, 1938). But as disciplines unfolded, he became more famous for his work as a psychologist on cortical mechanisms for learning and memory. He was also well known for his often-expressed ambivalence about the conditioned reflexology of I. P. Pavlov (1849–1936) as a foundation for a general theory of behavioral biology, even though it was embraced in Watson's behaviorism, and became an inspiration for B. F. Skinner (1904–1990). Although Lashley was drawn more and more deeply into psychology, he nevertheless broke faith with behaviorism, and it appears that he and Skinner were never on the best of terms. My own mentor, William Homan Thorpe, sensed this when he lectured at Harvard in 1951. In the description of his visit, he gives us a portrait of Lashley so perceptive and prescient that I quote it in full (Thorpe, 1979).

Thorpe says he found Lashley to be "an extraordinarily attractive character; a thin, hyperactive man with a delightful sense of humor and great mental agility. He was an accomplished musician, particularly as a string player. His thinking was so quick that when he lectured he poured out an almost overwhelming torrent of words which must have been incomprehensible to the elementary student. His mind was completely devoted to the discovery of truth even though this meant pulling to pieces and destroying a beautiful theory of his own". Thorpe describes how "He would come up with some exciting results or some improvement of technique in the study of animal learning or of brain function, would publish this and then immediately think of a new technique which would give a fresh angle or more accurate results. He would employ this and when, as not infrequently happened, he showed his earlier theory to be wrong: instead of being crestfallen, he would be hugely delighted and would exult in publicly knocking down his own theoretical structure". This trait was so marked that he (W.H.T.) believed that "it resulted in his not having the research following in the United States that his great eminence and ability might have lead one to expect. It seems that his mental agility and self criticism confused all

except the most brilliant students; for, they thought, if the great Lashley can be as wrong as this, what chance is there in this field for poor 'bods' like ourselves?" Be this as it may, Thorpe suggests that "it offers a plausible reason for his failure to achieve the full conceptual theme of animal behavior which we now regard as the central achievement of Konrad Lorenz. The more one studies the American situation at that time the more extraordinary it seems that the American group did not become the modern founders of ethology" (Thorpe, 1979, p. 50).

At the time, Thorpe also had in mind Wallace Craig, whose few gem-like contributions to the behavioral literature make you yearn for more. His writings on themes like "The voices of pigeons regarded as a means of social control" (Craig, 1908–1909), and "Appetites and aversions as constituents of instincts" (Craig, 1918) are still worth reading. His answer to the question "Why do animals fight? (Craig, 1928) in the International Journal of Ethics is still an effective riposte to Konrad Lorenz's argument for endogenous roots to aggression published 40 years later (Lorenz, 1966). Again Thorpe has a fascinating and telling anecdote. Lecturing on ethology at Harvard, Thorpe dwelt at some length on Craig's contributions and on Lorenz's acknowledgement of the debt to him. Afterwards, Edward Boring (1886–1968), the distinguished historian of experimental psychology, who attended the lecture asked Thorpe if he had been aware that Wallace Craig was actually in the audience. Such was Craig's shyness he remained a silent and anonymous spectator, slipping away afterwards without even identifying himself. With even a fraction of Konrad Lorenz's confidence and charisma, Craig's contribution to history might have turned out very differently. Even so, I believe that both he and Lashley had a considerable influence on the maturing of ethology and the emergence of behavioral endocrinology, both providing us with glimmerings of antecedents that may have encouraged the emergence of the discipline that we see flourishing today. Now we have a new, vigorously active generation with its own champions emerging, in turn making their own contributions to posterity, destined to further enrich the discipline's unique and distinctive heritage. As pressures to become more reductionistic, already on the horizon, grow more intense, I hope that future benders will not relinquish the unique focus on the physiological underpinnings of behavior writ large, that has made the contributions of behavioral endocrinology to contemporary neuroscience so valuable.

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