Rethinking the language bottleneck: Why don't animals learn to communicate?

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Abstract

While most work on the evolution of language has been centered on the evolution of syntax, my focus in this paper is instead on more basic features that separate human communication from the systems of communication used by other animals. In particular, I argue that human language is the only existing system of learned arbitrary reference. While innate communication systems are, by definition, directly transmitted genetically, the transmission of a learned learned systems must be indirect. Learners must acquire the system by being exposed its the use in the community. Although it is reasonable that a learner has access to the utterances that are produced, it is less clear how accessible the meaning is that the utterance is intended to convey. This particularly problematic if the system of communication is symbolic – where form and meaning are linked in a purely conventional way. Given this, I propose that the ability to transmit a learned symbolic system of communication from one generation to the next represents a key milestone in the evolution of language.

1 Features of human language

To theorize about the evolution of human language is to theorize about how human communication differs from the communication systems used by other species, and what biological basis underlies these differences. The features of human language that I would suggest we need to account for are as follows:

- **Syntax:** Human language is compositional, conveying structured meanings through the use of structured forms.
- **Learning:** Human language is passed on from one generation to the next via cultural transmission.
- **Symbolic reference:** The mapping between basic lexical elements and their meanings is arbitrary and conventional.

In distinguishing human language from other forms of communication, the attention has largely been focused on the evolution of syntax. (Bickerton, 1990; Pinker and Bloom, 1990;

No lanterns	$\Longleftrightarrow$	No attack
One lantern	$\Longleftrightarrow$	Attack by land
Two lanterns	$\Longleftrightarrow$	Attack by sea

Figure 1: A simple signaling system, consisting of a set of signals and their associated meanings.

Newmeyer, 1991). This is unsurprising, as syntactic structure is certainly the most salient feature of human language. Because other species seem to have no means of combining simple signals with each other to form more complex meanings, the prime objective of most research on the evolution of langauge has been to explain how such an ability arose in humans.

In this paper, I will instead focus on the other, perhaps more basic, features of human language that make it unique – learning and symbolic reference. While there are other forms of communication that are *learned*, and there are other forms of communication that are *symbolic*, I will argue that human language is the only existing system of communication that is both learned *and* symbolic. Moving from a simple (non-syntactic) innate system of communication to an equally simple learned system is non-trivial. Making such a transition is particularly difficult if the mapping between forms and meanings is an arbitrary convention.

2 Innateness and symbolic reference

Because I am putting aside the issue of syntax, the systems of communication that I am concerned with are what Lewis (1969) termed *signaling systems* – systems that map between unstructured signals and unanalyzed meanings. Lewis gives as an example a communication system used in Boston during the American revolution. In this system, immortalized in the phrase "one if by land, two if by sea", lanterns were used to signal the existence and nature of an impending British attack. 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 there was no attack coming. This signaling system is diagrammed in Figure 1.

I will refer to each bi-directional association between a signal (such as displaying two lanterns) and the meaning it denotes ("attack by sea") as a *sign*, after de Saussure (1959). In classifying a system of communication, I will ask two questions about the signs that compose it. First, are the signs innate or learned? An innate sign is an association that is specified genetically and passed on from one generation to the next through reproduction. A learned sign, on the other hand, is established experientially through the use of some learning mechanism. Rather than being passed on genetically, if a learned sign is to be perpetuated it must be culturally transmitted from one generation to the next.

The second question that I want to ask is whether or not the signs are *symbolic*. Peirce (1932) defines a symbol as "a sign which refers to the Object that it denotes by virtue of a law, usually an association of general ideas, which operates to cause the Symbol to be interpreted as referring to that Object" (276). A symbol, then, is linked with its referent by convention. Symbols are arbitrary, bearing no inherent relationship to that which they denote. There is no sense, for example, in which the word "dog" has any "dogness" in it, in either its spoken

	Non-Symbolic	Symbolic
Innate	Threat displays Bee dance Facial expressions	Most alarm calls
Learned	Chimpanzee gestures Road signs	Human language

Figure 2: Classifying communicative behavior with respect to innateness and symbolic reference.

or written form. One might object that any particular individual's use of the word "dog" is in fact *not* arbitrary – an individual's use of any particular word is determined by the way that word is used in the language community. This objection makes it clear that in stating that a sign is arbitrary, we must state exactly what it is arbitrary with respect to. We can thus clarify the definition of a symbol in the following way:

> **A symbol is a sign that refers to the object that it denotes in a way that is arbitrary with respect to the process of conventionalization that established it.**

In the case of learned signs, then, we would say that they are symbolic if they are arbitrary with respect to the relevant learning mechanism. A child's use of the word "dog" is symbolic because this use simply reflects the convention used by the language community. We can evaluate the signs used in innate animal communication systems in a similar way. Although it may seem strange to talk of innate symbols, it is completely consistent with the definition of what it is to be symbolic. In the case of innate communication, the process of conventionalization is natural selection. Animal signaling behavior is symbolic if it is arbitrary with respect to the process of natural selection.

3 Classifying communicative behavior

The distinctions made in the previous section give us the means to classify systems of communication based on whether they are innate or learned, and whether they are symbolic or not.[1] Figure 2 shows the four possible combinations under this classification. In the following sections, I will look at each of these classes of communication in turn.

3.1 Innate non-symbolic systems

One way in which reference can be non-symbolic is for the sign to be what Peirce calls *iconic*. An icon refers by virtue of resemblance, such as the way a road sign indicates that a road is slippery by using wavy lines. In the realm of animal communication, iconic signaling often occurs in threat display behavior, where aggressive intent is conveyed by such actions as the lowering of antlers or the revealing of teeth. Another example of iconic communication is

[1] A similar analysis, though broken down based on different features, can be found in Burling (this volume).

the dance done by honeybees to convey information about the information of food sources to other bees in the hive. 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 hive. 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.

Communicative behavior need not be iconic to be non-symbolic. Many animal signals derive from intention movements through a process of ritualization (Tinbergen, 1952). Consider the problem faced by flocks of birds that take flight as a group. If one bird is preparing to fly, the others need to recognize this and prepare to fly as well. To accomplish this, selection can tune the behavior of the birds such that the preparatory motions of other birds trigger the initiating of flight. In Peirce's terms, this form of reference is *indexical* – the preparatory motions signal a bird's intent to take flight by virtue of being part of the same causal chain of events.

3.2 Innate symbolic systems

Humans are not the only species that have a symbolic system of communication (contrary Deacon (1997)). Many non-human animals have innate symbolic systems of communication – arbitrary systems of reference that have been tuned by natural selection. The process by which natural selection can tune such systems is well understood, both mathematically (Warneryd, 1993; Blume, Kim, and Sobel, 1993; Kim and Sobel, 1995; Skyrms, 1996) and computationally (see for example Oliphant, 1997, and the papers in this volume by Di Paulo, Livingstone and Fyfe, and Noble).

Perhaps the most commonly cited example of an innate system of arbitrary reference is the alarm call behavior 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 chuttering 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 call, the monkeys to look up or run into bushes, the calls given in response to large cats cause vervets to run into trees, 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.

The vervet system is symbolic because there is no sense in which the acoustic properties of the alarm calls are intrinsically related to either the predators they correspond to, or the appropriate evasive behavior. In fact, it is difficult to imagine what an iconic alarm call would be like, unless it imitated some sound that the predator made.

While the vervet alarm call system involves a learned component, it is best thought of as an innate system of communication. 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,

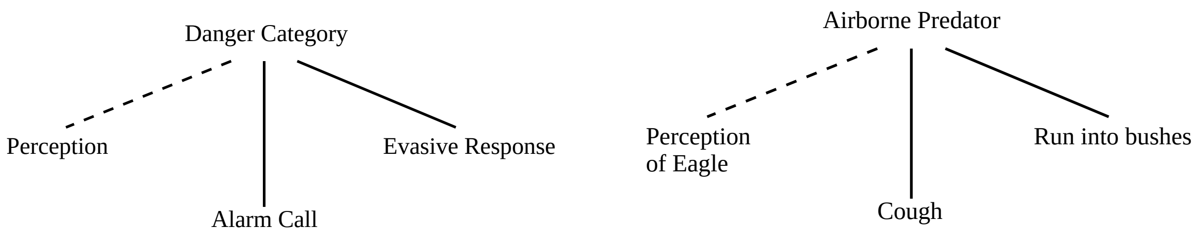

Figure 3: Innate and learned components of the vervet alarm call system. The left diagram represents the system as a whole, while the diagram on the right shows the alarm call behavior in response to eagles. Solid lines represent innate associations, while dashed lines represent associations that are learned.

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.

A schematic diagram of this view of the vervet call system is shown in Figure 3. Solid lines represent associations that are innate, while dashed lines represent learned associations. The association between a given danger category (such as "airborne predator") and the corresponding alarm call (a coughing sound) is innately specified. The association between a danger category and the precise nature of the perceptual stimulus that represents it is learned. The plasticity in the system involves perception, rather than communication. What is the reason for this plasticity? It may give some flexibility in the class of predators an alarm call can refer to. Perhaps more likely, however, is the possibility that the plasticity only exists because it isn't feasible to genetically encode the precise perceptual description of a predator.

3.3 Learned non-symbolic systems

Learned systems of communication are extremely rare. By far the more common case is for communication to involve an innate mapping between signal and meaning. One of the few cases where we do find evidence of learned communication is, perhaps unsurprisingly, in the apes. Chimpanzees use a wide variety of gestural signals to mediate social interaction, using them in situations such as play, care-giving, and aggressive and sexual interactions. At least some aspects of this gestural communication appear to be learned. Evidence that this is the case comes both from observation of the animals in their natural habitat (Goodall, 1986), and from 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). The communicative behavior shows variation across groups and individuals, and also 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, this communicative behavior is of a specific and limited kind. The 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). Tomasello (1996) calls this process *ontogenetic ritualization.* As the name suggests, this process can be seen as a learning equivalent of the ritualization of innate behaviors described in section 3.1.

Chimpanzee gestural communication, then, is indexical rather than symbolic, with the signal being related causally to the meaning it represents. Because of the derived nature of the signals that are used, the ritualization process limits what meanings can be refered to. Communication involving more arbitrary relationships between signal and meaning would be much more difficult to establish through such ritualization.

3.4 Learned symbolic systems

While, as the previous several sections have shown, there are a variety of non-human communication systems that are either learned or symbolic, human langauge seems to be the only system that is both. I would argue that this is true despite the results of a large number of studies demonstrating the ability of a variety of species to learn to use symbolic systems of communication (Hayes and Hayes, 1951; Gardener and Gardener, 1969; Premack, 1971; Herman, Richards, and Wolz, 1984; Pepperberg, 1987). The key issue here is what it means to say that a system of communication to be learned. In the cases cited above, the system was designed by the researchers and explicitly taught to the animals using a reinforcement-based training program. These studies do not constitute evidence that the species in question are capable of supporting a learned symbolic system of communication because there is no evidence that the system would perpetuate in a population of animals without human intervention.

Work done by Savage-Rumbaugh and colleagues with bonobo chimpanzees comes closer to providing such evidence. The observation that an infant chimpanzee showed evidence of having learned in a communication task that not he, but his mother was being trained in indicated that perhaps explicit reinforcement was not required (Savage-Rumbaugh, Mcdonald, Sevcik, Hopkins, and Rubert, 1986). This finding has been followed up in a more controlled setting, examining whether the chimpanzees can learn the meaning of spoken words simply by observing them in use (Lyn and Savage-Rumbaugh, this volume).

While this kind of study is exactly what is needed to refine our understanding of the differences (and similarities) between humans and other apes, it has not yet demonstrated learned symbolic communication among bonobos. Instead, it has shown that, under the right conditions, bonobos can learn symbolic system of communication from humans. We still have no evidence that bonobos can use and maintain such a system over time, passing it from one generation to the next. The fact that we do not see such systems in the wild would seem to indicate there must be *some* reason for their absence.[2]

[2]This assumes, of course, that we have an accurate picture of what the animals are doing in the wild. While it is possible that learned symbolic systems exist that we are unaware of, and we must be open to this possibility, it seems best to theorize based on what evidence we currently have available to us.

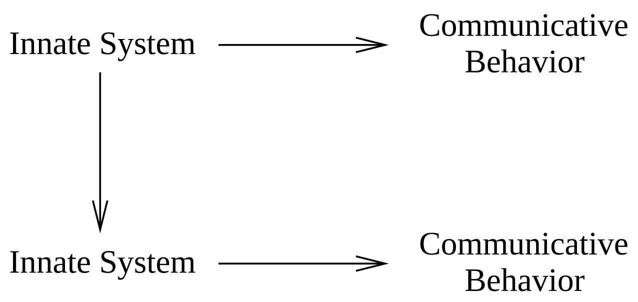

Figure 4: Transmission of an innate communication system. The representation of the system is passed on genetically.

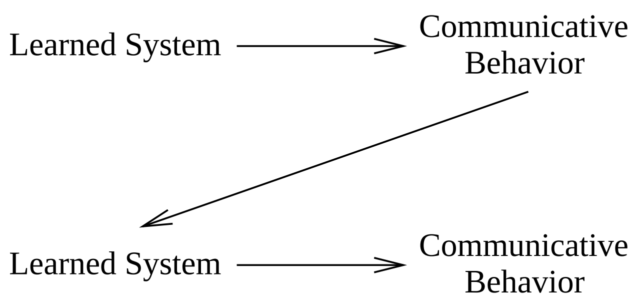

Figure 5: Transmission of a learned communication system. The representation of the system cannot be passed on directly, but must be mediated by the production of and exposure to communicative behavior.

4 Why is learning hard?

If we accept that human language is the only existing system of learned symbolic communication, the next step is to come up with an explanation as to why this might be the case. What is it that makes a simple learned system more problematic than an equally simple innate system? One possible answer to this question lies in differences in how innate and learned systems are transmitted.

For a system of communication to persist in a population, it must be heritable from one generation to the next. In the case of an innate system, such heritability is trivial. If the innate system has been tuned by natural selection, it is simply transmitted genetically (see Figure 4). In the case of learned communication, however, the system cannot be passed on directly from one individual to another. Instead, transmission must be mediated by the communicative behavior itself (see Figure 5). The extent to which such transmission is possible will be determined by how difficult it is to learn a communication system by being exposed to its use by others.

The results of computational simulation work has given us a good understanding of what is required for a population of individuals to establish and maintain a learned system of communication. This simulation work can be separated in to two forms of learning: those which use some form of reinforcement learning (Yanco and Stein, 1993; Hutchins and Hazelhurst, 1995; Steels, 1996; Murciano and Millan, 1996; Livingstone and Fyfe, this volume), and those which use a purely observational model (Oliphant and Batali, 1997; Oliphant, 1997). Reinforcement learning makes use of some form of error signal (generally whether or not an attempt at communicating was successful) to allow individuals to adapt their communicative behavior. In a purely observational learning paradigm, a communication system is learned solely on the basis of observing the communicative behavior of others.

The value of these simulation studies is that they give us information about what is computationally required of a learner, and what they tell us is quite startling. Very simple learning mechanisms seem to be sufficient. In fact, Hebbian learning, perhaps the simplest form of learning one could imagine, has been found to be sufficiently powerful to establish and sustain a learned system of communication in a population of observational learners (Oliphant, 1997).

This result would seem to indicate that making a transition from innate to learned systems of communication should not be particularly difficult. How are we to reconcile this with the fact that learned communication is so rare? The answer, I think, lies in assumptions that are made by the simulation studies with regard to what information a learner has access to. In the case of reinforcement learning, it is assumed that there is a reliable error signal that tells a learner whether they are communicating appropriately or not. It is not clear, however, that such an error signal exists. In the case of human language, for example, it is argued that children do not get sufficient reinforcement from their parents (Wexler and Culicover, 1980; Crain, 1991).

In the case of observational learning, what is assumed is that learners have access to the communicative behavior of others in the form of signal/meaning pairs. Having access to the signals that others are producing seems reasonable, but how is a learner to have reliable access to the meanings that others are intending to convey?

5 The problem of observing meaning

Understanding the problem a learner faces in determining the meaning a signal is intended to convey is central, I think, to explaining the rarity of learned communication. In the case of innate communication, the problem does not exist, simply for the reason that learning is not required for the system to be transmitted from one generation to the next.

The difficulty of observing meaning also accounts for why learned symbolic communication is so rare. In an innate system, transmission of an arbitrary sign is no more difficult that transmitting an iconic one – such distinctions are unimportant to the process of biological reproduction. This is not the case with respect to the transmission of a learned system. Iconic or indexical signs refer by resemblance and causal relationship respectively. In both cases, the signal gives direct information about the meaning it refers to. In contrast, a symbol will, by definition, bear no discernible relationship to the meaning to which it refers – the association is purely conventional.

Learned symbolic systems of communication are rare, then, because it in the case of symbols that the problem of observing meaning is most difficult. Humans seem to be the only species that have managed to find a way to cope with this difficulty. Children are able to learn to use words because they are adept at determining their meaning from the context in which they appear. They seem to simplify the task of deciding what a word denotes through knowledge of the existence of taxonomic categories (Markman, 1989), awareness of the pragmatic context (Tomasello, 1995), and reading the intent of the speaker Bloom (1997, this volume). In addition, human adults seem, at least to some degree, to make the meaning of their utterances more salient to the child. When talking to young children mothers modify their speech along a number of dimensions, and this may aid the child in acquisition (Snow, 1977).

6 Discussion

I have argued in this paper that human language is the only existing system of learned symbolic communication. While other species use innate symbolic systems, or learned non-symbolic systems, cultural transmission of arbitrary reference seems to exist only in humans. This uniqueness can be explained by looking at how the problem of transmission is different in the case of learned communication, even if the communication system itself is no more complex. While innate systems can simply be transmitted genetically, learned systems must be acquired ontogenetically. Learned systems cannot be transmitted directly, but must instead involve acquisition of the behavior produced by others.

Although simulation work has shown that very simple learning mechanisms are sufficient to support this process of acquisition, this has been based on the assumption that a learner has easy access to the meaning that a signal is intended to convey. Getting such access is likely to be a non-trivial process, particularly in the case of symbolic reference, where the signal and meaning are linked purely by convention.

Given this, I propose that a key milestone in the evolution of language is the ability to transmit a learned symbolic system of communication from one generation to the next. It is only when this ability is in place that the stage is set for the development of linguistic complexity. At this point, perhaps the addition of syntactic structure will require additional biological change. It is possible that the ability to communicate by combining sequences of signals requires cognitive skill that other animals do not have.

It is also possible, however, the the problem of transmitting a learned symbolic system is the primary factor limiting the evolution of language ability. Perhaps, the achievement of syntactic communication is an extension that is comparatively less difficult. That this might be true is supported by evidence of the use of syntactic forms in non-human animals (Greenfield and Savage-Rumbaugh, 1990; Kako, this volume), and computational work showing that syntactic structure can emerge on a cultural, rather than evolutionary time scale (Batali, 1997; Hutchins and Hazelhurst, 1997; papers in this volume by Batali, Hurford, Kirby, Steels, and Worden). In any case, we should not be preoccupied with the evolution of syntax, and should give careful examination to more basic features that may separate the communicative ability of humans from that of other animals.

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References

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. (1998). The negotiation and acquisition of recursive grammars as a result of competition among exemplars. See Knight and Hurford (1998).

Bickerton, D. (1990). *Language and species*. Chicago: Chicago University Press.

Bloom, P. (1997). Intentionality and word learning. *Trends in cognitive sciences 1*(1), 9–12.

Blume, A., Y. Kim, and J. Sobel (1993). Evolutionary stability in games of communication. *Games and Economic Behavior 5*, 547–575.

Burling, R. (1998). Comprehension, production and conventionalization in the origins of language. See Knight and Hurford (1998).

Crain, S. (1991). Language acquisition in the absence of experience. *Behavioral and Brain Sciences 14*, 597–611.

de Saussure, F. (1959). *Course in general linguistics*. New York: McGraw-Hill.

Deacon, T. (1997). *The symbolic species: the co-evolution of language and the brain*. New York: W.W. Norton.

Di Paulo, E. (1998). Spatio-temporal and structural constraints in the evolution of communication. See Knight and Hurford (1998).

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.

Greenfield, P. and E. Savage-Rumbaugh (1990). Grammatical combination in *pan paniscus*: Processes of learning and invention in the evolution an development of langauge. In S. Parker and K. Gibson (Eds.), *"Language" and intelligence in monkeys and apes*, pp. 540–578. Cambridge University Press.

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.

Herman, L., D. Richards, and J. Wolz (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition 16*, 129–219.

Hurford, J. (1998). Social interaction favours linguistic generalization. See Knight and Hurford (1998).

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.

Kako, E. (1998). Reconstructing proto-language from the capacities of language-trained animals. See Knight and Hurford (1998).

Kim, Y. and J. Sobel (1995). An evolutionary approach to pre-play communication. *Econometrica 65*(5), 1181–1193.

Kirby, S. (1998). Syntax without natural selection: How compositionality emerges from vocabulary in a population of learners. See Knight and Hurford (1998).

Knight, C. and J. Hurford (Eds.) (1998). *Procedings of the 2nd International Conference on the Evolution of Language*, London.

Lewis, D. (1969). *Convention: A philosophical study.* Harvard University Press.

Livingstone, D. and C. Fyfe (1998). A computational model of language-physiology co-evolution. See Knight and Hurford (1998).

Lyn, H. and E. Savage-Rumbaugh (1998). Observational word learning in bonobos (*pan paniscus*). See Knight and Hurford (1998).

Markman, E. (1989). *Categorization and naming in children: Problems of induction.* Cambridge, MA: MIT Press.

Murciano, A. and J. Millan (1996). Learning signaling behaviors and specialization in cooperative agents. *Adaptive Behavior 5*(1), 5–28.

Newmeyer, F. J. (1991). Functional explanation in linguistics and the origins of language. *Language and Communication 11*, 3–28.

Noble, J. (1998). The evolution of communication with and without conflicts of interest: An argument for modelling proto-proto-language. See Knight and Hurford (1998).

Oliphant, M. (1997). *Formal approaches to innate and learned communication: Laying the foundation for language.* Ph. D. thesis, University of California, San Diego.

Oliphant, M. and J. Batali (1997). Learning and the emergence of coordinated communication. *Center for Research on Language Newsletter 11*(1).

Peirce, C. (1932). *Collected papers of Charles Sanders Peirce*, Volume 2: Elements of logic. Harvard University Press.

Pepperberg, I. (1987). Evidence for conceptual quantitative abilities in the african parrot: Labeling of cardinal sets. *Ethology 75*, 37–61.

Pinker, S. and P. Bloom (1990). Natural language and natural selection. *Behavioral and Brain Sciences 13*, 707–784.

Premack, D. (1971). Language in chimpanzee? *Science 172*, 808–822.

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.

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.

Skyrms, B. (1996). *Evolution of the social contract.* Cambridge University Press.

Snow, C. (1977). Mothers' speech research: From input to interaction. In C. Snow and C. Ferguson (Eds.), *Talking to Children: Language input and acquisition*, pp. 31–49. Cambridge: Cambridge University Press.

Steels, L. (1996). Self-organizing vocabularies. In *Proceedings of the V Alife Conference*, Nara, Japan.

Steels, L. (1998). The origins of linguistic categories. See Knight and Hurford (1998).

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. (1995). Pragmatic contexts for early verb learning. In M. Tomasello and W. Merriman (Eds.), *Beyond Names For Things: Young Children's Acquisition of Verbs.* Lawrence Erlbaum.

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.

von Frisch, K. (1974). Decoding the language of the bee. *Science 185*, 663–668.

Warneryd, K. (1993). Cheap talk, coordination, and evolutionary stability. *Games and Economic Behavior 5*, 532–546.

Wexler, K. and P. Culicover (1980). *Formal principles of language acquisition.* Cambridge, MA: MIT Press.

Worden, R. (1998). Words, memes and language evolution. See Knight and Hurford (1998).

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.