ADVANCES IN CHEMORECEPTION

Edited by

JAMES W. JOHNSTON, JR.
Schools of Medicine and Dentistry
Georgetown University
Washington, D.C. 20007

DAVID G. MOULTON
Monell Chemical Senses Center
University of Pennsylvania
Philadelphia, Pennsylvania 19103
and Veterans Administration Hospital
University & Woodland Avenues
Philadelphia, Pennsylvania 19104

AMOS TURK
Department of Chemistry
The City College of the City University of New York
New York, New York 10031

Volume I

COMMUNICATION BY CHEMICAL SIGNALS

APPLETON-CENTURY-CROFTS
Educational Division
MEREDITH CORPORATION
New York

2

Defining "Communication"*

GORDON M. BURGHARDT†

Department of Psychology
University of Tennessee
Knoxville, Tennessee 37916

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 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.

* 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.

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).

The Animal Restriction

Perhaps, however, we can eliminate plants and restrict communication to events between *animals*. "In the most general sense, communication includes any stimulus arising from one animal and eliciting a response in another" (Scott, 1968). But here again there are certain problems. What about, for instance, the flowers that give off insect-attracting scents? What about the orchid whose flower parts mimic the visual sexual signals of female insects to the extent that the male attempts to copulate with the flowers and in the process polinates them (Wickler, 1968)? In other words, there are the symbiotic, commensal, and parasitic associations, the first of which Marler (1967) is willing to consider communicative. Although the label "communication" might not seem appropriate at first, it would seem that these examples involve stimuli which "work" differently than the rough bark of a tree which leads to its avoidance. In other words, they differ as they treat another organism, plant or animal, as an interbehavioral event, and not merely as a physical entity.

The Species-Member Restriction

Perhaps, however, we should qualify the statement to read as follows: Communication is the transfer of information between *species members*. In other words, communication is limited to intraspecific events. Diebold (1968) has utilized this distinction, as have Frings and Frings (1964). This is, however, a rather arbitrary restriction of communication, since interspecific phenomena that would come under most usages of communication are well known, such as the so-called threats and warning stimuli shown by one species to another species. Anyone owning a cat, dog, or almost any other pet also knows that this just won't do. Cross-fostering and imprinting experiments show that social signals can be given to normally inappropriate organisms. Bastian (1968), while not specifically eliminating interspecific behavior, would restrict communication to "interactions of a social nature." He goes on to state: "This restriction is surely warranted because the interactions of an animal with its social environment are most often marked by some degree of specialization and by relatively greater reciprocity of influence and concomitant fluidity than interactions with its nonsocial environment" (p. 576). The arguments of reciprocity and specialization will be dealt with below. Note that the implication of the definition is that communication is identical with *social behavior*, which Bastian recognizes. Again, what does the term communication add. Here we also need some clarity on what is "social" if restriction to intraspecific events is not sufficient. The best operational technique would call "social" all those instances where one animal treats another *as if it were* one of its own species. This is not only difficult to apply in practice, but it also breaks down upon consideration of cannibalism (predation on one's own species).

Two organizations appear to be needed as a minimum in communication. But this is not universally accepted. For instance, Sebeok (1965), who uses basically an information-transfer criterion based on encoding and decoding of messages, states that communication can take place within one organism. His example is echolocation in bats and porpoises. However, this, if looked at carefully, is quite unsatisfactory. The groping of a person in the dark for a light switch is exactly the same sort of

phenomenon, and calling this "communication" certainly does not aid our analysis. As a matter of fact, an authority on echolocation made the following point in a recent volume on communication (Griffin, 1968):

> While the source of echoes may be the body of another animal, only passive physical reradiation of sound waves is involved rather than active reply by the second animal. Hence, echolocation does not properly fall within any reasonable definition of communication behavior, and its discussion in the present volume is justified only by its indirect relevance to the physiological and behavioral phenomena that may be important both in echolocation and in communication (p. 155).

Therefore, although communication does involve stimuli, and two organisms are needed at a minimum, we can conclude that an approach limited to an analysis of responses to stimuli alone is inadequate to distinguish communication. Let us then begin to look at another series of distinctions.

The Necessity of Reciprocity

One way of viewing communication is to define its occurrence only when *reciprocal responding* occurs between organisms. That is, A responds to B, B then responds to the response of A, and so forth. There are variations of this approach (e.g., Bastian, 1968), but they could all be characterized minimally as follows: Communication occurs when one organism (sender) acts as a stimulus for another organism (discriminative stimulus, transfer of information) and the second organism (receiver) responds, which response can itself act as a stimulus (signal) for the first organism. Let us look at an example: If a predator attacks an animal, the victim often responds. For instance, when a garter snake strikes a worm, the latter will at least squirm. The responses of the prey are more vigorous the more tightly the predator holds on. These are certainly reciprocal interactions, but to call them "communication" would vitiate any distinctive meaning of the term.

Conversely, if B does not respond to A rather quickly, this does not imply that no communication has taken place. The temporal factor alone may be such that the experimenter does not see the response. In other words, it may take place a week or a year later. Certainly, we refer to letters or memos as communications, although no response may ever be made. In addition, books, television shows, and commercials are all, I think, properly considered communications even though they do not necessarily elicit an overt response. The soap salesman is communicating with me although I may never buy the product. Of course, it is fallacious to argue here that no response is a response: "no response"—failure to respond—is not to be confused with no movement, passivity, or freezing which may be directly attributable to a stimulus. This comment is not meant to imply that responses by the receivers never occur or are unnecessary.

The Necessity of Specialization

The Frings, in their interesting little book on animal communication (1964), are aware of many of the points discussed above. They, too, are concerned with a

definition of communication. The one they arrived at required the sender, the source of the message, to use some specialized structure or behavior to produce the signal.* Now, as one thinks about this definition, it does seem to be attractive. Wing markings, color patches, head bobbings, ritualized movements, and facial expressions can all be properly considered to be involved in communication. Are there some flaws in this definition? First of all, one might quibble with the reductionistic implications involved in the need for some specialized morphological structure. They do mention behavioral methods, but a specialized behavioral method is even more difficult to determine than a specialized structure. Nonetheless, let us assume that the criteria of specialized structures or methods are possible to ascertain.

Consider the response of snakes to chemical cues from their prey. On the basis of this definition, we can certainly exclude it as communication. In other words, the trailing by snakes of worm trails would not be communication because the worm is presumably not using a structure specialized for laying it, especially for snakes to follow. But I submit that the problem is not that easy. Let us consider the classical example of chemical communication, trail pheromones in ants. If there is anything which one would want to call chemical communication, this would certainly appear to be a strong contender, and usually it is so considered (Frings and Frings, 1964; Wilson, 1968). There are specialized structures and behavior involved in the depositing of the trail, and other worker ants respond to this trail, hence—communication. But looking at the behavior or structure of the sender is inadequate, as it is if we define the response as following the trail, and does not differentiate it as communicatory behavior. How can this statement be supported? Ants indeed follow a pheromone trail back to the nest. However, recently it has been shown (Watkins, Gehlbach, and Baldridge, 1967) that the small blind snake (*Leptotyphlops*) also follows pheromone trails of worker ants—it trails them right back to the nest, where it feeds upon the ant brood. Now, it seems reasonable to view the behavior of the blind snake as no more involving communication than the response of a garter snake to worm extracts or trails. Here, then, is a paradox.† It could be argued that if the ant trailing a worker ant's trail is considered communication and the snake trailing the identical trail is not, then the success of any attempt to define communication wholly on a physicalistic basis is impossible.‡ On the other hand, to consider both these examples (the snake trailing as well as the ant trailing the pheromone trail) as communication renders the concept of communication rather empty. For instance, the snake's orientation to prey cues is not basically different from a cow's orientation to its food source, grass, and to consider the latter communication only emphasizes the absurdity involved. But to deny communication in the pheromone trails of ants would eliminate not only chemical communication in general, but also many similar examples in the animal kingdom using other modalities as well.

* They further stated (p. 4) that the receiver be of the same species as the sender. This requirement has already been eliminated here as a necessity.
† The Frings' intraspecific requirement would allow them to resolve the problem. However, since the present author argues against the requirement, he obviously cannot use it.
‡ A good case against a model for psychology based on the model of the physical sciences has recently been made by Deese (1969), who has had impeccable S-R behaviorist credentials. Actually, the image of the physical sciences held by most "scientific" students of behavior is based on the outmoded Newtonian view, which is considerably different from modern theoretical physics (for example).

How, then, can we distinguish communication if specialized structures, mutual responding, limitations to intraspecific events, and other frequent distinctions are inadequate? Before answering this question, we should note the view that all predator-prey relationships be omitted from consideration as communication (Klopfer and Hatch, 1968). Then what remains with the above criteria will leave a satisfactory residue on the question of communication. However, I have already alluded to threats and warnings; for example, the stomping of skunks and hissing and rattling of snakes, which are associated with predator-prey relationships, but which certainly appear to be examples of communication.

The Appeal to Levels

It is clear that the biological world is composed of organisms that differ greatly in the complexity of their morphological, physiological, and behavioral characteristics. Therefore, the making of comparisons between different species always should be performed cautiously, especially when common mechanisms are implied. After stating this somewhat neglected truism, what more should we do? Considerably more according to Schneirla (1953) and, concerning communication, Tavolga (1968). Although complexity in biology is usually viewed as relative and continuous, Schneirla postulates a hierarchical series of levels of behavioral integration. These are not continuous, but are qualitatively different. The tendency has been to associate these levels with phylogenetic position. This is not always possible, and there is a regrettable propensity to ignore the behavioral differences within a group (i.e., fish, birds). The tendency becomes almost a rule in the study of comparative animal intelligence (e.g., Bitterman, 1965).

Another characteristic of the "levels" approach is that the behavioral level is usually tied to a specified degree of structural complexity. This opens the door to a reductionism not yet warranted by our knowledge of the physiological and anatomical correlates of behavior. An essential conservatism would be introduced into the study of behavior if we had to have a "reasonable" physiological mechanism before studying new behavioral phenomena in animals.

But given these caveats, how does the approach by levels contribute to the discussion of animal communication?* Briefly, there are six major levels of interorganismic interaction: vegetative, tonic, phasic, signal, symbolic, and language. The last three are said to comprise communication. The definition of communication, however, turns out to be only a more restricted version of Frings and Frings thesis (described above), and many of the same criticisms apply.

> "For communication to take place, the emitter most possess a specialized stimulus-producing mechanism (chemical, morphological, or behavioral). The stimulus must occupy a narrow portion of the available spectrum of the channel (frequency range, duration, patterning, chemical specificity). The receiver must possess specialized receptors and respond in a specific manner." (Tavolga, 1968, pp. 275-276.)

* Tavolga (1968) has attempted this task and should be referred to for a more complete explication.

The following of ant pheromones by the blind snake (which utilizes specialized chemical-sense organs) would have to be classified communication by this definition, while the following of worm "mucus" by a garter snake utilizing an equally specialized receptor would not be communication. In addition, the so-called qualitative levels are not that easy to discriminate. In other words, it is much easier to discuss them in the abstract than to deal with a specific example. I, at least, found the crucial distinction (as far as communication is concerned) between "phasic" and "signal" difficult to apply.

Another complication discussed briefly by Tavolga is that "the emitter and the receiver need not necessarily operate on the same level" (p. 276). This complicates the problem to the point where the use of this approach would eliminate the possibility of any precise meaning of the term communication. It is another bit of evidence that the concept has little scientific value.

The Multi-criterion Approach

Finally, we might conceive of communication as involving an injunctive definition similar to a definition of life (Lorenz, 1965). In other words, no one criterion is necessary and sufficient; certain combinations are required. While there may be some merit in that approach to communication, the parallel is far from exact. I have tried to make a list of criteria that, when taken in combination, would separate commonly accepted examples of communication from those not considered to be communication. I met with little success unless the position advocated below is made a necessary, but not necessarily a sufficient, criterion.

An Attempted Resolution

Is it, therefore, possible to define or to identify communication? Should we accept the conclusion that communication is a scientifically useless or redundant term? It will be argued here that it need not be this way if we make a certain criterion central to our definition. This criterion might be, at least on the surface, unacceptable to many scientists. However, at the present time there seems to be no other way of rescuing the term "communication." My position is that communication is indeed a valid term if we realize how we have, in fact, been using it.

The central criterion of the concept of communication must involve *intent* in some manner. This is implicit in the definitions of the Frings and of Tavolga, where the sender uses a specialized structure or method of behavior—specialized for what? They wanted to avoid the problem of purpose, and so they made a reductionistic jump that does involve "intent", but not so blatantly. Now intent, however, defined, characterizes all generally agreed upon examples of communication from protozoa to man. Must this mean vitalism and unscientific, unanalyzable types of arguments? Does it mean an incompatibility with a broad operational, experimental, and empirical approach to behavior? I do not think so. Intent can be looked at scientifically merely by considering that *it is to the real or perceived advantage of the signaler or the signaler's group for it to get its message across to whatever organism is involved.* In other words, it is adaptive. The signal mechanism has either been phylogenetically or ontogenetically "built" into the organism via natural selection in the first instance or probably via reinforcement in the other, acting, of course, upon the consequences of previous events. This crucial distinction between the "innate" and the "learned" has been recently elaborated on by Lorenz (1965) and Skinner (1966), although the present case does not depend on any given viewpoint in this controversial area. It does depend on the acceptance of both evolutionary and experiential determinants in behavior, although complex interactions certainly occur. In addition, the probabilistic nature of this approach must be emphasized. To be evolutionarily adaptive, communication must enhance survival value and reproductive success (Klopfer and Hatch, 1968). When identifying behavior as communicative, we are implying this. I submit that we must build our approach to communication on this conceptual base and not rely on concepts that are associated with biological and behavioral phenomena (such as signal characteristics, receiver mechanisms, reciprocity, and so forth), but that are by no means the most important parameters involved. In fact, this approach is based upon the use of a highly restricted teleology (see Ayala, 1968).

It is certainly empirically possible to determine whether it is to the signaler's advantage to get his message to another organism.* Obviously it needs to be received before a completed communicatory interchange can occur. Associated with this would be an energy expenditure by the signaler involving overt behavior and evolved morphological characteristics, such as colors, patterns, odors, and the like. Their use by the wrong animal, such as a predator, is irrelevant.† By this approach, we clearly see the blind snake's following of the pheromone trail is *not* communication. It is an unfortunate mistake from the sender's viewpoint. It is similar to tracing a murderer from clues left at the scene of the crime. Certainly the criminal was not attempting to communicate his identity to the authorities (psychoanalytic interpretations notwithstanding). This reliance on the "motivation," "intent," or as I would prefer, the *adaptive significance to the sender (or his group)* alone is intentional; a receiver, such as a predator, can be rewarded for responding to a signal at a distinct disadvantage to the sender.‡ For this reason it is not possible to completely accept the definition advanced by Klopfer and Hatch (1968, p. 32) in which communication "necessitates the existence of a code shared between two or more individuals" and is "mutually beneficial to its possessors." Emphasis on the signaler also neutralizes the problem encountered with the levels approach of having an act communicatory as far as either the signaler or receiver are concerned, but not both. Hockett and Altman (1968)

* In some cases, such as alarm cries, the sender might indeed be increasing his chance of capture, which may be maladaptive to the sender as an individual while conferring some advantage upon the signaler's "group," which is, by the way, not necessarily identical with all its species members. Consequently, the approach has room for altruistic behavior, however defined.

† "Intent" has been used in discussions of language as communication (Fearing, 1953). Although the usage in the present sense would include that covered by Fearing, the converse would not necessarily be true. However, his abstract definition would come close to encompassing that implied here. ". . . intent . . . refers to the fact that the act of producing content is *directed* rather than random or aimless, and implicitly or explicitly assumes future effects" (p. 76). Nonetheless, his usage is clearly "psychological" rather than "biological" or "ethological" as used here.

‡ That it might be an advantage to a species to have some of its senders picked off by predators (elimination of the less fit or excess numbers) is a legitimate point (witness the problems with ungulate herds in areas where predators have been eliminated by man). However, this consideration effectively moves the level of discourse to another sphere which is not appropriate here.

in contrast go even further and place all their chips on the receiver: "To count as communicative . . . a particular act of an animal in a setting must be, from the point of view of some receiver, one of a set of two or more acts any one of which *might* occur in just that perceived setting, but each of which precludes all the others" (p. 69). This is, in essence, a sophisticated statement of the information-transfer theory.

In complex behaviors, such as courtship, long chains may be involved where the response of B is simultaneously a stimulus for the original sender A. However, "reciprocity" of this type is not a necessary situation. Human communication, in this approach, does not contradict the above but involves merely the elaboration and extension of processes having the same ends.

The definition also allows us to make certain relevant distinctions that should be made. It is important to keep in mind Cherry's notion (1957) that to tell a man to jump off a bridge involves communication. To push him off the bridge is not communication. Therefore, a stimulus from A which has a direct effect on the responses of B, by dint of the physical or chemical force of the stimuli involved, is not communicating. This is a crucial distinction for the present argument. Obviously all signals, communicatory or not, are received through chemical or physical energy of some kind. However, a stimulus that is not intense enough to elicit the response directly, and yet does so, is qualitatively different from one that elicits the response passively as far as the receiver is concerned (such as a push), or, perhaps even reflexively (such as a startle response to a loud sound). Hockett and Altman (1968) also recognize this distinction and state the problem as follows: "To what extent is the communicative act (the signal) effective in itself, via direct energetic consequences, and to what extent only via triggering?" (p. 68). Another way to phrase the difference is that a communicatory signal is referring to something beyond itself (i.e., a future event) as shaped by prior events. This is implicit in the use of the term information. If this point were clearly emphasized, the distinction between information and stimulus control might be maintained, with the former being stimuli associated with communication as defined here.

Limitations and Extensions

It might be thought that certain instances would pose problems for this distinction. If a person is told to avoid a falling piano, or if he is pushed out of the way, what is the difference? The adaptive value is clear. However, the push itself contained no information. Indeed, he could have been pushed into the path of the descending ivories and associated structures. In neither case was information passed that would elicit a learned or evoked response. This example raises another point. The receiver of the verbal warning would presumably save his life or prevent serious injury by responding appropriately. This is clearly adaptive for the receiver, and since he is a member of the signaler's group, communication in the present sense is involved.

Let us apply the definition of communication to another phenomenon. We have heard recently of chemical interspecific or cross-specific communication where very potent noxious fumes are emitted by certain animals to ward off predators—especially in certain arthropods, as shown by Eisner and Meinwald (1966). Is this communication, as they claim? Is the spray of a skunk chemical communication? By the present approach, these are not examples of communication, but are much

more closely akin to the pushing of a person off a bridge. The warning movements of a skunk and its body markings are involved in the communicatory phases of its defensive behavior. The actual defensive behavior which the animal is warning against is not communication. In the example of arthropods, only if we can find some warning stimuli associated with the animal before it gives the spray can we say communication occurs. If we only have the chemical spray, then we do not have chemical communication. Indeed, Eisner and Meinwald do refer to these sprays as weapons. To accept them as also legitimate communication would logically extend the concept of communication to the use of Mace (a chemical spray used by police) and tear gas. Eisner and Meinwald even mention a defensive spray in nasute termites which acts as an alarm pheromone for its own species. Here is an example where exactly the same stimulus can mediate a communicatory act and also serve as a weapon. It is legitimate, however, to ask which came first evolutionarily and which function was derived.

In the psychological learning experiment, such as the lever pressing of a rat in a Skinner box, adaptive behavior is certainly evidenced if the animal "learns" to get food, escape shock, or whatever. The question now arises as to whether the rat is communicating with the experimenter, as implied in the famous cartoon of the talking rats ("Boy, have I got this guy conditioned"). Perhaps experimental psychologists have really been studying animal communication intensively for several decades. If this is true, then what is new about the study of animal communication outside of the use of more species-characteristic signals and behavior? Both a little and a lot.

The rat pressing a bar is responding to an inanimate physical object on a level similar to the rocks and trees mentioned earlier. That a human is programming reinforcement dependencies is irrelevant. It is merely a way of controlling environmental events to an extent unobtainable in nature. Indeed, if some external agent is controlling events in the world at large, every adaptive response of an organism could be considered communication with God. The latter's friends here on earth (or the moon) would object, of course, since the recognized method of communication with the Deity is prayer. Since only selected anecdotal evidence can be adduced for the efficacy of prayer, the advantage of this rapprochement between religion and science is clear. The converse of the argument, however, is that the psychological experimenter is behaving like the God he generally disavows. The direction of this argument, by the way, is a good reason why lever pressing as communication should not be seriously argued in the author's presence!

A more serious claim for communication between experimenter and subject involves the effect of the experimenter bias, where the subject picks up inadvertent cues from the experimenter as to the correct response as in the case of Kluge Hans, the mathematical genius horse (Pfungst, 1911). Clearly this is adaptive for the subject, but not so for the experimenter (*qua* experimenter), and so communication in the present sense is not involved. In general, an *experimenter* cannot be a communicator unless such communication is part of the problem under study, such as training guide dogs for the blind.

Recently, the study of nonverbal communication in humans has been intensively studied (e.g., Mehrabian, 1969). While many gestural signals are "unconscious" or "unintentional," they can clearly be viewed as communication here. Intent viewed in the present sense as applying to the behavior of all organisms is not to be confused

Frings, H., and Frings, M. 1964. Animal Communication. New York, Blaisdell Publishing Co.
Griffin, D. R. 1968. Echolocation and its relevance to communication behavior. *In* Sebeok, T. A., ed. Animal Communication. Bloomington, Indiana University Press, pp. 154-164.
Hockett, C. F., and Altman, S. A. 1968. A note on design features. *In* Sebeok, T. A., ed. Animal Communication. Bloomington, Indiana University Press, pp. 61-72.
Klopfer, P. H., and Hatch, J. J. 1968. Experimental considerations. *In* Sebeok, T. A., ed. Animal Communication. Bloomington, Indiana University Press, pp. 31-43.
Lloyd, J. F. 1965. Aggressive mimicry in *Photuris*: Firefly femmes fatales. Science, 149:653-654.
Lorenz, K. Z. 1965. Evolution and Modification of Behavior. Chicago, University of Chicago Press.
Marler, P. 1961. The logical analysis of animal communication. J. Theoret. Biol., 1:295-317.
——— 1967. Animal communication signals. Science, 157:769-774.
Mehrabian, A. 1969. Significance of posture and position in the communication of attitude and status relationships. Psychol. Bull., 71:359-372.
Pfungst, O. 1911. Clever Hans (The horse of Mr. von Osten). New York, Henry Holt and Company.
Schneirla, T. C. 1953. The concept of levels in the study of social phenomena. *In* Sherif, H., and Sherif, C., eds. Groups in Harmony and Tension. New York, Harper & Row, Publishers, pp. 52-75.
Scott, J. P. 1968. Observation. *In* Sebeok, T. A., ed. Animal Communication. Bloomington, Indiana University Press, pp. 17-30.
Sebeok, T. A. 1965. Animal communication. Science, 147:1006-1014.
——— 1968. Animal Communication. Bloomington, Indiana University Press.
Shannon, C. E., and Weaver, W. 1949. The Mathematical Theory of Communication. Urbana, University of Illinois Press.
Skinner, B. F. 1966. The phylogeny and ontogeny of behavior. Science, 153:1205-1213.
Smith, W. J. 1969. Messages of vertebrate communication. Science, 165:145-150.
Stevens, S. S. 1950. A definition of communication. J. Acoust. Soc. Amer., 22:689-690.
Tavolga, W. N. 1968. Fishes. *In* Sebeok, T. A., ed. Animal Communication. Bloomington, University of Indiana Press, pp. 271-288.
Verplanck, W. S. 1957. A glossary of some terms used in the objective science of behavior. Psychol. Rev., 64 (6), Part 2, pp. 1-42.
——— 1962. Unaware of where's awareness. *In* Erikson, C. W., et al., eds. Behavior and Awareness. Durham, North Carolina, Duke University Press, pp. 130-158.
Watkins, J. F., II, Gehlbach, F. R., and Baldridge, R. S. 1967. Ability of the blind snake. *Leptotyphlops dulcis*, to follow pheromone trails of army ants *Neivamyrmex nigrescens* and *N. opacithorax*. Southwest. Natural., 12:455-462.
Wickler, W. 1968. Mimicry in Plants and Animals. New York, McGraw-Hill Book Company.
Wilson, E. O. 1968. Chemical systems. *In* Sebeok, T. A., ed. Animal Communication. Bloomington, Indiana University Press, pp. 75-102.

3

Purity, Identity, and Quantification of Pheromones

P. Z. BEDOUKIAN

Tech. Director, Compagnie Parento, Inc.
40 Ashley Road
Hastings-on-Hudson, N. Y. 13076

INTRODUCTION

This chapter attempts to acquaint the reader with some of the pitfalls and difficulties which face the investigator of communication through chemoreception. An awareness of these problems is necessary in order to avoid the possibility of arriving at erroneous conclusions. Results of investigations which do not give details of the methods of purifiction, identification, and measurement of the chemical employed are open to criticism and doubt.

In the realm of chemoreception, we enter a somewhat bizarre area far beyond the usual concepts of purity, identity, or measurement. A "pure" substance is no longer sufficiently pure; positive identity is not assured by the generally accepted methods, nor are the quantities involved measurable by usual laboratory procedures.

Nevertheless, one need not be discouraged from attacking problems of chemoreception because some of the demands are too exacting. Although we may not be able to achieve absolute purity and identity, or measure infinitesimal quantities with absolute exactitude, we can at least show what the limitations are. The important