6. Conclusions

Much progress has been made on our understanding of the mechanisms and functions of LTP since its discovery in 1968. At the beginning of the twenty-first century there might still be a few unanswered questions, but there is little doubt that (a) these questions will receive definite answers rapidly and (b) the knowledge gained from the study of this phenomenon will be instrumental in designing new tools to study and improve various forms of learning impairments.

See also: Learning and Memory: Computational Models; Long-term Depression (Cerebellum); Long-term Depression (Hippocampus); Long-term Potentiation and Depression (Cortex); Memory Models: Quantitative

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M. Baudry

Lorenz, Konrad (1903–89)

1. Biography

1.1 Family

Konrad Zacharias Lorenz (born November 7, 1903 in Vienna, Austria) grew up within the upper crust of pre-World War I Vienna: his mother Emma (née Lecher) from a family of writers and scientists; his father, Adolf Lorenz, world-renowned orthopedic surgeon, Nobel prize nominee (A. Lorenz 1936). Konrad spent his formative years in Vienna and at his family's country estate in Altenberg on the banks of the Danube. At that time the river was still lined by large tracts of virgin riverine forest, and his inquisitive mind became fascinated by nature. He became a passionate observer and skilled caretaker of any swimming, crawling, or flying creature. These interests did not interfere, however, with his early socialization into the network of learned relatives and their friends (e.g., Karl Popper; see *Popper, Karl Raimund (1902–94)*).

1.2 Education

After visiting a 'progressive' elementary school, he was sent to the esteemed *Schotten-Gymnasium*, where his biology teacher, an enthusiastic Darwinist, introduced him to evolutionary reasoning. At his father's suggestion, he began to study medicine at Columbia University, New York in 1922. Homesick, especially for his wife-to-be, he continued his studies in Vienna, receiving his Dr.med. degree in 1928. During his first appointment as *Demonstrator* ($\sim$ assistant professor) at the department of anatomy at the University of Vienna, he studied zoology (J. Versluys), paleontology (O. Abel), and psychology (K. Bühler, his assistant E. Brunswik); he received his Dr. phil. degree in 1933.

1.3 Scientific Career

Lorenz's meager salary as *Demonstrator* and his wife's (Margarethe née Gebhardt) income as physician at a local hospital provided just enough to raise their family. Lorenz was always short of funds for the private research facility he had established in Altenberg. His negotiations with the (German) Kaiser-Wilhelm-Gesellschaft for funds to create a special institute for behavioral studies date back to 1937, but at the outbreak of World War II this project was shelved. In 1940 E. Baumgarten (a nephew of Max Weber (see *Weber, Max (1864–1920)*) and a pupil of J. Dewey (see *Dewey, John (1859–1952)*) and, hence, a representative of the pragmatist school of philosophy) accepted the famed chair of philosophy at Königsberg University, once occupied by Immanuel Kant (see *Kant, Immanuel (1724–1804)*), and looked for a biologically oriented psychologist who, at the same time, was interested in theory of knowledge, to share with him the prestigious appointment. E. von Holst became the match-maker, and Lorenz was chosen (Lorenz 1974, Leyhausen 2000).

One year later, however, Lorenz was drafted into the German Army as a motorcycle rifleman (in his papers he had not mentioned his medical training because of his limited experience with patients, and stressed only his proficiency in motorcycle racing and repair). When the authorities discovered that he held a medical degree and was a professor of psychology, he was assigned to a unit of the *Heerespsychologie* (Army Psychology) in Posen. Two months later, however, this unit was dissolved, and he was transferred to the Posen Army field hospital for neurology and psychiatry, where he worked as *Unterarzt* (medical noncommissioned officer) in a unit of 285 beds with patients suffering from war injuries, psychoses, and psychosomatic disorders. During a field assignment on the Russian front in 1944 he was captured by the Red Army. After that, he served in various POW camps as field surgeon until his release in 1948.

In post-World War II Austria career prospects for a biologist were worse than ever, while in Britain Lorenz's colleagues became especially interested in the Darwinian approach to behavioral studies. Niko Tinbergen became reader at Oxford University and, in 1950, Lorenz received a similar offer from the University of Bristol. German colleagues, notably E. von Holst and G. Kramer, both meanwhile directors at the newly founded Max Planck Institute for Marine Biology (Wilhelmshaven), were able to revive the old project of an institute for behavioral studies. A matching offer was made, and Lorenz accepted the appointment as head of a small behavior research unit in Buldern, Westfalia, founded in spring of 1951 as precursor to a special Max Planck Institute for Behavioral Physiology. Construction started in Seewiesen, Bavaria in 1955, and the institute opened in 1958: Lorenz was Director of his own division there until he retired in 1973.

1.4 Retirement

Upon retirement, Lorenz returned to his home in Altenberg, Austria. Shortly thereafter, he was awarded, together with Niko Tinbergen and Karl von Frisch, the 1973 *Nobel Prize for Medicine*. During retirement, he tidied up his work on evolutionary epistemology, on the social behavior of greylag geese and reef fishes, and became an eloquent spokesman for environmental conservation (Schleidt 1988). Lorenz died in Vienna on February 27, 1989 at the age of 85 and was buried near Altenberg at St. Andrä-Wördern cemetery (Wuketits 1990).

2. Contribution to Knowledge

Lorenz, cofounding with Niko Tinberger the science of Ethology as 'the study of the biology of organismic behavior', ranks among the most important stewards of Darwin's (see *Darwin, Charles Robert (1809–82)*) heritage of the twentieth century. In the 1930s and 1940s, most psychologists, sociologists, and biologists tried to understand behavior within the framework of Aristotelian (see *Aristotle (384–322 BC)*) philosophy, theology, Marxism (see *Marx, Karl (1818–89)*), or Behaviorism. Lorenz, on the other hand, viewed behavior as playing a central role in the process of evolution, and shaped primarily by 'natural selection', rather than by learning. By applying the methods of comparative morphology and paleontology to the study of 'species specific' behavior, he created a scientific approach which rapidly provided a wealth of data and new insights (Lorenz 1931, 1932, 1950a, 1965b, 1978). Contrary to the claim of his critics, Lorenz ignored neither the conventional schools of thought nor their observations, but was cautious in accepting their theories and conclusions. For example, he never denied the importance of environmental factors in learning, but he challenged the behaviorists' claim that innate behavior was restricted to only a few basic vital reflexes. In fact, he emphasized especially the interlocking of modular innate and learned behavioral (e.g., as in 'imprinting,' Lorenz 1935, and in his analysis of the channels through which information can enter a living system, Lorenz 1961, 1965 b).

2.1 Observation as Research Tool

Fundamental to Lorenz's approach to behavior is his rigorous adherence to the doctrine of *induktive Naturwissenschaft* (inductive natural science; Lorenz 1942, 1959, 1978), i.e., first establish a solid base with meticulous observations, supported by objective records (photos, film), tainted as little as possible by theories, and—only after a solid data base (*Induktions-Basis*) has been established—let patterns emerge from the data.

2.2 Behavioral Modules

Lorenz considered behavior to be composed of basic modules: e.g., classical reflexes, species specific *Instinktbewegung* 'Fixed Action Pattern' (FAP), in later years *Erbkoordination*, *erbkoordinierte Bewegung* (1978) (in English: 'fixed motor pattern'), specific circuits for the environmental control of reflexes and FAPs: 'Innate Releasing Mechanisms' (IRM, *angeborener Auslösemechanismus*), 'appetites and aversions' (*Stimmungen*), etc. Such modules provide each organism with basic behavioral skills to navigate within its environment, detect necessary resources, avoid danger, and interact with conspecifics. Learning can enter in various ways at the level of each of these modules, e.g., in the case of a reflex as 'conditioned reflex.'

This FAP/IRM diad is basically an extension of the classical Stimulus/Response concept, enhanced by several new features: the classical reflex, activated only by a specific external stimulus, cannot account for the observation that 'a healthy animal is up and doing' (as W. McDougall so aptly remarked). Consequently, the spontaneous nature of behavior, in general, and especially in many typical FAPs (locomotion, courtship behavior, certain types of bird song, etc.) became a topic of special interest (FActionP). FAPs constitute much more complex patterns than any of the classical reflexes (FAPatterns) and particular spatiotemporal parameters of FAPs are highly stereotyped within any one species (FixedAP), but different between species. Lorenz exemplified the complex interaction between internal and external variables in his 'psychohydraulic' model (1950 a, 1978), and applied this reasoning to explain the control of aggression in animals and humans (1963).

It was basically for this work on behavior modules, which are central to ethology, that Lorenz, Niko Tinbergen, and Karl von Frisch shared the distinction of winning the 1973 Nobel Prize for Medicine 'for their discoveries concerning the organization and elicitation of individual and social behavior patterns.'

2.3 Ethograms

Given the existence of species specific behavior, a behavioral study of individuals of any given species starts with an assessment of the modules of its behavioral repertoire, working towards the open-ended task of a complete 'ethogram' of that species. Lorenz had already touched on this in his first publication (1931), and a decade later published an exemplary comparative study of the courtship modules of ducks (1941). He delayed publishing of his ethogram of the graylag goose until 1988 … as a sort of swan-song.

2.4 The Innate Forms of Possible Experience

This heading is a translation of *Die angeborenen Formen möglicher Erfahrung*, the title of Lorenz's 1943 seminal paper dealing with the evolution of cognition, as a new paradigm. The results of many years of research into 'learning'—from the classical curves of learning and forgetting by I. Pavlov and E. L. Thorndike (see *Thorndike, Edward Lee (1874–1949)*)—indicate that it is a slow process. If an animal's survival depended solely on learning, it would be dead long before it had completed its first set of learning trials. Thus, it should not be surprising that an animal, entering into its world, is equipped with (a) certain 'innate' skills, behavior patterns to satisfy vital needs and escape danger, and (b) '*a priori* knowledge' to detect essential features of resources and danger —innate in the sense that particular patterns of behavior or relevance of particular environmental features are available prior to individual experience. In other words: a reflex, FAP, or IRM not only enables survival enhancing action, but it also constitutes organismic 'knowledge' about the environment and its contingencies, to which that individual's ancestors had been exposed in the evolutionary process (Lorenz 1941, 1943, 1953, 1965 b, 1973, 1978).

2.5 Imprinting

This peculiar process of forming an irreversible association between a behavior pattern and a 'stimulus' (object), without any reward other than the presence of that object, has been used for ages in animal breeding, and noted in the literature, but Lorenz was the first to recognized imprinting's far-reaching theoretical significance (1935, 1965 b, 1978).

2.6 *Nature–Nurture*

Much ink has been spilled on this duality, not much because of any intellectual challenge posed by these two concepts, but because of deeply rooted beliefs, religious or political, touching upon free will, accountability, and fate. Lorenz was attacked early on for his use of 'innate' as though he had excluded the possibility of learning, while all he suggested was that innate behavior was essential for the survival of individual organisms. Early on, he pointed to the intertwining of innate and learned behaviors (e.g., *Trieb-Dressur-Verschränkung*, drive-training-interlacing 1935), and with imprinting, provided a splendid example of such a process, which was ignored by the ruling psychologists of his time. He was attacked relentlessly for defending the concept of innateness, despite numerous attempts to respond to his critics (1961, 1965b, 1978, etc.).

2.7 *Epistemology*

'Philosophy is the academic abuse of those human potentials which have evolved by natural selection for the individual's survival in his struggle with the daily contingencies of his world.' This definition, attributed to Lorenz's mentor O. Heinroth, encapsulates the insight that human ability to acquire knowledge is not merely a matter of the reasoning individual *Homo sapiens* within a literate society, but is based on a long, evolutionary process, preceding the emergence of humanity by millions of years. Lorenz, having been elevated to Immanuel Kant's former chair in Königsberg in 1940, and facing the challenges by contemporary philosophy, and specifically by resident neo-Kantians, took a radically new approach to Kant's concept of *a priori* (Lorenz 1941, 1943), pioneering what is now called Evolutionary Epistemology (Popper 1972, Vollmer 1980). The most detailed discussion of this is contained in his posthumously published *Russian Manuscript* 1944–48 (1992), written with the fresh memories of his encounter with Kant's Königsberg in mind, while a more concise discussion can be found in the English edition of his textbook (1978/81).

2.8 *Moral Analogous Behavior, Human Morality, and Environmental Awareness*

Lorenz, throughout his life, struggled with his belief that morality could well have an evolutionary basis (as he had shown convincingly for the evolutionary basis of cognition in his evolutionary epistemology). He coined the term 'moral-analoguous behaviour' (moral-analoges Verhalten): special behavior that channels the individual's selfish struggle for its individual existence and reproductive success into an altruistic contribution for the good of its community. Based on his observations of a variety of highly social animals, Lorenz noticed that domesticated forms had lost certain elements of their moral-analoguous social behaviors which their wild ancestors had evolved as essential part of their sociality. Lorenz concluded, by analogy, that human evolution in general, and especially our own modern civilization, has led to comparable domestication effects ('self-domestication'), which have become a mixed blessings. Modern humans have freed themselves from the firm guide of instincts and consequently have more freedom to learn, and to make their own choices, but they also have lost some of their instinctive inhibitions to inflict damage to, and even kill conspecifics to an extent not known in any other species (1940, 1943, 1963, 1983).

In his early papers Lorenz proposed to counter these dangers to humanity with eugenic measures (before the atrocities of Hitler's Germany a widely respected field, especially in England and the USA), especially by encouraging ethically guided (not ethnically, as often misread) mate choice (1940, 1943). Starting in the mid-1950s, Lorenz's proposal of an evolutionary basis of human moral were attacked for various reasons or dismissed as unfounded. As competing hypotheses—especially those claiming sole environmental control of ethical behavior—have failed so far to resist falsification, these issues are, on the scientific level, far from resolved.

Lorenz's concern about human evolution running awry and leading us to extinction by our destruction of the environment was not merely a consequence of the atrocities of World War I, World War II, and of the nuclear demise scenarios of the Cold War, but had been deeply rooted in both his trust in science and in his allegiance to the Hippocratic oath. Thus, when by the vagaries of political and economic interests a nuclear power plant was built near his home in Altenberg, at a location that had been flawed by previously undisclosed risks, he opposed completion of its construction violently. Soon he found himself the revered leader in this fight that ultimately prevented the key ready nuclear power plant from going into service. A few years later, Lorenz was equally successful in a fight to save the last stretch of wetlands along the Danube.

3. *Relevance*

Lorenz's impact on behavioral and social science is linked closely to his collaboration and friendship with Niko Tinbergen, and it is difficult to measure each one's individual contribution. Both were curious naturalists endowed with outstanding skills: in observing, in detecting regularities—patterns of nature—and in formulating testable hypotheses; and, both were outstanding teachers (e.g., Lorenz 1949, 1950b).

While Tinbergen was more inclined toward an experimental approach, as exemplified in their joint paper (Lorenz and Tinbergen 1938), Lorenz's imprint on ethology is obvious in matters of pure observation, inductive reasoning, and formulating a comprehensive theory: the modular concept of action patterns and releasing mechanisms, these modules being shaped by evolution as well as by learning, and imprinting as a special type of learning.

3.1 Selected Topics

Lorenz achieved his scientific breakthrough in 1936. At an invited lecture before the German scientific elite of the Kaiser-Wilhelm-Gesellschaft in Berlin he proposed to stop arguing about how many drives and instincts one can define and instead start describing and analyzing behavior patterns as though they were anatomical features. In a discussion following the lecture, Max Hartmann, doyen of German biology, remarked that 'Konrad Lorenz's approach opens up to causal analysis a field that was previously just a playground for fruitless philosophical speculation' (Lorenz 1992).

World War II severely restricted research and exchange. But soon after the war had ended, Tinbergen traveled in the UK and the USA, presenting the new, ethological approach to behavioral studies, his effort culminating in his book *The Study on Instinct* (1951). Lorenz, who, up to then, had established an international reputation only among ornithologists, argued the case for a biological approach to the study of behavior and soon became the leading theoretician in the new science of ethology.

The high esteem for ethological research resulted in generous support by the Max Planck Gesellschaft, and subsequently by various national funding agencies, notably National Institutes of Health in the USA. Small informal meetings soon turned into international affairs. The biennial *International Ethological Conferences*, dominated by the Lorenz–Tinbergen School and 'converts' from a variety of related fields, became the central event for discussing new results and theories. The German journal *Zeitschrift für Tierpsychologie*, founded in 1937 with Lorenz as one of its editors, the first journal to favor ethological publications, soon got an English language companion in the Dutch journal *Behaviour*. A few years later *Animal Behaviour* was introduced, as the official organ of Animal Behavio(u)r Societies, founded in the US and UK, as publications in the new science steadily increased. While *animal psychology* and *comparative psychology* had been little known specialties, dealing mainly with the learning abilities of rats, the Lorenz–Tinbergen-inspired new *animal behavior* became a hot topic for lectures in academic departments both in biology and psychology, resulting in a demand for teachers and textbooks (e.g., Eibl-Eibesfeldt 1967/99), and spawning new opportunities and funding for behavioral research.

Since Lorenz, Tinbergen' and their colleagues were not only qualified biologists, but equally well-established in neighboring fields, the popularity of ethology soon led to fruitful cooperation, notably with sensory physiology, brain sciences, and psychiatry (e.g., Lorenz 1953). This process had considerable impact on the emergence of neurobiology, psychobiology, and evolutionary psychiatry, emphasizing a naturalistic, Darwinian approach at a time when the general trend in biology was toward molecular biology and biochemistry.

Subjects of ethological research at first were mainly vertebrates—birds, mammals, and fishes—and insects. The new approach was tested succesfully and applied to all kinds of species, including our own. Even though the magnitude and difficulties of a task like establishing a human ethogram may appear mind-boggling, 'human ethology' becomes workable as a special case of primate ethology (e.g., Eibl-Eibesfeld 1997). A healthy human newborn faces similar tasks as any other primate baby and behaves very similarly.

By applying ethological methods within the framework of natural science and evolutionary reasoning, similarities and differences between human and nonhuman animals are no longer a matter of poetic license, but causal analysis—not, however, without drawing heavy critique from the old religious and political establishment. *On Aggression* and *The Waning of Humaneness* (Lorenz 1963, 1983) are examples of an ethological approach to the moral strongholds of the humanities.

Human Ethology has become a domain of its own, of broad overlap not only with primatology, but anthropology (physical and cultural), psychology, and sociology, leading toward a new synthesis of knowledge which proves that the old distinction between hard sciences and humanities has become obsolete.

3.2 Politics

Fame has its price. Especially since having been awarded the Nobel Prize, Lorenz has been branded a racist and an anti-Semite and alleged to have provided a pseudoscientific justification for the Holocaust (e.g., Klopfer 1999).

In regard to these allegations, we must consider first that Lorenz grew up within a part of the Viennese society that was enmeshed intimately by friendship, marriage, and professional ties with the wealthy Jewish elite. He maintained these connections throughout his life by hosting many guests and being a guest on many in his frequent travels of old and new friends especially in England and the USA, and was certainly more pro-Semitic than average, and far less racist, especially than some of those who are now raising their voice. Thus, the charge that he advocated racist and anti-Semitic genocide is unfounded.

With respect to the allegation that Lorenz provided a pseudoscientific justification for the Holocaust, it must be considered that there is a long chain of inferences necessary to connect between his—always controversial—writings on the potentially dangerous effects of human self-domestication on the biological basis or ethical (not, and never ethnical!) behavior or Lorenz's proposed use of eugenics to combat the rise of unethical behavior, and the atrocities of the Third Reich. And, there is no indication—inspite of many inquiries and searches (summarized in Klopfer 1999) that prior to the end of World War II anybody in power was aware of such a link. Lorenz being called to the army early in World War II, his first assignment as a rifleman and later as medical NCO (never promoted to a higher rank) give ample evidence that he lacked political pull (Schleidt 2000).

Lorenz became active in politics only after his retirement. Given all the academic and public honors he had received, people listened when he spoke—as he proudly proclaimed—and he spoke loudly and clearly for environmental preservation and moral responsibility.

4. Concluding Remarks

When in the mid-1970s sociobiology made the headlines and behavioral ecology started riding the new wave of environmental awareness, the glamor of ethology began to fade. In 1999, the crown jewel of ethology, the Max Planck Institute for Behavioral Physiology at Seewiesen, was downgraded to an ornithological research station. However, the ideas conceived and publicized by Lorenz, Tinbergen, and their contemporaries as the foundations of ethology have become so much public property that their original sources are now rarely cited. This may be the best indicator of the importance of the work of Konrad Lorenz, and of ethology.

See also: Animal Cognition; Behaviorism, History of; Birdsong and Vocal Learning during Development; Comparative Psychology; Darwinism: Social; Evolutionary Epistemology; Psychological Development: Ethological and Evolutionary Approaches; Sensitive Periods in Development, Neural Basis of

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Lotka, Alfred James (1880–1949)

When A. J. Lotka died on December 5, 1949 his obituary in the *Journal of the American Statistical Association* began 'A brilliant chapter in modern demography came to a close with the death of Alfred James Lotka.' David Smith, translator of his major work in the field (Lotka 1939), calls him 'the father of mathematical demography.' And these were understatements of his contribution, for demography was only a part of Lotka's scientific interests—he was also described as chemist, physicist, biologist, and actuary, everywhere seeking better understanding through the use of mathematics.

Lotka was born on March 2, 1880 in Lemberg (Lvov), a Polish town of the Austro-Hungarian Empire, of American parents who were traveling Moravian missionaries; he died in Red Bank, New Jersey. His training was international: a boyhood mostly in France; a degree at the University of Birmingham (B.Sc. 1901, D.Sc. some 10 years later); graduate work in physics at Leipzig. Coming to the USA in 1902, he worked for the General Chemical Company, briefly for the US Patent Office as a patent examiner, and for the National Bureau of Standards as a physicist. He was editor of the *Scientific American Supplement* (1911–14), finally settling in the Statistical Bureau of the Metropolitan Life Insurance Company (1924–47). He was for long a bachelor, somewhat shy, described as quiet, learned, modest, and gently humorous. In 1935 he married Romola Beattie; they had no children. He was elected President of the Population Association of America (1938–9) and of the American Statistical Association (1942).

In his terminal year of graduate school, at Cornell in 1908–9, he began work with Professor F. R. Sharpe that led to the famous renewal equation—a mathematical description of the replacement of the generations:

$$B(t) = \int_{\alpha}^{\beta} B(t-a)p(a)m(a)da \tag{1}$$

In the simplest case, rates of birth and death are constant over time, there is no migration to or from the defined area and the female sex only is considered. These conditions make possible a strict accounting of the relation between two generations. For on the right side is $B(t-a)$ the number of births a years earlier ($\alpha \leqslant a \leqslant \beta$ where α is the youngest age of childbearing and β the oldest); $p(a)$, the probability that a child born a years ago survives to time t; $m(a)$ is the birth rate for women aged a; integrating gives current births and so should be comparable to the births $B(t)$ on the left side. The unknown quantity that should make the two sides equal is the trajectory of births, to be provided in terms of the known functions $p(a)$ and $m(a)$. If the trajectory of $B(t)$ in Eqn. (1) is simplified down to a curve of geometric increase, as Lotka initially assumed, then the question posed by the renewal equation is what rate of increase of births would equate the two sides of Eqn. (1). If that rate is r, taken either arbitrarily or from past data, then the age distribution of the population would stabilize over time to numbers proportional to $\exp(-ra)p(a)$ at the several ages a.

In finite intervals of time and age, Eqn. (1) can be expressed naturally as a recurrent series and this was done by Lotka himself late in his career. P. H. Leslie formulated it in matrix terms. To these can be added a fourth version in partial differential equations (Keyfitz and Keyfitz 1997), that also shows and compares the three other formulations.

Like most other discoveries, this one had predecessors who in part anticipated, as well as followers who marginally improved on, Lotka's work. Leonhard Euler (1760) came close on the theory; Edwin Cannan (1895) in the nineteeth century published an arithmetic calculation projecting the population of England and Wales that forecast the (then surprising) fall in births. R. Kuczynski (1931) and Richard Böckh of the Berlin Statistical Office were important predecessors working with the ratio of change per generation, the Net Reproduction Rate (NRR), $R_0 = \int p(a)m(a)da$. Willy Feller (1941), Princeton mathematician, noted that the solution to the renewal equation fell out simply and rigorously if each of the functions involved is translated into its unique Laplace Transform. Golubitsky et al. (1975) published an even more compact and more general solution.

Lotka went on to other demographic questions. He was curious to know why old populations have so few surnames and found the answer in a pure probability accounting for the extinction of family lines (1931a). He ascertained the frequency of orphanhood as a

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