The 1973 Nobel Prize for Physiology or Medicine

The 1973 Nobel prize for Physiology or Medicine has been awarded jointly to three zoologists: Karl von Frisch, 86 years old, of the University of Munich; Konrad Lorenz, 69 years old, of the Max Planck Institute for Behavioral Physiology at Seewiesen, near Munich; and Nikolaas Tinbergen, 66 years old, of the Department of Zoology at Oxford University, for their discoveries concerning organization and elicitation of individual and social behavior patterns. The award is a new departure for the Nobel Committee of the Karolinska Institute, acknowledging for the first time major advances in our understanding of sociobiology, especially in the area of behavioral science known as ethology. At a time when studies of learning in animals were generally conducted in the laboratory, thereby posing problems largely irrelevant to their natural biology, these three men discovered in the natural behavior of animals both learned and innate patterns, exquisitely adapted to their particular phylogenetically determined ways of life. At one stroke they explained some of the most remarkable examples of the fine control of elaborate patterns of behavior by external stimuli known to science, sometimes learned, sometimes not, while leaving in no doubt the crucial importance of genetic differences in understanding the development of behavior.

Karl von Frisch, inspired pioneer of comparative physiology, has opened our eyes to several unsuspected "sensory windows" through which animals view the world, and to complex and versatile communication behavior controlled by insect nervous systems formerly thought capable only of rigid mechanical responses. Stimulated by a distinguished family background in Vienna, including the physiologist Sigmund Exner, his boyhood enthusiasm for biology matured through studies with Richard von Hertwig, whom he later succeeded as professor of zoology at Munich. Shortly before World War I von Frisch demonstrated that, contrary to prevailing scientific opinion, fish and honeybees could discriminate colors. After the war he turned to experiments on olfaction and showed that bees could distinguish among dozens of odors, including the scents of closely related flowers. His thorough experiments in the 1920's settled in the affirmative the long-standing question whether fish could hear. Unsophisticated in the best sense, these experiments have been amply confirmed in later years with appropriate monochromators and hydrophones. An ardent Darwinian who successfully defended his views at his oral examination in philosophy against a professor who did not believe in evolution, von Frisch was motivated by a naturalist's faith that phenomena such as the colors and scents of flowers, or the Weberian ossicles of catfish, must have an adaptive biological significance.

In 1923 he described as a simple language the round and waggle dances of honeybees. In that heyday of behaviorism he observed simply that round dances occurred when foraging bees brought sugar solutions into the hive from artificial feeders, whereas waggle dances accompanied the gathering of pollen. But in 1944 he found the real "Rosetta Stone" to decipher the language of bees: Round dances mean a food source nearby, waggle dances one at some distance. More important, the direction of the straight portion of the waggle dance points the way to the food, and its duration signals the distance. On a horizontal surface the dancing bee points directly toward the food, but ordinarily the dances take place inside a dark hive on a vertical surface. Here *straight up* corresponds to the direction of the sun, which serves as a directional reference point. But if the sun is obscured by broken clouds, the bees use instead the plane of polarization of light from patches of blue sky. Thus behavioral experiments that had stemmed from earlier studies of sensory physiology disclosed a new sensory channel.

Von Frisch also demonstrated that odors are very important to identify the exact food source, and we now know that sounds or vibrations are also involved in the communication process. Bees dance only when the colony is in severe need of something, but dances are used not only for food but also for water when it is needed in hot weather to cool the hive. The most remarkable use of the dances was discovered by Martin Lindauer, one of von Frisch's leading students. When a colony of bees is swarming, scouts fly out from the teeming cluster of bees that have left their former hive and search for a cavity where thousands of bees can fly to establish a new colony. When a scout has located a suitable cavity, she signals its location by the same dance pattern used for food. Individual bees exchange information about the suitability and location of various cavities, sometimes the same bee acting alternately as transmitter and receiver of information.

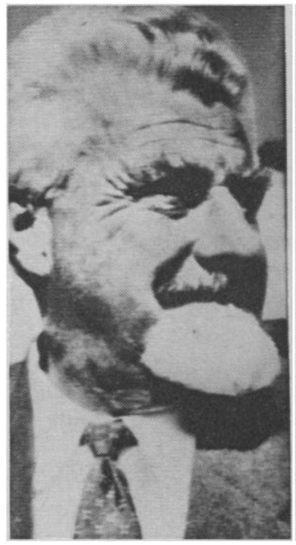
Questions have been raised about the accuracy with which information is actually transmitted, and about the relative importance of the dances, odors, and sounds or vibrations. Philosophers and linguists may debate whether the term language is appropriate. But, for behavioral scientists, the revolutionary discovery was that an insect sometimes communicates with fellow members of a closely integrated society by flexible, iconic, graded gestures about distant objects that are urgently needed by the social group as a whole. Behavioral continuity between animals and men extends even to fruitful comparisons between animal communication and human language.

Konrad Lorenz, acknowledged founder of the science of ethology, derived his insights into the causation and organization of behavior from studying fish and birds. At Altenburg in Austria, the house of his father, a Viennese orthopedist, was always full of animals and birds. A precocious naturalist, Lorenz developed early what became a lifelong passion for raising both wild and domestic animals by hand, and for living with them in the closest quarters, and so gaining insights into the relation between genome and experience in ontogeny. Medical training at the University of Vienna was followed by excursions, inspired by Ferdinand Hochstetter, Karl Bühler, and others, into comparative anatomy, psychology, and philosophy. One senses early tension between the attractions of a career in medicine and academia, and fascination with the beauty and diversity of animals. During a two-semester stint in the Columbia Medical School in New York in 1922, he is said to have spent more time studying the inhabitants of the New York Aquarium than at lectures. Comparative ethology was deemed an inappropriate pursuit in the department of anatomy, so to his M.D. degree he added, in 1936, a Ph.D. in zoology at the University of Munich, and remained in that department until 1941. The major features of his theory of behavior were laid during that period. After World War II, under the aegis of the Institute for Marine Biology, a Max Planck Institute was established at Büldern in Westphalia for Lorenz' group, and, in 1958, it became the Max Planck Institute for Behavioral Physiology, at Seewiesen in Bavaria.

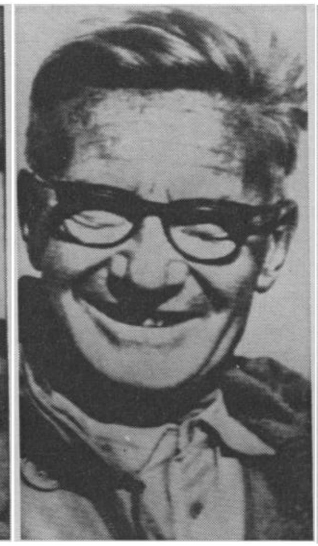
Ethological findings derive much of their force and generality from insightful use of comparative techniques and subjects selected appropriate to the problem. If Lorenz has a totem animal, it is surely the greylag goose in which, with his revered teacher Oskar Heinroth, he discovered imprinting, an especially rapid and relatively irreversible learning process with an optimal critical period early in the gosling's life. Imprinting has repercussions not only on what constitutes an acceptable parental object, or companion as Lorenz called it, but also on what becomes an appropriate sexual companion when the gosling grows up, one of many findings that have proved heuristically valuable in psychoanalysis and psychiatry.

This and other discoveries were incorporated in the panorama of ethological theory presented in 1935, and translated into English soon afterward by Margaret Nice, that was at once a treatise on the social behavior of animals and how the structure of a society relates to its component parts, and a manifesto for the objective analysis of the natural behavior of animals. A central conception complementary to that of imprinting, is the "innate release mechanism." These were visualized as genetically determined sensory mechanisms that predispose an organism to be especially responsive to stimuli, from the environment or from companions, that have assumed special valence in the course of evolution of behavioral adaptations for survival and reproduction. They match behaviors evolved for social communication that generate key "releasing schemata" or "sign stimuli," in turn evoking or guiding particular patterns of behavior in the respondent.

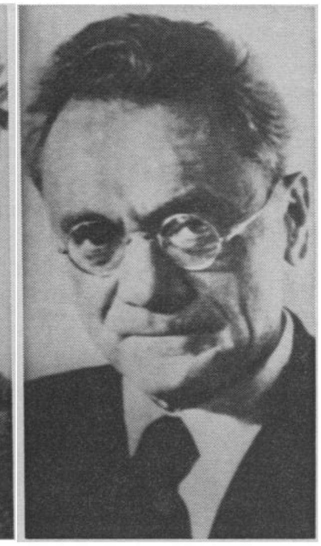
A series of germinal papers over the next 15 years defined more sharply inadequacies of purely reflexive and behavioristic theories of behavior, demonstrating that endogenous changes in



Konrad Lorenz



Nikolaas Tinbergen



Karl von Frisch

motivation to perform certain activities and endogenous changes in responsiveness to different kinds of stimuli cannot be omitted from a behavioral theory if it is to have any general validity.

Some of his viewpoints as expressed in the popular book *On Aggression*, which suggests an endogenous motivation to seek out opportunities for fighting in fish, and perhaps in man as well, proved highly controversial. However one senses deeper roots to the outrage with which some react to analogies between animal and human behavior. In the introduction to the 1970 translations of his work, Lorenz reflects wryly

> The fact that the behaviour not only of animals, but of human beings as well, is to a large extent determined by nervous mechanisms evolved in the phylogeny of the species, in other words, by "instinct", was certainly no surprise to any biologically-thinking scientist. It was treated as a matter of course, which, in fact, it is. On the other hand, by emphasizing it and by drawing the sociological and political inferences I seem to have incurred the fanatical hostility of all those doctrinaires whose ideology has tabooed the recognition of this fact. The idealistic and vitalistic philosophers to whom the belief in the absolute freedom of the human will makes the assumption of human instincts intolerable, as well as the behaviouristic psychologists who assert that all human behaviour is learned, all seem to be blaming me for holding opinions which in fact have been public property of biological science since *The Origin of Species* was written.

The young Niko Tinbergen, an avid naturalist from his boyhood in the sand dunes and pine forests of Hulshorst in Holland, saw the intricacies of insect behavior, specifically that of digger wasps hunting other insects and provisioning nest burrows with the corpses, as a testing ground for hypotheses about the sensory control of behavior. An opportunity while a graduate student in zoology at the University of Leiden to participate in 1931–32 in an Arctic expedition added snow buntings, phalaropes, and Eskimo sled dogs to a growing list of animals into whose behavior Tinbergen was to cast profound evolutionary insights. Returning to join the zoology faculty at Leiden, a seminal meeting with Lorenz in 1936, followed by a 6-month visit to Altenberg, gave rise to their only joint paper, in 1938, on the egg-rolling behavior of the greylag goose, and to more than 30 years of mutual cooperation, criticism, and stimulation that brought the new science of ethology into full flower. When he went to Oxford University in 1951, where he became a professor of animal behavior, he left the seeds of ethology firmly planted in Holland, and Groningen and Leiden continue as fertile research centers where aspiring students become versed in ethological discipline. One senses environmental imprinting in Tinbergen's choice of research sites while he was at Oxford. The sands of the Farne Islands, Scolt Head, and most recently Ravenglass are the Hulshorsts of England, permitting expansion of a research theme, already broached in Holland, on the social behavior of gulls, which led to fundamental insights into relationships between the behavior and ecology of animals.

From a theoretical framework established in his 1942 paper on "an objectivistic study of the innate behavior of animals," Tinbergen and his colleagues concentrated on the stimulus control of behavior. In both laboratory and field conditions, with butterflies, fish, and birds as subjects, he demonstrated that, by using inanimate models whose properties are systematically varied, experimental demonstration can replace intuitive judgment in deciding which elements of a stimulus complex control a response. New insights into how signaling behavior originates in the course of evolution were summarized, together with a general development of ethological theory in his 1951 book, *The Study of Instinct*, which introduced many English-speaking readers to the subject. Many patterns of social behavior, often with a signaling function, were understood as the outcome of social conflicts, a point of view that Tinbergen, with his wife Elizabeth, has since applied to the genesis of autistic behavior in children.

Perhaps most distinctive in the breadth of Tinbergen's research is his frontal attack in the 1950's and '60's on the problem of adaptiveness, which was for so long the subject of judgments from zoologists' armchairs. However, Tinbergen and his associates demonstrated that one can actually measure in animals preyed upon by others the cost or benefit of such traits as the color of a moth's wings or a bird's eggs, the spines of a three-spined stickleback, habits such as a gull's removal of egg shells from the nest after young have hatched, or living on the edge of a gull colony rather than in the center. The studies of gull behavior illustrate beautifully how an ecological decision made in phylogeny can reverberate through many aspects of the biology of a species. With von Frisch and Lorenz, Tinbergen has expressed the view that ethological demonstrations of the extraordinarily intricate interdependence of the structure and behavior of organisms are relevant to understanding the psychology of our own species. Indeed, this award might be taken not only as fitting recognition of the outstanding research accomplishments of these three zoologists, but also as an appreciation of the need to review the picture that we often seem to have of human behavior as something quite outside nature, hardly subject to the principles that mold the biology, adaptability, and survival of other organisms.

P. MARLER
D. R. GRIFFIN

Rockefeller University, New York 10021

Interstellar Molecules: New Theory of Formation from Gases

On the first of September, the 27th interstellar molecule was announced, this time sulfur monoxide. It was found with the same instrument used to detect many other molecules—a relatively small radio telescope operated by the National Radio Astronomy Observatory at Kitt Peak, Arizona. That interstellar molecules were discovered at all is a story of near oversight on the part of astronomers (see box), but once they were found at millimeter wavelengths (the radio wavelength the Kitt Peak telescope detects so well) it seemed that every new observation turned up a new molecule.

The pace of discovery was nearly a gallop from 1970 until about 1 year ago. Since then no further molecules except sulfur monoxide have been found, apparently because the limit of sensitivity of the Kitt Peak telescope—with its present electronic configuration—has been reached. In the meantime, the study of interstellar molecules has entered a period of consolidation, in which the scientists who were earlier quite busy simply reporting new findings are beginning to use their results to try to understand the dynamics of interstellar clouds, and others are proposing detailed schemes for the chemistry by which the interstellar molecules might have evolved. A chemical process that has been proposed recently—formation of complex molecules by collisions of ions and simpler molecules in a gas—seems particularly attractive as a working hypothesis, especially in conjunction with an older hypothesis that some molecules are formed on dust grains.

The environment in which interstellar molecules are found is far different from conditions on the earth, even in the laboratory. Some species, like CH, CH^+, OH, H_2, and atomic hydrogen, are found in very diffuse clouds of gas. The density of atomic hydrogen in these clouds is typically only 100 atoms per cubic centimeter; the clouds are transparent and permeated with intense ultraviolet light. But most of the molecular species have been found in a few huge clouds, toward the center of the galaxy and in the constellation Orion, that are opaque to visible or ultraviolet light. (Only the radical OH has been reported in another galaxy. The report has not so far been confirmed.) The clouds appear as dark patches in optical surveys of the sky, and are often associated with a bright nebula that is presumably created and illuminated by hot stars embedded in the cloud.

Dense interstellar clouds are principally composed of dust grains and molecular hydrogen. The reddening of starlight passing through the edges of the clouds reveals the presence of dust grains, smaller than a micron in diameter. The fact that molecular emissions are quite intense reveals the presence of a gas with a density of 10^4 to 10^7 molecules per cubic centimeter, but lack of correlation between 21-cm emissions and cloud positions rules out atomic hydrogen, so the gas is thought to be mainly molecular hydrogen. Radio measurements of other molecules indicate that the temperature is probably below 100°K, possibly as low as 20°K. The concentrations of the various complex molecules, relative to that of H_2, are 10^{-3} to 10^{-4} for CO; 10^{-6} to 10^{-7} for NH_3, OH, CS, CH_3OH, and HCN; and even lower for the rest. Because the concentrations of complex molecules are so low, three body collisions, which contribute significantly to chemical reactions at the earth's surface, are completely inconsequential. (Only two body collisions occur.) Therefore, many scientists previously thought gas phase reactions were unimportant.

Instead, until several years ago, most astronomers thought that interstellar molecules formed on the dust grains. Either by physical adsorption or by the stronger process of chemical adsorption, gas particles could be bound to grain surfaces, and despite the great uncertainties about the processes that occur on surfaces, William D. Watson at the University of Illinois, Urbana, and E. E. Salpeter at Cornell Univer-