

UNIVERSITY OF CALIFORNIA, SAN DIEGO

Formal Approaches to Innate and Learned Communication:
Laying the Foundation for Language

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Cognitive Science

by

Michael Oliphant

Committee in charge:

Professor John Batali, Co-Chairperson
Professor Jeffrey Elman, Co-Chairperson
Professor Edwin Hutchins
Professor Joel Sobel
Professor Ted Case

1997

TABLE OF CONTENTS

	Table of Contents	ii
	Acknowledgements	iv
	Abstract	v
I	Introduction	1
II	The behavior of communication	3
	A. Animal communication systems	3
	1. Flowers and pollinators	3
	2. Insect pheromones	4
	3. Bee dances	4
	4. Vervet monkey alarm calls	5
	5. Human language	5
	B. Defining communication	5
	1. Previous definitions of communication	6
	2. Incompatible definitions	7
	3. A causal definition of communication	8
	4. The chicken or the egg?	11
	5. Defining communication in practice	13
	6. An inclusive definition of communication	13
III	Communication system formalism	15
	A. Signals and meanings	15
	B. Communicative accuracy	16
	C. Communicative accuracy of a population	17
	D. Optimal communication	18
	E. Game-theoretic notions of communication	20
IV	Evolved communication systems	22
	A. Evolutionary game theory	22
	B. Evolutionary Computation	23
	C. Related work	24
	D. Simulation framework	25
	1. Structure of the genetic representation	25
	2. Fitness and reproduction	26
	E. Simulation parameters	27
	F. Situations of common interest	27
	G. Lack of common interest	28
	1. The evolution of altruism	30
	2. The prisoner's dilemma	30
	3. Reciprocal altruism	32
	4. Kin selection and spatial organization	39
	H. Discussion	46

V	The evolution of exploitation and manipulation	47
	A. Exploitation of random drift	47
	B. Exploitation of reliable behavior	50
	C. Manipulation	52
	D. Suppression	53
VI	Learned communication systems	56
	A. Reinforcement learning	56
	B. Observational learning	57
	C. The observational learning model	58
	1. Population dynamics	58
	2. Observing the behavior of others	59
	3. Creating a new individual	60
	4. Simulation framework	61
	D. Statistical learning procedures	61
	1. Imitative learning	62
	2. Saussurean learning	64
	3. Bayesian learning	67
	4. Normalization	73
	5. Analysis of Hurford	75
	E. Network learning mechanisms	77
	1. The network model	78
	2. Willshaw networks	79
	3. Cumulative-Association networks	81
	4. Hebbian networks	82
	F. Discussion	86
VII	Learned communication in non-human animals	87
	A. Why are the so few learned communication systems?	87
	1. Evolution may be sufficient	87
	2. Learning has associated costs	88
	3. The ability to learn is absent	88
	B. Observational learning and communication	89
	1. Bird song	89
	2. Vervet monkey alarm calls	90
	3. Communicative gestures in chimpanzees	90
	4. Language-trained animals	91
VIII	Discussion	93
	A. Natural selection and its limitations	93
	B. Observational learning is required	93
	C. Imitation is not enough	94
	D. Observational learning as a bottleneck in language evolution	95
A	Simulation software used	97
	Bibliography	98

ACKNOWLEDGEMENTS

I would like to thank the members of my committee for their helpful comments on earlier drafts of this dissertation. In particular, John Batali has been very much involved in helping to shape the ideas I present here. I would also like to thank Simon Kirby and Jim Hurford for stimulating, if heated, discussions on the topic of language evolution, and Deborah Forster for making sure that I did not forget that there are real animals out there. I would also like to thank the Collegium Budapest Institute for Advanced Study for providing the ideal working environment in which part of this work was done. Finally, I would like to thank Sherry Patheal for her moral and financial support and just for being really, really cute.

Much of the work on evolved communication systems presented in chapter IV is based work published in Oliphant (1995) and Oliphant (1996). The simulations on the spatialized prisoner's dilemma presented in section IV.G.4 are based on work published in Oliphant (1994) and Oliphant (1995). Some of the work on statistical learning procedures presented in section VI.D is based on work originally described in Oliphant and Batali (forthcoming).

ABSTRACT OF THE DISSERTATION

Formal Approaches to Innate and Learned Communication:
Laying the Foundation for Language

by

Michael Oliphant

Doctor of Philosophy in Cognitive Science

University of California, San Diego, 1997

Professors John Batali and Jeffrey Elman, Co-Chairs

This dissertation identifies the conditions necessary to establish a system of communication in a population of individuals, whether through evolution or learning. A definition of communication is proposed that encompasses the behavior of species ranging from flowers to human beings, and a formal framework for modeling such behavior is presented. Through the use of computational simulations, it is shown that systems of communication evolve in cases where such behavior conveys a selective advantage to both sender and receiver. It is also demonstrated that factors such as kin selection and reciprocal altruism can result in the establishment of communication even when there is no direct pressure on the transmission of signals. In the case of learned communication, it is argued that observational learning is the appropriate learning model. Learning strategies that simply imitate the behavior of others, however, are not suitable. Instead, a learning mechanism must optimize its behavior so as best to communicate with the population it is observing. A Bayesian learning procedure designed to maximize the probability of communicative success is shown to be capable not only of learning an existing communication system, but also constructing such a system from random initial signaling behavior. To examine how animals might actually implement such a procedure, network learning models are considered. It is shown that a simple form of Hebbian learning, well within the grasp of most animals, has the required properties. Given this, it is surprising that learned systems of communication are not more frequent. Evidence from the animal social learning literature suggests that the primary reason for this may be that observational learning is difficult, if not impossible, for non-human animals. Given this, the most basic explanation for why only humans have language may not lie in the ability of learn a complex, syntactic form of communication, but rather in the ability to learn any system of communication at all.

Chapter I

Introduction

The research that I will present in this dissertation has two related, but distinct goals. The first, and primary goal is to give a formal analysis of what is required for communication to be established in a population of animals, either through evolution or through learning. I believe that laying this formal foundation is critical. A clear understanding of the requirements involved in constructing and maintaining a system of communication will allow us to know when we should be surprised that such behavior exists, and when we should be surprised that it does not.

The second, and more speculative goal is to use the formal framework I develop to begin to answer some questions about communication and language that I feel are important. Why do animals communicate in situations where it seems not to be in their own best interest to do so? Why, when virtually every animal species has a system of communication, are so few of them learned? Why do human beings seem to be unique in their communicative abilities? Such questions represent both the motivation for the work in this dissertation, and the future directions that I hope to pursue as a result of it.

In the next chapter, I outline the behavior of communication, giving examples of some of the communicative behaviors that animals exhibit. I then formulate a definition of communication that encompasses all of these examples. In chapter III I give the formalism that will be used as the basis for simulations I present and analyze the conditions that are required of an effective system of communication.

Having established a definition of communicative behavior, and a formalism with which to describe it, I then turn to an investigation of mechanisms capable of establishing systems of communication. Chapter IV is an exploration of the establishment of innate systems of communication. Through the use of computational simulations, I demonstrate that communication

evolves in cases where sender and receiver each have a common stake in its success. I also show that factors such as kin selection and reciprocal altruism can result in the establishment of communication even when there is no direct pressure on the transmission of signals.

In chapter V, I use the evolutionary simulation framework I have developed to experimentally explore the differences between behavior that is communication and behavior that just involves the exploitation or manipulation of one individual by another. I then apply these results to simulation work done by others, showing that the behavior they observe is best described as exploitation or manipulation, rather than communication.

Chapter VI explores how systems of communication might be established through learning. I argue that observational learning is the appropriate learning model, and describe a number of plausible learning procedures that might be used. I show that learning strategies that simply imitate the behavior of others are not suitable. A learning mechanism must rather optimize its behavior so as best to communicate with the population it is observing. To examine how such learning might be implemented, I turn to network learning models. I demonstrate that a simple form of Hebbian learning is sufficient to result in the creation and maintenance of a system of communication in a population of individuals.

Because the computational requirements of learned communication seem to be so modest, in chapter VII I consider possible explanations for why we do not see more such systems. I point to a lack of observational learning ability among non-human animals as the primary reason, and give an overview of the animal social learning literature supporting this claim. In conclusion, I argue in chapter VIII that the ability to learn by observing others presents a key bottleneck in the evolution of language.

Chapter II

The behavior of communication

Before turning to an investigation of how systems of communicative behavior might be established, it is necessary to first give an overview of the behavior itself. First, I will discuss examples of the communicative behavior that I intend to model. Then I will attempt to give a definition of communication that is sufficient to account for all of these examples.

II.A Animal communication systems

This section gives a brief overview of the diverse examples that should be included in an account of animal communication. There is an enormous literature on this subject. For more detailed treatments, I recommend Smith (1977), Sebeok (1977), Lewis and Gower (1980) and Hauser (1996). My intent here is simply to show that communication systems are used by a wide variety of animals, using a number of different signaling techniques in a diverse set of types of interaction.

II.A.1 Flowers and pollinators

While communication occurs most frequently among conspecifics, it sometimes involves interactions across species. Bees obtain nectar from certain species of flower, and as a result, act as pollinators to the flower. Because it is in the flower's best interest to attract bees, their appearance has evolved to facilitate this (Daumer, 1958). Bees cannot see the color red, and very few of the flowers the bees pollinate are that color. This color bias of the flowers is quite possibly an adaptation that has occurred because of the symbiotic relationship between the flowers and the bees that pollinate them.

Some bee-pollinated flowers do even more to make the bee's job easier. The evening primrose, for example, has a distinctly colored central region. When the petals of the flower are removed and rotated so that the distinctive central region now faces outward, the bees probe at the corners, rather than at the center. Thus, the coloration of the flower helps the bee find the source of the nectar (and the site of pollination).

This interaction between bees and pollinators not only demonstrates that communication can be interspecific, but also that it can occur in clearly non-sentient species.

II.A.2 Insect pheromones

Pheromones are chemical signals used by certain species to communicate in a oral or olfactory manner. The use of pheromones is particularly widespread in among the social insects, who used them to coordinate much of their activity. Wilson (1965) identifies a variety of ways in which such signals are used by social insects, including alarm, recruitment, grooming, and recognition of others.

Termites use odor trails to recruit works to repair breaks in the nest wall, as well as to construct trails that lead to food resources. Pheromones also control caste recognition in termites. Both royal males and royal females identify others of their kind through pheromones. When a queen termite encounters another queen, the pheromones they release produce fighting behavior.

II.A.3 Bee dances

One the most famous examples of animal communication is the dance done by honeybees to indicate food sources. The bee "language", decoded by von Frisch (1974), is used by a bee that has discovered a source of food to inform others of its approximate angle and distance from the hive¹. A bee, upon returning to the hive, performs a tail-wagging dance in the shape of a figure-eight. The amount of time it takes the bee to traverse the straight, central portion of the dance indicates the distance to the food source, while the angle of this traversal gives its angle of the source using the position of the sun as a reference. The degree of vigorousness of the dances indicates the quality of food at the source. In addition, scent from the flower becomes attached to the bee, and indicates the flower type to others. This effectively gives an indirect signal from the flower to the other bees.

¹ von Frisch won the Nobel Prize in 1973 for this work, a prize he shared with Nikolaas Tinbergen and Konrad Lorenz.

II.A.4 Vervet monkey alarm calls

While many animal species have some form of alarm call system, perhaps the most studied is that of the vervet monkey (Strusaker, 1967; Seyfarth, Cheney, and Marler, 1980a; Seyfarth, Cheney, and Marler, 1980b). Vervets use a system of alarm calls that distinguishes the different kinds of danger posed by various species of their predators. When a vervet sees an eagle, it gives an alarm call that sounds like a cough. When a large cat such as a leopard is seen, a barking sound is made. When a vervet sees a snake, it utters a chattering sound. Each of these alarm calls causes other vervets that hear them to engage in evasive behavior appropriate to the predator: in response to the eagle's call, the monkeys look up or run into bushes, the calls given in response to large cats cause vervets to run into tress, and the snake call causes the monkeys stand up and look in the grass. That the monkeys are responding to the alarm calls, and not to the predators themselves is indicated by the results of playback studies. Seyfarth, Cheney, and Marler (1980b) have shown that vervets make the appropriate response to recorded calls in the absence of an actual predator.

II.A.5 Human language

No survey of animal communication, however brief, would be complete without making mention of human language. Human language, due to its unique complexity, is generally considered separately from communication in other species. Human beings are animals, however, and human language is a form of communication. It is therefore my intent that the results of the research presented in this dissertation apply to human communication, linguistic or otherwise.

The primary focus of this dissertation, however, will be on the properties of a subset of communication systems that I will call *simple*. Simple communication systems are those which make use of signals that are independent and discrete. In other words, the signals have no meaning-bearing internal structure, and cannot be combined together to create more complex utterances. This is to be contrasted with the combinatorial, syntax-governed structure of human languages, for which the term *language* will be reserved. Thus, while not all communication systems have the properties required of language, human language is a system of communication.

II.B Defining communication

The goal of this section is to establish a definition of communication that is general enough to encompass all of the examples given in the previous section, while still remaining sufficiently specific to exclude cases that common sense would rule as not involving communication.

This is an extremely difficult task, and one that has been attempted by many other researchers – each of whom, more often than not, differs with the others. A selection of these previous definitions will be reviewed here, as they will both contrast with, and provide a basis for the definition that will subsequently be formulated and used throughout the rest of this dissertation.

II.B.1 Previous definitions of communication

Attempts to define communication have, to a large extent, come from two different groups of researchers: those studying human language and those studying communication in other animals. Despite the similarities underlying communication in both cases, these definitions have proceeded more or less independently, and tend, at least on the surface, to seem incompatible with one another.

The study of human communication is closely intertwined with the philosophical notion of *intent*. Grice (1957), in defining what he calls *true* meaning, requires that individuals take into account the mental states of others. In particular, Grice wanted to distinguish cases of true meaning from events that have what he called *natural* meaning. In the nautical saying “Red sky at night, sailor’s delight. Red sky at morning, sailor take warning,” the color of the sky is taken to carry information about impending weather. There is no sense, however, in which the sky *intentionally* conveys this information.

According to Dennett (1987), individuals are intentional systems to the degree that they have mental states (beliefs, desires, emotions), and are capable of attributing them to others. He argues that communication requires that an individual has at least what he calls *second-order intentionality* – not only having their own mental states, but being capable of attributing such states to others. The more complicated nuances of human language, such as sarcasm, require even higher-order levels of intentionality.

In contrast, definitions of communication put forward in the more general context of animal behavior tend not to make reference to intentionality. Instead, the defining feature is generally whether or not the potentially communicative behavior results in a selective advantage to one or more of the participants involved in the exchange. There seems to be no general consensus, however, on whether communicative acts must benefit the sender, the receiver, or both. Wilson (1975), for example, considers an interaction to be communicative if it is adaptive from the perspective of either participant.

Communication is seen by some to be a primarily manipulatory behavior. In this case, it is only important that the behavior convey a selective advantage on the transmitter (Burghardt, 1970; Dawkins and Krebs, 1978). Dawkins and Krebs (1978) define communication as occurring

		Receiver:	
		Benefit	No Benefit
Sender:	Benefit	Communication	Manipulation
	No Benefit	Exploitation	Spite

Figure II.1: Classification of interaction types. Communication is differentiated from manipulation and exploitation based on the selective advantage conveyed to sender and receiver. Modified from Bradbury and Vehrencamp (forthcoming), after Wiley(1983).

when “an animal, the actor, does something which appears to be the result of selection to influence the sense organs of another animal, the reactor, so that the reactor’s behavior changes to the advantage of the actor” (p. 282). While this is a perfectly reasonable definition of manipulative behavior, others find it to be somewhat lacking as a definition of communicative behavior. This results, most likely, from a difference of opinion over what classes of behavior should be included and which should be excluded from the definition.

Bradbury and Vehrencamp (forthcoming) differentiate communication from other forms of interaction, such as manipulation and exploitation, based on the selective advantage conveyed to the sender and the receiver. As can be seen in Figure II.1, manipulative interactions convey an advantage to the sender, but not to the receiver. Exploitative interactions involve the opposite situation, conveying an advantage to the receiver, but not to the sender. They call interactions that are beneficial to neither party *spite*. By their definition, then, an interaction is only communicative if *both* the sender and the receiver benefit from it.

Because certain interactions that we will want to call communicative may not involve direct benefits to sender and receiver, this framework requires a small modification. In situations involving kin selection, for example, selection is best seen as operating at the level of the gene rather than the individual. In order to account for such situations, the benefit to the individuals involved in an interaction should be expressed in terms of inclusive fitness. Lewis and Gower (1980) approach this problem by being appropriately vague about the locus of a selective advantage, defining communication as “the transmission of a signal or signals between two or more organisms where selection has favored both the production and the reception of the signal(s)” (p.2).

II.B.2 Incompatible definitions

While intent-based notions of communication are sufficient to characterize human behavior, and fitness-based notions of communication provide a good classification of innate be-

havior, neither provides a general definition of communication.

A Gricean approach will conclude that most, if not all, non-human animals are incapable of communication – it is probably safe to assume that second-order intentionality is a great deal to ask of a bee or a flower. Even vervet monkeys, whose alarm calls are so often used as an example of animal communication, are unlikely to possess the level of sophistication that Grice requires (Cheney and Seyfarth, 1990; Cheney and Seyfarth, 1996). Because of this, although I believe that the study of intentionality, and of theory of mind in general, is relevant to attempts to ascertain the cognitive abilities of a species, I will argue that such issues are not germane to the task of determining what classes of behavior should be termed communicative. Although a vervet monkey may not intend, or even be aware that its leopard alarm call may indicate the presence of a leopard to other monkeys, there is still something more to this interaction than the way the color of the sky may indicate to a sailor that a storm is approaching. Because the requirement of intent excludes many animals whose behavior I believe should be called communication, it is necessary to look elsewhere to make the appropriate classification.

The definitions of communication based on selective advantage put forward in the animal communication literature are equally limited. They are tied quite tightly to communication systems that are innate, having been tuned by natural selection. In the case of human language, it is difficult to determine what, if any, selective advantage an interaction conveys on its participants. Even if it were possible to trace back intentional behavior to its evolutionary roots, the resulting connections would likely be too remote and convoluted to prove useful.

Because the communication systems that will be explored in this dissertation involve both innate and learned behavior, it will be useful to have a definition that encompasses all communicative interactions: innate systems, simple learned systems, and even human language. The following section attempts to formulate such a definition.

II.B.3 A causal definition of communication

Consider the communication system set up during the American revolution to warn of impending British attacks, and immortalized as “one if by land, two if by sea.” One lantern was lit to signal that Paul Revere should warn of a land attack, two lanterns were lit to warn of an attack across the Charles river, and no lanterns indicated that no attack was coming. The reason that this system is communicative has to do with the way various parts of it interact with one another. Why would an impending attack by sea cause two lanterns to be lit? Because this would signal to the defenders that they should defend against an attack on the shore. Why would a two-lantern signal cause preparations for a coastal defense? Because if the British were

$$X \rightarrow Y \rightarrow Z$$

Figure II.2: The form of a causal interaction. The sender, in situation X , exhibits behavior Y , and the receiver, upon observing this behavior, has a reaction Z .

going to attack across the river, two lanterns would be lit.

While this kind of reasoning seems circular, I argue that it is this very circularity that is at the heart of a definition of communication. An interaction is communicative only if the send and receive behaviors are such that, in some sense, each is an explanation for the other. The sender behaves the way it does because of how this behavior can be expected to be interpreted by the receiver.² The receiver interprets the sender's behavior the way it does because the sender can be expected to behave this way in particular situations. In the case of the lantern signaling system, the two halves of the system, while operating independently, have been structured to correspond to one another. In this case, this correspondence was explicitly established, but such design is not required.

The kind of interaction we are interested in, then, is one involving a causal chain of events. An interaction is causal when one individual, the sender, exhibits a behavior in response to a particular situation, and a second individual, the receiver, responds to this behavior (Figure II.2). Not all such causal interactions are communicative, however – the abovementioned synergistic relationship between send and receive behavior is required.

Exploitation and Manipulation

It is important that communication can be distinguished from situations that simply involve exploitation or manipulation of one animal by another. A causal interaction is exploitative if the fact that the receiver responds to the sender's behavior the way it does has, to some degree, been determined by the fact that the sender can be expected to behave this way in response to a particular situation (Figure II.3a).³ For example, consider the detection of bluffing in the game of poker. Suppose that one player has noticed that another player has a habit of blinking when he is bluffing a hand. The first player can then take advantage of this regularity to raise the bet in such situations. In this situation, the reason that the first player raises the bet is that there

²It is important to note that, while this could involve an explicit expectation on the part of the sender, all that is required is that the sender's behavior has been tuned in some way to be responsive to regularities that exist in the receiver's behavior.

³The qualification "to some degree" is used here because a myriad of different causes are likely to contribute to any given behavior. What is important in this case is that the sender's behavior is one of the factors that has shaped the receiver's response.

$$(X \rightarrow Y) \implies (Y \rightarrow Z)$$

a)

$$\left(\begin{array}{l} \text{Player 1 is} \\ \text{bluffing} \end{array} \rightarrow \text{Player 1 blinks} \right) \implies \left(\text{Player 1 blinks} \rightarrow \text{Player 2 raises} \right)$$

b)

Figure II.3: The form of an exploitative interaction. The general framework is shown in diagram a). Diagram b) gives an example where, in a poker game, one player exploits the habit of another who blinks when he is bluffing.

$$(X \rightarrow Y) \Leftarrow (Y \rightarrow Z)$$

a)

$$\left(\begin{array}{l} \text{Female} \\ \text{firefly is} \\ \text{hungry} \end{array} \rightarrow \begin{array}{l} \text{Female imitates} \\ \text{mating flash} \end{array} \right) \Leftarrow \left(\begin{array}{l} \text{Female imitates} \\ \text{mating flash} \end{array} \rightarrow \begin{array}{l} \text{Male of other} \\ \text{species responds} \\ \text{and is eaten} \end{array} \right)$$

b)

Figure II.4: The form of a manipulative interaction. The general framework is shown in diagram a). Diagram b) gives an example where a female firefly imitates the mating flash-code of another firefly species, attracting a male and eating him.

is a regularity between the other player's blinking and bluffing. This interaction is diagrammed in Figure II.3b.

A causal interaction is manipulative if the fact that the sender behaves the way it does in a given situation has, to some degree, been determined by the fact that the receiver can be expected to respond in a particular way (Figure II.4a). An example of this kind of behavior is the hunting technique of certain female fireflies, who imitate the mating flashing code signal of another firefly species (Lloyd, 1984). The males of the second species, arriving prepared to carry on their genetic line, are promptly eaten by the female deceiver. This interaction is shown in Figure II.4b.

Communication

A causal interaction is communicative if it can be described both as a manipulative interaction and as an exploitative interaction, as shown in Figure II.5a. This allows us to define communication in the following way:

An act of communication is a causal chain of events, whereby one individual, the sender, exhibits a behavior in response to a particular situation, and a second individual, the receiver, responds to this behavior. Such an interaction is communicative if it involves manipulation on the part of the sender, and exploitation on the part of the receiver.

Two examples of communicative behavior are shown in Figure II.5. The first is an example of human communication: attracting a waiter's attention in a restaurant (Figure II.5a). The customer wants to pay, so she raises her hand. The waiter sees the customer's raised hand and comes over to the table. The reason that the signal is transmitted is that it will have a particular outcome, namely attracting the waiter's attention. The reason the waiter comes over to the table is because of a known association between customers wanting to pay and the hand signals that they make.

The second example involves an innate behavior – the threat displays observed in the hostile interactions of many species. One animal, being in an aggressive state, makes a particular display with its body. The other animal, upon observing the display, may withdraw from the interaction. The withdrawal of the second animal is a result of an innate response to the display behavior. This response has been tuned by natural selection because of the association of the display with another animal's state of aggression. The display behavior itself has also been tuned by evolution, being selected for because it has the response that it does – namely causing another animal to back down.

II.B.4 The chicken or the egg?

The circular nature of this definition of communication may still seem to be problematic. Consider the chattering sound used by vervet monkeys as an alarm call for snakes. It seems circular to say that the response of vervets to a chattering sound caused vervets to chatter when they see a snake, and also to say that the fact that vervets chatter when they see a snake caused vervets to respond with the appropriate evasive action. Two things can not cause each other if neither of them initially existed. The solution to this problem is the same as the solution to most “chicken and egg” problems: neither was initially present in its current form, but small tendencies were exaggerated over time in a feedback loop. The initial correlation may have been

$$(X \rightarrow Y) \begin{array}{c} \Longrightarrow \\ \Longleftarrow \end{array} (Y \rightarrow Z)$$

a)

$$\left(\begin{array}{ccc} \text{Customer wants} & \rightarrow & \text{Customer raises} \\ \text{to pay} & & \text{his hand} \end{array} \right) \begin{array}{c} \Longrightarrow \\ \Longleftarrow \end{array} \left(\begin{array}{ccc} \text{Customer raises} & \rightarrow & \text{Waiter comes to} \\ \text{his hand} & & \text{the table} \end{array} \right)$$

b)

$$\left(\begin{array}{ccc} \text{Animal 1 is in} & \rightarrow & \text{Animal 1 gives} \\ \text{an aggressive} & & \text{a threat display} \\ \text{state} & & \end{array} \right) \begin{array}{c} \Longrightarrow \\ \Longleftarrow \end{array} \left(\begin{array}{ccc} \text{Animal 1 gives} & \rightarrow & \text{Animal 2} \\ \text{a threat display} & & \text{withdraws} \end{array} \right)$$

c)

Figure II.5: The form of a communicative interaction. Diagram a) gives the general framework. Diagram b) gives an example of human communicative behavior, where customers attract the attention of waiters by making hand gestures. Diagram c) gives an example of innate communication, where a threat display is used to mediate a hostile interaction.

small and randomly introduced, or, as seems often to be the case, derived from some aspect of a related behavior (Tinbergen, 1952; Moynihan, 1970; Brandon and Hornstein, 1986).

II.B.5 Defining communication in practice

Because of the historical nature of the causal links between transmission and reception behavior, it will often be difficult to tell whether a given behavior is truly communicative or not – there will often be multiple possible explanations. In the case of an alarm call system, for example, the animals could respond with cries of alarm because of biological reasons unrelated to the effect they have on others. The animals might then have been tuned by evolution to respond to these cries, resulting in a form of interaction that would be exploitation. On the other hand, the animals might be startled by certain sounds, again for reasons unrelated to any tendency of others to make them. Selection might then result in individuals that produce such sounds in response to predators, resulting in a manipulative form of interaction.⁴ Or the alarm behavior might truly be communication, with both alarm production and the response to it being tuned based on one another.

To determine whether any particular interaction is communicative will tend to require a historical argument. Such arguments will be *a priori* and, as such, must be speculative. In some cases, the situation will be relatively clear. For example, a common form of manipulation in insects is the imitation of another species' mating calls by a predator in order to attract prey (such as the firefly behavior described earlier). In this case, it is unlikely that the receiver's behavior has been tuned in response to the signals of the predator. Other situations, such as seemingly altruistic alarm calls that are made despite possible danger to the sender, are more difficult to assess. This difficulty is the primary motivating factor for the use of simulation, the main analytic technique that will be used in the research I present. In contrast to the study of real-world communication systems, the history of a simulation is accessible, and the selective pressures on an individual are manipulatable. In section V, I will return to these issues, using evolutionary simulations to demonstrate situations of exploitation and manipulation.

II.B.6 An inclusive definition of communication

In defining communication, I have focused on the synergistic relationship that must exist between transmission and reception behavior. This synergy can occur as a result of a variety of different pressures. It could result from the action of a learning mechanism, or it may, as is the

⁴Such behavior is *still* manipulative even if the receiver benefits. This points out a key difference between the present definition of communication and those that are based directly on selective advantage to sender and receiver.

case with most communication systems, be a result of natural selection. It might be established explicitly by agreement, or it may involve rational agents trying to predict each other's behavior. The failing of most existing definitions of communication is that they confound the relationship that exists between send and receive behavior with the pressure that established it. This leads to definitions that are limited in scope. They are designed to account for systems that have been established by a particular mechanism, and fail to apply in other cases. By separating the mechanism from the results it produces, the definition of communication proposed in this chapter is able to encompass a more general class of behavior.

Chapter III

Communication system formalism

In order to study communicative behavior within a computational or mathematical framework, it is necessary to come up with a formalism with which to describe it. As is always the case with such a formalism, it will be an abstraction from the reality, and will involve numerous simplifying assumptions. Previous models of communication have been presented by Lewis (1969), Hurford (1989), and Skyrms (1996). The present model shares much in common with this previous work, particularly that of Hurford.

III.A Signals and meanings

We will assume that there is a set, E , of environmental states that an animal is capable of distinguishing between, and a set, A , of distinct actions that the animal can perform in response to these states of the environment. Let us further assume, for the sake of simplicity, that these sets E and A are the same size, and that there is a one-to-one function, a , that determines, for each state $\epsilon \in E$, a unique action, $\alpha \in A$, that is appropriate. The animal in the course of its everyday behavior will, when it observes some state ϵ (such as the presence of a particular predator), perform action $a(\epsilon)$ (such as appropriate evasive behavior).

This describes the behavior of an individual animal interacting with its environment. Often, however, one individual has privileged information about some state of the environment (including, perhaps, its own internal state) that another, uninformed individual does not have access to. Communication provides a way for the uninformed individual to react appropriately to the state of the environment by using the informed individual as an intermediary.

In order for communication to be possible, the animals must have at their disposal a set, S , of low-cost behaviors which are observable and can be distinguished by others. We will call

these behaviors *signals*. Because the set of environmental states and their appropriate responses are linked to each other in a one-to-one fashion, it will be convenient to refer to each associated pair together as a single *meaning*, $\mu \in M$.

A communicative interaction, then, involves one individual observing an environmental state ϵ , and producing a signal, $\sigma \in S$. A second individual observes the signal σ , and performs an action, α .¹ Communication is said to be successful if the action is appropriate to the environmental state ($a(\epsilon) = \alpha$).

An individual's communicative behavior will be characterized in two distinct parts. The first, *transmission*, determines what signal will be sent for a given meaning. The second, *reception*, determines what meaning a given signal will be interpreted as. Both of these behaviors will be described by probability functions. $s(\mu, \sigma)$ represents the probability that a signal σ will be sent for a meaning μ by a transmitter, and $r(\sigma, \mu)$ represents the probability that a signal σ will be interpreted as meaning μ by a receiver. The send function s , then, gives a probabilistic mapping from meanings to signals, while the receive function r maps back from signals to meanings.

III.B Communicative accuracy

Consider two individuals involved in a communicative interaction, the transmitter with send function s and the receiver with receive function r . For a particular meaning μ , $r(\sigma, \mu)$ is the probability that, if a given signal σ is sent for μ , it will be correctly interpreted by the receiver. The probability, then, that meaning μ will be correctly communicated is the weighted average of this conditional probability across all possible signals, with the weighting term being the probability, $s(\mu, \sigma)$, that the transmitter will use a particular signal:

$$\sum_{\sigma} s(\mu, \sigma) r(\sigma, \mu) \tag{III.1}$$

We can now compute the expected probability that signals sent using send function s will be correctly interpreted by receive function r . This probability, which we will write as $ca(s, r)$, will be called the *communicative accuracy* from s to r . If we assume that all meanings are equally likely to serve as the subject of a communicative interaction, then this value is the average probability that any given meaning will be correctly communicated:

$$ca(s, r) = \frac{1}{|M|} \sum_{\mu} \sum_{\sigma} s(\mu, \sigma) r(\sigma, \mu) \tag{III.2}$$

¹Interactions involving groups of animals can generally be reduced, for the purposes of analysis, to simple interactions between two individuals. If one animal gives an alarm call that is heard by a group of others, each of these other animals can be considered to be involved in a communicative interaction with the calling animal.

s	a	b	c
1	1.0	0.0	0.0
2	0.0	0.6	0.4
3	0.0	0.4	0.6

a	b	c	r
1.0	0.0	0.0	1
0.0	0.4	0.6	2
0.0	0.6	0.4	3

Figure III.1: An example communication system.

where $|M|$ is the number of meanings. The maximum value of $ca(s, r)$ is $|S|/|M|$, giving a maximum communicative accuracy of 1.0 as long as there are at least as many signals available as there are meanings to be conveyed.

Figure III.1 shows sample send and receive functions for communication involving three meanings (1,2, and 3) and three signals (a,b, and c). To calculate $ca(s, r)$, we calculate the accuracy for each meaning using Equation (III.1):

$$\begin{aligned}
 \text{Meaning 1} &\rightarrow (1.0)(1.0) + (0.0)(0.0) + (0.0)(0.0) = 1.00 \\
 \text{Meaning 2} &\rightarrow (0.0)(0.0) + (0.6)(0.4) + (0.4)(0.6) = 0.48 \\
 \text{Meaning 3} &\rightarrow (0.0)(0.0) + (0.4)(0.6) + (0.6)(0.4) = 0.48
 \end{aligned}$$

The communicative accuracy between s and r is the average of these three values, or 0.65.

In addition to knowing how well a given transmitter will be understood by a given receiver, it is often important to calculate how well two individuals will intercommunicate. This probability, called *two-way communicative accuracy* (ca_2), is simply the average of the two one-way probabilities (assuming each takes turns sending and receiving with equal frequency). For two individuals with send and receive functions s_1, r_1 and s_2, r_2 respectively, the calculation would be:

$$ca_2(s_1, r_1, s_2, r_2) = \frac{1}{2} (ca(s_1, r_2) + ca(s_2, r_1)) \quad (\text{III.3})$$

III.C Communicative accuracy of a population

The communicative behavior of a population can be represented in much the same way as that of an individual. Assuming that each individual in the population is given equal weight, the behavior of the population can be characterized as the expected behavior of an individual selected randomly from it. This expected behavior can be expressed in terms of average send and receive functions for the population. These functions, S and R , can be calculated by averaging

the send and receive probability functions (s_i and r_i) of all individuals in the population:

$$S(\mu, \sigma) = \frac{1}{N} \sum_i s_i(\mu, \sigma) \quad R(\sigma, \mu) = \frac{1}{N} \sum_i r_i(\sigma, \mu) \quad (\text{III.4})$$

where N is the number of individuals in the population.

These two new probability functions represent the transmission and reception behavior of an average member of the population, and can themselves be used in the equations formulated in the previous section. This allows us to calculate values for communicative accuracy involving entire populations. The probability with which a particular individual (with send and receive functions s and r) will communicate accurately with a population (described by send and receive functions S and R) is $ca_2(s, r, S, R)$. The average communicative accuracy within the population is $ca(S, R, S, R)$, which will simply be written as $ca(S, R)$.

III.D Optimal communication

As mentioned earlier, if we assume that there are at least as many signals as there are meanings, the maximum communicative accuracy achievable is 1.0. In order to achieve this optimal state of communication, a population must satisfy three independent requirements:

Coordination: Each individual's send and receive functions must communicate with each other at least as well as either would communicate with any other system. Thus, for any individual in the population with send function s_i and receive function r_i :

$$ca(s_i, r_i) \geq ca(s_i, r_o) \quad (\text{III.5})$$

for any other receive function r_o and:

$$ca(s_i, r_i) \geq ca(s_o, r_i) \quad (\text{III.6})$$

for any other send function s_o .

Distinctiveness: In each individual's send function, each signal must be sent for exactly one meaning. In each individual's receive function, each signal must be interpreted as exactly one meaning. Thus, for each meaning μ , there is a signal σ such that $s(\mu, \sigma) = 1.0$, and $s(\eta, \sigma) = 0.0$ for all meanings $\eta \neq \mu$. Also, for each meaning μ , there is a signal σ such that $r(\sigma, \mu) = 1.0$, and $r(\kappa, \mu) = 0.0$ for all signals $\kappa \neq \sigma$.²

²This condition only holds strictly if there are equal numbers of signals and meanings. In cases where there are more signals than meanings, it is possible to have equivalence classes of signals, where each member of the class is interpreted identically to the others by the population. In cases where there are fewer signals than meanings, the requirement of distinctiveness cannot be satisfied, and optimal communication cannot be achieved.

Consensus: All individuals must have the same communication system. Thus, for any two individuals with send and receive functions s_i, r_i and s_j, r_j :

$$s_i(\mu, \sigma) = s_j(\mu, \sigma) \quad r_i(\sigma, \mu) = r_j(\sigma, \mu) \quad (\text{III.7})$$

for any meaning μ and signal σ .³

If any one of these requirements is not fully met, the population will not communicate optimally. To prove this, we will consider each requirement in turn.

Lack of coordination

Suppose that a population has consensus and that each individual's system is fully distinctive, but that some individual's system is not fully coordinated. This means that there is some other communication system that would communicate more accurately with this individual than this individual communicates with itself. Because all individuals in the population have the same system, this means that, for any two individuals, there exists a communication system that would communicate with either one of them more accurately than they communicate with each other. In this case, the population's communicative behavior cannot be optimal.

Lack of distinctiveness

Suppose that a population has consensus and that each individual has a fully coordinated communication system, but that some individual's system is not fully distinctive. This individual, then, transmits the same signal for more than one meaning, or interprets a signal as more than one meaning. This results in an ambiguous situation, and the individual will not communicate optimally with any member of the population. Thus, the population's communicative behavior cannot be optimal.

Lack of consensus

Finally, suppose that each individual has a fully coordinated, fully distinctive communication system, but that not every individual has the same system. This means that there exists some individual that, for a given meaning sends a different signal than some other individual does, or, for a given signal, interprets that signal differently than does some other individual. If we assume equal numbers of signals and meanings, this will necessarily result in a miscommunication between the two individuals.

³The requirement of consensus has a similar exception to the requirement of distinctiveness in cases where there are more signals than meanings. If there is an equivalence class of signals, individuals can then transmit any member of the equivalence class without affecting communicative accuracy.

		Player 2:	
		Go to A	Go to B
Player 1:	Go to A	2,2	0,0
	Go to B	0,0	1,1

Figure III.2: An example game. Two people want to meet for dinner, and they would both prefer to go to restaurant *A*.

III.E Game-theoretic notions of communication

The mathematical theory of games, first put forward by Von Neumann and Morgenstern (1953), is a technique for describing behavior in economic situations. The basic model involves an interaction between a finite number of participants, each of whom can take one of a number of possible courses of action. Depending on the combination of actions taken by the players, each receives a payoff. Nash (1951) laid the foundation for the study of games in which the participants choose actions independently. By assuming that people behave in a rational, self-interested manner, it is possible to predict the outcome of such interactions. More specifically, certain pairs of actions are stable and others are not. Stable action pairs (called Nash equilibria) are those where no player can better their situation by unilaterally changing their course of action.

Consider the example of two people meeting for dinner. Suppose that there are two possible restaurants (*A* and *B*), and they each must decide independently which one to go to. If they do not want to end up at different restaurants, and furthermore, both prefer restaurant *A*. A payoff matrix for this situation is shown in Figure III.2. This game has two pure-strategy Nash equilibria – the situation where both players go to restaurant *A* and the situation where they both go to restaurant *B*. Despite the fact that both players would prefer to eat at restaurant *A* (making it an *efficient* equilibrium in the terminology of game theory), classical game theory simply predicts that the result of the game will be one of the two Nash equilibria.

The inability of classical game theory to rule out inefficient equilibria serves as the motivation for the introduction of communication into a game. The idea here is that if the players were able to communicate with one another, they would be better able to coordinate on an efficient equilibrium. While this seems true intuitively, it has proven difficult for economists to demonstrate it formally. The basic problem is that communication, implemented as a cost-free interaction before the game itself (termed *cheap-talk*), does not alter the payoff structure. The result is that the signals are meaningless and inefficient equilibria still cannot be eliminated.

Farrell (1988) considered a version of a communication game very similar to the model presented earlier in this chapter. He showed that, while optimal systems of communication are Nash equilibria, there are also other, inefficient equilibria. This is true even in cases where the individuals' interests coincide. These sub-optimal equilibria involve situations where a signal is sent for more than one meaning, or more than one signal is interpreted as the same meaning.

This result is rather disturbing, as it fails to predict that rational individuals will communicate effectively with each other even when it is in their best interest to do so. One possible explanation of this apparent dilemma is that the apparatus of classical game theory is too simple to account for the phenomenon. More satisfactory results have been achieved within the framework of evolutionary game theory. This framework will be discussed in section IV.A and the results obtained from it will be reviewed in section IV.F.

Chapter IV

Evolved communication systems

The vast majority of existing communication systems are innate, the behavior of transmitting and receiving signals being present at birth and remaining fixed throughout an individual's lifetime. These systems of communication, then, have been tuned by natural selection. This chapter will investigate the conditions necessary for such systems to emerge.

IV.A Evolutionary game theory

Evolutionary game theory is an extension to classical game theory. The basic model remains the same, but is extended to apply to populations of individuals in an evolving population (Hamilton, 1964; Hamilton, 1967; Maynard Smith, 1982). In the evolutionary case, the action an individual takes in a game is determined by natural selection, rather than rational choice. The payoff an individual receives from playing the game against other members of the population provides a fitness metric that can be used as the basis for selection.

Evolutionary game theory allows predictions to be made about what conditions are required for a population of individuals to maintain a stable state. Maynard Smith formalized this by introducing the notion of Evolutionary Stable Strategy (ESS) (Maynard Smith and Price, 1973; Maynard Smith, 1982). A strategy of play in a game is evolutionarily stable if a population of individuals all playing this strategy cannot be invaded by any other strategy. This means that a strategy A is an ESS if the payoff it receives by playing others of strategy A is greater than the payoff any mutant B gets playing individuals with strategy A . Mathematically:

$$P(A, A) > P(B, A) \tag{IV.1}$$

A strategy can also be stable if:

$$P(A, A) = P(B, A) \text{ and } P(A, B) > P(B, B) \quad (\text{IV.2})$$

One can see from this formulation that any ESS will also be a Nash equilibrium. Since no mutant can play better against strategy A than A can play against itself, there is no motivation for either of two players playing strategy A to switch to anything else.

While evolutionary game theory can determine whether a strategy is stable, it says nothing about whether such a strategy could come to dominate a population in the first place. Such claims about achievability rather than simply stability turn out to be much more difficult to make. This difficulty serves as the primary motivation for the use of computational, rather than purely mathematical techniques when studying evolutionary dynamics.

IV.B Evolutionary Computation

Evolutionary computation, variants of which have been introduced under different names by different people, refers to the use of simulation techniques inspired by biological evolution to try to solve computational problems. It involves creating populations of simulated “individuals” and subjecting them to simulated, fitness-based selection pressures. The most commonly referred-to variants are *genetic algorithms* (Holland, 1975), *evolutionary programming* (Fogel, Owens, and Walsh, 1966), and *evolutionary strategies* (Rechenberg, 1973).

More recently, similar techniques have been used in an area somewhat dubiously known as *Artificial life* (Langton, 1989). In this framework, rather than using evolution to as a means of computation, computation is used as a means for studying evolution. The simulations that will be presented in this chapter are of this latter kind, using computational simulation techniques as a means of exploring changes that may have occurred in real biological systems over evolutionary time.

Most of the simulations I will present are generation-based. In a generation-based model, the individuals in a population are evaluated and reproduce (based on fitness) to create a new generation of individuals. It is important to clarify how the word *fitness* is generally used in the area of evolutionary computation. In biology, fitness is a technical term that is generally defined as the number of offspring an individual has during the course of their lifetime. In evolutionary simulations, the programmer decides on some relevant means of measuring an individual’s ability to perform the task of interest. This evaluation, often called a *fitness function* yields a number which I will refer to as the individual’s *fitness-evaluation*. The number of offspring an individual has is determined based on this fitness-evaluation.

There is a key difference between the way evolutionary computation techniques are used in the simulations presented in this dissertation, and the way it they are used when applied typical problems of function optimization. Optimization problems generally have a fixed fitness function. This means that there is a static function that, when applied, gives the quality of a genome with respect to a particular, fixed problem. The simulations presented here use what is called *relative fitness*, where the fitness-evaluation of a particular individual depends on interactions with the rest of the population (the class of behavior that evolutionary game theory is designed for). The use of relative fitness is required when the fitness-relevant task is social. In the case of communication, it does not make sense to evaluate the ability of a particular, isolated individual to communicate. What is important is an individuals ability to communicate with others.

IV.C Related work

A number of other researchers have used evolutionary computation techniques to study the evolution of communication. This work has generally focused on the emergence of communication as a way of mediating activity in some other task. Werner and Dyer (1991) studied the evolution of mating signals that allowed immobile “females” to direct mobile but blind “males” to their location. MacLennan and Burghardt (1994) evolved populations of finite-state machines in a task where communication provided a mechanism for cooperative behavior. Ackley and Littman (1994) looked at the evolution of signals that allowed simulated organisms to help each other avoid predators. Levin (1995) used genetic algorithm techniques to study the evolution of correspondences between agent’s internal states and externally observable behaviors. A number of researchers have used a grid-like environment scattered with “food” particles to study how communication might evolve to facilitate coordinated foraging behavior. Cangelosi and Parisi (1996) use such a model to evolve networks to classify edible/inedible food and pass this information on to others via a communication system. Di Paolo (1996) presents a similar simulation framework.

While the evolutionary simulations that will be discussed in the next sections share much in common with the work described above, they are generally more abstract and less tied to a particular ecological context. This allows for the investigation of the pressures necessary to evolve systems of communication independently of the pressures imposed by any particular task.

Transmission Genes			Reception Genes		
Signal made			Meaning interpreted		
Meaning to encode	0	d	Signal observed	a	1
	1	a		b	2
	2	b		c	3
	3	c		d	0

Figure IV.1: Structure of an example genome. Note that this is a perfect communication system, as the reception system is the inverse of the transmission system. It is perfect in the sense that if all individuals in a population used it, communication would always succeed. For example, in response to meaning '0', signal 'd' is sent. Signal 'd' is interpreted as '0', which is the original meaning.

IV.D Simulation framework

IV.D.1 Structure of the genetic representation

To use evolutionary computation techniques in conjunction with the communication system formalism describe in section III, a suitable genetic representation must be found. The communication system formalism is, by its very nature, probabilistic. For ease of representation, however, the systems used in the following simulations will be deterministic. This can be thought of as constraining the system to send a single signal with probability 1.0 for each meaning, and interpreting a each signal as a single meaning with probability 1.0.¹

This simplification allows us to express a communication system in the form of a look-up table. For each meaning, we keep track of what signal is sent for it. For each signal, we keep track of what meaning it is interpreted as. An example of such a look-up table can be seen in Figure IV.1.

This look-up table is then used as an individual's genome. The signals given in response to each meaning are put on the genome in order, followed by the meanings each signal is interpreted as. The look-up table shown in Figure IV.1 would be represented in genetic form as is shown in Figure IV.2.²

¹It is important to note that this does not mean that the system will be forced to be fully distinctive. The same signal can be sent for multiple meanings, and multiple signals can be interpreted as the same meaning.

²To ensure that this specific genetic representation is not critical to my results, I have also tried other representations. The results I will report here are robust with respect to such changes.

d	a	b	c	1	2	3	0
---	---	---	---	---	---	---	---

Figure IV.2: The genetic representation of a communication system. The entries in lookup-tables representing the transmission and reception systems are simply placed one after another.

IV.D.2 Fitness and reproduction

Now that we have a genetic representation, we need to define a fitness function in order to evaluate individuals and allow the process of selection to operate. The fitness functions used in the simulations I will present are all based on the communicative accuracy measure described in chapter III. The evaluation of an individual is done by placing it in a number of communicative interactions with randomly selected other members of the population. In each interaction, one individual is designated to be the transmitter, and produces a signal based on a meaning. The other individual, designated to be the receiver, produces a response to the signal provided by the transmitter. Successful communication between the two individuals is considered to have occurred when the receiver's response to a signal produced by the transmitter matches the meaning the transmitter encoded. The process is then repeated, with the roles of transmitter and receiver reversed.

After each interaction, both individuals involved receive a contribution to their fitness-evaluation that depends on the success of the interaction and the particulars of the simulation involved. An individual's final fitness-evaluation is determined by summing all of the contributions it has received and then dividing this value by the number of interactions the individual was involved in.

The number of offspring an individual has is proportional (probabilistically) to its fitness-evaluation. This means that if an individual has twice the fitness of another, will be expected to be represented with twice the frequency in the new population. For each slot to be filled in the new population, an individual is selected to reproduce. The probability that a particular individual is chosen is proportional to its fitness-evaluation. This results in a new population consisting of copies of individuals from the previous population.

The new population is then subjected to the process of mutation in order to provide new genetic variation. Because the entries that make up the genome have no inherent ordering, if one is effected by a mutation it will change randomly to any value in the valid range (including, possibly, the original value). When a mutation rate is given for a particular simulation, this value is the percent chance that any particular gene (look-up table entry) on any individual's genome will be changed in a generation.

	Success	Failure
Transmitter	1.0	0.0
Receiver	1.0	0.0

Figure IV.3: Payoff matrix for common interest communication. Both the sender and the receiver get a high (1.0) payoff when communication between them is successful, and a low (0.0) payoff when it is not.

IV.E Simulation parameters

Unless otherwise stated, the size of the populations used in all simulations is 100 individuals. The mutation rates used are generally quite low (on the order of 1 in 1000) and will be only be reported where variation in the mutation rate has been found to qualitatively affect the results of the simulation.

IV.F Situations of common interest

Now that the simulation framework has been defined, the only additional requirement needed to do an evolutionary simulation is a fully-specified fitness function for communicative interactions. The first scenario that I will consider assumes that communication between two animals is a matter of common interest. That is to say that both sender and receiver have a fitness-related stake in the outcome of a communicative exchange. Through the use of evolutionary game theory, it has been shown analytically that optimal communication is the only outcome that is evolutionarily stable in this situation (Warneryd, 1993; Blume, Kim, and Sobel, 1993; Kim and Sobel, 1995; Skyrms, 1996). Furthermore, it can be proven that such optimal systems are not only stable, but guaranteed to emerge (Batali and Oliphant, forthcoming).

Simulations can be designed in which the fitness function reflects this common interest scenario. After an interaction, both the sender and the receiver receive a high contribution to their fitness-evaluation if communication between them was successful, and a low contribution if it was not. This can be done via a very simple payoff matrix, as shown in Figure IV.3. Based on this payoff scheme, the best fitness-evaluation an individual could hope to achieve would be 1.0 (resulting from successful communication in every interaction) and the worst fitness would be 0.0 (resulting from communication failure in every interaction). The fitness-evaluation, then, is an estimate of the individual's two-way communicative accuracy with the population, as defined in section III.C.

Bearing out the theoretical prediction, simulated populations using such a payoff matrix

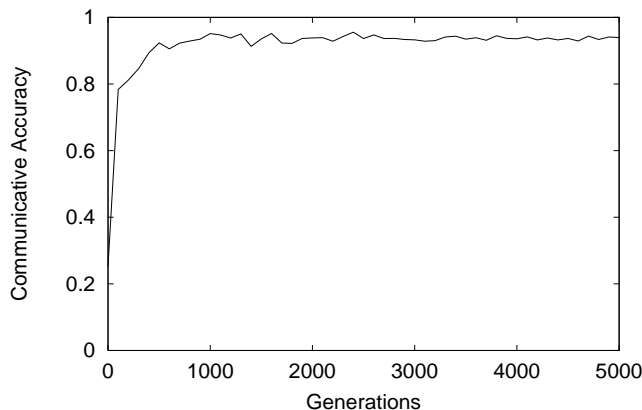


Figure IV.4: Communicative accuracy increasing to near optimality using a common interest regime. Four meanings and four signals are used. Results are averaged over ten simulation runs.

always converge on one of the possible optimal communication systems.³ Figure IV.4 shows simulation results using a common interest payoff as a fitness function. After approximately 1000 generations, the population is communicating at near optimality. The variability observed after generation 1000 is due to the new mutations occurring in each generation.

MacLennan and Burghardt (1994) use a common-interest framework similar to that described above. While their results are somewhat difficult to assess, as they use a measure of entropy rather than communicative accuracy, their populations seem to fall significantly short of optimal communication (although performance is above chance). Because their simulations involved a more complicated form of interaction amongst individuals, it seems likely that this additional complexity is responsible for the discrepancy between their results and those shown here.

IV.G Lack of common interest

In the previous simulation, the consequences of a communicative interaction were the same for both the sender and the receiver. If communication was successful, both benefited. If communication failed, both paid the price. Communication in the real world may not always reflect this assumption, however, and it is probably often the case that the environment in which communication evolves is not quite like the simulations just described.

³Making the simplifying assumption that the number of signals available for use is the same as the number of meanings (say, N), the number of optimal systems is the factorial ($N!$). This simply reflects the number of possible ways that the signals can be arranged, while still conveying each meaning uniquely. If there are more signals than there are meanings, the number of optimal systems increases. If the number of signals is less than the number of environmental states, no optimal system is possible.

	Success	Failure
Transmitter	n/a	n/a
Receiver	1.0	0.0

Figure IV.5: Payoff matrix for communication without common interest. Selective pressure is placed only on the receiver.

Consider the example of animal alarm call systems. The main problem with applying a common-interest framework in such cases is that, while the benefit to the receiver clear, it is much less obvious that the transmitter of an alarm gets any direct benefit from successful communication. After all, the animal giving the signal has already seen the predator. In fact, giving an alarm call may be detrimental if it calls attention to the transmitter (although there is evidence that some species have evolved calls that are difficult to localize (Marler, 1955; Marler, 1957; Konishi, 1973)). While arguments can be made that alarm calls are given to reduce risk to the transmitter (Trivers, 1971; Charnov and Krebs, 1975), they are difficult to assess. Regardless, an explanation of communication that does not require a direct benefit to the transmitter is desirable.

In order to investigate the effects a lack of common interest has, it is possible to carry out simulations identical to the previous ones, except that instead of evaluating both the transmitter and the receiver based on the success of an attempted communication, only the receiver is evaluated⁴. The payoff matrix reflecting this non common interest situation is shown in Figure IV.5.

Figure IV.6 shows simulation results using this new payoff matrix. After 5000 generations, communicative accuracy is still low. The population is far from achieving an optimal communication system. This failure results directly from the payoff matrix. In a communicative interaction, only the receiver is evaluated, resulting in a lack of selection pressure on genes used to determine transmission behavior. These genes are left only to the action of genetic drift.

Communicative accuracy hovers around 50%, meaning that communication is successful half of the time, on average. This is surprising, as chance performance given four signals and four meanings would be 25% accuracy. Even though there is no selective pressure on transmission, there is still an above-chance level of communication occurring. The reason for this will be discussed in Section V. For the moment, the important result is that while optimal communication systems are achieved in situations of common interest, communicative accuracy remains

⁴This reflects the assumption that transmission behavior is neutral with respect to fitness. As was mentioned previously, it may be the case that such behavior is actually detrimental. Simulations using such a payoff matrix will be considered in section V.D.

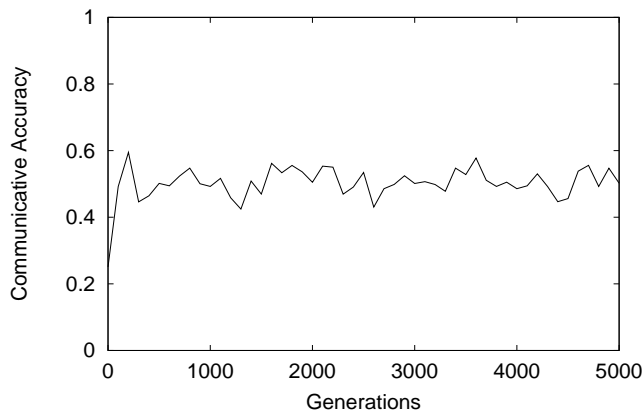


Figure IV.6: Communicative accuracy when no selective pressure is placed on the transmitter. Four meanings and four signals are used. Results are averaged over ten simulation runs.

sub-optimal in cases where the transmitter has no stake in the outcome of the exchange.

IV.G.1 The evolution of altruism

The results of the previous section demonstrate that transmitting accurately when there is no fitness benefit to be had by it is something that will not, as a rule, be favored by natural selection. Accurate transmission does, however, bestow a fitness advantage on the receiver of the interaction. Hence we have a situation where a behavior that is not advantageous to an individual itself is beneficial to others. In this way, communication in the absence of common interest can be seen as an altruistic act. Given this, the study of communicative behavior can gain from drawing on ideas from the evolution of altruism literature.

IV.G.2 The prisoner's dilemma

Much attention has been focused on studying the evolution of apparently altruistic behavior. A formalism known as the prisoner's dilemma has been adopted as the standard for studying the evolution of cooperative behavior.

Consider the following situation. Both you and an accomplice have been arrested for a crime that the two of you have committed and you have been placed in separate cells and are not allowed to communicate with each other. The prosecutor gives you each the opportunity to give evidence against the other. You are told that if neither of you give evidence, you will both be put in prison for two years. If, on the other hand, you both give evidence, you will each serve four years. Finally, if only one of you gives evidence, that person will go free, while the other

	Coop	Defect
Coop	R/R	S/T
Defect	T/S	P/P

Figure IV.7: Payoff matrix for the prisoner's dilemma

serves a five year sentence. What should you do?

Taken from a rational, self-interested point of view, the correct decision is simple. Your accomplice can do one of two things – give evidence against you (termed *defection*) or keep silent (termed *cooperation*). If they cooperate, your best decision is to defect on them, because then you will go free. If, on the other hand, they defect on you, you had still better defect on them and serve only two years, because if you cooperate and stay silent you will serve five years. Thus, each of you, acting in your own best interest, should defect on the other and you will both serve four years. This result, while perfectly rational, is frustrating because if only you both had cooperated you would each serve only two years.

If we convert the penalties into positive payoffs, the structure of the prisoner's dilemma can be expressed as a payoff matrix, as shown in Figure IV.7. In each cell of the matrix, the payoff to the row player listed first, followed by the payoff to the column player. The dilemma occurs when $T > R > P > S$ and $2R > T + S$ (an example of suitable values would be $T=5$, $R=3$, $P=1$, $S=0$). Although mutual cooperation is the best solution from the joint perspective of both players, defection is the best choice on a self-interested basis. If an individual can expect to encounter a percentage of cooperators F_c and a percentage of defectors F_d (where $F_c + F_d = 1$) over the course of an evaluation cycle, then the expected average payoff for a cooperator would be:

$$P_c = R \cdot F_c + S \cdot F_d \quad (\text{IV.3})$$

and the expected average payoff for a defector would be:

$$P_d = T \cdot F_c + P \cdot F_d \quad (\text{IV.4})$$

Because $T > R$ and $P > S$, defectors always have an advantage, regardless of the makeup of the population. Although each player is acting in their own perceived best interest, they end up with a result that is non-optimal for both of them.

To demonstrate this result in simulation, we can create a population of simulated individuals and represent them using a single gene denoting a playing strategy of cooperation or defection. We can then simulate evolutionary change in such a population using a genetic algorithm. For a measure of fitness for natural selection to operate on, we can use the average success

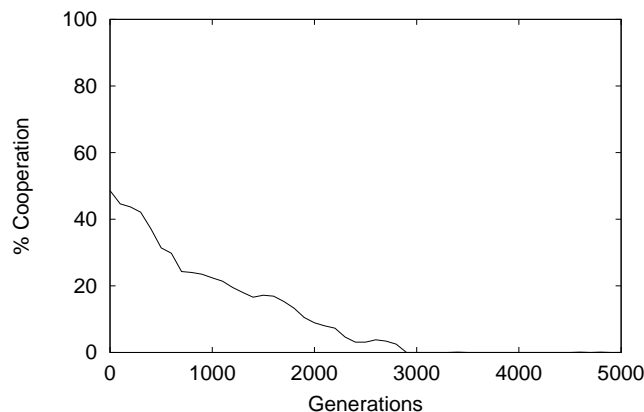


Figure IV.8: Percentage of cooperators in a population playing the prisoner’s dilemma over the course of 5000 simulated generations. The unavoidable result is that all cooperation disappears from the populations. Results are averaged over 10 simulation runs.

an individual has when it is placed in the dilemma against other members of the population. The classic result found in simulations of this kind is that the entire population quickly evolves to be defectors. This makes perfect sense because, as we saw earlier, it is always in one’s best interest to defect. An example of such a simulation can be seen in Figure IV.8. The population is initialized with roughly 50% cooperators and 50% defectors. By generation 3000, there are no cooperators left.

Despite this mathematically airtight conclusion, there are numerous examples of seemingly altruistic behavior in the animal world. Attempts at reconciling this apparent contradiction within the prisoner’s dilemma framework involve modifying the nature of the game in a number of different ways. Two of these ways, each also used to approach the dilemma of altruistic communication, are presented in the next two sections.

IV.G.3 Reciprocal altruism

Dissatisfied with mathematical inevitability of defection in the standard formulation of the prisoner’s dilemma, researchers turned to a more complex version of the game (Axelrod, 1980a; Axelrod, 1980b; Axelrod and Hamilton, 1981). This variant, called the *iterated* prisoner’s dilemma, involves individuals playing each other more than once. In order to benefit from experience gained in previous games against the same opponent, individuals are given a multiple-game history that documents both their actions and those of their opponent. They are also given a mechanism that allows them to modify their future behavior based their history of interaction

with an opponent. This gives the potential for individuals to cooperate with those who have cooperated with them in the past and defect on others. Such strategies involved what is called reciprocal altruism (Trivers, 1971), and allow cooperation to arise in the iterated game.

The simplest, and most commonly referred to of these strategies is called Tit-For-Tat (TFT) because its behavior in a particular interaction just involves doing exactly what its opponent did in the last interaction.⁵ Thus, if its opponent cooperated last turn, TFT will cooperate and if its opponent defected, TFT will retaliate by defecting as well. This provides a cooperative strategy (TFT will cooperate with those that cooperate with it) that is resistant to exploitation by defectors (TFT will defect on those that defect on it). While defectors do slightly better than TFT (getting an initial defection in, before TFT retaliates), they do much worse against other defectors than TFT does against itself. This gives TFT an overall advantage in a mixed population. In simulations of the iterated game, cooperative strategies like TFT come to dominate the population (Axelrod, 1987).

Reciprocal communication

It seems reasonable that reciprocal altruism might provide a means for establishing perfect communication much as it facilitates cooperation in the prisoner's dilemma. To investigate this experimentally requires modifications to the structure of the genome that was used in prior simulations. Individuals must now have some mechanism to respond differentially based on past interactions. In the simplest case, being able to act based on one past interaction makes it necessary to have two modes of action – one if the past interaction resulted in successful communication and another if communication was unsuccessful. This can be done by encoding not one, but two transmission systems in the genome. The individual playing the role of transmitter then uses one of their two transmission systems: one if the last interaction was successful, and the other if it was not.

It is also necessary to have another gene in order to specify the initial assumption an individual makes about other players. This gene is used to determine which of an individual's two communication systems will be used in the first round that is played against a new opponent (the result of the previous round can not be used, because there is not yet any history of interaction between the two individuals).

The only other required modification to the simulation framework is that, instead of being based on single interactions between a pair of individuals, a number of interactions are required in order to allow the role of past interaction to have an effect. The number of interactions

⁵The Tit-For-Tat strategy first appeared as an entry by Anatol Rapoport in a competition held by Axelrod. Although it was the simplest of all the strategies, it was the winner of the tournament.

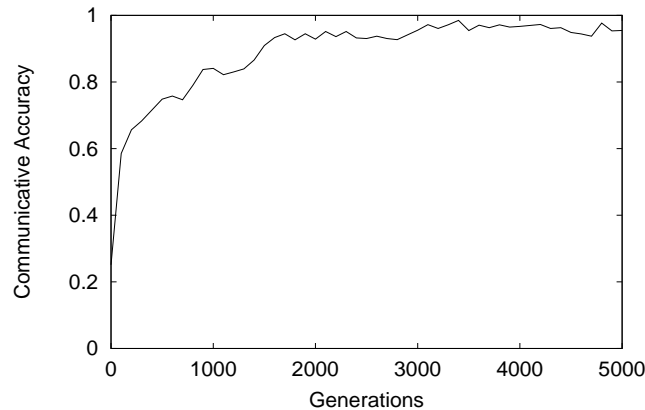


Figure IV.9: Communicative accuracy in a reciprocal altruism scenario. No direct selective pressure is placed on the transmitter. Four meanings and four signals are used. Results are averaged over ten simulation runs.

is not especially important, as long as it is more than one. For reasons of efficiency, the simulations reported here are done using two interactions.

Figure IV.9 shows the results of a simulation using this new, iterated form of communication. The fitness function is identical to that used in section IV.G where pressure is placed only on the receiver. As can be seen in the graph, the iterated version of the game allows communicative accuracy to approach the optimum. This occurs because of the evolution of a communication system that operates much like the Tit-For-Tat strategy in the prisoner's dilemma.

How the reciprocal strategy works

The mechanism underlying the reciprocal strategy can be seen by looking at the communication system settled on by the population when it has reached a high level of communicative accuracy. The *cooperative* transmission system (the one used if the last interaction was a success) evolves to send a unique signal for each meaning. A corresponding reception system evolves such that, when paired with the cooperative transmission system, communication is successful. The *retaliatory* transmission system (the one used if the last interaction was unsuccessful) is not tuned to be the same as the cooperative system, and hence will tend not communicate successfully with the reception system. Finally, the gene that determines an individual's initial assumption about others evolves such that interactions always start by using the cooperative communication system.

An example of the kind of genome the populations converge on is shown in Figure

c	b	c	b	c	b	a	d	2	1	0	3	1
---	---	---	---	---	---	---	---	---	---	---	---	---

Figure IV.10: A sample genome encoding a reciprocal strategy. The first group of four entries represent the retaliatory transmission system, the second group of entries encode the cooperative system, the third group of entries encode the reception system, and the last entry represents the initial assumption made about other individuals. This genome is unpacked in Figure IV.11.

Transmission Genes				Reception Genes		
		Retaliatory Signal	Cooperative Signal	Meaning interpreted		
Meaning to encode	0	c	c	Signal observed	a	2
	1	b	b		b	1
	2	c	a		c	0
	3	b	d		d	3

Figure IV.11: The operation of the reciprocal strategy encoded by the genome in Figure IV.10. The cooperative transmission system encodes each meaning with a unique signal that is understood by the reception system. The retaliatory transmission system encodes the set of meanings ambiguously, using only two signals. Because the initial assumption gene is set to '1', the cooperative system will always be used to begin a series of interactions.

IV.10, with its two transmission systems and the reception system being explained in Figure IV.11. This strategy results in a population that both communicates successfully and is resistant to exploitation by other strategies. The high level of communicative accuracy occurs because the reception system in use by the population accurately receives signals produced by the cooperative transmission system, and because individuals default to using the cooperative system when they interact with a new individual. The resistance to exploitation results from the retaliatory transmission system not matching the population's reception system. This means that if a mutant that does not transmit accurately enters the population, they will be responded to through the use of a less accurate transmission system. This maintains pressure on accurate transmission, even though it is not directly enforced by the fitness function.

Stability of the reciprocal strategy

One would expect, then, that after a reciprocally altruistic communication strategy evolved in a population, it would remain fixed from that point on. This is not what happens, however. Instead, the population transitions from one reciprocal strategy to another, equally ef-

fective but different, reciprocal strategy. This happens repeatedly over the course of evolutionary time.

Such a transition can be seen in Figure IV.12a. Because the effects of such transitions are damped out when results are averaged over a number of simulations, the graph shows the results of a single simulation run. Communicative accuracy begins at an optimal level because the population is seeded with an effective reciprocal strategy. The transition from one system to another is evidenced by the drop in communicative accuracy that reaches its lowest level around generation 600.

The reason for this drop in communicative accuracy is complex, and depends on a number of factors. As can be seen in Figure IV.12b, the drops in communicative accuracy are closely associated with drops in the frequency of the seeded cooperative transmission system (shown in the dashed line). This occurs because the matching reception system (shown in the solid line) is still dominating the population. Any reduction in the frequency of the seeded cooperative transmission system causes a mismatch with the reception system and leads to a decrease in accuracy.

The pressure that maintains the cooperative transmission system depends on the retaliatory transmission system mismatching with the reception system. This allows the retaliatory system to fulfill its retaliatory function – transmitting non-optimal signals when the previous interaction with another individual was unsuccessful. As can be seen in Figure IV.12c, the cooperative transmission system declines in frequency at the time of an increase in the frequency of a retaliatory transmission system that is identical to it. When the cooperative and retaliatory transmission systems are identical, the retaliatory system no longer has any negative impact, and there is no longer any positive pressure for individuals to maintain their cooperative systems. In this situation, the cooperative transmission system is allowed to drift, decreasing the accuracy with which it transmits signals.

Figure IV.12d shows how the system recovers and completes the transition to a new system. A new cooperative transmission system (dashed line) becomes established in the population, and the corresponding reception system (solid line) is then selected for. By generation 700 this has resulted in a new, optimal system.

The problem of drift

This kind of phenomenon is also seen in simulations of the iterated prisoner's dilemma. The Tit-For-Tat strategy shows instability over long periods of time (Lindgren, 1991; Batali and Kitcher, 1995). Once a population has converged on a cooperative, reciprocal strategy, there

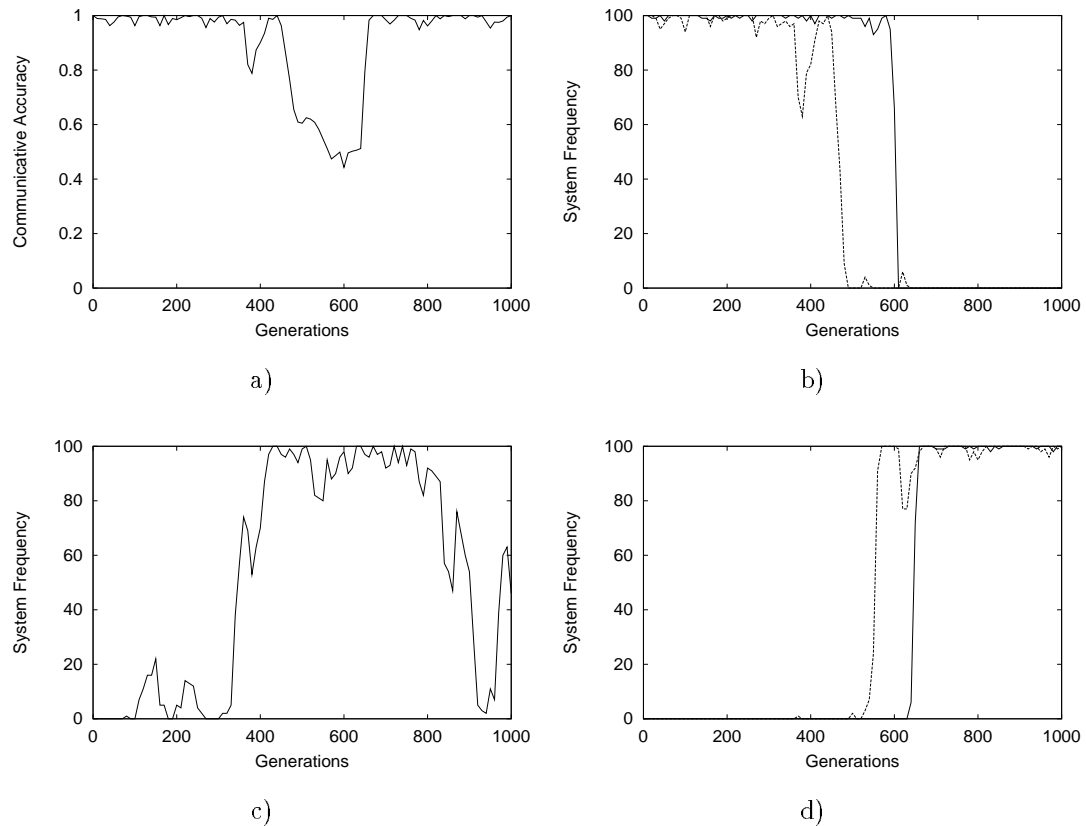


Figure IV.12: A single run of a reciprocal altruism scenario. Two meanings and two signals are used. The initial population has been seeded to an optimal system. Plot a) shows that the system does not remain stable over time. Plot b) shows the frequencies of the seeded reception system (solid line) and cooperative transmission system (dashed line) system. The decline in these systems causes the decline of communicative accuracy. Plot c) shows the frequency of the retaliatory transmission system that matches the seeded cooperative transmission system. The increase in this frequency allows the frequency of the cooperative transmission system to drift. Plot d) shows the frequency of the other possible optimal reception system (solid line) and its corresponding cooperative transmission system (dashed line). The increase in these values account for the recovery in the population's communicative accuracy.

is no longer any pressure to maintain the part of the strategy that reciprocates defection with defection. Because all individuals in the population always cooperate, this part of the genome is never indexed, and is thus subject to drift without selective pressure. Once it has drifted sufficiently, the TFT strategy is compromised and is unable to retaliate against any mutant strategies that always defect.

In the case of communication, the situation is both worse, and better than that of the prisoner's dilemma. It is worse because not only is there no pressure to maintain the retaliatory part of the reciprocal strategy when the entire population is communicating cooperatively, there is no pressure to maintain it under any circumstances. The payoff matrix in the prisoner's dilemma is such that responding to defection with defection carries a fitness benefit over responding with cooperation. In the communication game, there is no such difference in fitness. An individual gains no selective advantage by retaliating to non-optimal transmission with non-optimal transmission of its own. This results in the retaliatory transmission system being in a continual state of drift.

This is compensated for, however, by the fact that the genome that defines an individuals' communication system is more complex than the one generally used in the prisoner's dilemma. A single point-mutation is enough to weaken TFT by changing its retaliatory behavior from defection to cooperation. In the case of communication, however, the retaliatory transmission system must match the cooperative one exactly in order for the effect of retaliation to be neutralized. As the number of signals and meanings increases, the chance of this happening becomes very small. For an equal number, N , of meanings and signals, the retaliatory transmission system must chance upon one system in N^N through random drift.

Cognitive requirements of reciprocation

Reciprocal strategies require a higher level of social sophistication than is needed in strategies involving only isolated interactions. In particular, in order to behavior reciprocally, an animal must be able to discriminate others and maintain a memory of past interactions. While reciprocal altruism may play an important role in explaining the behavior of animals with a high degree of social intelligence, its cognitive requirements have led some to discount it as an explanation for communicative behavior in other species, such as alarm calls in birds (Trivers, 1971). In the next section, an alternate explanation for altruistic behavior that requires less social sophistication is explored.

IV.G.4 Kin selection and spatial organization

Another possible solution involves changing the locus at which selection is presumed to operate. Ethologists have argued that this locus, rather than being at the level of the individual, is better understood as being at the level of the gene (Hamilton, 1963; Hamilton, 1964; Maynard Smith, 1965; Dawkins, 1976). Because a given gene will exist in more than one individual, an apparently altruistic act may well be selfish with respect to a gene. In particular, related individuals will generally expect to share genes in common (50% for siblings and parent/child relationships, reducing by half at each additional level of removal), providing a potential motivation for altruistic behavior through what is known as *kin selection*. In such cases, an individual is not seen as maximizing just their individual fitness, but rather they are maximizing their *inclusive* fitness – taking into related individuals into account.

One of the most striking examples of altruistic behavior is that of social insects, where the majority of individuals do not reproduce. Among bees, the workers exist solely to support the queen bee and her offspring and never mate themselves. This situation is difficult to explain from the perspective of individual fitness. Because the workers have no offspring, their individual fitness would be zero. It so happens, however, that the workers are very closely related to the offspring of the queen that they take care of. In fact, in the common case where the worker is the daughter of the queen herself, such a worker can expect to share a full 3/4 of her genes with her sisters. This is because the queen bee mates only once in her lifetime, and all of a male bee's sperm are identical genetically. Because of this, while a worker's actions may not be in her own best interest, they may well be in the best interest of her genes.

The key factor that allows for the apparently altruistic behavior in such situations is that interactions take place in such a way that an altruistic individual's selfless actions often benefit related individuals. One way to accomplish this is for individuals to be intelligent enough to recognize their degree of relatedness to others, acting in a more altruistic manner the more genes they expect to share. This seems, however, to require a level of sophistication in the individual's perceptual and cognitive abilities above and beyond that which can be expected in many species.

A more realistic solution, perhaps, is to rely on the structure of the environment to ensure that most interaction occurs among individuals that are sufficiently related that altruistic behavior is warranted (as is the case with the worker bee). It is often some form of spatial organization (such as grouping into hives) that provides the mechanism for biasing the distribution of interactions to favor those between related individuals. The next two sections present the potential for the spatial organization of a population to allow for the emergence of altru-

istic behavior where none evolves in a non-spatial population. First, simulations involving the prisoner's dilemma will be presented, and then the framework will be applied to the problem of communication.

Evidence from prisoner's dilemma simulations

The earliest work done on spatializing the prisoner's dilemma was done by Nowak and May (1992). They used the prisoner's dilemma as an update rule for two-dimensional cellular automata. In their simulations, cells could be in one of two states (cooperate or defect), and at each time step, every cell was replaced by the cell bordering it that had the highest summed payoff from playing the game with its eight neighbors. The result they found was not the mathematically-expected convergence on defection. Instead they saw intricate patterns of cooperation and defection.

While this result seemed encouraging, it has been criticized as being an artifact of the simulation conditions used. Huberman and Glance argued that the results depend on the use of a synchronous updating mechanism in which all cells in the space are updated simultaneously (Huberman and Glance, 1993). They demonstrated that when asynchronous updating (updating one cell at each time step) is used, the population quickly degrades into the typical situation where all members are defecting.

Despite this result, it still seems intuitive that organizing a population spatially should facilitate cooperative behavior. Consider a population where spatial organization is taken into account. In a such a population, individuals will be more likely to interact with others that are close to them than they will be with those farther away. Also, if offspring are placed into the population at a location near that of their parents, individuals will tend to be more closely related to those near them. Because individuals are biased toward interacting with those close to them, and because those individuals close to them tend to be related to them, we get a situation where individuals are biased toward interacting with others that share their playing strategy, providing the mechanism for a kind of kin selection effect.

To investigate the effect of adding a spatial component, simulations can be carried out where the population is organized in a one-dimensional space (a ring). Individuals play the prisoner's dilemma game against others picked from a normal distribution around them, averaging five positions away. As can be seen in Figure IV.13, this simple change is enough to provide a situation where cooperators have the advantage. Because selection for interaction and reproduction is stochastic, this result is significantly different than that of Nowak and May, where the persistence of cooperation depended on the deterministic nature of the update rule

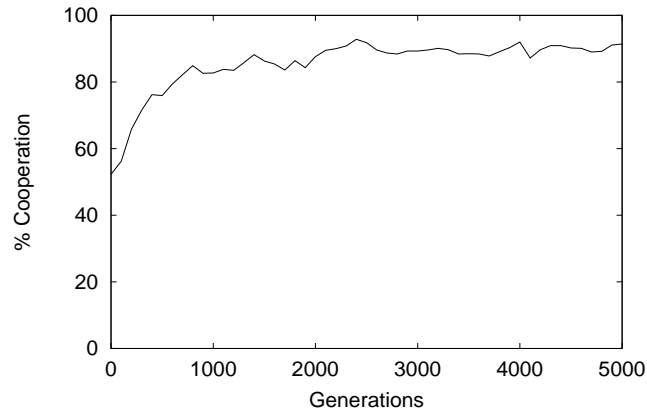


Figure IV.13: Percentage of cooperators in a spatially organized population where prisoner's dilemmas interactions are more likely to occur with others that are spatially close. This spatial organization allows cooperation to dominate the population. Results are averaged over 10 simulation runs.

and the stable patterns it produced. In order to be completely sure that these simulations are not subject to objections of Huberman and Glance, I have done similar simulations using an asynchronous updating mechanism. In this situation, where a single member of the population reproduces and another individual dies, the results are not significantly different.

Why space helps

The dramatic change from convergence on defection to convergence on cooperation occurs because organizing a population spatially increases the chances that cooperators will play cooperators and defectors will play defectors. The cooperators thus increase each other's fitness-evaluations, while defectors have a negative impact on each other. The end result is a situation where cooperators prevail.

The convergence on cooperative behavior can be accounted for by looking at how spatial organization affects the expected payoffs of the game. The original formulation of the payoffs (shown in equations IV.3 and IV.4) is based on the assumption that individuals will interact with the same percentage of cooperators and defectors regardless of their own game-playing strategy. If this assumption does not hold, neither does the mathematical result the predicts defection as the outcome. A more generalized version of the payoff equations can be formulated as follows:

$$Pc = R \cdot F_{cc} + S \cdot F_{cd} \quad (\text{IV.5})$$

$$Pd = T \cdot F_{dc} + P \cdot F_{dd} \quad (\text{IV.6})$$

where F_{cc} is the percentage of the time a cooperator plays against a cooperator and F_{cd} is the percentage of the time a cooperator plays against a defector, etc. In the non-spatial case $F_{cc} = F_{dc} = F_c$ and $F_{cd} = F_{dd} = F_d$, but this symmetry is broken when spatial organization is added.

As a result, the expected number of cooperators and defectors an individual will play against depends on their own status, providing a mechanism for cooperation to spread through the population. Getting back to equations IV.5 and IV.6, what spatial organization does is to increase the probabilities F_{cc} and F_{dd} , thereby increasing the $R \cdot F_{cc}$ and $P \cdot F_{dd}$ terms. Since $R > P$, this benefits the cooperators.

How this plays out spatially over the course of a simulation can be seen if we look at the structure of the population as it unfolds over time. Figure IV.14 shows a contour map of a sample spatial population evolving from generation to generation. The vertical axis represents the members of the population (the ring of individuals has been cut, and laid out as a line). The higher, darker areas of the plot represent concentrations of defectors, while the lower, lighter regions are areas of cooperation. Initially, there is an even mix of cooperation and defection, but cooperation quickly takes hold. Subsequently, defectors can appear in the population due to mutations, but they are not able to last for long and cannot infiltrate the existing group of cooperators.

Space in the iterated game

In addition to providing pressure to cooperate in the non-iterated prisoner's dilemma, spatial organization has been shown to strengthen cooperation in the iterated game (Grim, 1996). Populations in such a game become dominated, not by Tit-For-Tat, but by a more generous strategy that will often cooperate even when it has been defected on once. ⁶

Kin selection and the evolution of communication

Evolving optimal systems of communication, while a more complex situation than the prisoner's dilemma, involves less altruism. While there is no positive pressure to transmit accurate signals, we are operating under the assumption that there is no explicit pressure against such transmission, either. Given this, it seems reasonable that organizing a population spatially could lead to convergence on perfect communication in much the same way that it lead to convergence on cooperation in the prisoner's dilemma. Further encouragement is given by analytic work in ethology showing that kin selection can provide a plausible account for the existence of alarm calls,

⁶The strategies that occur in Grim's simulations are a more generous version of the strategy called Generous Tit-For-Tat by Nowak and Sigmund (1992).

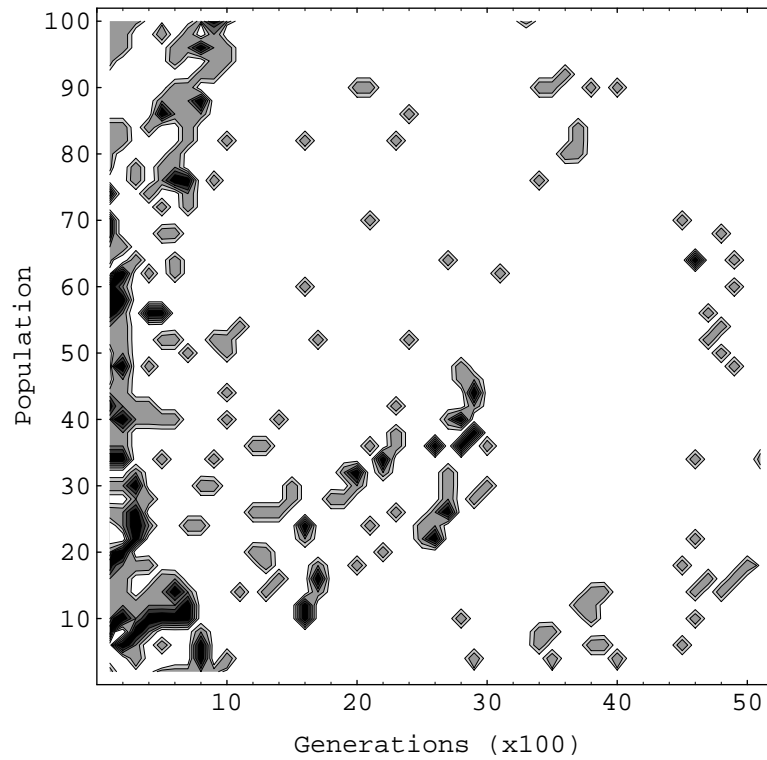


Figure IV.14: A contour map of a spatial population evolving over time. The vertical axis represents the 100 individuals in the population. Shaded areas represent areas containing defectors. The population begins with an even mix of cooperators and defectors, but the cooperators quickly take over. Once cooperation has been established, defectors can appear through mutation, but soon die out again.

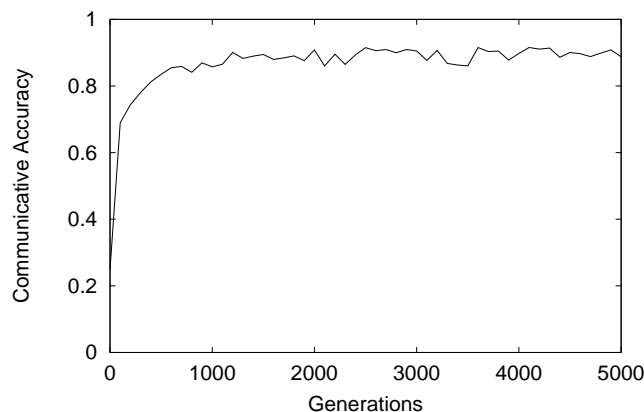


Figure IV.15: Communicative accuracy when spatial organization is used and no selective pressure is placed on the transmitter. The standard deviation of the spatial distribution is 5 locations in the population. Four meanings and four signals are used. Results are averaged over ten simulation runs.

given that the degree of relatedness is sufficient (Hamilton, 1963; Hamilton, 1964; Maynard Smith, 1965). This theoretical work is supported by field evidence in animals such as the Belding's ground squirrel, where alarm call frequency is related to the expected presence of related individuals (Sherman, 1977).

Following the structure used in the spatialized version of the prisoner's dilemma, similar simulations can be carried to investigate the effect of space on the evolution of communication. The structure of these simulations is identical to those shown in figure IV.6, where optimal communication failed to evolve when no pressure was placed on the transmitter. The only difference here is that selection of communication partners is biased spatially, as is the location of an individual in a new population relative to the position of its parent in the previous population. Both are based on a normal distribution, averaging five population locations away. As can be seen in Figure IV.15, the addition of spatial organization results in the population quickly converging to an optimal communication system.

Why space helps

The reason coordinated communication evolves in such cases is analogous to the reason cooperation evolves in the spatialized prisoner's dilemma. With respect to communication, cooperation means having a transmission system that sends a unique signal for each meaning. Reception systems that understand any such transmission system can easily be evolved through direct selective pressure. Once such reception behavior has become established in the popu-

lation, a cooperative transmission system must send signals that match this reception system. Transmission systems are uncooperative to the degree that they are ambiguous or send signals that others cannot understand, with the worst possible system sending the same signal for each meaning, or sending signals that are maximally uncoordinated with the population's reception behavior.

Communication fails to evolve in the non-spatial case because individuals will be expected to interact with cooperative and uncooperative transmitters with a probability that is just based on the frequency of these systems in the population. Whether their own transmission system is cooperative or not makes no difference. Spatial organization changes this. Just as it increased the likelihood of cooperator/cooperator and defector/defector interactions in the prisoner's dilemma, it also increases the likelihood that cooperative transmitters will interact with other cooperative transmitters and that uncooperative individuals will interact with other uncooperative individuals. This results in a change to the expected payoff of an individual based on its transmission strategy, and provides selective pressure for cooperative transmission.

Varying the distance of spatial interactions

A factor that is critical to the particular results of spatial simulations is the size of the standard deviation of the normal distribution that is used to define the space. Increasing the standard deviation increases the average distance over which individuals interact, and places new individuals farther away in the population from the location that their parents were in. This weakens the effect that promotes like-individual interactions, and reduces the benefit that spatial organization gives to cooperative behavior. This can be seen in Figure IV.16a, where the standard deviation has been increased to 10 population locations. Weakening the spatial effect has resulted in a lower attained level of communicative accuracy. As the size of the standard deviation is increased to large numbers relative to the size of the population, the spatial effect becomes negligible. By the time that the deviation is up to 20 population locations, as shown in Figure IV.16b, the results are essentially the same as in the non-spatial case.

Related work

Similar results have been shown by Di Paolo (1996), who attributes the degree of communicative success in his model of foraging behavior to the formation of spatial clusters of individuals. Ackley and Littman (1994) present a model where predator avoidance is facilitated by communication among individuals. They suggest that the communicative success that they observe may be due to spatial effects.

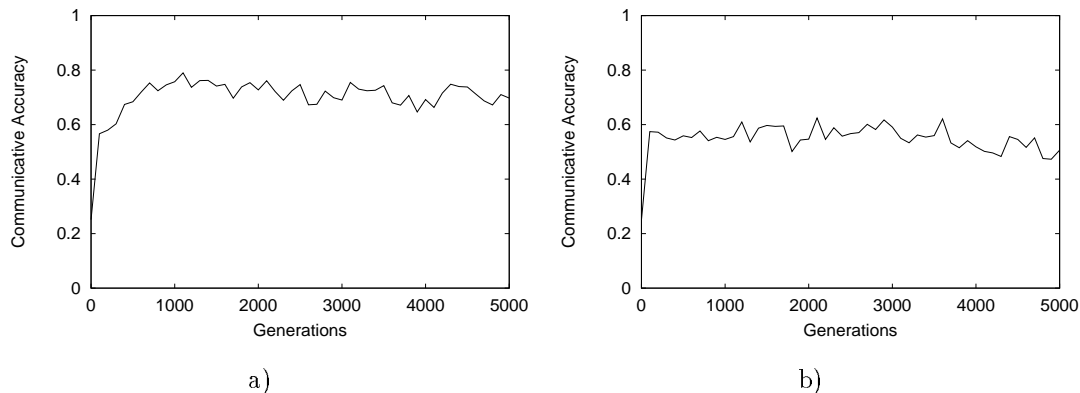


Figure IV.16: Communicative accuracy with weakened spatial effects. Plot a) shows results where the standard deviation of the spatial distribution is 10 locations in the population, and Plot b) shows a deviation of 20. Four meanings and four signals are used. Results are averaged over ten simulation runs.

IV.H Discussion

The simulation work presented in this chapter has shown an number of situations in which innate systems of communication can be tuned to near-optimal performance by natural selection. If the situation involves a common-interest scenario, where coordinated activity results in a selective advantage to both sender and receiver, both analytic and simulation work indicate that communication will emerge. Because many communicative situations do not seem to fit the common interest framework, it is important to show that, in such cases, communication can still evolve. In particular, when accurate communication bestows no direct selective advantage on the transmitter, some additional mechanism is required. In these situations, it has been demonstrated that factors such as reciprocal altruism and kin selection can impose the necessary pressure to tune the system.

The existence of common interest, kin effects, and reciprocal effects, acting in isolation or in concert, are likely to account for the majority of the innate communicative behaviors observed in animal species. Possible additional effects, such as the imposition of honest signaling through costly signals (Zahavi, 1975; Zahavi, 1977; Grafen, 1990), may account for additional data. Natural selection, acting through these mediums, seems well equipped to tune innate systems of communication, and the origin of this innate behavior, when examined carefully, appears relatively unmysterious.

Chapter V

The evolution of exploitation and manipulation

In section II.B, true communication was contrasted with the related behaviors of manipulation and exploitation. In this chapter, this distinction will be explored further with the use of evolutionary simulations.

V.A Exploitation of random drift

In section IV.G it was observed that, in simulations where there is only selective pressure placed on the reception behavior of an individual's communication system, communicative accuracy is still above chance performance. The simulation results are re-shown in Figure V.1. Given four signals and four meanings, chance performance would be 25%, while the performance observed centers around 50% accuracy. Figure V.2 shows simulation results for a set of simulations identical to those in Figure V.1, except that all selective pressure has been removed from the system. In this case, the expected value of 25% is seen.

The difference in the observed results in the two simulations shows that selection can play a role to increase communicative accuracy above chance performance even when transmission behavior is subject only to random drift. The reason for this is that random drift is not the same thing as random behavior. If the transmission behavior is truly random, then selection is powerless to improve performance. If simulations are run with selective pressure on reception, but with a random signal transmission (rather than using the transmission genes of a transmitting individual), performance is at chance levels (results not shown).

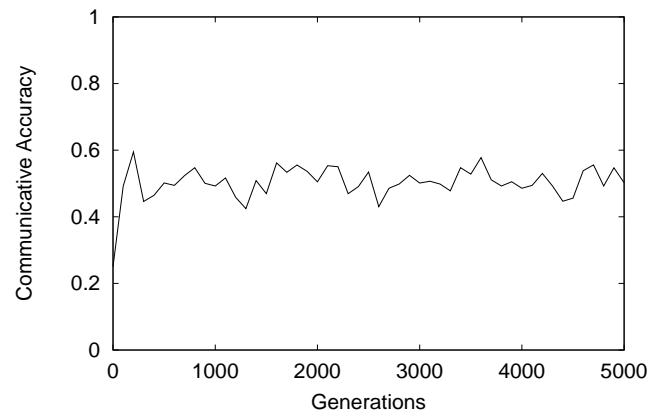


Figure V.1: Communicative accuracy when no selective pressure is placed on the transmitter. Four meanings and four signals are used. Results are averaged over ten simulation runs.

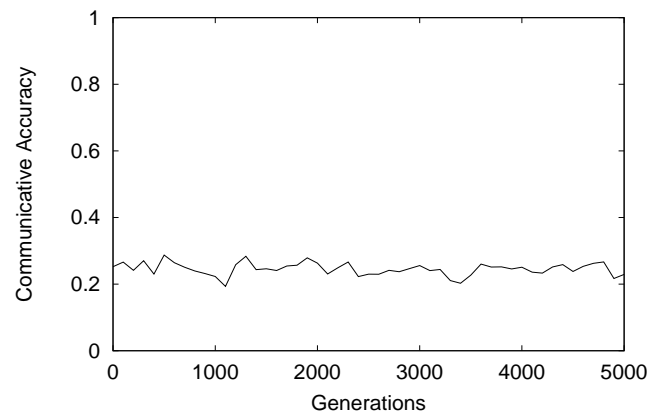


Figure V.2: Communicative accuracy when there is no selective pressure on either transmission or reception behavior. Four meanings and four signals are used. Results are averaged over ten simulation runs.

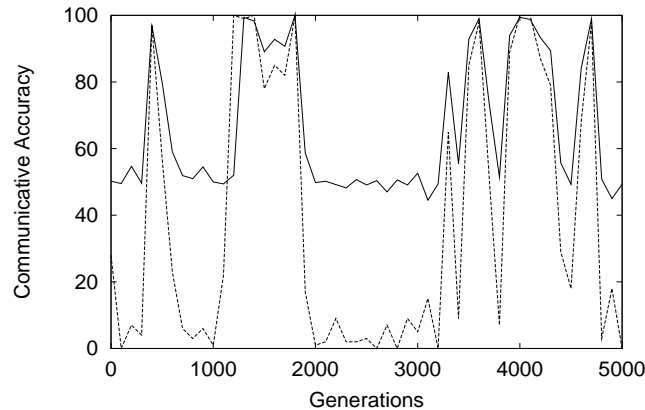


Figure V.3: Communicative accuracy (in the solid line) and the frequency of the most frequent of the two informative transmission systems (in the dashed line). There is no selective pressure on transmission. Two environmental states and two signals are used. Results are from a single simulation run.

The above-chance performance observed in Figure V.1 must then be attributed to some degree of regularity in transmission behavior, even though this behavior is subject only to drift. Selection then operates on the reception behavior, tuning it to exploit these regularities in transmission.

To analyze this situation more closely, it is helpful to use the simplest possible communication task: two meanings and two signals. In this task, there are four possible transmission systems and four possible reception systems. Two of the transmission systems are completely uninformative, as they involve always transmitting a single one of the two signals, regardless of the meaning. The other two transmission systems are potentially fully informative, as they send a unique signal for each meaning.

Figure V.3 shows a single simulation run done using this simple task, with pressure only on the receiver. Plotted are both communicative accuracy (in the solid line, here expressed as a percentage) and the frequency in the population of the most frequent of the two informative transmission systems (in the dashed line). From the figure, it can be clearly seen that the reception behavior of the population is closely tracking the most frequent of the informative transmission systems. It is often the case that one of these transmission systems is at a relatively high frequency in the population, allowing for a high level of communicative accuracy with the corresponding reception system. Because selection can tune reception behavior faster than the transmission behavior drifts, exploitation is possible. A mathematical analysis of this effect has been done by Batali (unpublished).

In general, the communicative accuracy of the population is roughly halfway between the frequency the most frequent informative transmission system and the optimal value. This happens because the non-informative transmission systems send the same signal in every situation, resulting in an additional communicative performance at chance levels. This results in a baseline performance of 50% accuracy when the population’s transmission behavior is maximally uninformative.

As has been pointed out, the above-chance performance is due to the reception behavior of the population being tuned by selection to exploit regularities in transmission behavior. Despite the fact that information is being transferred from the sender to the receiver, this exploitative behavior is not communicative under the definition given in section II.B. Because the transmission behavior of the population has not been tuned in response to reception behavior, individuals in these simulations are not truly communicating with one another.

V.B Exploitation of reliable behavior

In the case of the exploitation shown in the previous section, the regularities in transmission behavior that were exploited were the result of random drift, and hence not very reliable. Exploitation is much more effective in cases where the regularities occur as a result of an observable manifestation of some relevant internal state of another individual. A striking example of this can be seen in Cangelosi and Parisi (1996). This paper looks at a particular set of conditions under which they claim that a system of communication emerges in a population of neural networks. The fitness-relevant task used in the simulations they present is the ability to discriminate food items based on their edibility. Some food is edible (resulting in a positive energy contribution to the individual eating it) and some is poisonous (resulting in a loss of energy). The observable characteristics of the food items are such that it is possible to learn to classify them.

Communication enters into the simulation by supposing that, in some cases, an individual is placed in a position of deciding whether or not to eat a food item without being able to see its observable characteristics. Another individual, however, can see the food item, and can give a signal to the first individual. This communicative interaction is shown in Figure V.4.

Simulations involving communicative interactions of this sort resulted in signaling behavior that was sufficient to allow individuals to successfully discriminate food items that they could not see. Because fitness was based only on how well an individual did at consuming appropriate food, and not on how well an individual’s signaling succeeded in giving information to the receiver, there was no selective pressure to favor accurate signaling. Thus the interactions among

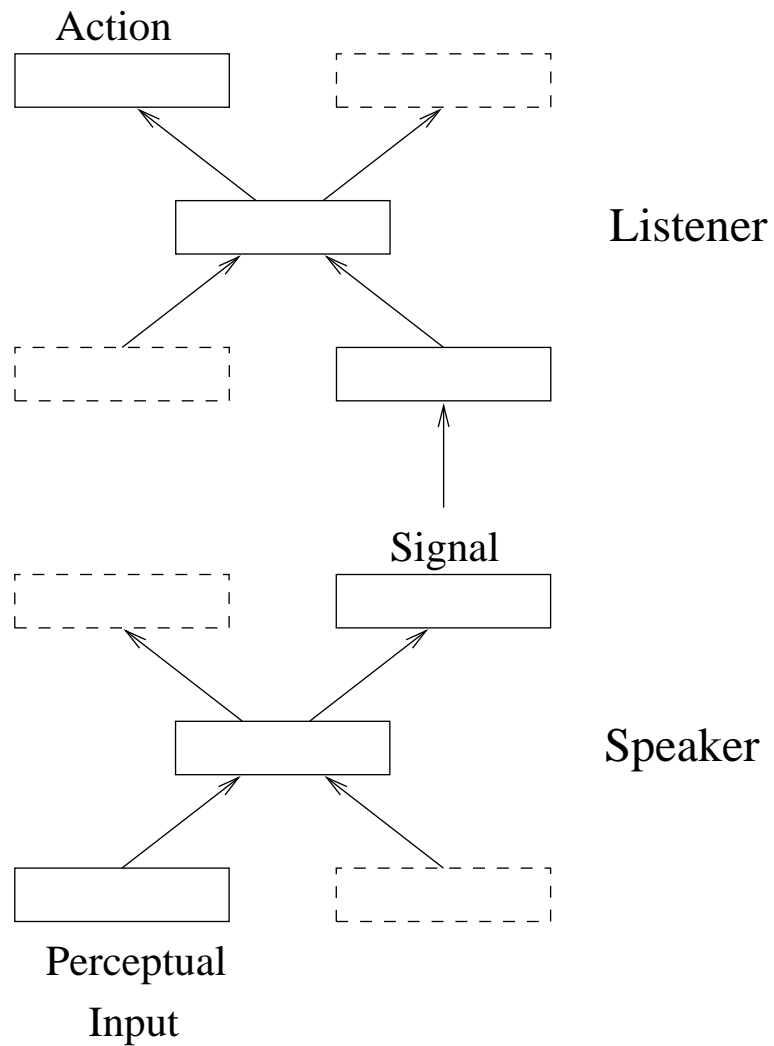


Figure V.4: A signaling interaction between two neural networks. The speaker can perceive a food item, but does not take a action itself. Rather, it sends a signal to another individual who takes action with the signal, but no direct perception, as input. The dashed boxes indicate parts of the network architecture that are not relevant for this interaction. After Cangelosi and Parisi (1996).

the individuals in the simulations are best described as exploitative, rather than communicative.

The exploitation observed in this case is particularly effective because of the network architecture used in the simulations. As Figure V.4 shows, the output layer responsible for action (to eat or not) and the output layer responsible for encoding a signal are both connected to the same hidden layer in the network. Because this hidden layer is intimately connected to the fitness-relevant task of discriminating food items based on direct observation, it must necessarily encode a useful representation of the perceived food item. Because the signal output layer is also connected to this same hidden layer, it will spontaneously produce output that is, at least to some degree, correlated with the perceived input. It is this correlation that the listening individual is tuned by selection to exploit, resulting in a higher level of performance than would otherwise be expected.

V.C Manipulation

Manipulation is simply the mirror-image of exploitation. It occurs in situations where selective pressure is placed on transmission behavior, but not on reception behavior. A clear example of such a situation occurs in simulations done by Levin (1995). Interested in how correspondences might be established and understood between an animal's internal states (such as anger or hunger) and externally observable behaviors (such as body position or display of teeth), Levin sets up an evolutionary simulation framework virtually identical to the one used here in the previous chapter.

Levin states that he is simulating a system in which selection “rewards mutual understanding” in an interaction population (p. 169). The fitness function he uses, however is based on the “average understanding of its internal states by others” (p. 170). Thus the fitness-evaluation of an individual is based only on how well others understand it, and not on how well it understands others. Selective pressure is therefore placed only on transmission behavior, with an individual's reception genes left to drift.

Levin's results are difficult to assess in detail because he reports only the performance of the best individual in each generation, rather than the average performance of the population. Even if the best individual is taken to be representative of the population, the results he observes, while above chance, are significantly below optimal. Levin points to the above-chance performance as an indication that some degree of communication has emerged in the population. I would argue, however, that the behavior he has observed would more correctly be described as manipulation. Just as reception behavior evolved to exploit random regularities in transmission in the simulations described in section V.A, Levin's results are due to transmission behavior

	Success	Failure
Transmitter	0.0	1.0
Receiver	1.0	0.0

Figure V.5: Payoff matrix for communication with negative pressure on transmission. Positive pressure is placed on the receiver.

evolving to manipulate random drift in reception behavior.

V.D Suppression

All of the simulations presented so far has assumed that there is either a positive pressure on transmission behavior or no pressure at all. It is possible, however, that in certain situations it is actually against the transmitter's best interest to provide the receiver with information. This would be the case in any situation where the receiver is exploiting regularities in the sender's behavior and using them against the sender (as is the case in the example given in Figure II.3 of chapter II.B, where one poker player exploits behaviors that give away the fact that another player is bluffing).

Negative pressure on transmission can be quite easily taken into account in the structure of a simulation. Figure V.5 shows a payoff matrix for a communicative interaction where there is pressure on the receiver to understand the transmitter, and pressure on the transmitter *not* to be understood. The results of an evolutionary simulation using this payoff matrix as a fitness function are shown in Figure V.6.

Performance, rather than being above-chance (as was the case with no pressure on transmission – see Figure V.1), has dropped to chance levels. This means that selection has succeeded in tuning the transmission behavior of the population so that any regularities that might be exploited have been effectively suppressed.

If we go one step farther, and change the payoff matrix such the positive pressure on reception is removed (see Figure V.7), we get the results shown in Figure V.8. The communicative accuracy of the population is essentially reduced to zero. This occurs because the reception behavior of the population is now subject only to random drift. This allows selection to tune transmission behavior so that, rather than being uninformative, it is now maximally misinformative. This is essentially a reversal of the results of Levin's simulations described in the previous section. Rather than transmission being tune to manipulate understanding in a receiver, it is tuned to manipulate misunderstanding.

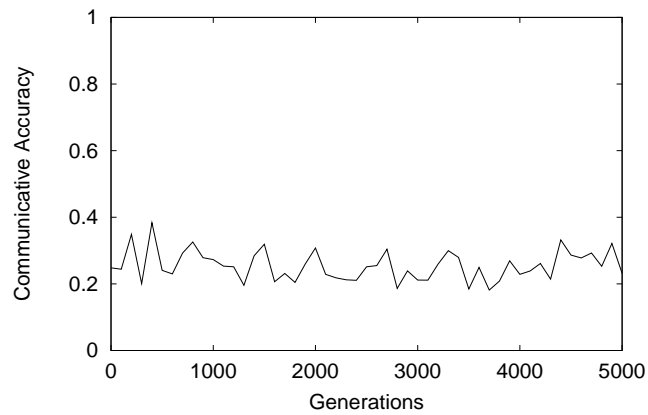


Figure V.6: Communicative accuracy with negative pressure on transmission and positive pressure on reception. Four signals and four meanings are used. Results are averaged over 40 simulation runs.

	Success	Failure
Transmitter	0.0	1.0
Receiver	n/a	n/a

Figure V.7: Payoff matrix for communication with negative pressure on transmission and no pressure on reception

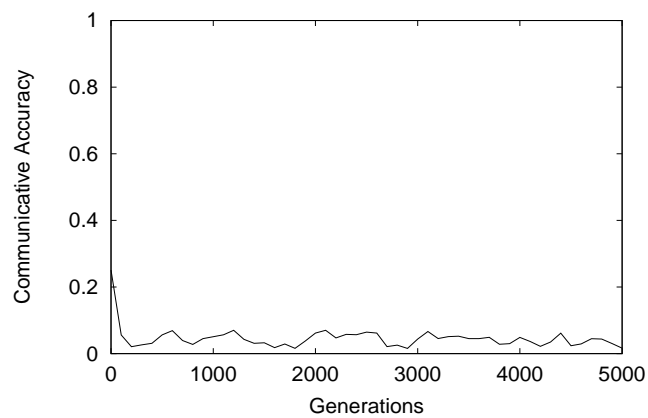


Figure V.8: Communicative accuracy with negative pressure on transmission and no pressure on reception. Four signals and four meanings are used. Results are averaged over 40 simulation runs.

Similar results are obtained if negative pressure is placed on reception behavior, rather than transmission behavior. In this case, reception can be seen as being tuned by selection to ignore signals that would cause it to behave against its own best interest.

Another interesting variation is to modify the nature of the negative pressure being applied. While the simulations presented in this section show that transmission behavior will be suppressed if there is a cost to transmitting accurately, it can also be shown that transmission behavior is suppressed if there is a cost imposed on signaling itself. Batali (unpublished) presents simulations where a transmitter is allowed the use of one cost-free signal, but the use of each additional signal is penalized. As this cost is increased, the communicative accuracy achieved by the population decreases (presumably because fewer signals are used by senders, resulting in ambiguities).

Chapter VI

Learned communication systems

All of the communication systems described up to this point have been innate systems, genetically specified and tuned by evolutionary processes. Natural selection is a very effective means of constructing and maintaining such systems. While innate behavior accounts for the vast majority of existing systems, there are some, most notably human language, that are learned. If the system is to be learned, rather than being directly specified genetically, the learning mechanism will now be responsible for establishing and maintaining coordination.

In order to do this, a satisfactory learning mechanisms must be able to:

- Acquire a pre-existing optimal system of communication when it is introduced into a population that uses it.
- Maintain a pre-existing optimal system of communication against reasonable levels of noise.
- Improve a non-optimal system of communication in such a way that, as new individuals who use the learning mechanism are added to a population, the communicative accuracy of the population increases and eventually reaches an optimal state.

Thus, we are requiring more of a learning mechanism than is generally demanded. We are not only interested in how a new individual might acquire an existing system, but also how such systems are created in the first place.

VI.A Reinforcement learning

One way in which a learning mechanism might operate is to essentially use the same method used by natural selection: trial-and-error with reinforcement. The majority of other

simulation approaches to the study of learned communication use some form of reinforcement learning paradigm. Hutchins and Hazelhurst (1995) simulate the establishment of communication in populations of interacting neural networks. The reinforcement regime that they use involves back-propagation of error based on mismatches between the signals used by two individuals involved in a communicative interaction. Yanco and Stein (1993) use reinforcement learning to develop a shared communication system among a small number of mobile robots involved in a coordination task. Steels (1996) uses a mixture of reinforcement and observational learning to explore the construction of shared vocabularies. The properties of this model in a spatially distributed environment are described by Steels and McIntyre (1997)

While these reinforcement learning techniques have reported varying degrees of success, all of them have resulted in significant or optimal levels of communicative accuracy in their simulated populations. Trial-and-error learning, then, does seem able to construct communication systems. As has been pointed out by Pulliam and Dunford, however, “the obvious problem with trial-and-error learning is error” (1980, p.435). An error signal that works quite well at the timescale of evolution may be rather less useful at the timescale of an individual’s lifetime. Much of communication occurs in situations where failure brings a high cost. Even in less costly situations, reinforcement learning is problematic. In many situations, it is not clear that a reliable error signal exists at all. In the case of human language, the clearest example we have of a learned communication system, it is argued that children do not get sufficient reinforcement from their parents (Wexler and Culicover, 1980; Crain, 1991).

VI.B Observational learning

Because of the problems with reinforcement learning in communication, the simulations presented in this chapter will involve learning by observing the behavior of others, rather than using trial-and-error. Observational learning does not require a reinforcement signal, making it both less costly, and free of the need for feedback that may not be available. Boyd and Richerson (1995) give a formal analysis of utility of observational learning under different conditions. They argue that the observational learning will outperform reinforcement learning as environmental stability increases (making it sensible to learn from others) and the probability of independent individual success decreases (making it costly for an individual to learn on their own).

Compared with those who have looked at communication within a reinforcement paradigm, fewer researchers have studied observational learning models. Billard and Dautenhahn (1997) uses a form of observational learning in a situation involving two robotic agents – one the teacher and one the learner – engaged in a simple following task. Hurford (1989) uses an observational

learning paradigm and addresses many of the same issues that will be discussed here. Because his work is so relevant, I will give an analysis of his results in section VI.D.5, relating them to the results I present.

Perhaps one reason for the comparative lack of research in this area is the difficulty that observational learning mechanisms have in improving the communicative ability of a population. It makes intuitive sense that it should be possible to learn an existing communication system by observing others, but it is less obvious how repeated observation might construct such a system. Because observational learning uses no reinforcement signal, there is no external feedback about the communicative utility of particular behavior. In constructing a system, a purely observational learning procedure must do “blind” hillclimbing – following a fitness landscape without being able to sample it directly. As will be seen in the simulations presented in this chapter, learning procedures will vary in their ability to do this.

VI.C The observational learning model

The simulations that will be presented in this chapter involve populations of individuals with send and receive functions as described in section III. These communication functions, rather than being tuned by evolution, will now be constructed through a learning procedure, taking observations of the behavior of others as data.

It is assumed that the life of an individual proceeds in two stages: a learning stage and a behaving stage. During the learning stage, an individual observes the behavior of the other individuals in the population, and uses these observations to construct its own communication system. After learning, this communication system remains fixed. During the behaving stage, individuals interact with one another, providing the basis for the learning of new individuals.

VI.C.1 Population dynamics

Beginning with an initial population with randomized send and receive functions, new individuals are periodically introduced, learning to communicate and becoming behaving members of the population. In addition, individuals are periodically removed from the population, modeling death. This occurs in a continuous cycle, as is shown in Figure VI.1.

In this way, the population can be seen as a dynamical system, with the addition of new individuals and the removal of old individuals determining the change in the population over time. More concretely, if we have a transition function, T , that determines the effects of adding a new individual (with send and receive functions s_{new} and r_{new} respectively) to a population,

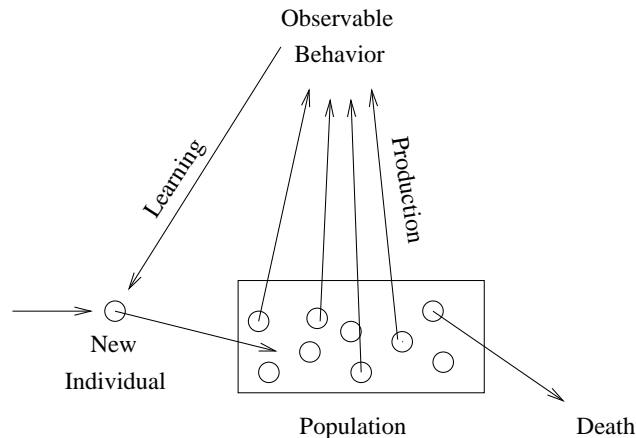


Figure VI.1: The learning cycle. Old individuals are continually replaced by new ones in the population. New individuals learn from an observed sample of behavior produced by the existing population.

the change in the population can be described by:

$$P_{t+1} = T(s_{new}, r_{new}, P_t) \quad (\text{VI.1})$$

where P_t represents the state of the population at a given time.¹

This dynamic describes the way the communicative behavior of the population will change over time. Because the function, T , that determines the transition from one state of the population to another is likely to be quite simple (such as simply adding the new individual to the existing set), the behavior of the system will be largely governed by how the send and receive functions of a new individual are determined by the learning procedure. In order to be able to construct and maintain effective communicative behavior, the learning procedure must be such that it results in a dynamical system in which accurate communication systems are attractors.

VI.C.2 Observing the behavior of others

New individuals learn their communication systems by observing others. The send and receive functions of the population are not available directly to a learner, however, but rather are reflected by an observed sample of behavior. The sample that a learner will see is determined by an observation function, O . This function maps the actual population send and receive functions, S and R , into samples of observable behavior, S_{smp} and R_{smp} , as is shown here:

$$S_{smp} = O_s(S) \quad R_{smp} = O_r(S_{smp}, R) \quad (\text{VI.2})$$

¹The function T will also reflect the effects of removing individuals from the population.

S	a	b	c
1	0.8	0.1	0.1
2	0.6	0.4	0.0
3	0.4	0.6	0.0

a)

S_{smp}	a	b	c
1	6	1	0
2	4	3	0
3	2	4	0

b)

R	a	b	c
1	0.6	0.1	1.0
2	0.2	0.1	0.0
3	0.2	0.8	0.0

c)

R_{smp}	a	b	c
1	7	1	0
2	3	1	0
3	2	6	0

d)

Figure VI.2: Dependence of reception on transmission. Figures a) and b) show the population's average send function, and an observed sample of it. Figures c) and d) show the population's average receive function and an observed sample of it (expressed as the number of observed instances of the signal/meaning pair). Because a signal must be sent in order for it to be received, reception behavior to signals that are sent rarely will be underrepresented or not represented at all.

The reason that observation function for reception O_r is dependent on the observed send sample is explained in Figure VI.2. Communication is by its very nature a directed process. Reception comes after transmission and operates on the signals that transmission produces. Because of this, it is impossible to observe a population's reception system directly. What is observed instead is the result of receiving the signals produced by a sample of transmission behavior. In Figure VI.2c, the probability with which an individual from the population will interpret signal c as meaning 1 is 1.0. In the sample of reception behavior, however, this mapping is never observed (Figure VI.2d). This occurs because member of the population rarely send signal c for any meaning, and in this particular sample of transmission behavior, it is never sent.

VI.C.3 Creating a new individual

Given that we now have samples of transmission and reception behavior, they can now be used to determine the send and receive functions of the new individual that is being exposed them. This is done using a learning function, L , that operates in the following way:

$$s_{new} = L_s(S_{smp}, R_{smp}) \quad r_{new} = L_r(S_{smp}, R_{smp}) \quad (\text{VI.3})$$

The majority of work in this chapter will be primarily devoted to exploring the properties of

various kinds of mechanisms that might be used to instantiate this learning function.

VI.C.4 Simulation framework

Unless otherwise specified, all simulations presented here will implement the functions described above in the following way:

- The transition function, $T(s_{new}, r_{new}, P_t)$, is simply a set operation on P_t . A randomly selected member of the population is removed from the set, being replaced by a new individual with send function s_{new} and receive function r_{new} . This ensures that the population remains at a constant size.
- The observation functions, O_s and O_r produce the observed samples of behavior, S_{smp} and R_{smp} , by sampling a fixed number of communicative interactions. Unless otherwise specified, three interactions are observed for each meaning². For each interaction, a transmitter and a receiver are randomly chosen from the population. The signal the transmitter produces in response to the given meanings is recorded in S_{smp} . This signal is then presented to the receiver, and the meaning the receiver interprets it as is recorded in R_{smp} . S_{smp} and R_{smp} , then, are simply matrices that contain counts of the number of times a particular signal/meaning pairing was observed in the send and receive behavior of the population.
- The learning functions, L_s and L_r vary with the particular learning strategy that is being investigated.

All simulations involve populations of 100 individuals, unless otherwise specified. The unit of time in the simulations is a *round*, which involves the removal of one individuals from the simulation at random, and the addition of a new individual to the population. Each new individual is learns according to the particular learning procedure being investigated in the simulation.

VI.D Statistical learning procedures

The following sections describe a number of statistical procedures that could be used to implement the learning functions L_s and L_r . The different learning procedures I present have varying degrees of success at constructing and maintaining systems of communication. I first

²This is slightly unrealistic, as it assumes that each meaning is actually observed with equal frequency. It allows simulation times to be faster, however, since fewer interactions are needed to have all meanings represented in the sample.

describe procedures that attempt simply to reproduce the statistical properties of a sample and then turn to procedures that attempt to take into account the communicative function of signals.

VI.D.1 Imitative learning

Perhaps the most obvious way to construct a communication system from the behavior of others is just to imitate the behavior that is observed. The word *imitate* is used here to mean “reproduce as faithfully as possible.” An imitative learning strategy, then, attempts to reconstruct the population’s send and receive behavior as accurately as it can from the observed sample. This can be done by simply sending and receiving signals with the probabilities observed in the sample.

This may seem to be the best way to learn a communication system; indeed, an imitative learning strategy can, given a large enough sample of behavior, learn an existing system. The problem with imitation is that learning an extant system is, as was pointed out in the previous section, only one of the requirements placed on a learning mechanism. Imitative learning strategies, because they are designed to faithfully reproduce a population’s communicative behavior, cannot improve sub-optimal systems. Faced with a system where individuals send and receive signals with low accuracy, an imitative strategy will learn to communicate in an equally inaccurate way. In addition, Figure VI.3 shows that such a strategy fails to maintain an optimal system against even very low levels of noise. The system quickly degrades to a chance level of performance.

Imitate-Choose

It is possible to improve an imitative strategy by imitating the statistical mode of the observed sample of behavior, rather than the actual observed distribution. This can be done by sending, for each meaning, the signal that the population most often sends for that meaning, and receiving each signal as the meaning the population most often receives that signal as. This learning procedure, which we will call *Imitate-Choose*, is outlined in Figure VI.4³.

Unlike the pure imitative strategy, the Imitate-Choose procedure allows a population to maintain an optimal system against moderate amounts of noise. The slight deviations caused by noise are ignored in favor of the dominant behavior of the population. Despite this, however, the Imitate-Choose strategy is unable to reliably improve sub-optimal communication systems, as is shown in Figure VI.5.

³In all cases where the a maximum value is calculated in the description of this and other learning procedures, if the maximum is shared over more than one value, one is chosen randomly.

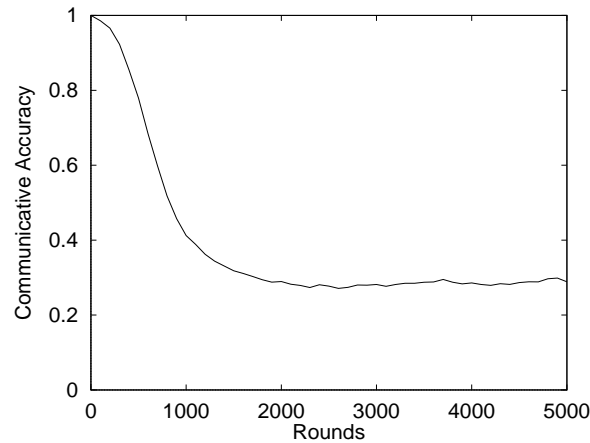


Figure VI.3: Starting with an optimally coordinated communication system, an imitative strategy fails to maintain it the presence of a low noise level. Sampling is done such that a signal is guaranteed to be observed being sent for every meaning. There is a 1% chance that the signal used in a communicative interaction will be observed incorrectly. Four signals and four meanings are used. Results are averaged over 10 simulation runs.

For each meaning μ :

s.1: Find the signal κ_μ for which $S_{smp}(\mu, \kappa_\mu)$ is maximum.

s.2: Set $s_{new}(\mu, \kappa_\mu) = 1.0$, and set $s_{new}(\mu, \sigma) = 0$ for all $\sigma \neq \kappa_\mu$.

For each signal σ :

r.1: Find the meaning η_σ for which $R_{smp}(\sigma, \eta_\sigma)$ is maximum.

r.2: Set $r_{new}(\sigma, \eta_\sigma) = 1.0$, and set $r_{new}(\sigma, \mu) = 0$ for all $\mu \neq \eta_\sigma$.

Figure VI.4: The Imitate-Choose learning procedure.

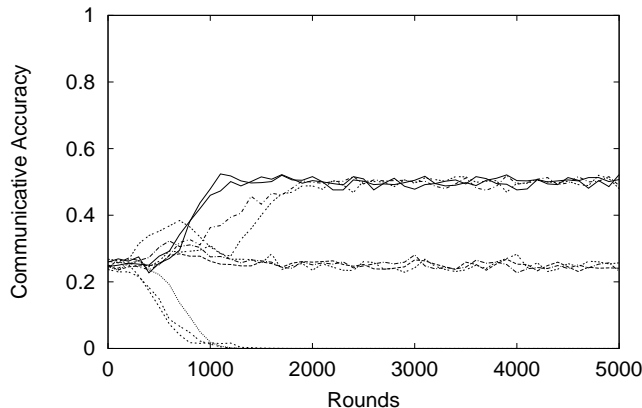


Figure VI.5: Performance of the Imitate-Choose learning procedure. Imitate-Choose fails to reliably improve populations with random initial communication systems. Four meanings and for signals are used. Results of 10 simulation runs are shown superimposed.

Recall that in section III.D, optimal communication in a population was characterized in terms of three requirements: coordination, distinctiveness, and consensus. The Imitate-Choose procedure enforces consensus, resulting in its ability to resist noise. It does not, however, enforce either distinctiveness or coordination. Essentially, all that Imitate-Choose does is to exaggerate the initial biases of the population. Because each new individual imitates the dominant behavior of the population, consensus is eventually reached. There is no guarantee, however, that the system that is converged upon will communicate accurately, as it is effectively chosen randomly. As Figure VI.5 shows, the communicative accuracy of the population stabilizes, communicating accurately about some particular number of meanings (in this case, 0, 1, or 2 out of four). The expected communicative accuracy of a population using the Imitate-Choose strategy is the same as the expected communicative accuracy of a random transmission system paired with a random reception system. This expected value is $1/|M|$. It is 0.25 in the case of the simulations shown in Figure VI.5, which is the approximate value of communicative accuracy observed.

VI.D.2 Saussurean learning

One of the things that the Imitate-Choose procedure described in the previous section failed to do was to enforce coordination between transmission and reception behavior. Because coordination is so critical to accurate communication, one might suppose that this linkage between transmission and reception behavior should be imposed directly by the learning procedure. Hurford (1989) calls such learning strategies that assume a bi-directional mapping between meaning

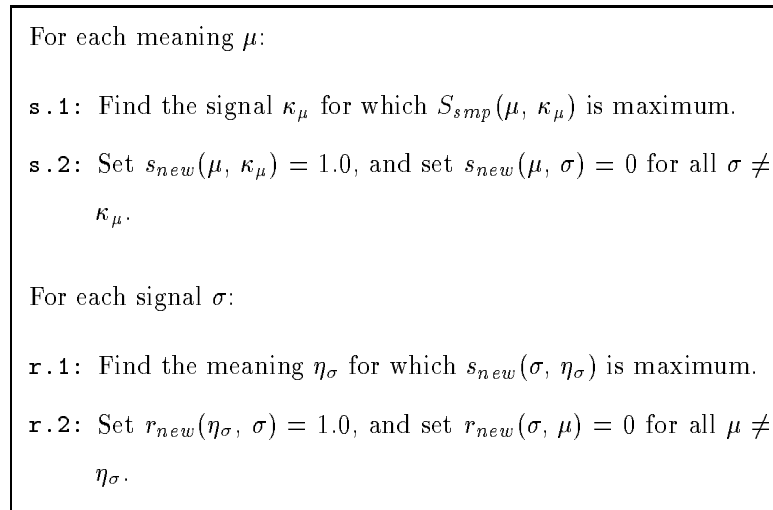


Figure VI.6: The Saussurean learning procedure.

and signal *Saussurean*, as this association between a form and a meaning is termed a *Saussurean sign*, after de Saussure (1959).

Figure VI.6 gives the definition of a Saussurean learning procedure. The send function of the new individual is derived in the same way as was done in the Imitate-Choose procedure. The construction of the reception function is also similar to Imitate-Choose, except that, instead of deriving from the population's reception behavior it derives from the individual's own newly constructed send function. The new reception function is forced to be the send function's "other half" of the Saussurean sign.

Figure VI.7 shows results of simulations using this Saussurean learning procedure. While performance is better than was achieved with the Imitate-Choose procedure, populations using the Saussurean strategy still fail to reliably converge on optimal communication systems. The reason that the Saussurean strategy performs better than Imitate-Choose is that, in addition to enforcing consensus, it also enforces coordination (in fact, it was designed to do so). The reason it does not always construct a perfect system is that it does not enforce distinctiveness.

The transmission portion of the Saussurean strategy is derived just as was done with Imitate-Choose. Just like Imitate-Choose, it simply exaggerates the dominant transmission behavior in the random initial population, resulting in the population converging on a random transmission system. This random system might send a unique signal for every meaning, but it is equally likely to send the same signal for every meaning.

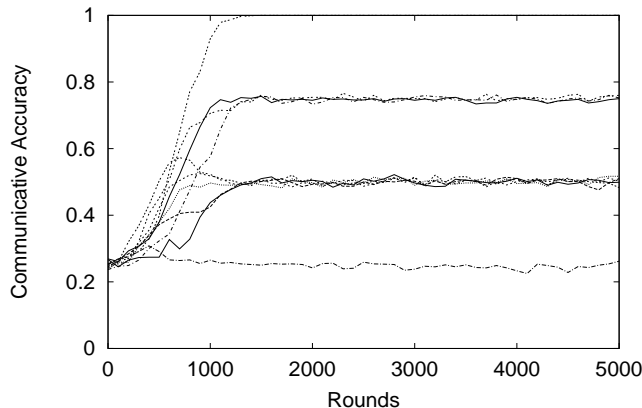


Figure VI.7: Performance of the Saussurean learning procedure. The Saussurean strategy exhibits performance that is better than chance, but fails to reliably produce an optimal system from random initial conditions. Four meanings and four signals are used. Results of 10 simulation runs are shown superimposed.

Expected performance of the Saussurean strategy

The expected performance of the Saussurean strategy can be mathematically predicted. Because the transmission system is constructed by the Saussurean procedure through imitation, biases in the random transmission behavior of the initial population will simply be exaggerated over time. This effectively results in the population converging on a random transmission system (just as was the case with the Imitate-Choose procedure). The expected number of unique signals expressed by a random transmission system encoding m meanings into s signals can be calculated as follows:

$$n_u = s(1 - (1 - (1/s))^m) \quad (\text{VI.4})$$

Because the Saussurean learning strategy mirrors its reception from its transmission, it will correctly receive every unique signal that it sends. This means that it will correctly communicate with itself for n_u of the m meanings, resulting in an expected communicative accuracy of n_u/m . Because the Saussurean strategy enforces consensus, this value will be the expected communicative accuracy of a population of Saussureans. A simulation averaging the performance of a number of runs involving populations is shown in Figure VI.8, along with the mathematically-expected performance of the strategy. The simulation results conform very closely to the level of accuracy that is predicted.

The expected performance of the Saussurean learning procedure depends critically on the number of meanings and signals that are used. More specifically, it depends on the ratio

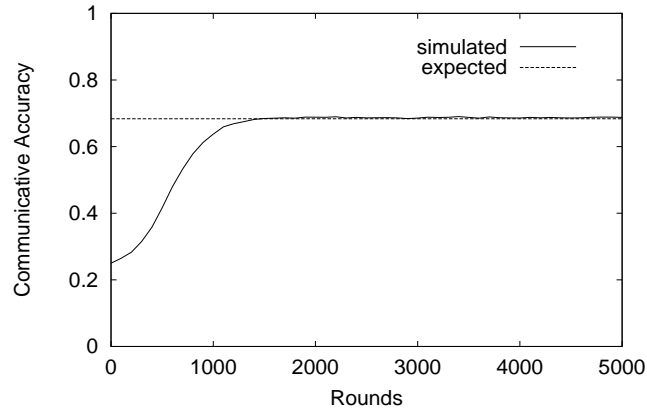


Figure VI.8: Average performance of the Saussurean learning procedure and the predicted value based on Equation VI.4. Four meanings and four signals are used. Results are averaged over 40 simulation runs.

of the number of signals to the number of meanings. As the number of signals increases for a fixed number of meanings, the probability of sending a unique signals for a given meaning also increases.

The expected communicative accuracy (n_u/m) can be closely approximated by the expression:

$$(s/m)(1 - e^{-m/s}) \quad (\text{VI.5})$$

Taking r to be the ratio s/m , the expected accuracy can be then expressed as:

$$r(1 - e^{-1/r}) \quad (\text{VI.6})$$

Figure VI.9 gives a plot of this expression for varying values of r . By the time the ratio has reached 10 : 1, the expected performance is very close to 1.0. Given this, the Saussurean strategy can be quite effective, provided that there are many more signals than there are meanings to express.

VI.D.3 Bayesian learning

Despite the success of the the Saussurean strategy, there are a number of reasons to look for a better learning procedure. First, the requirement that signals be plentiful is one that may or may not be met in a given ecological scenario. Second, the *a priori* incorporation of the Saussurean sign as a part of the learning mechanism is less satisfying than the possibility of having it emerge as a consequence of the learning dynamic.

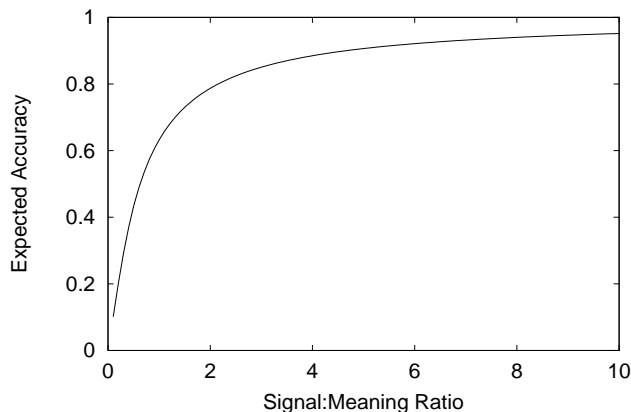


Figure VI.9: Expected Saussurean performance as the number of signals increases relative to the number of meanings.

To attempt to address these issues, we will consider another way to think about the task of the learner. Rather than imitating the behavior of the population (and the Saussurean strategy is still, at its heart, an imitative strategy), a learner could instead try to construct a communication system based on its expected utility for communicating with the population. In other words, a learner should try to maximize its ability to communicate with the average member of the population. To do this, it is necessary to a) create a send function that maximizes the probability of being understood by the population's average reception behavior, and b) create a receive function that maximizes the probability of correctly interpreting the population's average transmission behavior.

This amounts to doing a bayesian maximization of the conditional probability of communicative success. The formulation of such a learning strategy, which we will call the *Bayesian* learning procedure, is shown in Figure VI.10. It is important to note that this learning procedure involves the direct use of the average receive function of a population, rather than a sample biased by transmission behavior. As was pointed out in section VI.C.2, this assumption is not realistic and it will be addressed shortly.

Proof of Bayesian optimality

It can be proven that the Bayesian strategy produces the best possible communication system for use with a given population. In order to carry out this proof, we will first consider the construction of the send function. For a particular meaning μ , let κ be the signal most often interpreted as μ by members of the population whose average receive function is R . Thus, for

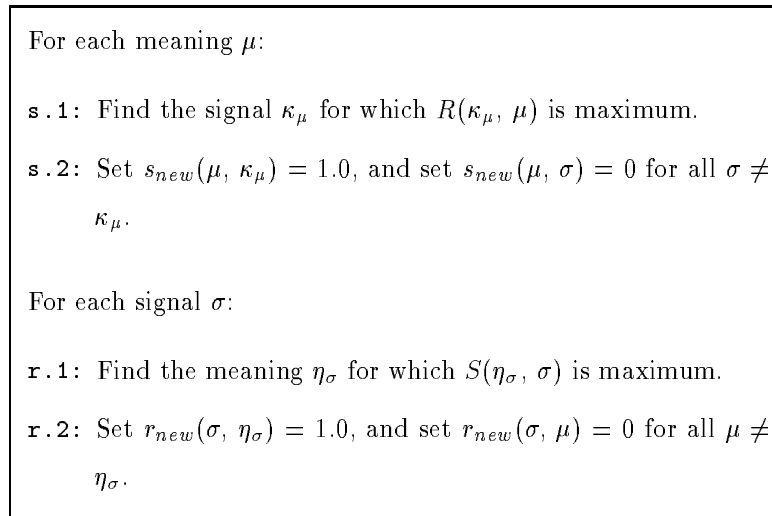


Figure VI.10: The Bayesian learning procedure.

any signal σ :

$$R(\sigma, \mu) \leq R(\kappa, \mu) \quad (\text{VI.7})$$

Because any weighted average of a set of numbers cannot exceed the largest number in the set, we know that, for any send function s :

$$\sum_{\sigma} s(\mu, \sigma) R(\sigma, \mu) \leq R(\kappa, \mu) \quad (\text{VI.8})$$

This means that the maximum possible communicative accuracy that any send function can have with respect to meaning μ is $R(\sigma, \mu)$ (see Equation III.1). Because the Bayesian procedure will construct a send function, s_b , that will send signal κ for meaning μ with probability 1.0, and will send other signals with probability 0.0, its probability of communicative success for meaning μ will be $R(\kappa, \mu)$. Thus, from Equation VI.8:

$$\sum_{\sigma} s(\mu, \sigma) R(\sigma, \mu) \leq \sum_{\sigma} s_b(\mu, \sigma) R(\sigma, \mu) \quad (\text{VI.9})$$

for each meaning, μ . Because we have shown that the send function produced by the Bayesian learning procedure will communicate any given meaning at least as well as any other possible send function, it follows from Equation III.2 that:

$$ca(s, R) \leq ca(s_b, R) \quad (\text{VI.10})$$

meaning that no other send function could communicate with the population better than s_b .

A virtually identical proof can be used to show that no other possible receive function performs better than the receive function, r_b , produced by the Bayesian procedure. Given this,

for a population whose average send and receive functions are S and R respectively:

$$ca_2(s, r, S, R) \leq ca_2(s_b, r_b, S, R) \quad (\text{VI.11})$$

for any possible send function, s , and receive function, r . The Bayesian learning procedure results in a communication system that communicates as accurately as is possible with a given population.

Increasing a population's communicative accuracy

It has been proven that that the learning strategy is guaranteed to produce the best possible system for communicating with the current population. It follows then, that such a system will communicate with the population as well or better than the population communicates within itself. Substituting the population average send and receive functions, S and R , for s and r in Equation VI.11, we get:

$$ca_2(S, R) \leq ca_2(s_b, r_b, S, R) \quad (\text{VI.12})$$

If new individuals continually replace old ones in the population, we can expect the communicative accuracy of the population to increase, until such time that the population communicates within itself as well as any send or receive function could possibly communicate with it.

Implementing the Bayesian learning procedure

Simulation results showing the average performance of populations of Bayesian learners is shown in Figure VI.11.

Approximating the Bayesian learning procedure

Although the Bayesian learning procedure produces optimal systems of communication, it is based on the use of an unrealistic sampling function for reception behavior. This can be easily corrected by modifying the Bayesian strategy outlined in Figure VI.10 so that it uses S_{smp} and R_{smp} rather than S and R directly. This procedure cannot truly be called Bayesian, since it is based on a biased sample of reception behavior, rather than the true conditional probabilities. The performance of this new strategy, which I will call *Invert*, is shown in Figure VI.12.

While performance is very good, perfect communication is not reliably achieved. Even if the number of rounds is increased, the average communicative accuracy fails to increase much beyond the value reached at round 5000. A closer look at these simulation results is shown in Figure VI.13. In one of the ten simulation runs shown, the communicative accuracy stops at a

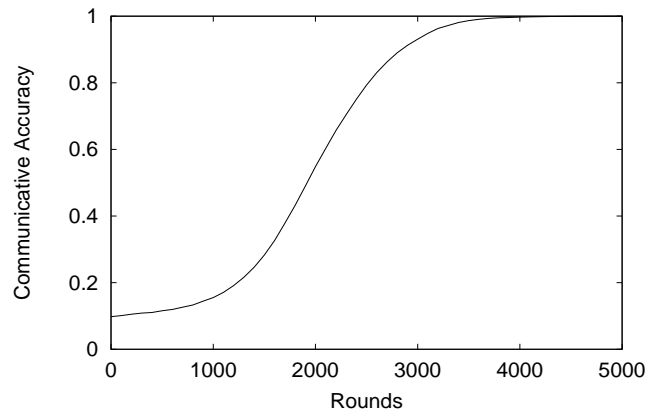


Figure VI.11: Average performance of the Bayesian learning procedure. Four meanings and four signals are used. Results are averaged over 40 simulation runs.

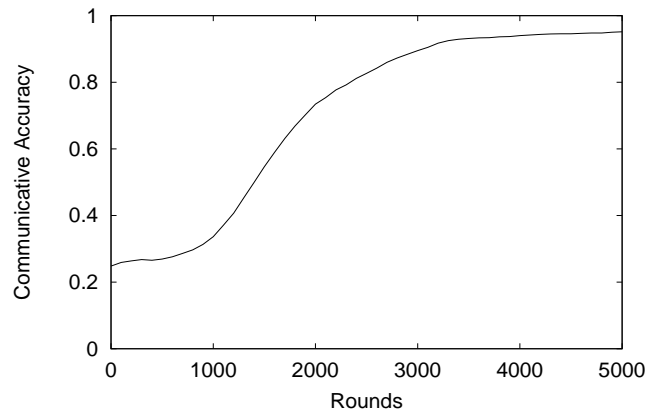


Figure VI.12: Average performance of the Invert learning procedure. Four meanings and four signals are used. Results are averaged over 40 simulation runs.

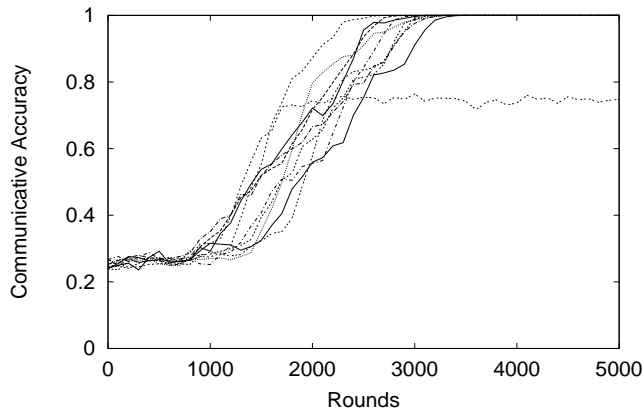


Figure VI.13: Failure of the Invert learning procedure. One of ten runs fails to reach perfect communication. Four meanings and four signals are used. Ten simulation runs are shown superimposed.

s	a	b	c	d
1	1.0	0.0	0.0	0.0
2	0.0	0.0	1.0	0.0
3	0.0	1.0	0.0	0.0
4	0.0	1.0	0.0	0.0

a	b	c	d	r
1.0	0.0	0.0	n/a	1
0.0	0.0	1.0	n/a	2
0.0	0.5	0.0	n/a.	3
0.0	0.5	0.0	n/a	4

Figure VI.14: A coordinated, but not optimal communication system. Signal 'b' is sent ambiguously for both meanings 3 and 4, and signal 'd' is never sent.

value of .75 (three of four meanings communicated accurately). Such sub-optimal performance is infrequent, but occurs reliably in approximately one run in ten.

In section III.D, it was shown that a population can be converged on a fully coordinated system, but still lack the required distinctiveness for optimal communication. This is exactly what is happening in the single failed run in Figure VI.13. The problem can be illustrated by looking at the communication system converged on in the single failed case in Figure VI.13. This system, shown in Figure VI.14, is ambiguous, sending signal 'b' for both meanings 3 and 4. Signal 'd' is never sent by members of the population. The reception system does the best it can, interpreting signal 'b' as meanings 3 and 4 with equal probability. The reception behavior with respect to signal 'd' is undefined, as it is never observed.

a	b	R_{smp}
4	3	0
6	1	1

a)

a	b	R_{norm}
0.4	0.75	0
0.6	0.25	1

b)

Figure VI.15: Normalizing a sample of reception behavior. Figure a) shows an example of a sample of a population's receive behavior. Figure b) shows the sample after it has been normalized, making all columns sum to 1.0.

Although this system is sub-optimal, it is still fully coordinated in that the send and receive functions communicate with each other at least as well as either would communicate with any other system. From observations of this system's send function, s , the Bayesian learning procedure will produce receive function r .⁴ From observations of receive function r , it will produce send function s . This system is an example of one of the inefficient equilibria discussed with respect to game theory in section III.E. The situation is inescapable, and the communicative accuracy of the population cannot increase.

VI.D.4 Normalization

The problem with the Invert strategy results from the fact that it is not a true Bayesian strategy. The observed sample of reception behavior is biased by the population's send behavior. Reception behavior to signals that are sent with low frequency is underrepresented in the sample. One way to correct for this is to normalize the sample of reception behavior so that it provides a better estimate of the true dispositions of the population. This normalization operation is shown in Figure VI.15. The columns are normalized so that they each sum to 1.0, representing the probability that a signal will be interpreted as a meaning, rather than the number of times the pairing was observed. As can be seen from the figure, this changes the signal that will be chosen for meaning '0'. Before normalization, signal 'a' would be chosen for both meanings. After normalization, signal 'b' will be chosen for meaning '0'. Normalization of the sample of transmission behavior can be carried out in a similar way, but is less critical if all meanings are equally likely to be signaled.

The performance of this new learning procedure, which I will call *Normalize*⁵, is shown in Figure VI.16. As can be seen from the figure, the normalization of the observed sample is

⁴ Actually, it will choose randomly to interpret signal 'b' as either meaning 3 or meaning 4, resulting in receive function r at the population level.

⁵ This learning strategy is functionally identical to the strategy called *Obverter* in Oliphant and Batali (1997).

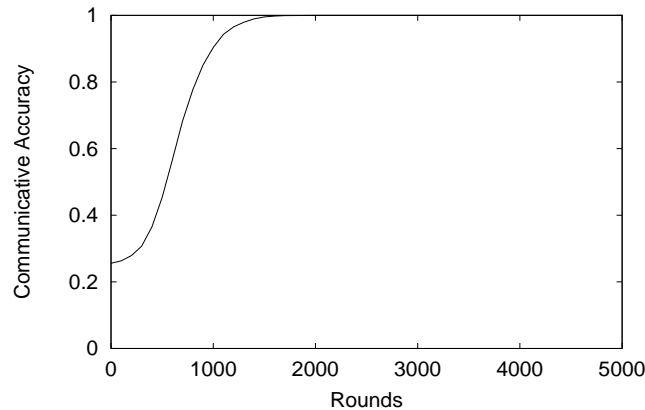


Figure VI.16: Performance of the Normalize learning procedure. In every simulation run, the Normalize strategy results in an optimal communication system. Four signals and meanings are used. Results are averaged over 40 simulation runs.

effective, and every simulation run achieves optimal performance. In fact, performance is better than that of the actual Bayesian learning procedure itself. This is likely due to the fact that normalization, in addition to countering biases due to skewed observation of reception behavior, also helps to compensate for the error involved in sampling in general.

Scalability

The performance of the Normalize strategy scales well for increased numbers of meanings. Figure VI.17 shows that, while the time it takes a population to converge on an optimal system increases with the number of meanings, optimal communication is nevertheless always achieved. The increase in convergence time is likely due to a lowered starting point – the chance level of communicative accuracy decreases as the number of meanings goes up.

It is important to be clear that the increase in time shown here is in terms of the number of rounds it takes the population to reach an optimal state, not the amount of time that it takes each new individual to learn. Learning involves observing three communicative interactions based on the transmission of each meaning. Thus, as the number of meanings increase, so does the number of observed samples of behavior. This reflects the number of observations required to get a representative sample of a larger system, and is not reflected by the number of rounds.

Time to convergence is also affected by the size of the population, as can be seen in Figure VI.18. As the number of individuals in the population increases, so does the number of rounds required to reach an optimal state of communication. This increase seems to be linear in

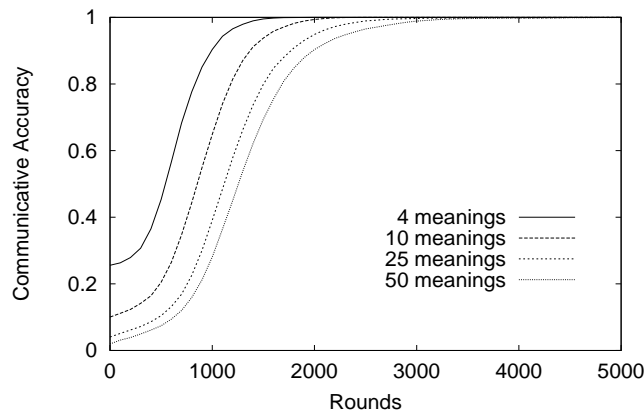


Figure VI.17: Performance of the Normalize learning procedure for varying numbers of signals and meanings. The number of signals and meanings is equal in each case. Time to converge increases only slightly with the number of signals/meanings. Results for each plot are averaged over 40 simulation runs.

the size of the population, and likely reflects the additional time to reach consensus in a larger population.

VI.D.5 Analysis of Hurford

The work presented in Hurford (1989) inspired many of the ideas presented in this section on statistical learning procedures. Hurford carried out a series of simulations closely related to the ones presented here. Because of this, it is useful to give an overview of the work that he did, and describe how it differs from the simulations presented here.

Hurford was primarily interested in the evolution of the Saussurean sign, investigating how an imposed bi-directional mapping between form and meaning might evolve as part of a language learning procedure. In order to do this, he pitted three different learning strategies against one another in an evolutionary scenario. The three strategies he proposed were:

Imitator: Equivalent to the Imitate-Choose learning procedure presented in Section VI.D.1.

Saussurean: Equivalent to the Saussurean learning procedure presented in Section VI.D.2.

Calculator: Equivalent to the Bayesian learning procedure presented in Section VI.D.3.

The performance of these three learning strategies in Hurford's simulations are largely consistent with the analytic and simulation results presented in the previous sections. Hurford examined the performance of populations of each of the three strategies, using a communicative

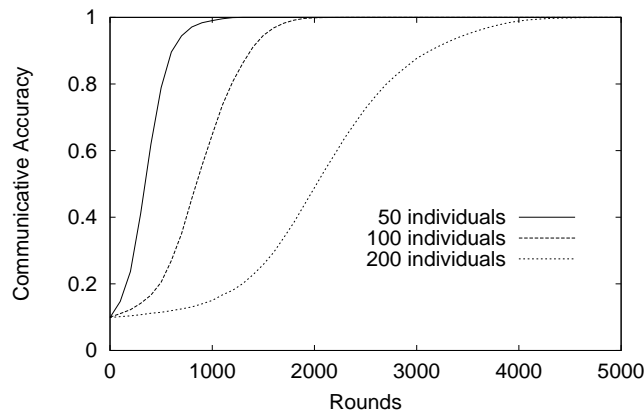


Figure VI.18: Performance of the Normalize learning procedure for varying population sizes. Time to converge seems to be linear in the size of the population. Results for each plot are averaged over 40 simulation runs.

task that involved 5 meanings and 7 signals. For a population of Imitators, Hurford had an average of 1 out of 5 meanings being communicated accurately (Hurford, 1989 p.220). Given the random performance of the Imitate-Choose strategy, this is exactly what would be expected.

For a population of Saussureans, Hurford had an average of 3.7 out of 5 meanings being communicated accurately (Hurford, 1989 p.221). For 5 meanings and 7 signals, the expected number of meanings communicated accurately by the Saussurean learning procedure is 3.76 (see Equation VI.4).

Hurford's results for the Calculator strategy, however, differ greatly from the results expected of a Bayesian learner. He found that Calculators failed to improve a population's communicative accuracy, and even reduced initially perfect systems to chance level performance. This seems surprising, as Bayesian learners should produce highly effective communication systems. This discrepancy can be reconciled by looking at a critical way in which Hurford's simulations differed from the ones presented here. While the present simulations maintain a steady flow of individuals into and out of the population, Hurford used a generation-based model, where the entire population of individuals was replaced all at once.

This difference, while not affecting the Imitator and Saussurean procedures, has a dramatic effect on the Calculator strategy. A Calculator models its transmission behavior on the reception behavior of others, and its reception behavior on the transmission behavior of others. As Figure VI.19 shows, a generation-based model causes the calculator to base its behavior on the population's behavior in the previous generation. This results in a situation where a calculator's behavior is optimized with respect to a population of individuals that no longer exists. What

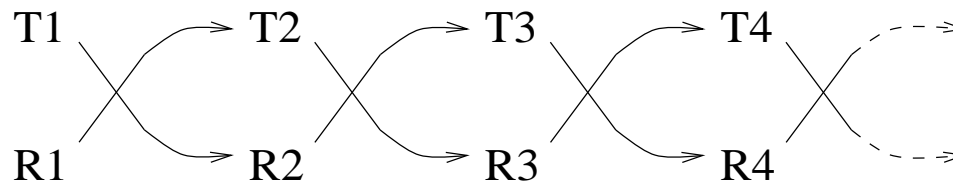


Figure VI.19: A population of Calculators over time. Because there is no overlap of individuals from one generation to the next, each generation is optimized to communicate with the previous generation, and not the other individuals in the current population. After Hurford (1989).

occurs in such a simulation is that the population constructs highly coordinated send and receive functions that are offset by one generation. Each generation is able to communicate well with the previous generation, but not their own.

As a result of this problem, Hurford concluded that the Saussurean procedure was superior to Calculator. The simulations presented here, however, show that Calculator (here called Bayesian) is the more effective strategy, and that it will produce optimal communication systems.

VI.E Network learning mechanisms

The statistical learning mechanisms described in the previous section all involve constructing a new learning system based on statistical properties of an observed sample of behavior. An important question that has not yet been addressed is whether we really expect animals to be able to carry out such statistical operations. It seems rather unlikely that any animal, including humans, are likely to carry out such complicated mental bookkeeping and calculation in the course of learning a communication system.⁶ However, it is also unlikely that when a little-league player learns to throw a baseball, she is doing the mental math required to calculate the trajectory. In both cases, we expect that the necessary calculation is done by exploiting properties of the underlying neural mechanism, rather than being done through conscious mental calculation. This section presents a number of different network models that might be used to instantiate some of the statistical learning procedures explored earlier.⁷

⁶ Although it can be shown that, under certain circumstances, such calculations can be reduced to a potentially reasonable level (see the *Unit-Statistic* learning procedure described in Oliphant and Batali (1997)).

⁷ It is slightly misleading to contrast *network* learning procedures with *statistical* learning procedures as network learning rules are, of course, also statistical. The distinction I intend is between learning that is explicitly statistical and learning in a network that is more implicitly statistical.

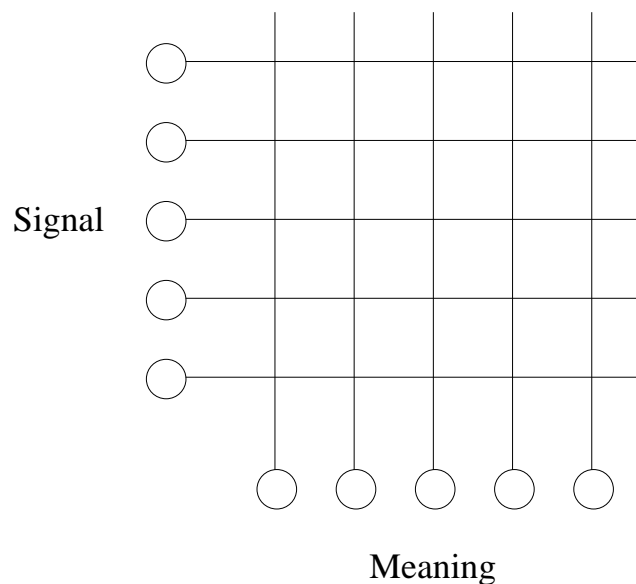


Figure VI.20: The associative network model. Signals and meanings are each represented by a layer of units, with the interconnecting weights storing the association between them.

VI.E.1 The network model

The networks used in the section use an associative learning framework, where an association between pairs of input and output patterns is learned. In this case, the input patterns are signals, and the output patterns are meanings. The general network architecture can be seen in Figure VI.20. A signal is represented on the input layer by turning on a single one of the input units. A meaning is represented on the output layer by turning on a signal one of the output units. Associations between signal and meaning are represented by the bi-directional weights that connect each input unit to every output unit.

More formally, the networks consist of a set of input units, S , and a set of output units, M . Individual units will be referred to as S_i and M_j , with w_{ij} designating the weight connecting input unit S_i and M_j . Because the weights are bi-directional, networks of this form are inherently internally coordinated, and the weights can be thought of as implementing a Saussurean sign.

The simulation regime used for populations of networks is virtually identical to the framework used for the statistical learning procedures presented earlier. There are only several small differences that should be noted. First, the networks begin with all weights set to zero, producing random initial behavior through having no bias, rather than giving the network a random bias (as was the case in with the statistical learning procedures). The second difference is that when an individual is used as a model for a learner, it is also trained on its own response.

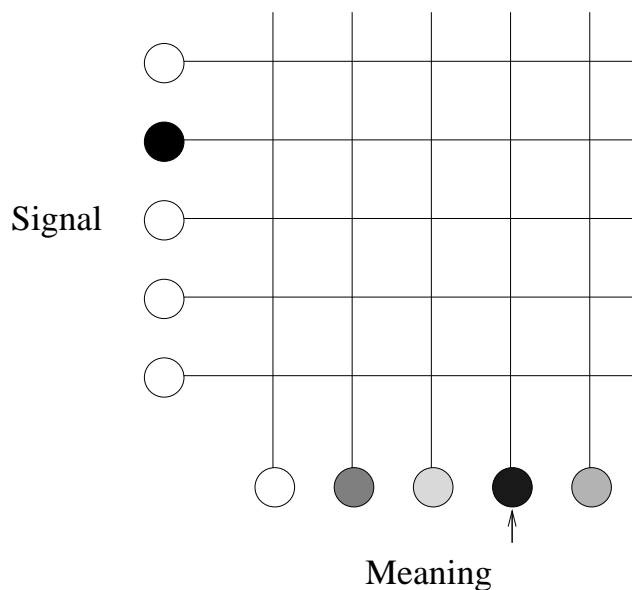


Figure VI.21: Winner-take-all recall. A particular signal is being interpreted by the network. The resulting meaning is the mostly highly activated unit, as indicated by the arrow.

This is necessary to ensure consistency in cases where the network has no bias in the current situation (something that happens very often in the early rounds, where the population consists almost entirely of the initial, unbiased networks used to begin the simulation).

All learning is done based on observed samples of transmission behavior only. Because the networks impose an inherent link between transmission and reception behavior, observations of either behavior are sufficient. While the learning rule that modifies the weights in response to the presentation of pairs of patterns will vary depending on the type of network, all of the simulations presented in this section use a winner-take-all output strategy. In this paradigm, the most highly active output unit is set to be active, while the other units are turned off. Thus, to use the network to interpret a particular signal, the unit corresponding to signal is activated, and the output unit, with the largest net input:

$$a_j = \sum_i S_i w_{ij} \quad (\text{VI.13})$$

is the winner. This procedure is diagrammed in Figure VI.21. Recall operates in a corresponding way for transmission behavior.

VI.E.2 Willshaw networks

Perhaps the most basic kind of associative networks are Willshaw networks, designed to associate pairs of sparse binary patterns (Willshaw, Buneman, and Longuet-Higgins, 1969;

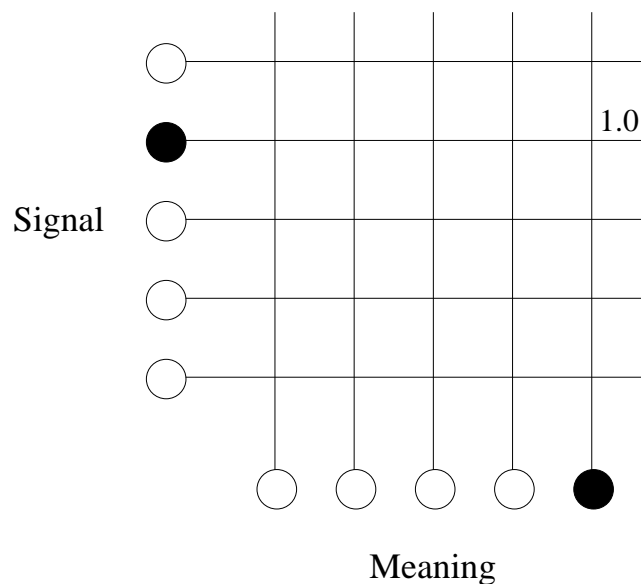


Figure VI.22: Training in a Willshaw network. A weight is set to 1 if the input and output units it connects are both active.

Willshaw, 1971). The learning rule used by these networks simply sets a weight, w_{ij} , to 1 if both S_i and M_j are activated for a given pair of input and output patterns. This learning rule is diagrammed in Figure VI.22.

In assessing the suitability of the Willshaw learning rule for communication, the issue is not whether or not such networks can learn an existing system, but rather whether they can construct a system. Any reasonable associative network should be able to learn an optimal communication system because the sets of vectors representing both the signals and the meanings are orthogonal, resulting in no intercorrelations. This results in the easiest possible data set to learn.

As can be seen in Figure VI.23, populations of Willshaw networks fail to construct a communication system. This occurs because, although the networks can learn a well-structured existing mapping, they are exceedingly bad at creating such structure. There is no way for a Willshaw network to represent one of two existing associations as being stronger than another. Because of this, there is no way for any one association to become exaggerated in the population. The networks maintain a collection of equally strong associations, resulting in random performance and a chance level of communicative accuracy.

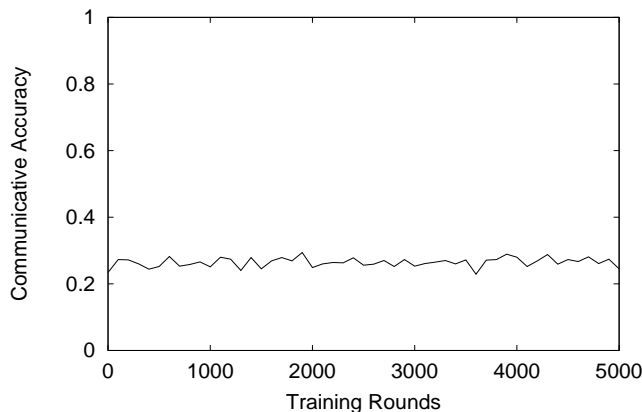


Figure VI.23: Performance of the Willshaw network. The Willshaw learning rule is unable to bring a population above chance performance. Four signals and four meanings are used. Results are averaged over ten simulation runs.

VI.E.3 Cumulative-Association networks

To correct the problem that Willshaw networks have in discriminating different levels of association, one can simply increment a weight when an association is perceived, rather than just setting the weight to 1. The weight update rule for such a network, which I will call a *Cumulative-Association* network, is as follows:

$$\Delta w_{ij} = \begin{cases} 1 & \text{if } S_i = 1 \text{ and } M_j = 1; \\ 0 & \text{otherwise;} \end{cases} \quad (\text{VI.14})$$

This new learning rule results in the performance shown in Figure VI.24. While populations of Cumulative-Association networks increase communicative accuracy above chance levels, they do not reach an optimum state. In fact, the performance is identical to that of the Saussurean learning strategy described in section VI.D.2. This is because the Cumulative-Association network is essentially a network implementation of the Saussurean procedure, resulting in similar disadvantages for similar reasons. Like the Saussurean procedure, the Cumulative-Association rule does not impose distinctiveness, resulting in the same signal being sent for multiple meanings, and the same meaning being interpreted for multiple signals.

One possible solution to this problem is to use the same technique that was used successfully to construct the Normalize learning strategy in section VI.D.4. Such a procedure will be explored in the next section.

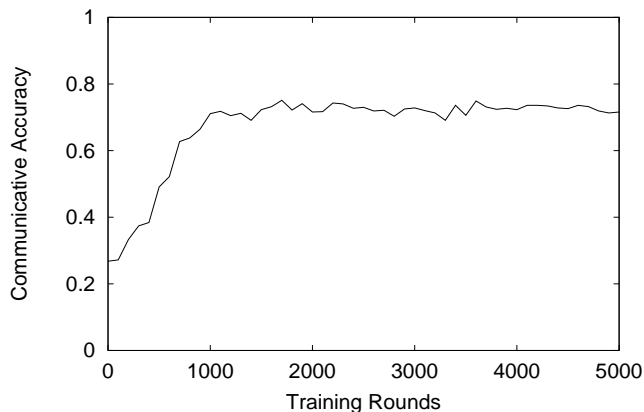


Figure VI.24: Performance of the Cumulative-Association network. The level of communicative accuracy reached is identical to the performance of the Saussurean learning strategy. Four signals and four meanings are used. Results are averaged over ten simulation runs.

VI.E.4 Hebbian networks

It turns out that there is a very simple way to obtain the effects of normalization in a network learning model. In the case of the statistical learning procedure, normalization involved converting a row or column in a sample matrix into probabilities. This can be done by summing all of the values in the row or column, and dividing each number by this sum. Normalization, then, can be seen as essentially a form of lateral inhibition, with each entry in the matrix being inhibited by its neighbors.

Lateral inhibition is a common operation in network learning. In this case, adding lateral inhibition to the Cumulative-Association rule described in the previous section results in a form of Hebbian learning rule (Hebb, 1949). Inhibition is implemented by decreasing the strength of a connection between a signal unit and a meaning unit if one, but not both of them are active. This results in the following weight update rule:

$$\Delta w_{ij} = \begin{cases} 1 & \text{if } S_i = 1 \text{ and } M_j = 1; \\ 0 & \text{if } S_i = 0 \text{ and } M_j = 0; \\ -1 & \text{otherwise;} \end{cases} \quad (\text{VI.15})$$

This new update rule is diagrammed in Figure VI.25.

It is important to note that this update rule does not increase the weights if both units are not firing, as is done in the most common formulation of the Hebbian learning rule. This results in better performance, and is in fact more compatible with the original hypothesis of Hebb (1949). It is also important that the networks use binary units rather than the signed (+1,-1)

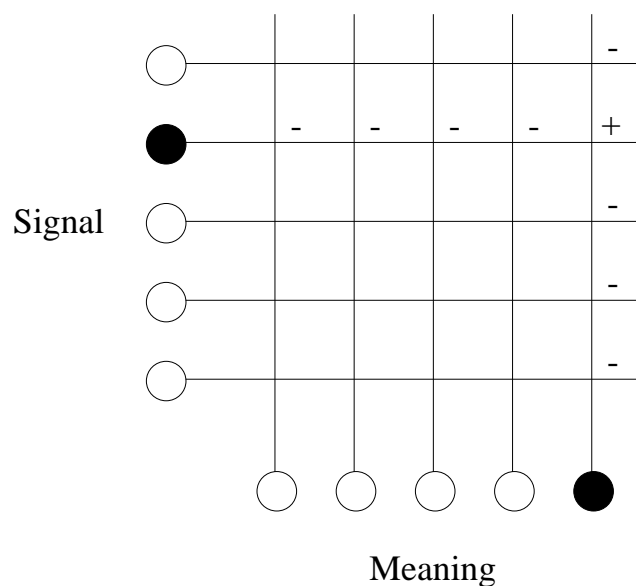


Figure VI.25: Training in a Hebbian network. A weight is increased if the input and output units it connects are both active. The weight is decreased if one, but not both of the units are active.

units that are used for mathematical convenience in the most standard formulation of Hebbian networks. Aside from the resulting problems in making analogies with real neural activity, using signed units in a task where patterns are sparse creates a great deal of spurious correlation. Two different patterns, each with one unit active, will be correlated in all but two of their units. This makes the task of the network unnecessarily difficult, and standard Hebbian networks cannot do the encoding task at all.

The performance of populations of networks using this formulation of the Hebbian learning rule is shown in Figure VI.26. As was the case with the Normalize learning procedure, the addition of lateral inhibition to the network learning rule results in the ability to achieve optimal performance.

Scalability

The performance of populations of Hebbian networks with varying numbers of meanings, and varying population sizes scales in much the same way as did the performance of the Normalize learning procedure. Figure VI.27 shows how performance changes with the number of signals and meanings. Figure VI.28 shows the effect of varying population sizes.

If each figure is compared with the corresponding one (Figure VI.17 and Figure VI.18) in section VI.D.4, it can be seen that, in general, populations of Hebbian networks converge

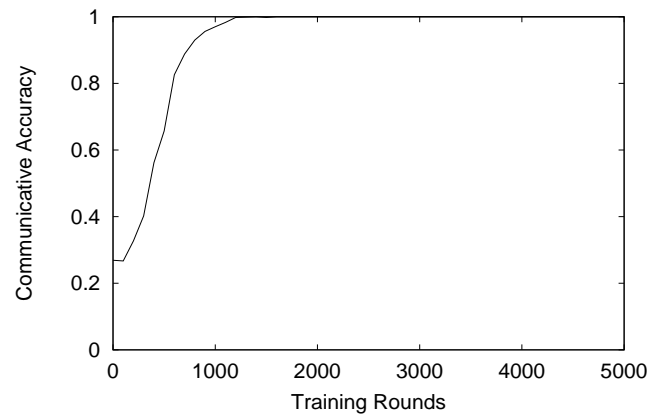


Figure VI.26: Performance of the Hebbian network. Populations of Hebbian networks are able to construct optimal communication systems. Four signals and meanings are used. Results are averaged over 10 simulation runs.

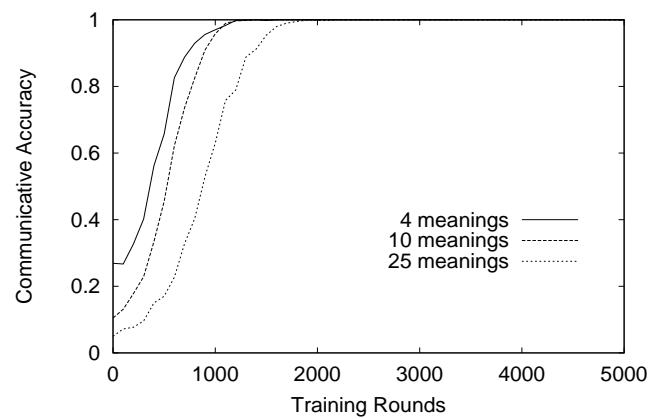


Figure VI.27: Performance of the Hebbian network using varying numbers of signals and meanings. The number of signals and meanings is equal in each case. Results for each plot are averaged over ten simulation runs.

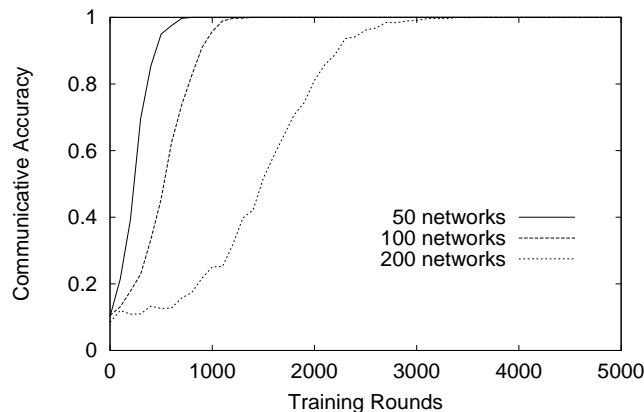


Figure VI.28: Network populations of varying sizes establishing a conventional encoding for ten input patterns. All plots are averaged over ten simulation runs.

faster than populations of learners using the Normalize strategy⁸. This is likely due to the fact that the coordination between transmission and reception behavior is inherently imposed in the network model, while it must be established by the Normalize learning procedure.

Multiple-unit meanings

Using Hebbian networks, it is also possible to deal with more complex meaning patterns than the ones used in the previous simulations. Instead of turning a single unit on in the vector to represent a particular meaning, a pattern across multiple units can be used. This allows the meanings to be structured according to some task-based metric. It also provides a way in which meanings can be more or less similar to each other, as patterns can overlap, sharing some of the same units.

The addition of structure transforms the problem into a form of vector quantization (Kohonen, 1989). The problem of correlations between the new structured meanings can be avoided by adding a conscience mechanism to the winner-take-all output threshold, as is done in other vector quantization tasks (Grossberg, 1976; Bienenstock, Cooper, and Munro, 1982). Additional details about this type of network, and results demonstrating its performance can be found in Oliphant (forthcoming).

⁸These simulations differ slightly from those done with the Normalize strategy in that the plots are only averaged over ten simulation runs. Also, Figure VI.27 does not include a plot for 50 signals/meanings. This is due to the combinatorial nature of these simulations – they are a serial simulation of a parallel task. These differences should not, however, significantly affect the comparison.

VI.F Discussion

This chapter has detailed the performance of a number of learning mechanisms operating within an observational learning paradigm. This kind of learning, while more realistic than reinforcement learning, has the disadvantage of lacking a feedback mechanism. Being unable to try a number of different communicative behaviors and choosing the one that *is* the most successful, an observational learning system must calculate, given a sample of the behavior of others, what communicative behavior *will be* the most successful.

Learning strategies that simply imitate the observed behavior of others are not sufficient. Imitation of a bad communication system results in a bad communication system. This means that perfect reproduction of observed behavior results in an inability to increase the population's performance. Rather than producing an individual communication system that mimics the communication of the population, a learning mechanism should construct an individual system that will increase the population's communication accuracy.

This is exactly what the Bayesian learning strategies do. From a sample of a population's behavior, they construct a communication system that will have the maximum possible communicative accuracy with that population. Such learning mechanisms, if used by a population of individuals, will increase the population's communicative accuracy over time. With the addition of lateral inhibition, the communicative accuracy of the population will eventually reach an optimal level.

It may seem that this kind of learning strategy would require that the learner possess an inordinate ability to calculate and predict. In the case of communication, however, this turns out not to be the case. Hebbian learning, perhaps the most simple, biologically plausible learning mechanism one could ask for, instantiates the required statistical properties. Given this, it seems that the ability to construct and maintain a learned system of communication should be, at least computationally, within the means of virtually any animal species.

Chapter VII

Learned communication in non-human animals

VII.A Why are the so few learned communication systems?

In the previous chapter, it was argued that the computational requirements of learned communication appear to be modest enough to be satisfied by most animals. Given this, why do we see so few examples of learned systems of communication in non-human animal species?

VII.A.1 Evolution may be sufficient

One reason why many species do not have learned communication may be that natural selection is doing a perfectly satisfactory job of maintaining the system. The animals may simply not have very much to say, and evolution is good enough to give them a way to say it. This scenario seems particularly likely in the case of animals that engage in relatively simple kinds of social interactions, the nature of which remain stable over long periods of time. Most animals really only need communication for a few basic purposes, such as attracting mates, defending territory, and sounding the alarm in response to predators. If communication boils down to a few variants of “I’m tough!” (for the benefit of both potential mates and competitors) and “Look out!”, evolution can, and does provide the means.

In animals with a more complicated social framework, however, it is more likely that learning will have advantages over evolution. As social interactions become more complex, the

number of communicative signals may increase. Learning is better able to keep pace with an enlarged signal repertoire than is a genetic representation in which each signal must be created and maintained by natural selection. In particular, evolution is unable to allow for communicative productivity within an individual's lifetime. Signals that referred to a particular individual in the population, for example, would be impossible.

VII.A.2 Learning has associated costs

It is also possible that, for a given species, the benefits of learning might be outweighed by associated costs. While evolution may be slow to respond to change, it has the advantage of making behavior available early on in life. If making accurate use of a communicative behavior is critical at a young age, a learned system which takes time to become established may be disadvantageous.

Learning to communicate, particularly in fitness-critical situations, may be a luxury that can only be supported by investing in an initial period involving a high level of parental care. This investment in childcare is made increasingly in the higher primates, culminating in the western model of human society where children are not considered full members of society until the age of 18.

VII.A.3 The ability to learn is absent

Let us assume that, at least in some situations, the advantages of learned communication are greater than the disadvantages. In such cases learned communication might still be absent because the animals lack a critical ability that such learning requires. Although I have shown Hebbian learning is computationally sufficient to establish communication in a population of animals, it was assumed that the data, in the form of observed signal/meaning pairs, were available to the learning mechanism.

The question remains, then, whether or not animals are capable of observing others, extracting the relevant information, and making it available to be learned. In doing observational learning¹, the animal may be capable of doing the learning, but not the observation. The degree to which animals are able to learn observationally is a controversial subject, particularly in the case of apes. In chimpanzees, it seems likely that the use of tools and communicative gestures is, to some degree, transmitted through some form of social learning (Goodall, 1986; Nishida,

¹I use the term *observational learning* to refer to learning that involves what others (such as Tomasello, 1990) call true imitation. This means that it is to be contrasted with other forms of social learning such as observational conditioning (Whiten and Ham, 1992). I reserve the use of the term *imitation* to refer to observational learning in which no additional structure is imposed on the input.

1987; Whiten and Custance, 1996). It is less clear, however, whether this social learning is truly observational (Tomasello, 1990; Tomasello, 1996).

VII.B Observational learning and communication

The next several sections present examples in which aspects of an animal's communicative behavior appear to be learned socially. These examples will be discussed with regard to two issues: what aspects of the animal's behavior are learned, and what form of learning is involved.

VII.B.1 Bird song

Song in male oscine birds, the most-studied example of which is the white-crowned sparrow, is often pointed to as a case of learned communication. In order to develop normal song, these birds must be exposed to the song of others of their kind. If a bird is raised in isolation, it develops a simpler song (Marler, 1970). Furthermore, such song has regional dialects, where birds of the same species but living in different geographical areas have distinct versions of song. While some birds learn to sing a single song, others, such as nightingales, learn to produce hundreds (Hultsch, 1993).

While it is clear that learning plays an important role in the development of song, it does not seem that the learned aspects involve tuning a system of communication. Bird song is certainly a form of communication, playing an important role in male-female courtship interactions and male-male territorial disputes, but this communicative function is innately specified. Birds do not learn a mapping between a song's form and its communicative function. In most species, even the basic form of the song is specified by an innate template (Konishi, 1965). This leads to the conclusion by avian researchers that "the ability to imitate sound may be as reflexive and cognitively uncomplicated as the ability to breathe" (West and King, p.172). Bird song appears to be a case which the learned behavior depends only on the behavior of the model, and not on a perceived relationship between the model's behavior and its consequence.

This is not to say that variations in singing behavior, such as increased song repertoire, have no utility. Evidence from song playback and other techniques indicates that females respond to variations in male song (Searcy, 1992). Increased song complexity and variability seem to mainly serve as an attention-getting device, operating much like the car alarms that cycle from one pattern of sound to another.

VII.B.2 Vervet monkey alarm calls

The alarm call system of vervet monkeys, as discussed in section ??, involves the use of specific vocal signals in response to a variety of predators. Unlike birdsong, the vocal calls do not appear to be learned. Comparisons of recordings of spontaneous calls given by immature animals to alarm calls given by adults indicates that learning is relatively unimportant in determining the acoustic properties of calling behavior (Seyfarth and Cheney, 1986; Hauser, 1996). The set of alarm calls appears to be innately constrained.

Vervets do, however, learn to fine-tune the use of alarm calls through experience. Seyfarth and Cheney (1986), in analyzing the use of the eagle alarm call, have found that it initially is used by infants and juveniles in response to perceptually similar non-predatory species such as vultures. Only later in life does it get narrowed to be a response to the eagles that prey on the vervets. While learning plays a role in tuning the specificity of an alarm call, it seems that the general danger categories such as “airborne eagle-like predator” are determined innately (Hauser, 1996). Because adult vervets generally ignore false-alarm calls by infants, it seems likely that these categories get narrowed through selective reinforcement; only in the case of a true predator will an infant’s alarm call generate a response from others.

Given the innate constraints on both the repertoire of signals and the general classes of meaning with which they are associated, it is difficult to call vervet communication, at least as it is observed in nature, a truly learned system. Furthermore, the learning that does take place is likely to be based on reinforcement, rather than observation of correlations between alarm calls and evasive responses in others. It would be very interesting, however, to know how closely tied the calls are to the danger category they are associated with. Could vervets learn through observation a system in which the usage of eagle and snake calls were switched? Such a question seems virtually impossible to test in the wild, however, and I am not aware of any study that addresses it.

VII.B.3 Communicative gestures in chimpanzees

Chimpanzees use a wide variety of gestural signals to mediate social interaction, using them in situations such as play, caregiving, and aggressive and sexual interactions. At least some aspects of this gestural communication appear to be learned. Evidence that this is the case comes from situations where a gesture is local to a particular population of animals (Nishida, 1987; Tomasello, 1990). If a gesture is wide-spread among one group of animals, and not used in another group of the same sub-species, it seems likely that the behavior was invented by some individual and then passed on through learning. It is difficult to be sure, however, as Tomasello

(1990) points out that it is always possible that the observed behavioral differences between different groups of animals result from subtle differences in the ecologies they inhabit.

Tomasello and his colleagues have carried out extensive observational studies of gesturing in captive chimpanzees placed in a physical and social setting designed to resemble that which exists in the wild (Tomasello, George, Kruger, Farrar, and Evans, 1985; Tomasello, Gust, and Frost, 1989; Tomasello, Call, Nagell, Olguin, and Carpenter, 1994). These studies have provided additional evidence that chimpanzees learn gestural signals. The communicative behavior of the animals changes ontogenetically, apparently adapting to the changing social environment as the animal grows from infant to adult (Tomasello, Gust, and Frost, 1989).

While the animals do seem to learn to use gestures, such learning is not necessarily observational. Many of the gestures learned by young individual, such as the solicitation of nursing, were never directed at them, and would have been difficult to observe in others. In addition, many of the gestures were unique, used only by a single individual. In light of this data, Tomasello argues that gesture learning occurs through a process of *ontogenetic ritualization*, which is essentially the learning equivalent of ritualization in the evolution of display behavior (Tomasello, 1996). He concludes that “each signal is created anew from individual, though perhaps common, social interactions, with no attempt to reproduce the behavior of a conspecific” (Tomasello, 1990, p.302).

VII.B.4 Language-trained animals

A large number of studies on animals such as apes, dolphins, and parrots have demonstrated the ability of the animals to learn to use human-designed systems of communication (Hayes and Hayes, 1951; Gardener and Gardener, 1969; Premack, 1971; Herman, Richards, and Wolz, 1984; Pepperberg, 1987). While such studies show that the animals in question do seem to be able to learn simple communication systems, they involve explicit language training through reinforcement. Thus they do not provide a test of the animal’s observational learning abilities.

Work done by Savage-Rumbaugh with the chimpanzee Kanzi is a possible exception (Savage-Rumbaugh, McDonald, Sevcik, Hopkins, and Rubert, 1986). Kanzi’s mother was being trained in an explicit language task like the ones mentioned above. While the mother failed to master the communication task, Kanzi showed communicative ability even though he had not been trained. He apparently picked the ability up by observing the training of his mother.

The case of Kanzi presents perhaps the strongest evidence for observationally learned communication in non-human animals. It is problematic for a number reasons, however. First, it is a single case, and did not occur within the context of an experimental setting. Second, the

behavior that Kanzi observed involved the carefully structured teaching of his mother, a situation very different than simply observing communication in everyday use by conspecifics.

Chapter VIII

Discussion

VIII.A Natural selection and its limitations

The vast majority of animal communication systems are innate. Evolution, as has been demonstrated in chapter IV, is well-equipped to construct and maintain simple systems of communication. This is particularly clear in situations where communication is in the direct best interest of both transmitter and receiver. In other cases, factors such as kin selection and reciprocal altruism help to modify the situation such that natural selection still manages to promote communicative behavior.

Evolution has its disadvantages, however. Any change to an innate system of communication requires modification of a genetically-encoded representation, and the timescale of such evolutionary change is very slow. This places limitations both on the possible complexity of an innate communication system¹ and on the ability of the system to respond quickly to changing demands. As has been mentioned previously, communication with respect to subjects introduced during an individual's lifetime is impossible.

VIII.B Observational learning is required

The solution to the limitation of innate systems of communication is for communication behavior to be learned. Not just any form of learning will do, however, and I have argued that communication must be learned through observing the behavior of others, rather than through individual trial-and-error.

¹I have done simulations looking at the ability of natural selection to construct and maintain a communication system as a function of the number of signals and meanings involved. Preliminary results indicate, not surprisingly, that the time to converge increases with the size of the system.

As was pointed out in section VI.A, reinforcement learning has the significant disadvantage of only being effective where error involves a low cost. Trial-and-error learning is also largely restricted to situations where experimenting with behaviors is likely to succeed. If an animal never finds a behavior that is successful, the behavior cannot be learned by reinforcement. Observational learning is essential in such situations. Even the behavior is difficult to acquire, it need only be discovered once, and can then be passed on to others by observation. Reinforcement learning requires that each individual create the behavior anew.

In the few cases (with the possible exception of Kanzi) where non-human animals seem to be able to learn communicative behaviors, this learning involves reinforcement rather than observation. Furthermore, the learning occurs in exactly the situations that reinforcement learning is suited to. In the case of vervet monkeys, the repertoire of signals and the categories of meaning are innately fixed. This facilitates trial-and-error learning by strictly limiting the set of behaviors an animal needs to try. In particular, stumbling upon the correct acoustical properties of a vocal signal would be extremely difficult if the set of possibilities was not restricted. Innately specifying the set of signals and meanings, however, negates what is perhaps the primary benefit of a learned system – extendability.

The examples of learned communication in chimpanzees are a result of a ritualized history of interaction between individuals. These gestures tend to be simple, ritualized shortcuts, where a component of a behavior is used as a signal for the entire sequence of action. An example is an infant touching its mother's arm as a nursing request. This signal is a ritualized version of an action that initially involved the infant moving its mother's arm to get access to the nipple (Tomasello, 1990). Communication involving more arbitrary relationships between signal and meaning would be much more difficult to establish through such ritualization.

Even if reinforcement learning was functionally able to establish any given system of communication, the timecourse involved still represents a severe limitation. Re-inventing the wheel over and over again makes it difficult to find time for building a cart. It is difficult to imagine, for example, a situation in which human language had to be re-negotiated for every pair of individuals, rather than a pre-established conventional system being learned.

VIII.C Imitation is not enough

Researchers studying social learning in animals have concentrated on whether or not animals can learn by imitating others, and have given less thought to the computational requirements of such learning (Heyes and Galef, 1996). The simulation work done here in chapter VI shows that the kind of observational learning strategy used makes a critical difference. While

simple imitation is sufficient to learn an existing system of communication under ideal conditions, it is not capable of maintaining such a system against noise, or constructing it in the first place. Because it lacks the benefit of a reinforcement signal, a purely observational learning procedure must not simply imitate the behavior it observes, but also impose structure on it. Without the imposition of such structure, imitators of ineffective communicative behavior will be equally ineffective themselves.

This distinction, contrasting a learning mechanism that can only learn an existing communication system and one that can also construct such a system, is extremely important. Pinker (1994) argues that children do not simply learn their language, but reinvent it in each generation. Strong evidence for this claim comes from work on creole languages (Bickerton, 1981; Bickerton, 1990). Children, when exposed to the relatively unstructured *pidgin* language that occur when members of different language communities are thrown together, do not simply reproduce the pidgin. Instead, they construct a much more richly structured creole language. Structure is continually imposed at each generation. If it was not, language would degrade over time.

Given that simple imitation is not enough to account for socially transmitted systems of communication, the simulation work I present could well have revealed some computational requirement above and beyond what could be expected of most animals. Instead the requirements seem to be rather modest. The basic principles of Hebbian learning happen to impose exactly the kind of structure that is necessary for a population of interacting individuals to construct and maintain a simple system of communication.

VIII.D Observational learning as a bottleneck in language evolution

Most approaches to the evolution of language point to the evolution of syntax as the primary barrier differentiating the communicative abilities of man and other species (Chomsky, 1990; Bickerton, 1990; Pinker, 1994). While the use of syntactic language certainly poses significant challenges that must be overcome, another, more basic, bottleneck exists. Although virtually every animal species uses some form of communication, very few of these systems are learned. Innate communication is the norm, while learned communication is a very rare exception.

Given this, a serious problem in the evolution of language seems to be the ability to utilize *any* form of learned communication system, be it syntactic or not. Because of the critical importance of the ability to observe from others in learning a communication system, I argue that a lack of observational learning contributes greatly to holding back the communicative ability of

even highly social species. This claim is supported by the evidence from social learning studies in animals. While human infants come into the world as virtual imitation machines (Meltzoff, 1996), it seems that the ability to learn by observing others is rare, if present at all, in other animals.

Because humans appear to be the only animals that possess either observational learning or syntactic language, it is difficult to assess the relative difficulty in achieving these skills. We do not know how long it took our human ancestors to make the progression from simple learned systems of communication to more complex, language-like systems. It is possible that the ability to communicate by combining sequences of signals requires cognitive skill that other animals do not have, significantly above and beyond the ability to learn observationally. That this might be true is supported, perhaps, by the failure of non-human animals to use syntactic language in reinforcement training studies.

It is also possible, however, that observational learning is the primary factor limiting the evolution of language ability. Perhaps, once animals can learn to communicate by observing others, the achievement of syntactic communication is an extension that is comparatively less difficult. Recent work involving computational simulations of the origins of syntax support this view (Batali, 1997; Worden, 1997; Kirby, 1997; Hutchins and Hazelhurst, 1997).

What, then, is unique about human language? It involves the use of syntactic structure and it is learned by observing others. While most attention is generally focused on syntax, I argue that the ability to learn observationally may be an equally, if not more important evolutionary milestone.

Appendix A

Simulation software used

All of the simulations reported in this dissertation were carried out using custom-designed software written in C++.

The evolutionary simulations were done using an open-ended package, designed to allow for use in a wide variety of studies. Creation of a new simulation involves specifying a genetic representation and a procedure that implements a fitness function. All other operations are carried out by general-purpose functions in the simulator. Because this software may be useful to others, a public release is possible at some point in the future.

The simulations involving learning were done using two different simulation programs: one implementing the statistical learning procedures, and the other implementing the network learning procedures.

Bibliography

- Ackley, D. and M. Littman (1994). Altruism in the evolution of communication. In R. Brooks and P. Maes (Eds.), *Proceedings of the fourth artificial life workshop*, Cambridge, MA, pp. 40–48. MIT Press.
- Axelrod, R. (1980a). Effective choice in the prisoner’s dilemma. *Journal of Conflict Resolution* 24, 3–25.
- Axelrod, R. (1980b). More effective choice in the prisoner’s dilemma. *Journal of Conflict Resolution* 24, 379–403.
- Axelrod, R. (1987). The evolution of strategies in the iterated prisoner’s dilemma. In L. Davis (Ed.), *Genetic algorithms and simulated annealing*, Chapter 3, pp. 32–41. Los Altos, CA: Morgan Kaufmann Publishers, Inc.
- Axelrod, R. and W. Hamilton (1981). The evolution of cooperation. *Science* 211, 1390–1396.
- Batali, J. (1995). Small signaling systems can evolve in the absence of benefit to the information sender. Unpublished manuscript.
- Batali, J. (1997). Computational simulations of the emergence of grammar. In J. Hurford, C. Knight, and M. Studdert-Kennedy (Eds.), *Evolution of Language: Social and Cognitive Bases for the Emergence of Phonology and Syntax*. Cambridge University Press.
- Batali, J. and P. Kitcher (1995). Evolution of altruism in optional and compulsory games. *Journal of Theoretical Biology* 175, 161–171.
- Batali, J. and M. Oliphant (forthcoming). A model of simple communication systems.
- Bickerton, D. (1981). *Roots of language*. Ann Arbor, MI: Karoma.
- Bickerton, D. (1990). *Species and language*. Chicago: Chicago University Press.
- Bienenstock, E., L. Cooper, and P. Munro (1982). Theory for the development of neuron selectivity: Orientation specificity and binocular interaction in visual cortex. *Journal of Neuroscience* 2, 32–48.
- Billard, A. and K. Dautenhahn (1997). The social aspect of communication: a case study in the use and usefulness of communication for embodied agents. In *1997 European Conference on Artificial Life*, Brighton, England.
- Blume, A., Y. Kim, and J. Sobel (1993). Evolutionary stability in games of communication. *Games and Economic Behavior* 5, 547–575.
- Boyd, R. and P. Richerson (1995). Why does culture increase human adaptability. *Ethology and Sociobiology* 16, 125–143.

- Bradbury, J. and S. Vehrencamp (forthcoming). *Principles of animal communication*. Sunderland, MA: Sinauer Associates.
- Brandon, R. and N. Hornstein (1986). From icons to symbols: some speculations on the origins of language. *Biology and Philosophy* 1, 169–189.
- Burghardt, G. (1970). Defining communication. In J. Johnston Jr., D. Moulton, and A. Turk (Eds.), *Communication by chemical signals*. Appleton-Century-Crofts.
- Cangelosi, A. and D. Parisi (1996, January). The emergence of a 'language' in an evolving population of neural networks. Technical Report NSAL-96-004, Institute of Psychology, National Research Council, Rome.
- Charnov, E. and J. Krebs (1975). The evolution of alarm calls: altruism or manipulation? *American Naturalist* 109, 107–112.
- Cheney, D. and R. Seyfarth (1990). *How monkeys see the world: Inside the mind of another species*. Chicago: University of Chicago Press.
- Cheney, D. and R. Seyfarth (1996). Function and intention in the calls of non-human primates. *Proceedings of the British Academy* 88, 59–76.
- Chomsky, N. (1990). Language and mind. In *Ways of communicating*, pp. 56–80. Cambridge, UK: Cambridge University Press.
- Crain, S. (1991). Language acquisition in the absence of experience. *Behavioral and Brain Sciences* 14, 597–611.
- Daumer, K. (1958). Blumenfarbend wie sie die bienen sehen. *Z. vergl. Physiol.* 41, 49–110.
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- Dawkins, R. and J. Krebs (1978). Title. In J. Krebs and N. Davies (Eds.), *Behavioral ecology: an evolutionary approach*. Blackwell Scientific.
- de Saussure, F. (1959). *Course in general linguistics*. New York: McGraw-Hill.
- Dennett, D. (1987). *The intentional stance*. Cambridge, Massachusetts: MIT/Bradford Books.
- Di Paolo, E. (1996). An investigation into the evolution of communicative behaviors. Technical Report Cognitive Science Research Paper 445, School of Cognitive and Computing Sciences, University of Sussex.
- Farrell, J. (1988). Communication, coordination and nash equilibrium. *Economics Letters* 27, 209–214.
- Fogel, L., A. Owens, and M. Walsh (1966). *Artificial Intelligence through Simulated Evolution*. New York: Wiley and Sons.
- Gardener, B. and P. Gardener (1969). Teaching sign language to a chimpanzee. *Science* 165, 664–672.
- Goodall, J. (1986). *The chimpanzees of Gombe*. Cambridge, MA: Harvard University Press.
- Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology* 144, 517–546.
- Grice, H. (1957). Meaning. *Philosophical Review* 66, 377–388.

- Grim, P. (1996). Spatialization and generosity in the stochastic prisoner's dilemma. *BioSystems* 37, 3–17.
- Grossberg, S. (1976). Adaptive pattern classification and universal recoding: II. feedback, expectation, olfaction, illusions. *Biological Cybernetics* 23, 187–202.
- Hamilton, W. (1963). The evolution of altruistic behavior. *American Naturalist* 97, 354–356.
- Hamilton, W. (1964). The genetical evolution of social behaviour (i and ii). *Journal of Theoretical Biology* 156, 1–52.
- Hamilton, W. (1967). Extraordinary sex ratios. *Science* 156, 477–88.
- Hauser, M. (1996). *The evolution of communication*. Cambridge, Massachusetts: MIT Press.
- Hayes, K. and C. Hayes (1951). The intellectual development of a home-raised chimpanzee. *Proceedings of the American Philosophical Society* 95, 105.
- Hebb, D. (1949). *The organization of behavior*. New York: John Wiley & Sons.
- Herman, L., D. Richards, and J. Wolz (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition* 16, 129–219.
- Heyes, C. and B. Galef (1996). *Social Learning in Animals: The Roots of Culture*. San Diego: Academic Press.
- Holland, J. (1975). *Adaptation in natural and artificial systems*. Ann Arbor, MI: The University of Michigan Press.
- Huberman, B. and N. Glance (1993). Evolutionary games and computer simulations. *Proceedings of the National Academy of Sciences (USA)* 90(16), 7715–7718.
- Hultsch, H. (1993). Tracing the memory mechanisms in the song acquisition of nightingales. *Netherlands Journal of Zoology* 43, 155–171.
- Hurford, J. (1989). Biological evolution of the saussurean sign as a component of the language acquisition device. *Lingua* 77, 187–222.
- Hutchins, E. and B. Hazelhurst (1995). How to invent a lexicon: the development of shared symbols in interaction. In N. Gilbert and R. Conte (Eds.), *Artificial Societies: The computer simulation of social life*. London: UCL Press.
- Hutchins, E. and B. Hazelhurst (1997). The emergence of propositions from the coordination of talk and action in a shared world. forthcoming.
- Kim, Y. and J. Sobel (1995). An evolutionary approach to pre-play communication. *Econometrica* 65(5), 1181–1193.
- Kirby, S. (1997). Language evolution without natural selection: From vocabulary to syntax in a population of learners. Manuscript in preparation.
- Kohonen, T. (1989). *Self-organization and associative memory* (3rd ed.). Berlin: Springer-Verlag.
- Konishi, M. (1965). The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Zeitschrift für Tierpsychologie* 22, 770–783.
- Konishi, M. (1973). Locatable and nonlocatable acoustic signals for barn owls. *American Naturalist* 107, 775–785.

- Langton, C. (1989). *Artificial Life*. Redwood City: Addison-Wesley.
- Levin, M. (1995). The evolution of understanding: a genetic algorithm model of the evolution of communication. *BioSystems* 36, 167–178.
- Lewis, D. (1969). *Convention: A philosophical study*. Harvard University Press.
- Lewis, D. and D. Gower (1980). *Biology of communication*. New York: Wiley.
- Lindgren, K. (1991). Evolutionary phenomena in simple dynamics. In C. Langton, C. Taylor, J. Farmer, and S. Rasmussen (Eds.), *Artificial life II*, pp. 295–311. Redwood City, CA: Addison-Wesley.
- Lloyd, J. (1984). On deception, a way of all flesh, and firefly signaling and systematics. In R. Dawkins and M. Ridley (Eds.), *Oxford surveys in evolutionary biology*, pp. 48–54. New York: Oxford University Press.
- MacLennan, B. and G. Burghardt (1994). Synthetic ethology and the evolution of cooperative communication. *Adaptive Behavior* 2(2), 161–187.
- Marler, P. (1955). Characteristics of some animal calls. *Nature* 176, 6–8.
- Marler, P. (1957). Specific distinctiveness in the communication signals of birds. *Behavior* 11, 13–39.
- Marler, P. (1970). A comparative approach to vocal learning: song development in white-crowned sparrows. *Journal of Comparative and Physiological Psychology* 71, 1–25.
- Maynard Smith, J. (1965). The evolution of alarm calls. *American Naturalist* 99, 59–63.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge: Cambridge University Press.
- Maynard Smith, J. and G. Price (1973). The logic of animal conflict. *Nature* 246, 15–18.
- Meltzoff, A. (1996). The human infant as imitative generalist: a 20-year progress report on infant imitation with implications of comparative psychology. In C. Heyes and B. Galef (Eds.), *Social Learning in Animals: The Roots of Culture*, pp. 347–370. San Diego: Academic Press.
- Moynihan, M. (1970). Control, suppression, decay, disappearance and replacement of displays. *Journal of Theoretical Biology* 29, 85–112.
- Nash, J. (1951). Noncooperative games. *Annals of Mathematics* 54, 289–295.
- Nishida, T. (1987). Local traditions and cultural transmission. In B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Strusaker (Eds.), *Primate Societies*. Chicago: University of Chicago Press.
- Nowak, M. and R. May (1992). Evolutionary games and spatial chaos. *Nature* 359, 826–829.
- Nowak, M. and K. Sigmund (1992). Tit for tat in heterogeneous populations. *Nature* 355, 250–252.
- Oliphant, M. (1994). Evolving cooperation in the non-iterated prisoner's dilemma: The importance of spatial organization. In R. Brooks and P. Maes (Eds.), *Proceedings of the fourth artificial life workshop*, Cambridge, MA, pp. 349–352. MIT Press.

- Oliphant, M. (1995). Selfish genes and altruistic behavior. In P. Enrado (Ed.), *Explorations in artificial life*, pp. 32–35. San Francisco, CA: AI Expert Presents.
- Oliphant, M. (1996). The dilemma of saussurean communication. *BioSystems* 37(1-2), 31–38.
- Oliphant, M. (1997). Self-organized coordination in populations of interacting associative networks. Forthcoming.
- Oliphant, M. and J. Batali (1997). Learning and the emergence of coordinated communication. Forthcoming.
- Pepperberg, I. (1987). Evidence for conceptual quantitative abilities in the african parrot: Labeling of cardinal sets. *Ethology* 75, 37–61.
- Pinker, S. (1994). *The language instinct*. New York: William Morrow.
- Premack, D. (1971). Language in chimpanzee? *Science* 172, 808–822.
- Pulliam, H. and C. Dunford (1980). *Programmed to learn*. New York: Columbia University Press.
- Rechenberg, I. (1973). *Evolutionsstrategie: optimierung technischer systeme nach prinzipien der biologischen evolution*. Stuttgart: Frommann-Holzboog.
- Savage-Rumbaugh, E., K. McDonald, R. Sevcik, W. Hopkins, and E. Rubert (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*pan paniscus*). *Journal of Experimental Psychology: General* 115, 211–235.
- Searcy, W. (1992). Song repertoire and mate choice in birds. *American Zoologist* 32, 71–80.
- Sebeok, T. (1977). *How animals communicate*. Bloomington: Indiana University Press.
- Seyfarth, R. and D. Cheney (1986). Vocal development in vervet monkeys. *Animal Behavior* 34, 1640–1658.
- Seyfarth, R., D. Cheney, and P. Marler (1980a). Monkey responses to three different alarm calls: evidence for predator classification and semantic communication. *Science* 210, 801–803.
- Seyfarth, R., D. Cheney, and P. Marler (1980b). Vervet monkey alarm calls: semantic communication in a free-ranging environment. *Animal Behavior* 28, 1070–1094.
- Sherman, P. (1977). Nepotism and the evolution of alarm calls. *Science* 197, 1246–1253.
- Skyrms, B. (1996). *Evolution of the social contract*. Cambridge University Press.
- Smith, W. (1977). *The behavior of communicating*. Cambridge, MA: Harvard University Press.
- Steels, L. (1996). Self-organizing vocabularies. In *Proceedings of the V Alife Conference*, Nara, Japan.
- Steels, L. and A. McIntyre (1997). Spatially distributed naming games. In *Fourth European Conference on Artificial Life*, Brighton, England.
- Strusaker, T. (1967). Auditory communication among vervet monkeys (*cercopithecus aethiops*). In S. Altmann (Ed.), *Social Communication among Primates*, pp. 281–324. Chicago: University of Chicago Press.

- Tinbergen, N. (1952). Derived activities: Their causation, biological significance, origin and emancipation during evolution. *Quarterly Review of Biology* 27, 1–32.
- Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signaling of chimpanzees? In S. Parker and K. Gibson (Eds.), *Language and intelligence in monkeys and apes: Comparative developmental perspectives*. Cambridge: Cambridge University Press.
- Tomasello, M. (1996). Do apes ape? In C. Heyes and B. Galef (Eds.), *Social Learning in Animals: The Roots of Culture*, pp. 319–436. San Diego: Academic Press.
- Tomasello, M., J. Call, K. Nagell, R. Olguin, and M. Carpenter (1994). The learning and use of gestural signals by young chimpanzees: a trans-generational study. *Primates* 35, 137–154.
- Tomasello, M., B. George, A. Kruger, J. Farrar, and E. Evans (1985). The development of gestural communication in young chimpanzees. *Journal of Human Evolution* 14, 175–186.
- Tomasello, M., D. Gust, and T. Frost (1989). A longitudinal investigation of gestural communication in young chimpanzees. *Primates* 30, 35–50.
- Trivers, R. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology* 46, 35–57.
- von Frisch, K. (1974). Decoding the language of the bee. *Science* 185, 663–668.
- Von Neumann, J. and O. Morgenstern (1953). *Theory of games and economic behavior*. Princeton: Princeton University Press.
- Warneryd, K. (1993). Cheap talk, coordination, and evolutionary stability. *Games and Economic Behavior* 5, 532–546.
- Werner, G. and M. Dyer (1991). Evolution of communication in artificial organisms. In C. Langton, C. Taylor, J. Farmer, and S. Rasmussen (Eds.), *Artificial life II*, pp. 659–687. Redwood City, CA: Addison-Wesley.
- West, M. and A. King (1996). Social learning: synergy and songbirds. In C. Heyes and B. Galef (Eds.), *Social Learning in Animals*, pp. 155–178. San Diego: Academic Press.
- Wexler, K. and P. Culicover (1980). *Formal principles of language acquisition*. Cambridge, MA: MIT Press.
- Whiten, A. and D. Custance (1996). Studies of imitation in chimpanzees and children. In C. Heyes and B. Galef (Eds.), *Social Learning in Animals: The Roots of Culture*, pp. 291–318. San Diego: Academic Press.
- Whiten, A. and R. Ham (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. In P. Slater, C. Rosenblatt, C. Beer, and M. Milinski (Eds.), *Advances in the Study of Behavior, Volume 21*, pp. 239–283. New York: Academic Press.
- Wiley, R. (1983). The evolution of communication. In T. Halliday and P. Slater (Eds.), *Animal behavior*. W.H. Freeman and Co.
- Willshaw, D. (1971). *Models of distributed associative memory*. Ph. D. thesis, University of Edinburgh.
- Willshaw, D., O. Buneman, and H. Longuet-Higgins (1969). Non-holographic associative memory. *Nature* 222, 960–962.

- Wilson, E. (1965). Chemical communication in the social insects. *Science* 149, 1064–1071.
- Wilson, E. (1975). *Sociobiology: the new synthesis*. Cambridge, MA: Harvard University Press.
- Worden, R. (1997). The evolution of language from social intelligence. In J. Hurford, C. Knight, and M. Studdert-Kennedy (Eds.), *Evolution of Language: Social and Cognitive Bases for the Emergence of Phonology and Syntax*. Cambridge University Press.
- Yanco, H. and L. Stein (1993). An adaptive communication protocol for cooperating mobile robots. In J. Meyer, H. Roitblat, and S. Wilson (Eds.), *From Animal to Animats 2: Proceedings of the Second International Conference on Simulation of Adaptive Behavior*. MIT Press.
- Zahavi, A. (1975). Mate selection - a selection for handicap. *Journal of Theoretical Biology* 53, 205–214.
- Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology* 67, 603–605.