Meetings

Communication by Chemical Signals

Many organisms extract information about their environment by detecting and analyzing its chemical constituents. Compounds with such signaling properties are called pheromones if they are secreted to the outside by one individual and elicit a specific reaction, a definite behavior, or a developmental process in another individual of the same species. Mice, for example, have at least five distinct odors that differ in their behavioral or physiological significance—individual, alarm, male urine, group, and alien male odors. Although the chemical identity of such compounds is known in relatively few cases, evidence concerning their impact on the receiving organism, at the receptor, behavioral and hormonal levels is increasing. These compounds are used in transmitting what is often remarkably precise and complex information that can exert a powerful control over the relations between an animal and its external environment.

What are the limitations and advantages of chemical as opposed to other forms of communication? How are pheromones able to alter the hormonal status of the individual? What are the receptor systems involved? Do such signals play a role in controlling primate behavior, including that of man? These problems were discussed by investigators representing psychology, zoology, physiology, organic chemistry, and perfumery at a meeting on "Communication by Chemical Signals" held in Auburn, Massachusetts, on 27 and 28 June 1968. The meeting was arranged by Clark University and sponsored by the U.S. Army Research Office.

It is one thing to demonstrate that pheromones are implicated in the control of behavioral or physiological processes, but quite another to establish what receptor systems are involved. (Is it the vomeronasal or the olfactory organ in mice?) The main exception to this has been among insects, where the electrophysiological method—particularly that of Schneider, Boeckh, and their associates—has proved especially effective. Two types of receptors occur among the great variety of odor-sensitive sensilla of insects: odor "specialists," showing similar sensitivities to a number of substances, especially those of vital biological significance (for example, sex attractants), and odor "generalists," showing different sensitivities. "Specialists" have also been found which respond with comparable sensitivity to either water, sugars, or salts; but no "generalists" responsive to taste solutions are known. B. Stuerckow (Northeastern University, Boston), who reviewed these and other properties of insect chemoreceptors, also stressed the similarities in neural and behavioral responses to chemical stimuli.

The role and significance of chemical communication in insect behavior was considered in relation to cockroaches (L. M. Roth, U.S. Army Laboratories, Natick), termites (A. M. Stuart, North Carolina State University), and ants (A. Gabba, Universita di Pavia, Italy). In these groups, pheromones serve as trail markers, alerting substances (many of which are terpenes), aphrodisiacs, aggregating substances, and sex attractants (of which about six have been isolated and identified chemically and biologically), and others. Roth spoke of a pheromone called "seducin," produced by males of the cockroach *Nauphoeta cinerea*. It attracts the female and functions as an arrestant, keeping her in proper position long enough for the appropriate connection to be made. Sometimes the glands responsible for pheromone secretion have been identified. Among these are Pavan's gland, which produces the trail substance in ants, and Dufour's gland, which produces the alarm substance in ants (and is also part of the venom apparatus).

During the past few years there has been an impressive revival of interest in the role of chemical signals in fish behavior. J. K. Bardach (University of Michigan, Ann Arbor) summarized recent findings. Both taste and smell are highly developed in certain species of fish, and these senses have been implicated in the control of migration, homing, and feeding; in social, schooling, and reproductive behavior; and in the relations between parents and young, predators and prey, and symbionts.

Bullheads and other fish that live in communities show complex social behavior. Group stability and individual recognition is based on olfaction. Individual recognition, once established, leads to the setting up of rank orders and status in the community. When the individual status of a fish changes through stress, such as a fight, these changes are communicated through chemosensory channels. Bullheads without a sense of smell are deprived of their ability to recognize another individual. They are incapable of forming stable communities and will continue to fight one another even to death. In contrast to such anosmatic animals with stereotyped behavior, bullheads in normal communities only engage in ritual fights—once community stability has been established—and even behave cooperatively to one another on occasion.

The individual's slime carries a species-specific odor distinguished by the animals themselves, as well as members of other species. There may also exist a group or school odor, carried by slime, comparable to the warning substances released from the skin when members of a school are maimed by a predator. They are then dispersed throughout the water and bring about species-specific, though variable, avoidance behavior that is adaptive to the ecology of the species.

In reptiles, an additional and curious chemosensory organ becomes prominent —the vomeronasal organ. It apparently has a part in a variety of behavioral responses in certain snakes and lizards, but in most species its function is largely unknown. These and other aspects of chemical perception in reptiles were discussed by G. M. Burghardt (University of Tennessee, Knoxville) in relation to his experiments with newborn snakes. When extracts of the snake's normal food are presented on cotton swabs, even blinded animals respond in a manner characteristic of the species, an indication that chemical cues alone may be involved. Thus the snake increases its rate of tongue flicking and attacks the swab. Newborn snakes of various species show differences when presented with a series of similar extracts. The differences are highly correlated with the natural feeding habits of the species tested even though the species were not exposed after birth to such different natural environments or food objects. This behavior might prove useful in studying the evolution of various Ophidian groups. However, litters of the same species from different geographical areas can differ in their responsiveness to various extracts. The effective substances are apparently nonvolatile and heterogeneous, and have a molecular weight of about 5000.

For most mammals, we have little or no reliable evidence of the role of chemical signals in guiding behavior. However, the prominence, diversity, and frequent occurrence of skin glands emitting strongly odorous secretions suggest a corresponding dependence on odor signals. Thus 40 different types of skin glands have been described; among them are the cutaneous, pedal, preorbital, chin, inguinal, retrocorneal, occipital, caudal, preputial, anal, and scapular glands. Urine and feces may be used to mark territory. In discussing the role of skin glands in mammalian communication, R. Mykytowycz (CSIRO, Canberra, Australia) pointed out that social interaction may play a decisive role in population dynamics. His own studies on experimental populations of wild rabbits have shown that the use of secretions from anal and chin glands varies among individuals, depending on factors such as social status, territoriality, reproductive stage, and age. The use of human panels revealed the existence of differences in the intensity of smell between sexes and age groups and among individuals of different social status. It is only recently, however, in the studies of Müller-Schwartze on mule deer, that attempts have been made to determine the communicative powers of the separate chemical components of skin-gland secretions.

Among primates, the Prosimii seem best equipped with skin glands, and skin secretions may also be exploited by at least one human cultural group to convey information. Thus in the Kanum-irebe tribe of southern New Guinea the secretion from the axillary sweat glands is used in a ritual performed by the host to demonstrate his friendship with a departing guest. Some mammals have the ability to control the flow of secretions voluntarily (the skunk, for example).

Much of the recent quickening of interest in pheromones stems from the demonstrations by Bruce, Whitten, Bronson and others that the volatile external secretions of mammals play an important intraspecific role in reproductive physiology. This evidence was reviewed by W. K. Whitten (Jackson

Laboratories, Bar Harbor, Maine). He used the term "primer" pheromone to describe a substance acting on the endocrine system (probably through the central nervous system) to produce a response which is generally slow to develop, as opposed to a "signaling pheromone" which elicits an immediate behavioral response. Studies on house mice provide most of our understanding of mammalian primer pheromones although they have also been found in deer mice and field voles. Three effects have been described: inhibition of estrous cycles in segregated female groups, induction of estrus by urine from male mice, and pregnancy block by strange males. The pheromones responsible for the last two effects both occur in the urine, are androgen-dependent, labile, and may, in fact, be the same pheromone, as Whitten suggests. An additional factor or identifier would be required to change the context. The pheromone that produces pregnancy block is highly strain-dependent, and strains exist in which no block occurs. The neuroendocrine pathways mediating the effects of these primer pheromones probably involve the hypothalamus and pituitary.

Whitten concluded that current evidence does not suggest that pheromones are effective in regulating population density, but they may provide alternative stimulatory pathways that enhance the probability of reproductive success.

Experiments on the role of odor in the control of reproductive behavior in higher primates were reported by R. E. Michael (Primate Research Center, Beckenham, Kent, England). Two adult male rhesus monkeys were trained to press a lever to gain access to ovariectomized females, certain of which were also estrogenized. After it was determined that they worked more consistently for estrogenized than non-estrogenized females, temporary anosmia was induced in the males, and estrogen was administered to the non-estrogenized females. However, the males showed no change in behavior toward the females until their sense of smell was assumed to have returned. This experiment suggests that odors play a role in the male's recognition of the hormonal states of the female.

T. Engen (Brown University) reviewed the detection, recognition, discrimination, and scaling of odors by man. He emphasized the value of applying signal detection theory as opposed to the classical concepts of threshold in the study of odor detection. He also argued that odors are not easily recognized unless the context has been established, and cited the finding that the channel capacity for odor quality is little more than four bits of information at best (and for intensity one and a half bits). This is a good performance when compared with certain other human capacities, for example, two to four bits for audition and vision.

In a thoughtful summarizing paper, J. Le Magnen (Collège de France, Paris) stressed the peculiar advantages and properties of chemical, as opposed to other forms of sensory communication, in regulating the relations between individuals, and between individuals and other aspects of their external environment. Such properties include the extreme specificity of chemical messages and their discriminative accuracy, depending, in some cases, on a single chemical structure. The equivalent in acoustic signals would be a highly specific call stimulating only one type of receptor and heard only by members of one sex of a given species—others being deaf to it. In addition, odors have a direct releasing action on endocrine systems, and chemical cues can acquire significant properties in consummatory acts such as mating and feeding.

Le Magnen also pointed out some disadvantages associated with chemical signals (as opposed to sound and light). In particular, they are unusually dependent on the condition of the channel of communication—for example, wind direction—which reduces their efficiency as direction and distance indicators. Possibilities for chemical modulation of the signals are also severely limited. In certain insects, which emit their sexual attractant rhythmically, the effect is probably detected over a distance of less than 1 meter. On the other hand, spatial modulation by the natural occurrence of stationary sources of stimuli may provide an effective means of communication resembling the use of arrows and road signals by man. Le Magnen mentioned experiments on service dogs in which some subjects could detect differences of less than 15 minutes in the age of a trail.

The papers presented, along with others, will be included in the first volume of a continuing series of monographs [*Advances in Chemoreception*, J. W. Johnston, Jr., D. G. Moulton, A. Turk, Eds. (Appleton-Century-Crofts, New York), in preparation].

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