Volume I

# COMMUNICATION BY CHEMICAL SIGNALS

APPLETON-CENTURY-CROFTS
Educational Division
MEREDITH CORPORATION
New York

Library of Congress Catalog Card Number
74-92664

PRINTED IN THE UNITED STATES OF AMERICA
390-48350-8

ADVANCES IN CHEMORECEPTION

Volume I

# COMMUNICATION BY CHEMICAL SIGNALS

# ADVANCES IN CHEMORECEPTION

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# PREFACE

Research on the chemical senses has been growing at a remarkable rate over the last decade. This growth has greatly expanded our understanding of the electrical properties and ultrastructure of chemosensory organs, of the role of chemoreception in the control of behavior, of the organization of higher centers in the chemosensory pathways, and of the chemical constituents of mixtures of biologic significance. But one area where advances have been especially impressive is concerned with the properties of pheromones and substances with similar biologic effects.

Pheromones are compounds, produced by certain animals, which have the effect of inducing one or more specific responses within members of the same or closely related species. Some of these substances—the "primer" pheromones—act on the endocrine system, probably through the central nervous system. The pregnancy block induced in mice by the odor of strange males is a striking example. Others, such as "signalling" or "releaser" pheromones, elicit an immediate behavioral response. Sex attractants are prominent examples of this group.

While the chemical identity of these compounds is known, in a relatively few cases (and these, mainly in insects) we now have extensive information about their impact on the receiving organism at the receptor, physiologic and behavioral levels. As a consequence, it is becoming increasingly clear that pheromones and related substances are exploited more intensively and by a far wider range of species than is generally assumed. They can transmit what is often surprisingly precise and complex information that can exert a powerful control over the relationship between an animal and its external environment.

The study of communication by chemical signals currently absorbs the activities of workers from a diverse range of disciplines, including zoology, perfumery, physiology, organic chemistry, electron microscopy, and psychology. Since this variety also reflects the diversity of approaches characteristic of the broader study of chemoreception, it is an appropriate topic for the first of a continuing series of monographs on chemoreception. It was only after the outline of this book had been prepared and authors had agreed to contribute that it became clear that many of them had not met each other or discussed their own work with more than a small group of workers in this area. At this stage the advantages of bringing them together began to emerge. A meeting was arranged and took place in Auburn, Massachusetts on June 27 and 28, 1968. A selection of the discussions which took place at that meeting is included in this book. The meeting was arranged by Clark University Biology Department, and sponsored by the U.S. Army Research Office.

The Editors

# CONTENTS

# 1

# Introduction

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Odors drift back and forth across the boundary of human consciousness. Never explicit, never freighted with exact information, they carry, above all, emotional meaning. Odors haunt, intrigue, repel, evoke, are redolent of. Unlike sights and sounds, they seldom instruct, command, guide, inform. It is appropriate that a poet such as Baudelaire could express what odors mean to us as incisively as any psychologist:

> *Some wardrobe, in a house long uninhabited,*
> *Full of the powdery odours of moments that are dead—*
> *At time, distinct as ever, an old flask will emit*
> *Its perfume; and a soul comes back to live in it.**

It seems natural that, given this character of human olfaction, biologists have found it difficult to approach the subject of chemical communication in a systematic fashion. The other obstacle is that odors are "invisible," which is another way of saying that we are microsmatic, generally inept at classifying and measuring odors. We have had to depend on machinery to do the job for us.

Yet in the past 10 years the study of chemical communication has been able to take shape as a discipline. Two developments, one conceptual and the other methodologic, have made this possible. The first is the concept of the releaser, or sign stimulus, as created by the ethologic school of animal behavior. A releaser, defined as simply as possible in the description of animal communication, is a discrete, relatively simple and specific signal produced by one animal that evokes a specific, and often complex, response on the part of another animal. The releaser and the

* Translation from the French by Edna St. Vincent Millay. Reprinted by permission of George Dillon and Washington Square Press.

response are adaptive with respect to both animals involved; and being adaptive, they tend to be genetically programmed (innate). What made the primitive physiologic models of ethology enticing at the outset was the notion they created that animal communication is isomorphic in nature: for one response there is one signal or set of signals, and vice versa, and it remains for the biologists to synthesize the signal to unlock the response. Such a view, held widely in the 1950's, was of course oversimplified, but it was also very heuristic. Those who worried about the analysis of chemical communication were bound to ask the question: if visual and auditory communication is so predominantly mediated by releasers, must not the same be true for chemical communication? Should we not be able to induce many behavior patterns by the simple presentation of appropriate synthetic chemicals? I believe it was a faith in this elementary proposition that brought many of us to the subject in the first place. Complexity and compromise in our explanations were to come later.

The methodologic advance that made the difference was organic microanalysis. In the late 1950's, when Butenandt and his associates isolated and identified the first sex attractant (bombykol), they had to extract 250,000 female moths to obtain on the order of 10 mg of pure pheromone; nothing less was feasible for structural identification. In the early 1960's gas chromatography came into general use, and it was then possible to analyze complex mixtures of odorants using less than milligram quantities. With the employment of the coupled gas chromatograph-mass spectrometer in the last several years, chemists acquired the ability to identify substances in microgram quantities or less. Since most pheromones are produced in nanogram or microgram quantities, or less, per individual animal, the new natural-products chemistry has made pheromone identification an all but routine matter.

The analysis of a communication system is tripartite: it considers the origin, the transmission, and the reception of the signals. And that covers a great deal of biology. With reference to the origin of a signal we must consider not only the chemistry of the pheromone but also its biosynthesis, its intracellular transport, and its secretion—topics that require modern methods of biochemistry and electron microscopy. In studying transmission we must employ the techniques of physical chemistry in order to estimate the shape and rate of spread of the "active space" within which the molecules are at or above threshold concentration. In studying reception we must consider chemosensory physiology, one of the most difficult and still inchoate topics of modern biology, and finally we must consider neurophysiology.

Additional complexity is added in that there is as yet no very efficient classification of chemical signals. The term pheromone applies only to signals functioning within a single species, but there also exist chemical releasers of comparable specificity and efficiency that operate between species. Some of the signals are mutually adaptive—for example those that operate in mutualism—and they are therefore part of a communication system in the strictest sense of the word. There also exist defensive secretions that repel rather than cripple or kill and can therefore be termed communicative in a looser sense. In fact, some of the volatile secretory substances of ants serve to cripple enemies, to repel them, as well as to alarm other members of the same colony. Perhaps the way out of the semantic difficulties is to refer to interspecific chemical signals as allomones and to the study of pheromones and allomones together as chemical semiotics.

The term *allomone* was suggested by W. L. Brown and T. Eisner in *The American Naturalist*, 102:188-191, 1968.

The Auburn Conference, the first to my knowledge ever specially convened at the international level, displayed the eclectic nature of chemical semiology. Chemists met with biologists of the widest range of persuasion—insect physiologists, mammalian endocrinologists, a herpetologist, an ichthyologist, an experimental psychologist, animal behaviorists, and zoologists and physiologists identified with various other research specialties. To an unusual degree the conferees were meeting each other for the first time.

A certain expected awkwardness and occasional semantic confusion in the discussion periods were more than made up for by the sense of excitement over being present at an early event in the development of what is quickly emerging as an important new biologic discipline. The papers to follow should convey to the reader these impressions, and also a sense that considerable coherence is already being attained in the subject. For the keynote in research on chemical communication is now the rapid discovery of new phenomena, and these phenomena exist all around us in rich abundance. The conference was marked by a common interest in bringing them to light and to deepen their analyses in all aspects of their origin, transmission, and reception.

# 2

# Defining "Communication"*

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## Introduction

The study of "communication" has been of great interest recently to students of animal behavior, psychology, ethology, and related fields. Until recently I was quite sure that I knew what the area of animal communication entailed. Now I am not so sure. This change came about because of some of my research, discussed elsewhere in this book, which shows that newborn garter snakes will respond to chemical cues from those organisms which constitute the species-characteristic diet, such as worms, fish, and frogs. This response was considered to be an example of interspecific chemical communication, as evidenced by an invitation to present this work at the symposium, "Communication by Chemical Signals," on which the contents of this book were based. I had not interpreted this behavior as communicatory, and somehow the label fit uncomfortably, but I was unable to resolve the conflict on the basis of some current defini-

* Originally presented as "The Communication Gap" at the annual meeting of the Psychonomic Society in St. Louis, November 1, 1968.

† Supported, in part, by grant MH-15707 from the National Institute of Mental Health. I thank Benjamen B. Beck, Lori S. Burghardt, Michael G. Johnson, and William S. Verplanck for reading the manuscript and making many helpful suggestions.

tions of communication. This led to discussing the topic of chemical communication, animal communication, and communication in general with a large number of people, as well as searching the literature. I soon discovered that if I was confused, many other people were confused also, although they, perhaps, did not realize it. Indeed, many authors neglect even to give a definition so that one may know which usage is being employed. While it is often possible to determine usage from context, and while "intuitively everyone knows what communication is," when workers in various areas of "communication" gather they feel constrained to grapple with the need for precise meaning. But is this possible? I rapidly approached the point where "animal communication" seemed merely one of the latest "in" or "vogue" fields labeled with a phrase which very well might turn out to be meaningless in the sense of being a scientifically valid or useful concept.

The present effort is an attempt to avoid such a pessimistic conclusion. This chapter brings together the types of definitions implicitly or explicitly used most frequently, with a brief critical analysis of each. Because of the multitude of approaches, each of the various definitions will be stated in an overly simplified manner. These definitions consist of the various characteristics of communication that have been advanced in attempts to set it apart as a scientific term.* Then I will evaluate briefly each definition, using as a primary criterion its applicability to certain examples of behavior that are generally acknowledged to be or not to be communication at the animal level. Those arguments which state that communication involves only high order symbolic or complex cognitive functions, which probably do not exist in nonhuman animals, will not be dealt with; in other words, communication viewed as involving an uniquely human type of language is not under consideration here. Indeed, if this is what is meant by communication, then I submit that we do not need the concept since we have the term language, which is generally restricted to that which occurs in humans. (Bees are sometimes excepted. Whether or not they should be is an interesting question but inappropriate here.) On the other hand, I am not unmindful of the "communication" processes found within an organism involving, for instance, the various organs or systems (such as the nervous system). Even on the cellular lever, communication is referred to in the analysis of interactions between the nucleus and the cytoplasm as implied in the name of the mediator—"messenger RNA." However, to restrict communication considerations to organisms appears no more arbitrary and as necessary tactically as the similar restriction usually placed on behavior in psychology and ethology (Verplanck, 1957).

## Definitions of Communication

### *The Act of Discrimination*

Perhaps the most elementary and straightforward definition of communication is simply that it "is the discriminatory response of an organism to a stimulus." This

* Since the original presentation of this paper, the valuable volume edited by Sebeok (1968) has become available and has been referred to extensively in this revision.

definition was proposed by S. S. Stevens (1950). By this definition a pigeon pecking at a green key is communicating. It is clear that if we accept this definition, the term "communication" is quite unnecessary since the term "stimulus control" is perfectly adequate and does not entail the excess implications of the term communication.

### *Information Transfer*

A definition, predicated on the concept of *information transmission* as the essential ingredient, is one commonly given initially by various scientists, whether physical, biological, or psychological. This is especially true of those for whom systems analysis, computers, and cybernetics have replaced the telephone switchboard as the model for behavioral study. This concept of communication has been greatly influenced by the writings of Shannon and Weaver (1949). Communication exists wherever a transfer of information is shown to occur. For example, Batteau (1968) sees communication as the "transformation of information from one carrier to another." Although clarity is not a major attribute of papers with this orientation, it appears that "carrier" is not synonomous with organism.* Indeed "any change in the physical world is a consequence of a message being written in it" (Batteau, 1968). Although couched in different language, it appears that this definition is essentially no different from the preceding one.† Consider the following example: If a person or animal detours around a tree or rock, he is indeed responding to information concerning the size, location, etc., of the object. While this example is rather crude, it demonstrates that information transfer is really not different from stimulus control, at least in the way it appears to be defined—although perhaps not in the way it is used. Therefore, information transfer is, by itself, an inadequate criterion for distinguishing communication. At best, "information" is merely a means of scaling stimulus control. A common procedure, especially in perception, is to quantify "physically" stimuli into bits with $\log_2 N$ alternatives. Although this gives an aura of preciseness, it is a mirage due to the utter lack of rigor possible in specifying the alternatives.

### *The Organism Restriction*

Suppose we tried to rescue the preceding distinction by requiring that two *organisms* (plant or animal) be involved in either the stimulus control or information transfer. This is also inadequate since there seems to be no basic difference in stepping aside to avoid stepping on a snake, bumping into a tree, or stubbing your toe on a rock.

* The origins of mathematical communications theory in electrical engineering make it abundantly clear that living organisms are unnecessary for the concept of communication in this technical sense.

† The stimulus control approach may even have an advantage over the information model as used by some, such as Batteau. It has the advantage of a clearly defined criterion (discriminatory response) and the inclusion of an organism. The first sentence in Shannon and Weaver also exposes a rather unstable stage. "The word *communication* will be used here in a very broad sense to include all the procedures by which one mind may affect another" (Shannon and Weaver. 1949. p. 3).