From Cultural Selection to Genetic Selection: A Framework for the Evolution of Language

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This paper is an attempt to construct a programmatic framework for the evolution of human language. First, we present a novel characterization of language, which is based on some of the most recent research results in linguistics. As these results suggest, language is best characterized as a *specialized* communication system, dedicated to the expression of a surprisingly constrained set of meanings. This characterization calls for an account of the evolution of language in terms of the interaction between *cultural* and *genetic* evolution. We develop such an evolutionary model on the basis of the mechanism of *culturally-driven genetic assimilation*. As we show, a careful analysis of the diverse effects of this mechanism derives some of the most crucial properties of the evolved linguistic capacity as a specific, functional communication system.

Keywords: Cultural evolution, genetic assimilation, linguistic semantics, syntax-semantics interface, island constraints

1. Introduction

In dealing with the evolution of human language, we are confronted with two fundamental questions. The first is the question of the *object* of the evolutionary process: what is language? What type of cognitive capacity is it? What is its function? What is the relationship between its function and its structure? The second question is that of the evolutionary process: how did the human species get to master this incredibly complex capacity, which, more than any other trait, distinguishes it from all other species? These two questions are indelibly interdependent: on the one hand, different answers to the *object* question, i.e., different characterizations of language as a cognitive capacity, naturally lead to different answers to the process question: what we think about language delimits what we can say about its evolution. On the other hand, what we think about evolutionary processes may suggest that some answers to the object question are more reasonable than others.

As far as the *object* question is concerned, linguists and cognitive psychologists usually subscribe to one of two traditional, and radically opposite, views. Unfortunately, both of these views seem to lead to a theoretical dead-end with respect to the question of the evolutionary process. The first traditional view is the structuralist one. In the second half of the 20th century, this view has mostly been associated with Noam Chomsky's theory of Generative Grammar. For Generative Grammarians, language is first and foremost an extremely complex and subtle *structural* system: as native speakers, we seem to know much more about the structure of our language than we are aware of, and it is this implicit knowledge which Generative Grammarians are trying to describe and explain. A very famous example of this type of knowledge is that associated with the phenomenon of island constraints. Speakers of English, as well as many other similar languages, know that the questions in (1a) and (2a) are grammatical, whereas those in (1b) and (2b) are ungrammatical:

- (1) a. Who did the girl kiss? (Answer: The girl kissed *the boy who delivered the pizza*.)
 - b. *What did the girl kiss the boy who delivered? (Answer: The girl kissed the boy who delivered *the pizza*.)
- (2) a. Who did your obsession with Madonna annoy? (Answer: Your obsession with Madonna annoyed *your father*.)

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b. *Who did your obsession with annoy your father? (Answer: Your obsession with *Madonna* annoyed your father.)

Characteristically, speakers who are presented with examples such as the above for the first time are genuinely surprised: nobody (apart from linguists) ever talks about such facts, and parents and teachers do not teach them to their children and students. Yet all speakers share the same clear grammaticality judgements concerning these examples, and many others. Two crucial questions, then, need to be asked about such examples and their likes: first, what type of knowledge do speakers possess that determines their grammaticality judgements? Second, how did the speakers get to possess this knowledge? Chomsky's answer to the first question is purely structural and formal. Speakers have a complex mental representation of the formal properties of grammatical structures, and these properties determine their grammaticality judgements. Take a look at the answers to the questions in (1) and (2). The noun-phrase the pizza, which is topic of the question in (1b), is structurally embedded within a larger noun-phrase, the boy who delivered the pizza. The noun-phrase Madonna, which is the topic of the question in (2b), is structurally embedded within the noun-phrase your obsession with Madonna. Informally, Chomsky's theory states that structural configurations of certain types (in our case, a noun-phrase embedded within a noun-phrase) disallow the formation of questions such as (1b) and (2b). In the answers to the questions in (1a) and (2a), on the other hand, the noun-phrases which refer to the topic of the question are not embedded within other noun-phrases. Their questions are thus perfectly grammatical. Chomsky's answer to the second question, that of the acquisition of this implicit, formal knowledge, is the following: children cannot possibly learn this type of knowledge from their linguistic environment, which means that they must come to the world with this knowledge encoded in their genes. Generative Grammar thus postulates innate knowledge of a rich set of grammatical rules and constraints, highly abstract and complex. This set is called Universal Grammar.

This characterization of the cognitive basis of language, as an innately-given set of formal rules and constraints, suffers from at least four major problems. Taken together, these problems strongly suggest that Chomsky's framework should *not* be adopted as the basis of a theory of the evolution of language. First, Chomsky's specific formal theories suffer from serious empirical problems. As far as island constraints are concerned, for example, there are many attested cases where noun-phrase embeddedness does not prevent question formation (cf. Dean, 1991; Dor, 2000a). Second, the rules and constraints of Universal Grammar are decidedly nonfunctional: they do not seem to be related in any real fashion to the function of language as a tool of communication. The constraint postulated to explain the distinction between (1a, 2a) and (1b, 2b) should make this very clear: there does not seem to be any communicative reason why language should impose a constraint of syntactic embeddedness on question formation. As strange as it may sound to the nonlinguist, Chomsky regards the communicative function of language as totally *contingent* to the essence of linguistic knowledge. According to his view, what we are capable of *doing with language* (for example, transfer information, tell stories, ask questions, make requests, and so on) cannot tell us anything significant about the structural properties of the linguistic system itself. This state-of-affairs implies that a Neo-Darwinian theory of the evolution of language is unattainable in principle, because the Neo-Darwinian mode of evolutionary explanation demands a satisfactory functional characterization of the relevant evolved trait (in our case, the linguistic capacity) as a descriptive platform. This is why Chomsky himself insists that the very attempt to say anything meaningful about the evolution of language is a total waste of time.

Different writers (e.g. Pinker and Bloom, 1990; Berwick, 1998; Newmeyer, 1998; Jackendoff, 1999) have attempted to show that Generative Grammar does make some evolutionary sense, and Maynard Smith and Szathmáry (1995) have adopted this strategy in their chapter on the evolution of language. Two claims are usually involved in this attempt: some writers (most notably Pinker and Bloom, 1990) claim that even perfectly-arbitrary syntactic regularities are still adaptive to the extent that they are conventionally adopted by an entire community of speakers. This is so, because they establish *parity* between speakers and listeners, senders and receivers of messages: an arbitrary convention is better than no convention at all. Other writers (e.g. Jackendoff, 1999) maintain that some aspects of Universal Grammar, although not all of them, are

related to general cognitive predispositions, and are thus, at least to some extent, functional. These claims are problematic: the parity hypothesis is partially right - selection for parity is an important element in the construction of any communication system. The problem, of course, is that we know of no complex system of communication, in biology or elsewhere, which can be explained on the basis of parity independently of the particular function served by the system. In computer communication, for example, parity between the different communicating elements is extremely important, and there is a certain arbitrariness in the selection of one communication system over another in a specific configuration. The point, however, is that each of the candidate systems is perfectly *functional* on its own right: it is designed to communicate certain specific types of messages. The idea that a complex set of formal, arbitrary rules of syntax evolved on the sole basis of meaning-blind parity seems to us to stretch the credibility of the argument beyond a reasonable point. Jackendoff's argument may also have some truth to it, but to the extent that it does - it actually undermines Chomsky's own characterization of language as a formal capacity and suggests a much more functionally-oriented view of it. Jackendoff's paper may thus have been written as an attempt to defend Universal Grammar, but we believe it can actually be *read* as an interesting argument against it. At any rate, we believe that Chomsky, rather than his defenders, is actually right here: from the evolutionary point of view, his innateness claim cannot be reconciled with his specific characterization of language as a non-functional cognitive apparatus.

The third problem with the generative framework has to do with the notion of innateness: Chomsky's specific innateness claim - not the general notion that humans are genetically endowed with the capacity to learn language, but the claim that *specific* grammatical rules and constraints are genetically encoded - cannot be reconciled with what we know about brain structures: neuroscientists from different disciplines seem to agree that the brain is an organ of extreme plasticity and generality (cf. Elman et al., 1996; Deacon, 1997), which means that the chances of finding explicit representations of linguistic specificities innately encoded in brain tissue prior to acquisition are very slim. The fourth problem is that Chomsky's view of linguistic knowledge is extremely *static* and *universalistic*. The Generative theory of *principles and parameters* is the most remarkable representative of this view: according to the theory, variability between different languages the fine-grained differences, for example, between island constraints in different languages - are also encoded in the genes: children come to the world with a few parameters for each linguistic rule or constraint, and choose the right one for the specific language they encounter. This conception faces some difficulties, which as far as we are concerned, seem pretty much insurmountable: (i) it cannot account for the obvious fact that languages are dynamic entities which constantly change and evolve in their social contexts - beyond the narrow margin of flexibility allowed by the theory; (ii) it cannot easily account for the enormous amount of variability attested between different languages - again, beyond the theory's scope; and (iii) it is forced to assume a genetic change, which enabled an individual in a community of hominids to use the full range of future languages in a situation when no languages existed - and then assume that this hardly-functional property spread in the whole community. Such a scenario either assumes a single mutation with a huge effect, or a whole series of initially-neutral mutations, all of which have become fixed in the population through genetic drift. Needless to say, such evolutionary assumptions are hardly defensible.

The opposite traditional answer to the object question is the *functional* one: according to this view, language is simply a general-purpose tool for the communication of meanings. A corollary of this view is that grammatical complexities in natural languages are theoretically reducible to principles of general cognition. As far as island constraints are concerned, for example, functionalists usually attempt to explain them as manifestations of the cognitive processing of language: the ungrammatical sentences in (1b) and (2b) are somehow more difficult to process than the grammatical ones in (1a) and (2a) (Dean, 1991). According to this view, there is nothing cognitively unique about the linguistic capacity: languages comply with the general constraints imposed on human cognition, and children simply acquire their languages on the sole basis of external input – just like they do with respect to any other socially-based type of knowledge. As far as the evolutionary question is concerned, adherents of this functional view naturally concentrate on the so*cial* foundations of the evolutionary process, and

equate the cognitive evolution of language with the evolution of general intelligence (Deacon, 1997; Dunbar, 1996). At first sight, this perspective may seem to fare much better than the Generative one, but it actually suffers from at least three problems, which make it very hard to defend. The first problem is, again, an empirical one: although the specific functional theories which attempt to reduce grammatical complexities to general cognitive principles (e.g. Langacker, 1987; Wierzbicka, 1988; Dean, 1991; Givon, 1995) may suggest first approximations of the cognitive precursors of linguistic complexities, these first approximations do not usually get anywhere close to an explicit and precise explanation of the relevant specific phenomena. As such, they do not offer a real alternative to the Chomskian characterization of the object of evolution. Second, the very attempt to reduce language to general cognition is problematic: we have ample evidence from the specific patterns of language acquisition and language breakdown, and from the formation of de novo languages, such as the sign language developed by the deaf children in Nicaragua (Kegl et al., 1999) – for the *unique* status of language as a highly specialized cognitive capacity. Whereas Chomsky's theory captures the uniqueness of language at the expense of its functionality, the functional theories attempt to salvage the functional aspects of language at the expense of its uniqueness. Third, the functionalists' attempt to characterize language as a general-purpose communication tool does not really enhance our understanding of the function of language - it is simply too general: the claim that we use language "for communication" is similar to the claim that we use our visual system "for seeing". As Marr (1982) so convincingly claimed, a functional characterization of any cognitive system should be a much more *specific* one.

It thus seems that both traditional views lead us to a theoretical dead-end. What we need is a characterization of language as a cognitive capacity that is both *empirically viable* and *functionally specific*. This characterization should be able to reconcile the *domain-specificity* of language on the behavioral level with the high level of *plasticity* of the brain, and account for both the obvious *universality* of language as a cognitive capacity *and* the equally obvious fact that languages are *dynamic*, *variable* entities. The most important challenge in here is that of the explication of the relationship between linguistic function and linguistic structure. Two questions have to be answered: first, can the seemingly non-functional complexities of grammar – those which have inspired Chomsky's formal theories – be explained in a functional *and* empirically viable manner? Second, can we define the general function of language in a *non-trivial* fashion?

As we will show below, a long series of empirical results, accumulated in the last two decades by semanticists and lexical semanticists, suggests that the answers to both of these questions lies in the nature of the semantic categories of linguistic communication – the specific types of meanings which are expressible through language (Dor, 2000b). On the one hand, we shall claim that grammatical complexities in natural languages are best explained on the basis of these specific types of meanings: grammatical complexities are neither autonomously formal (as the structuralists claim), nor reflections of general cognitive principles (as the functionalists claim), but structural reflections of linguistic meaning. On the other hand, it turns out that the types of meanings which are expressible through language constitute a very constrained subset of the types of meanings which can be thought: we can use language to express only a fraction of what we can think and feel. In technical terms, semantic categories are a subset of conceptual categories. This state-of-affairs allows for the construction of a non-trivial functional characterization of language, as a unique and highlyconstrained communication system, dedicated to the communication of this specifically restricted set of meanings. Technically, again, this communication system is best described as a mapping-system between linguistic meaning and linguistic form. The representational level of Linguistic Meaning determines the set of the semantic categories of linguistic communication; the representational level of Linguistic Form determines the structural properties of the speech-channel.

This characterization of language as a cognitive capacity allows for a major re-framing of the *evolutionary* question, as the question of the gradual *expansion* and *sophistication* of the linguistic mapping-system, i.e., the expansion and sophistication of the set of semantic categories, their interactions, and their modes of mapping onto the speech channel. The re-framing of the evolutionary question naturally calls for an answer in terms of the interaction between *cultural evolution* and *genetic evolution*. The idea that the evolution of language consisted of a complex interaction between genes and culture has been discussed by Pinker and Bloom (1990), Maynard Smith and Szathmáry (1995), Jablonka and Rechav (1996), Deacon (1997) and Kirby and Hurford (1997). In this paper, we shall attempt to develop and explicate this idea both in terms of the evolutionary *properties* of the interactive process and in terms of its linguistic *object*.

As we shall claim, the process of cultural linguistic evolution consisted of the selection of, social agreement on, and cultural evolution of the semantic categories for linguistic communication, and the gradual sophistication of the mapping-system for these categories. In this long, gradual, and complex process, a social group gradually isolates certain aspects of its epistemology, sharpens and develops them, reaches social agreement about them, and develops sophisticated structural means for communicating them within the community. Here we part way with Kirby (1999), who assumes the cultural evolution of the syntactic mapping-system on the basis of a pre-given semantic platform (see section 3.2 for further discussion). Needless to say, the semantically-based cultural evolution of language is a permanent process, which goes on until today. As we shall claim, this cultural process was made possible, throughout most of evolutionary time, by the great behavioral plasticity of hominids. This plasticity included all aspects of linguistic behavior: production, comprehension, acquisition and transmission.

Crucially, however, at various points in evolutionary time, the behavioral plasticity of the speakers was stretched by cultural evolution, to the point where differences in the ability to learn language became selectively important. At these points, genetic assimilation occurred - on all cognitive fronts. At every step of the way, linguistic culture constituted the selective environment in which genes that contributed to linguistic performance, acquisition and transmission, were selected. The interaction between continuous, directional cultural evolution and partial genetic assimilation resulted in a consecutive set of evolutionary stages, in which the expressive envelope of language was expanded and sophisticated, and speakers were selected on the basis of their linguistic performance. We will claim that this process of cultural evolution and genetic assimilation gradually created what we think of as linguisti*cally-biased cognition*: a cognitive make-up which, without encoding linguistic specificities on a genetic basis, is still biased towards *rapid learning of the linguistic mapping-system*.

In section 2 of the paper, we present our characterization of language as a specialized communication system. As this paper is mainly addressed to a biologically-oriented readership, the characterization will be presented in a decidedly informal and general fashion, and many of the controversial linguistic claims will not be argued for in a fully technical and detailed fashion. A more elaborate discussion can be found in Dor (2000a, b, c) and in Dor and Jablonka (in press). In section 3, we provide preliminary evidence for our assumption that both cultural and genetic evolution were involved in the development of this system. We then discuss the interaction between cultural and genetic evolution, and explicate the fundamental features of the mechanism of genetic assimilation. In section 5, we describe the process of the evolution of language, and suggest that some of the constitutive properties of the evolved system are actually derivable from the characteristics of the evolutionary process. In section 6, we conclude with a few remarks regarding the more general consequences of the analysis.

2. On language as a cognitive capacity

As we have already indicated, a long series of empirical results, accumulated throughout the last decade or two in the domains of semantics and lexical semantics, suggests that grammatical complexities in natural languages are best accounted for on the basis of a careful examination of the specific meanings involved – the meanings of the words, expressions and constructions which combine to create the relevant grammatical structures (cf. Dowty, 1979, 1991; Jackendoff, 1983, 1990; Levin and Rappaport-Hovav, 1991, 1995; Frawley, 1992; Levin, 1993; Goldberg, 1995; Dor, 1996, 2000a, b, c; Alsina et al., 1997; Van Valin and LaPolla, 1997, and references therein). Note that this type of explanation runs counter both the structuralists' and the functionalists' views. To demonstrate, let us look at the following examples:

- (3) a. John broke the stick.
 - b. The stick broke.

(4) a. John hit the tree.b. *The tree hit.

Why is (4b) ungrammatical whereas (3b) is a perfectly good sentence? The explanation lies in the meanings of the verbs break and hit. Break is what lexical semanticists call a change-of-state verb: it denotes an event, the event of *breaking*, in which an entity (in our case, the stick) changed its state as a result of some activity (in our case, John's action). Hit, on the other hand, is a surface-contact verb: it denotes an event in which an entity (in our case, the tree) was touched on its surface by something or someone (in our case, John). Now, as it turns out, all change-of-state verbs behave like break (we can say 'the tree bent, folded, shattered, cracked); all surface-contact verbs behave like hit (we cannot say *the tree *slapped*, *struck*, *bumped*, *stroked* and so on). The distinction between the patterns of grammatical behavior is thus correlated with a parallel distinction between the meanings of the verbs involved in the construction. Different technical theories have been developed throughout the years to explain how the meanings of the verbs determine the grammatical patterns, and these theories will not interest us here. The crucial point for the purposes of this discussion is that we need to assume that speakers (of English, in this case) have an implicit mental representation of the semantic distinction between the types of events denoted by the different verbs. In other words, we have to assume that speakers mentally categorize, or classify, events according to their semantic properties. As it turns out, speakers implicitly classify events according to a very rich and detailed scheme of categories: thus, for example, events are classified in terms of their telicity: telic events (like the event of breaking a window) are bounded in time; they have a necessary end point (the event of breaking the window must include the point in time in which the window is *broken* – and that is where it necessarily ends). Atelic events (like the event of swimming in the pool) do not have such a necessary end point. Events can also be classified on the basis of their thematic structure (the number of their participants and their specific modes of involvement in the events); their epistemic status (whether we know for a fact that they took place in the real world, or we *think* that they did, or *hope* so), and so on and so forth. Each of these categorical distinctions determines some aspects of grammar.

Sometimes, grammatical complexities are determined by a combination of two or more of these semantic categorizations. Needless to say, speakers are totally unaware of this relationship between semantic categorization and grammatical behavior.

The semantic categorization of events is a major determinant of grammatical knowledge, but it is not alone: some grammatical phenomena seem to be determined by other schemes of semantic classification. We classify entities in the world, for example, on the basis of a set of categories, including animacy (dogs and people are *animate*; chairs and tables and are inanimate), gender (male and female), and countability (you can count bottles and people; you cannot count rice and water). Each of these categorical schemes, and others, determines some grammatical patterns in natural languages. Some other classifications are more abstract: we classify *times* (past, present, future); spatial relations (an entity is behind, above, below another entity); and logical relations (negation, conditionals). These, too, determine grammatical patterns. As our understanding of these schemes of categorization deepens, more and more grammatical complexities turn out to reflect them in interesting ways - including those complexities which have for the last forty years been thought of as the ultimate proof of the formal, non-functional nature of grammar. In a recent paper, for example, Dor (2000a) develops a semantically-based account of island constraints, which we have mentioned in the beginning of the paper. Here are the examples we have looked at:

- (5) a. Who did the girl kiss? (Answer: The girl kissed *the boy who delivered the pizza*.)
 - b. *What did the girl kiss the boy who delivered? (Answer: The girl kissed the boy who delivered *the pizza*.)
- (6) a. Who did your obsession with Madonna annoy? (Answer: Your obsession with Madonna annoyed *your father*.)
 - b. *Who did your obsession with annoy your father? (Answer: Your obsession with *Madonna* annoyed your father.)

Dor's (2000a) technical account derives these phenomena, together with a wide range of related facts from a set of formal semantic considerations, which we shall not deal with here. For our present purposes, it will suffice to take an informal look at the semantic underpinnings of the above simple examples. The sentences in (5) and (6) are interrogative sentences: they are used for asking questions. When a speaker asks a question of this type, he or she actually performs a rather complex speech-act: the speaker (i) tells the interlocutor that a certain event occurred (or may have occurred, or did not occur, and so on), and (ii) asks the interlocutor to provide a certain piece of information about this event. Thus, for example, when a speaker asks, "who did the girl kiss?", he or she tells the interlocutor that "the girl kissed someone", and asks the interlocutor to provide the identity of that person. When a speaker asks, "who did John say that the girl never kissed?", he or she tells the interlocutor that, according to John, the event in which "the girl kissed a particular person" never occurred, and asks the interlocutor to provide the identity of that person. Technicalities aside, Dor (2000a) shows that speakers can ask questions concerning the entities which participated in the event they told their interlocutor about, and concerning the general properties of the event - its time, place, cause and so on. Crucially, however, speakers cannot ask questions concerning entities which did not participate in the event they reported. Now, as we have said, speakers know a great deal about the semantics of events, including the semantics of kissing and annoying events. Among other things, speakers know that both types of events involve two necessary participants: kissing events involve the kissing participant and the participant being kissed; annoying events involve the annoyed participant and the annoying participant. Now, in (5a) and (6a), the speaker tells us about a kissing event, and an annoying event respectively, and asks about participants in these events: (5a) is about the participant being kissed; (6a) is about the participant being annoyed. In (5b) and (6b), on the other hand, the speaker tells us about the very same events, but asks about entities which do not participate in them: (5b) is a question about the pizza, which does not participate in the kissing event; (6b) is a question about Madonna, which does not participate in the annoying event – the father is annoyed by the obsession, not by Madonna herself. (5b) and (6b) are thus ungrammatical because they violate a semantic constraint on linguistic communication. Rather than constitute the prototypical example of the formal character of grammatical complexities, island constraints actually demonstrate the functional nature of grammatical structures.

Now, the following point is crucial: in principle, it seems that we may classify our knowledge of the world (our knowledge of events, entities, properties and so on) on the basis of an infinite number of categories. Indeed, when we perceive the world, think about it, or have *feelings* about it, we use a very large, diverse and constantly-changing set of categories: we may, for example, categorize people on the basis of the categorical distinction between friend and foe; we may classify physical entities on the basis of their practical utility, or their price; we may categorize species as endangered or not; and so on and so forth. We usually classify events as interesting or boring; and we distinguish between events in which someone we know participated, and events in which only strangers took part. It would seem reasonable, therefore, to expect that grammars of natural languages would reflect this infinitely large and diverse set of categories, or at least that different languages would reflect radically diverse subsets of these. Crucially, however, a survey of the world's languages reveals a very surprising fact: languages are definitely not all alike, but the semantic categories which are reflected by grammatical complexities in natural languages belong to a very constrained subset of all the categories which we can use to think, feel and conceptualize about the world: some semantic categories turn out to be grammatically marked in language after language, whereas some others consistently do not participate in the grammatical game. Specifically, no language we know grammatically marks the distinction between friend and foe, or between interesting and boring events. The categorical distinctions between animate and inanimate entities, telic and atelic events, factual and hypothesized events are reflected in virtually every language we know, and so are the distinctions between different spatial relations and time configurations. (Note that different languages may relate to the same categorical scheme in different ways. Thus, for example, different languages carve up time in different ways: some languages mark the distinction between *future* and *non-future*; some mark the distinction between *past* and *non*past; some have much more elaborated systems.) It seems as if all natural languages went through a very similar process of *epistemic selection* – where a specific subset of all possible categorical distinctions

was isolated, highlighted and marked by grammars for the purposes of linguistic communication.

Circumscribing the set of semantic categories which universally determine grammatical structures allows for the formulation of a non-trivial functional definition of language: language is not just a general-purpose communication system. It is a communication system, structurally designed to communicate messages which are grounded in a specific and constrained categorical scheme. This categorical scheme is centered around a specific set of events and situations (not all types of events and situations), their participants, their time and place, their properties, and some of the properties of their participants. Thus, these categories determine the expressive envelope of language - they determine which meanings, and which meaning combinations, are expressible by the means provided by natural languages. Again: the expressive envelopes of different languages are different in interesting and subtle ways, but they all share a common core. Types of messages which fall comfortably within this core are best suited for communication through language. Types of messages which do not comfortably comply with it turn out to be more difficult to communicate through language. Many other types of messages, which do not comply with this scheme at all, turn out to be virtually impossible to communicate through language. Interestingly, many of the messages which turn out to be very difficult to communicate through language seem to be very well suited for communication through other means of communication: we can mime and dance them, use facial expressions and body language to express them, *paint* and *draw* them, write and play *music*, prepare charts and tables, write mathematical formulae, screen movies and videos, and so on.

To take a simple example, think about a simple knot, a figure of eight. Suppose you know how to make the knot, and want to teach someone how to make it. There are at least two very simple ways to do this: you can either take a piece of rope and *demonstrate* the procedure, or draw a simple drawing which accomplishes the same goal. Suppose, however, that you insist on communicating this knowledge *through language*. Now, the communicative task becomes surprisingly more difficult to achieve. You may want to formulate the following set of instructions (from Aitchison, 1996):

1. Pass the end of the rope over the standing part.

2. Take the end under the standing part away from the loop.

3. Bring the end of the rope back up over itself towards the loop.

4. Pass the end down through the loop.

5. Pull tight.

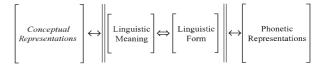
This description of the procedure is accurate, but note that the cognitive effort needed to formulate the instructions, and the effort needed to understand them, are much greater than that involved in the face-to-face demonstration. This is so, because the message itself-the procedure of tying the knot-has to be *reframed* and *broken down* in order to comply with the categorical scheme of language. The instructions break down the event of tying the knot into a series of smaller events, each of which separately meets the conditions set by the semantics of events. In each of these smaller events the first participant, an agent (the person holding the rope), causes another participant, the theme (e.g. the end of the rope) to move in space and reach a new position in relation to a third participant, the goal (e.g. the standing part, or the loop). This is a type of event which semantic categorization recognizes. Note, and this is a crucial point, that if you learn to tie the knot in non-verbal ways - from a picture, or by looking at someone doing it - you may never have to conceptualize about such entities as the end of the rope, the standing part or the loop. Neither will you have to conceptualize about the different stages described in the instructions. You will probably conceptualize about one entity (i.e. the rope itself, a single physical unit, the object which is tied into a knot) and one event (i.e. tying the rope). This event, however, does not fall comfortably within the categorical scheme of language: specifically, the rope which participates in it plays both the role of theme and of goal in the event. A major component of event semantics does not seem to allow this: informally, language is not designed to describe events in which the same participant plays two different spatial roles.

The linguistic communication of simple, practical instructions of this type is more cumbersome than the communication of the same information in non-verbal terms, but, as we have seen, it is still possible. In more complicated cases, such communication is virtually *impossible*. Think about learning to play basketball, practice karate, or play the violin, through the sole means of linguistic communication. Anyone who is engaged in these activities knows that language plays a rather negligible role in their instruction. They are best taught by mimesis (cf. Donald, 1991). Moreover, emotional meanings are best communicated through facial expressions, body language, music and dance. Language may sometimes help in categorizing the emotion, but is rather helpless when it comes to complex, holistic emotions. As Deacon (1997) notes, "a rich and complex language is still no substitute for a shocked expression, a muffled laugh, or a flood of silent tears, when it comes to communicating some of the more important messages of human social relationships". And think about visual information. As Donald (1991) says, "visual thinking is now seen as largely autonomous from language". Visual meanings are best communicated by visual means - pictures, drawings, hand waves – and this is another domain where language is practically useless: to convince yourself of that, make a simple, abstract free-hand drawing on a piece of paper, and try to verbally communicate the drawing to a friend – without showing him or her the drawing itself, and without moving your hands about. As you will realize, this is incredibly difficult. You will probably be able to give your friend a general idea of the drawing, but you will not be able to provide a detailed description which will allow your friend to *reduplicate* the drawing. In this sense, a picture is really "worth a thousand words": there are many types of visual meanings which simply cannot be communicated through language. As Donald (1991) argues, then, "a significant part of normal human culture functions without much involvement of symbolic language. Examples are found in trades and crafts, games, athletics, in a significant percentage of art forms, various aspects of theater, including pantomime, and most social ritual. ... When humans lack language, provided they do not suffer some brutal brain lesion that robs them of other, more fundamental, cognitive skills, they can continue to participate in all those forms of human culture that do not require language."

The last paragraphs concentrated on that set of meanings which are virtually inexpressible through language, but there is, obviously, a remarkable set of meanings which are *exquisitely* expressible through language – and this is where the *other* means of

communication are hopelessly lost. Language allows us to perform a rich set of speech-acts - make claims, tell stories, ask questions, make requests, promise and threat - concerning events of different types, their *participants*, their *properties*, their epistemic status, their location and time, and so on. Informally, we use language to *tell* each other that we know, or think, or guess, that an event of a certain type occurred, in which someone did something to someone, at a certain place, at a certain point in time, for a specific reason. Or we can use language to ask each other whether such a event happened, or who was involved in it; or to *promise* that an event of a certain type will happen; or to request that such an event will take place; and so on. These meanings are very difficult to communicate through mimesis, and almost impossible to communicate through dance, facial expressions and so on. (We can communicate a general plea by a facial expression, but we cannot express a specifically detailed request, such as "Can you please drive me to the airport tonight? I need to catch a plane".)

Natural language, then, is a communication tool which is structurally designed for the communication of a constrained set of meanings. The structural medium for the communication of this set of meanings is mostly the *auditory* channel – although signlanguages use the visual channel with the same level of efficiency. In terms of traditional cognitive science, this characterization of language is best captured by the notion of a *mapping-system*: a cognitive system which maps representations of one type (in our case, meanings which fall within the expressive envelope of language) onto representations of another type (in our case, the set of grammatical markers which are visible on the speech-channel). The following is a schematic representation of this view of language:



In this schematic representation, language is characterized as a transparent mapping-system between the levels of *Linguistic Meaning* and *Linguistic Form*. The representational level of Linguistic Meaning constrains the set of meanings which are expressible through language: as we have seen, a major set of Conceptual Representations is not lin-

guistically expressible. The level of Linguistic Form, which we have not discussed up to this point, includes all the structural tools which are visible on the speech-channel, and are used to mark linguistic meanings in natural languages: phonological regularities, morphological markers, linear order, adjacency, and so on. What is missing from this picture is abstract, non-functional, syntax, of the type envisioned by Generative Grammarians: as we have seen before, we have good reasons to assume that such syntactic representations are no longer needed. Note, moreover, that this schematic characterization allows for both linguistic variability and universality, on all fronts: we know that a core set of semantic categories is universal, but different languages may, in principle, choose to occupy the level of *Linguistic* Meaning with different semantic categories, and different categorical combinations. Different languages obviously use different subsets of Linguistic Form to mark their meanings, but some such markers are universal. Finally, different languages may map different semantic categories onto different markers; this is an essential property of the system. Thus, for example, thematic roles (the roles played by participants in events) may be marked by linearorder in some languages, and by morphological case-markers in others: in English, we know that John was the active participant in the event described by a sentence like John invited Bill for a meeting, because the noun-phrase John appears before the verb; we know that Bill was the more passive participant because it appears after the verb. In Russian, on the other hand, the noun-phrases John and Bill are marked by special morphological casemarkers, which specify their mode of involvement in the event. Linear-order in Russian is thus much more flexible.

This characterization of language immediately re-frames the question of the evolution of language. It is now neither the question of the evolution of a formal, meaning-blind system, nor the question of the evolution of a general-purpose communication system. It is the question of the evolution of a *specific* communication system, dedicated to the communication of a *constrained* set of meanings by means of sound concatenation. In the above cognitive terms, it is the question of the evolution of a mapping-system: The gradual *expansion* and *sophistication* of the representational levels of Linguistic Meaning and Linguistic Form, and their transparent mapping onto each other. As we shall show in the remainder of this paper, this novel evolutionary question calls for an answer in terms of a specific interaction between *cultural evolution* and *genetic evolution*.

3. Cultural evolution and genetic evolution

Like all other evolutionary processes, the process of the evolution of the linguistic mapping-system is a multi-faceted one. Different questions may be asked about it: we may, for example, inquire about the types of selection pressures that played a role in the evolution of language; or ask about possible stages in the evolutionary process, trying to draw a reasonable line of progression, or a branching pattern; or focus on the dynamic patterns of the process. In the following, we will suggest an answer to the last question, that of the dynamics of the process, and address the other questions only to the extent that they directly relate to it. We will suggest that the dynamics of the evolutionary process was that of the interaction between cultural evolution and genetic evolution. More specifically, we will present the backbone of an evolutionary model, where the cultural evolution of language drives the process of genetic evolution through the mechanism of genetic assimilation. Before we delve into the model, however, we need to justify the very preliminary notion that both cultural and genetic evolution were involved in the process. Two questions need to be answered: first, Why do we need to assume a cultural component in the evolution of language in the first place? Why is genetic evolution not sufficient? Bickerton's (1990) model of the evolution of language, for example, seems to ignore the role of cultural evolution altogether: for him, the evolution of language is the genetic evolution of a specific language organ. Why is that not enough? Second, why do we need to assume a specific genetic component in the evolution of language? Note that this is not simply the question of whether the hominid mind went through a general process of evolution, which resulted in a more powerful intelligence: this much is beyond dispute. The question is why we need to assume that the evolutionary process resulted in a genetic make-up which is in some way specifically suited for language. Deacon (1997), for example, believes that such an assumption is unwarranted: according to him, the human mind went through a general process of evolution, which resulted in higher intelligence, capable of symbolic (non-linguistic) representation and communication. Language simply adapted itself to this sophisticated mind. So, why is general intelligence not a rich enough substratum for the cultural evolution of language? Why do we need to assume that genetic evolution *for language* was a significant component of the process?

3.1. Why assume cultural evolution?

There are many things we do not know about our ancestors. However profound our ignorance, one thing seems beyond dispute: our ancestors did have cultural traditions, and these played a major role in their life. We know that traditions are ubiquitous in higher animals, and that they involve every aspect of the animal's life: modes of foraging; criteria for selecting mates; ways of avoiding predators; criteria for choosing a habitat; practices of parental care; and so on (Avital and Jablonka, 2000). Traditions are particularly well studied in primates. Whiten et al. (1999), who summarize the long-term studies of seven populations of the common chimpanzee in Africa, describe 39 different cultural traditions, five of which have something to do with communicative functions. As the systematic and comprehensive study of animal traditions has only recently started, this is clearly an underestimation. Our current understanding of the cultures of our close extant relatives, as well as a whole host of archaeological findings from the early hominids' period, strongly suggest that hominids did indeed live in cultural settings, and that these cultural settings reflected local, evolving traditions.

Traditions are the result of the transmission, over generations, of patterns of behavior through social learning. They are the result of *cultural evolution*. In this sense, cultural evolution can be thought of as the change in the frequency and nature of sociallylearned and socially-transmitted behaviors in a population. When cultural evolution is *cumulative*, the process often leads to the gradual sophistication of the cultural practice, each evolutionary step building on previous ones. A good example of such a cumulative process of cultural evolution may be the evolution of *tool-making* techniques. In a process of this type, a cultural innovation, invented by a single individual or by a whole group, is adopted and absorbed (and often extended and improved) by the other members of the community – most often by younger individuals, whose behavioral plasticity is extensive. Such innovations, once they are accepted by the community, become the behavioral norm for the next generation (Morgan, 1994). This behavioral norm may then provide the basis for the next innovation, and so on and so forth. The process, of course, need not be continuous, and may proceed by fits and starts. So, although we still know very little about the dynamics of the process, it seems quite reasonable that cumulative cultural evolution played a major role in the development of hominid's material culture.

In many respects, linguistic culture is similar to material culture: first, languages are extremely important tools used by individuals in societies for the narration of stories, for the transfer of information, and for the construction of a socially-based worldview. Second, just like material artifacts, languages change constantly - in ways which are intimately related to social modification and transformation. There is no real reason to assume that this dynamic aspect of language is only a very recent development. Moreover, recent experimentation with higher primates (e.g. Savage-Rumbaugh and Lewin, 1994) demonstrates that even common and pigmy chimpanzees, who do not communicate linguistically in the wild, are capable of developing this capacity, at least to some extent, when exposed to language in a structured cultural environment. (Researchers estimate that the language-tutored chimpanzees reached the proficiency level of two-year-old human children.) This demonstrates that the culturally-based capacity for language can develop, at least to some preliminary extent, in the absence of a specific genetic basis. It is thus reasonable to assume that cultural evolution played at least some role in the evolution of language.

3.2. Why assume genetic evolution for language?

It has been argued (e.g. Donald, 1991; Lieberman, 1991; Deacon, 1997) that language may have emerged as a by-product of the evolution of hominid's general intelligence (reflected in the increased size of hominids' brain). According to this hypothesis, a host of diverse processes of selection resulted in the emergence of language, but none of these processes involved the selection of properties or capacities *which are specifically linguistic*. According to this hypothesis, individuals were selected throughout the evolutionary process on the basis of better motor control, better sequencing of motor activities, better memory capacity, more sophisticated social intelligence, more elaborate communication skills, better learning skills, and so on. Somewhere along the way, language emerged as a cultural product – either en bloc, in a few generations, or gradually through a lengthy process of cultural evolution.

This hypothesis is parsimonious, and therefore attractive. It suffers, however, from several interrelated problems. None of these problems is sufficient to disprove the hypothesis on its own. Taken together, however, they seem to suggest that at least a certain degree of language-specificity on the genetic level is necessary, beyond the obvious contribution of the evolution of hominid's general intelligence.

The first argument for linguistic specificity on the genetic level comes from language acquisition. As much as we disagree with Chomsky's views on language, we acknowledge his huge contribution in constructing this argument. The process of language acquisition is unlike any other learning process we are aware of: it is incredibly fast and seemingly effortless. Before they reach the age of two, children already master linguistic complexities of the type that adults find extremely difficult to grasp when they try to learn a second language (Bloom, 1993). Acquiring a native language does not seem to depend on the social status, economic privileges or general intelligence of the children. Language acquisition does not seem to depend on some special, conscious teaching activity on the parents' part: children are known to acquire a native language in conditions of extreme neglect, where no adult makes a point of speaking to them, as long as they are exposed to language being spoken around them. It is extremely difficult to account for this achievement on the sole basis of the external input which children are exposed to. When a complex pattern of behavior is learned very quickly, on the basis of poor input, we usually assume some innate basis. For example, many small mammals show fear of hissing snakelike sounds, even if they were never exposed to such sounds before. These mammals are born with a nervous system, which predisposes them to react to such sounds with fear. Crucially, this innate predisposition is *specific* to hissing noises; it is not a general predisposition to associate sounds with fear. Unlike the fear reaction, linguistic knowledge does require a significant amount of learning, but the above general point seems to hold with respect to language, too: children are *not* such efficient and fast learners of *other* types of knowledge. The unusual capacity to acquire language seems to be a specific one.

The formation de novo of new languages is probably the most extreme illustration of this fact. The best example of such a process is that of the development of the Nicaraguan sign language (Kegl et al., 1999). A group of deaf children, who were never exposed to sign language, and only communicated through a very limited system of conventionalized gestures, were gathered in a school in Managua with the goal of teaching them to lip-read. The attempt was a total failure: the children did not even understand what the goal of the exercise was. In a few months, however, a miraculous development occurred: the children developed an elaborate system of signs, which they used to communicate among themselves. When a group of younger, deaf children joined them, a few years later, this communication system rapidly evolved into a fully developed sign language - with a level of grammatical complexity similar to that of any other human language. In this case, the complexities of the new language could not have been acquired from the environment, for the simple reason that they were not there. It is highly likely that the creative formation of the language was based on some innately-given foundation, and that this foundation was language-specific.

This achievement is all the more remarkable, because the specific properties of the new language seem to be similar to properties which are *universally* manifested by languages around the world. When a system exhibits universal features (at the behavioral or anatomical level), despite the diversity of environments in which the system develops, this indicates that the developmental process is independent of variations in experience. Independence from variations in experience is often equated with *developmental canalization*. In principle, this does not necessarily mean that the genetic basis for canalized development is *specific* to the system. It may be the case, for example, that the universal properties of language result from strong, general constraints on brain development in the child. This is the essence of Deacon's (1997) universality argument. However, the fact that some of the universal properties of language are so specific and complex suggests that the genetic basis is likely to be more specific, too. The fact that all languages share the same core expressive envelope, and that the Nicaraguan children zoomed in on the same set of functions, cannot be easily explained on the basis of the general properties of the brain.

In general, then, no dynamic model which we are aware of is capable of deriving the above phenomena - the patterns of language acquisition, the formation of new languages, the universal intricacies of the system - from the properties of general intelligence and learning. This, of course, does not mean that such a model is impossible, but it substantially weakens its feasibility. Interestingly, recent dynamic models (e.g. Batali, 1998; Kirby, 1999, to appear, a, to appear, b) provide partial demonstrations of the way grammatical complexities may have culturally emerged in evolution on the basis of pre-existing social agreement on the semantic underpinnings of the system - in line with our framework. In Kirby's model, for example, individuals in the simulation are provided with a set of meanings, which they are then supposed to express by arbitrarilychosen strings of sound. The individuals are assumed to be able to assign semantic interpretations to the strings produced by the others, remember them, compare them to previous strings, and extract grammatical regularities from them. After a large number of trials, regularities do emerge: the community of individuals reaches social agreement on lexical items, word order and syntactic compositionality. This is indeed an impressive result. It is based, however, on certain presuppositions regarding the semantic foundation of linguistic knowledge, which we think of as a major part of the evolutionary question: within our framework, such constitutive semantic notions as event structure and thematic roles, and such capacities as semantic memory and interpretation, which play an explanatory role in Kirby's model, are themselves objects of cultural evolution and genetic assimilation.

Having established the possibility that both cultural and genetic evolution played a role in the evolution of language, we may now take the next step, and try to figure out how the two processes interacted. As we shall show, the properties of this interaction provide the key explanatory tool for our account of the evolutionary process. The major mechanism driving this interaction is that of 'genetic assimilation', or 'the Baldwin effect'.

4. The Baldwin effect

The Baldwin effect is the transformation, through Darwinian selection, of a learned response into a more genetically-fixed or 'instinctive' response. This process has been independently described, more than a 100 years ago, by Lloyd Morgan, J. M. Baldwin, and Fairfield Osborne, and was named the Baldwin effect by Simpson (1953). The crux of the phenomenon is this: when faced with a new challenge in their environment (e.g. a new predator), individuals first adapt to the challenge by *learning*. If the selective pressure is ongoing, and if the necessary learning process is lengthy and costly, individuals will be selected for their ability to respond appropriately to the challenge without the full investment in the learning process: in other words, individuals who are more 'instinctive' responders to the challenge will be selected.

Originally, Baldwin, Morgan and Osborne thought about this process in terms of the selection of new mutant individuals. They believed that the learning process allows the individuals in the population to survive long enough for congruent adaptive mutations to appear. C. H. Waddington, the British geneticist and embryologist, however, argued that the transformation occurs through the formation of new combinations of genes, following sexual reshuffling and continuous exposure to the selective environment. He also believed that the same process leads to the transition of acquired or induced physiological and morphological characters into constitutively expressed characters. He called this process 'genetic assimilation'. Waddington experimentally demonstrated this process for several morphological and physiological characters in the fruit fly, Drosophila melanogaster. Thus, for example, Waddington induced the development of four wings in fruit flies, by treating fertilized eggs with ether. He then selected the fraction of flies who responded to the ether by developing four wings, bred from them, treated their fertilized eggs with ether, allowed them to develop to the adult stage, selected again, and so on. In the first 20 generations, the appearance of the

four-wing phenotype in the selected line was dependent on the ether treatment of the eggs. After 20 generations of systematic selection, however, few flies with four wings appeared in the selected line without ether treatment. The character whose development was at first dependent on external induction became genetically fixed and independent of the ether treatment (Waddington, 1953). Waddington showed that the ether treatment exposed variations in genes that could lead to an induced 4-wing phenotype. During the 20 generations of selection, genecombinations that produced an ether-induced, fourwinged phenotype were constructed through the process of sexual reshuffling and selection, until a threshold was eventually crossed: a particular combination of genes, which enabled the development of four wings, now appeared with no need for an external inducer (for a more detailed explanation of the experiment and its significance, see Avital and Jablonka, 2000).

Waddington's analysis was applied by Ewer (1956), Haldane (1959), Hardy (1965) and others, in an attempt to explain the evolution of behavioral instincts: Ewer, for example, explained the evolution of filial imprinting in the chick in terms of genetic assimilation, and Haldane used the same strategy to explain the innate, excited response of sheep-dog pups to the smell of sheep. Avital and Jablonka (2000) suggest that the innate fearful reaction of many small mammal and bird species to hissing snake-like noises, and the fearful reaction of spotted hyenas to the smell of lions, may be additional examples of assimilated responses (Kruuk, 1972; Edmunds, 1974). In all these cases, individuals were selected on the basis of their ability to learn to respond to the particular stimulus. The individuals who were selected were those who managed to learn to respond adaptively very fast – on the basis of a minimal number of trials. Eventually, after many generations of selection, some individuals could respond to the stimulus after a single exposure: the learned response became innate. It is important to understand that in these extreme cases, where the response to the stimulus becomes independent of learning, it is in fact the ability to learn the stimulus which was selected: throughout the process, learning becomes more and more efficient and rapid, up to the point where it is 'internalized'. It is also important to realize that most assimilation processes do not end up with a completely internalized, instinctive response. In most cases, the assimilation process will be *partial*: it will significantly reduce the number of learning trials, and make the learning of the stimulus, which will still be needed to some extent, much more rapid and efficient (Hinton and Nowlan, 1987; Behera and Nanjundiah, 1995). The speed of assimilation is expected to vary in different cases, depending on the intensity of selection, the number of genes involved, and the nature of their interactions.

In some interesting cases, adaptation through learning does not only expose hidden genetic variation - it also creates persistent changes in the environment. The new learned response changes the environment in which the individuals and their descendants live. If individuals learn to avoid a new predator by digging burrows and hiding in them, for example, individuals will be selected on the basis of their ability to dig effectively. Crucially, however, the ability to dig the burrows actually creates a new physical environment, which means that individuals are now also selected for their ability to live in this environment. Thus, those individuals who will be positively selected will be both efficient diggers and efficient burrow-dwellers. In this case, the pressure to avoid the predator leads to what is called *niche construction* by the organisms – they actually construct the environment in which they live and in which they and their offspring are selected (Lewontin, 1978; Odling-Smee et al., 1996). This makes selection more directional and more reliable, and enhances its effectiveness. A famous example of this process in humans is the evolution of lactose-absorption following the domestication of cattle, and the drinking of fresh milk (Durham, 1991).

There is still more to the effects of genetic assimilation: it can sometimes lead to the *sophistication of behavior*. Avital and Jablonka (2000) have described three major ways in which this can occur. We will describe two of these ways, which will turn out to play important and interesting roles in our model of the evolution of language. The first process which leads to the sophistication of behavior is that of *stretch-assimilate*.

Imagine a bird capable of reliably learning a sequence of four consecutive acts, culminating, for example, in the building of a simple nest. Learning beyond this is very difficult. Assume, for the sake of simplicity, that there is a constraint on the learning capacity of this species of bird, so that improved learning ability is unlikely to evolve (perhaps because a big brain needs more energy to maintain, or there may be some developmental constraint on brain growth). Assume, however, that there is consistent selection for the efficient and reliable performance of the nest-building behavior sequence so that one of the steps becomes genetically assimilated: it becomes innate. The bird now needs to learn only three steps, and will construct its simple nest much more quickly. Crucially, part of its unchanged learning capacity is now "liberated". If selection for building good nests continues, the bird can now learn an additional nest-improving behavior. This novel behavior may be acquired in several different ways: individual learning through trial-and-error, learning from an experienced individual of another species, and so on. The bird may learn, for example, to tie the nest to the branch with plant strips, so it is more safe and less likely to fall when the wind blows. Once acquired, the new behavior will be able to spread in the population through social learning. There will now be five consecutive acts, one of which is innate. If building nests rapidly and efficiently continues to be advantageous, another previously learned act can become assimilated, and yet another new learned one can be added, so that behavioral sequence is lengthened by yet another step. It is thus possible to gradually lengthen the sequence of acts without changing the capacity to learn: genetically assimilating some previously learned behaviors "frees" the individual to learn additional acts, without extending the limits set by its learning capacity. This process, which involves the assimilation of a part of the behavioral sequence, and the resulting *stretching* of the sequence by learning may explain the evolution of many complex behavior patterns in nature.

The second effect of genetic assimilation is that of the evolution of *categorization*. Imagine a population of monkeys, which is threatened by a new dangerous aerial predator, a monkey eating eagle. Predation pressure is very severe, and individuals do their best to learn to avoid the predator. Monkeys who are better at identifying and memorizing the shape of the eagle, its mode of flight, and so on, will have a better chance to survive. As in previous examples, this process will expose hidden genetic variation, which is specifically relevant to the threat. Now, after several monkey-generations, the selection pressure may weaken, and even become negligible, because the population is now composed of individuals with a genetic make-up, which enables them to identify and avoid the predator much more efficiently than before. Note that this will result in partial genetic assimilation, rather than in a fully innate response, because the degree of assimilation depends on the intensity (and also on the duration) of the selection pressure. This result, however, has an interesting consequence: whereas a fully assimilated response would associate the avoidance response with a highly specific stimulus (the monkey eating eagle), partial assimilation will result in the association of the avoidance response with a larger, and much more diffuse, set of stimuli: it will include all aerial predators whose shape and mode of flight are similar enough to that of the Monkey Eating Eagle. Effectively, the monkeys will have formed the conceptual category of 'aerial predator'.

Avital and Jablonka (2000) suggest that a process of this type underlies the evolution of poison avoidance in rats. In the 1950s and 1960s, Garcia and his associates experimentally showed that rats learn to avoid poisonous food on the basis of its taste and smell, but find it difficult to learn to avoid poisonous food on the basis of an associated clicking sound (Rose, 1993). From the evolutionary point of view, this bias makes sense, because food-poisoning is associated with taste and smell rather than with sounds. If during evolution, many different food types commonly caused food poisoning in rats, each particular food-type for a limited time, an association between a particular food and poisoning would not evolve to the point of becoming innate. However, a very general bias for associating the taste and smell of food with subsequent gastric illness could be established through *partial* genetic assimilation: this is so, because the only two properties which all poisonous foods share are (i) the fact that they caused illness, and (ii) the fact that they all have a taste and a smell. This categorical generalization allows rats to behave in a rule-governed manner: 'avoid any food (whatever its specific taste and smell) if you felt sick after you ate it last'.

To sum up: the process of genetic assimilation transforms learned behaviours into more genetically-fixed, or 'instinctive' behaviours. The selection pressure for more efficient learning exposes hidden variation in the ability to learn the specific behaviour, and leads to the selection of better, specialised learners. As we have seen, the process may also lead to the construction of a new selective environment, and to the sophistication of behaviour through the stretch-assimilate process, and through category-formation. For the process to work, some conditions need to be met: populations must have abundant genetic variation that is relevant to individuals' ability to respond to the stimuli; different sets of genes should become selectively relevant under new circumstances; phenotypically visible genetic variation should be able to be recruited and organised into new adaptive genotypes through sexual reshuffling and selection; and selection for the adaptive genotypes (genotypes that enable the more adaptive responses) should be maintained for several generations. What we know of the nervous system, and of the abundance of genetic variation in animals, not only allows us to make these assumptions, but also suggests that such processes must have been very common during evolutionary history. The evolution of hominids is no exception.

The effects of genetic assimilation are all the more dramatic when the set of learned behaviors is itself developing through cultural evolution. In the following section, we will propose that this is the mechanism by which the linguistic mapping-system evolved.

5. The evolutionary spiral

Let us think about an arbitrary stage in the evolution of language. Assume that at this stage, stage N, a community of hominids used some preliminary, culturally-transmitted communication system – a system which mapped a very constrained set of meanings onto a set of phonetic markers. The meanings and their markers may have been very different from those we use in present-day languages. They may have included, for example, some conventionalized alarm-calls, emotional-social vocalizations, some referential lexical items, and so on. As is the case with other mammalian species, such signs are often transmitted culturally through social learning (Avital and Jablonka, 2000). In terms of our functional characterization of language, this communication system was defined by a very limited expressive envelope. The set of meanings expressed by this system was obviously narrower than that of fullfledged human languages, but more importantly, it was also narrower than the set of conceptual meanings which individuals at this stage were capable of representing: in other words, individuals at this stage were capable of thinking and feeling much more than they could say. This is a very reasonable assumption: it has been dramatically demonstrated in experimental settings involving chimpanzees. Assume that individuals at this stage used their quasilinguistic system comfortably and naturally, and that their children comfortably acquired it. Assume further, that the community was characterized by a particular genetic constitution, which allowed for the acquisition and usage of the system – with the necessary amount of variability: some individuals were better at acquiring and using the system than others. Last but not least, assume that all members of the group shared the necessary cognitive precursors for linguistic communication: they had some preliminary form of a theory of mind, some level of conceptualization, some implicit understanding of social relations and hierarchies, and the motivation for information sharing. This last assumption has recently been scrutinized by Knight (1998) and others. It has been argued that language is particularly prone to evolutionary instability, resulting from the usage of language for cheating, because linguistic messages are cheap, and can therefore be easily used to convey false information. We believe that Knight overestimates the role of deception in the evolution of linguistic communication, for at least two reasons: first, linguistic communication is multi-functional, and some of its most important functions cannot be reduced to the sharing of verifiable information: questions, requests, threats, ritualized stories, poems and prayers are neither true nor false. Second, the socially-oriented nature of linguistic communication, and what we think about the cohesive nature of early human societies, may provide various effective types of controls against systematic cheating (Dor and Jablonka, in preparation). At any rate, the assumption that early hominids may have shared the motivation for the social communication of information seems to us to be quite a reasonable one.

Assume, then, that at different points in time, throughout stage N, individuals or groups of individuals came up with *linguistic innovations*. We may imagine a very wide range of *types* of linguistic innovations, which must have occurred during the entire evolutionary process, and most of them must have happened *again and again*. Assume that at stage N, they included new lexical items for specific referential meanings; some more abstract markers for existing and novel conceptual distinctions; new pragmatic conventions for linguistic communication, and so on. How did these innovations come about? Well, like all cultural innovations, they may have been arrived at by accident, through conscious effort, or as part of social play, by individuals who were clever enough, or explorative, or just lucky, and happened to be in the right social context at the right time. Many of the innovators must have been inquisitive youngsters, and in some cases, the innovation may have been the result of group effort (think about the achievement of the Nicaraguan children). The social driving force for the innovations must have been associated with a growing pressure for better communication within the group, and this pressure may have been causally related to a whole host of processes: an increase in group size (Dunbar, 1996); significant changes in ecological conditions; changes in tool usage; changes in the need for social co-operation; or changes in the patterns of interaction between different hominid populations. Different sets of causal factors may have been involved in each particular case, but we may confidently assume that we do not need to invoke a genetic explanation for any of the innovations: by their very definition, the linguistic innovations of stage N were within the genetically-based capacity of their inventors.

What happened to each of these linguistic innovations, once it was invented? Well, if it was not too remote from the cognitive and linguistic world of the community, the innovation may have been learned by some of the other members of the community. Although only a small minority in any community is capable of real innovation, a much larger group of individuals is capable of learning to understand and use the innovation once it is there. Here, again, we do not have to invoke a genetic explanation: hominid cognition is extremely plastic, and social learning takes advantage of this plasticity. Moreover, research on child language and on chimpanzees teaches us that at every developmental stage, individuals' achievements in linguistic comprehension are much more impressive than their achievements in linguistic *production*. The innovator thus has a good chance of being understood, especially by those individuals who are closely related to him or her – family members, close friends and so on. Note, moreover, that different individuals probably differed with respect to their ability to understand and use the innovation, and that at least some of this variability resulted from variability in individuals' genetic make-up: some individuals understood the innovation better than others; some learned to use it themselves; others managed to passively comprehend it; some others may not have been able to keep up with it.

What happened, then, to the innovation once it was learned by a few members of the community? Its fate depended to a significant degree on its propagation and dissemination across the population. These, in turn, probably depended upon a large set of considerations, including the functional significance of the innovation, the social status of the innovator and the first learners, the level of social cohesion within the first subgroup of learners, and so on. We may assume that in the innovator's own generation, the propagation of the new linguistic tool was unstable and uncertain. Many innovations, including some very adaptive ones, probably disappeared at this stage, because the significance of the innovation can sometimes be fully appreciated only when it is used by a significantly large and cohesive group of communicators (there is positive frequency dependent selection, up to a point, at least). We may, however, assume that the innovation had a better chance of establishing itself after the first learners transmitted it to their offspring, because children play a significant role in the establishment of cultural traditions (e.g. the role of juveniles in the establishment of food washing by Japanese macaques in Koshima island). We may also assume that for a long period of time, after the original invention, the innovation went through a process of cultural evolution: it may have been improved upon in all sorts of ways, and it may have become conventionalized and streamlined, in a long dynamics of learning and relearning (cf. Kirby, 1999).

As noted above, the chances of an innovation to establish itself crucially depend upon its *adaptive value* as a tool of social communication. For an innovation to survive, its usage should be beneficial for the speakers who decide to adopt it. In general, the adaptive value of a linguistic innovation is a direct function of its *information potential*, and an inverse function of its *processing effort* (Sperber and Wilson, 1986). An innovation carries high information potential if it allows for the transfer of more information which is relevant for the community; if it adds relevant elements to the expressive envelope of the system; and if it allows for more precise production and interpretation. An innovation requires low processing effort to the extent that it is relatively easy to acquire and use in contexts of social communication. (This is why parity considerations are not enough: meaning-blind conventions have no information potential whatsoever.) Note that the information potential of an innovation does not necessarily have to be related to the practical considerations which are usually discussed in the literature, such as the efficiency of co-operation in hunting or fighting, or the sharing of information about the natural environment. Although these considerations are probably important, it seems to us that the information potential of an innovation is also a social issue: it has to do with the sharing of social information (social relations, social events and social hierarchies), with the sharing of social narratives and myths, and with the construction of social epistemology (cf. Knight 1998, and Heeschen, in press). The construction of social epistemology, in turn, plays an important role in linguistically-based social identity - which strengthens the adaptive value of the innovation to an additional degree. The semantic categories we discussed in section 1 of this paper - event structure, *epistemic status, animacy* – seem to be especially functional in this respect (see Dunbar, 1996).

Now, for a linguistic innovation to survive and propagate it has to be adaptive for a sufficient amount of time, and preferably in a wide array of changing circumstances. This is especially true for categorical markers. New lexical items may come and go, depending on circumstances, but persistent categorical markers were those which survived throughout social changes over long periods of time. Moreover, for linguistic innovations to survive they have to meet the conditions set by system constraints. These are of at least two types: first, linguistic innovations have to comply with psychological constraints. Those innovations which corresponded to pre-existing cognitive, or developmental biases, were probably selected, as they were the ones most easily learned, remembered and transmitted (cf. Sperber, 1996). Second, as the linguistic system evolved, it set its own constraints on new innovations: they had to comply with the already established system. This means that, at least from a certain point in the evolution of language, the system

itself dictated the directional nature of its own future evolution. Moreover, as the system became more complex, it gradually set more and more constraints on its own ability to go through major changes. Thus, although full-fledged languages as we know them are still very flexible, the universal expressive envelope of human languages may not be expanding today at the rate we assume for the early hominid period. Note, moreover, that some types of information - such as emotional messages, or manual instructions - were probably very effectively communicated by *non-linguistic* means, such as body language, facial expressions, mime, song and dance, and so on. Linguistic innovations directed at these types of information did not survive (or may have not be invented in the first place), because the other means of communication rendered them unnecessary. Thus, division of labor between the different systems of communication may have had a significant role in the cultural evolution of the highly-constrained expressive envelope of language.

Let us assume, then, that some of the adaptive linguistic innovations of stage N managed to spread and establish themselves in the community. This establishment was very enduring, because it was both dependent upon, and constitutive of, the social structure, and because social traditions are by their very nature self-perpetuating. This cultural change enhanced the communicative capacity of individuals within the community, thus increasing the fitness of the best individual communicators, as well as the fitness of the entire group. Crucially, however, the establishment of the innovation also raised the demands for social learning imposed on individuals in the community: they did not only have to acquire the new innovations in order to be able to participate in social communication - they also had to learn to look at the world in new ways, direct attention to new aspects of reality, process and remember new types of information, and so on. In short: the linguistic innovations which established themselves in the community changed the social niche, and the inhabitants of this new niche had to adapt to it - just like the small mammals which dig burrows in order to hide from predators. In adapting themselves to the niche, the individuals could probably count on the built-in residual plasticity of their minds. Those individuals, and cohesive groups of individuals, who made better use of the innovations for efficient communication – for whatever cultural or social reason – probably benefited: they were probably reproductively more successful than others, and more likely to thrive.

Very gradually, however, the increasing cognitive demands set by the evolving linguistic niche started to expose hidden genetic variation. In our terms, residual plasticity was gradually stretched, and individuals found the accumulating linguistic demands more and more demanding. This process must have taken a long time. Eventually, however, after a very long period of consistent, directional cultural selection, genetic assimilation occurred: some individuals dropped out of the race; other survived. The frequencies of those gene combinations which contributed to easier language acquisition and use increased in the population. Eventually, in stage N + 1, we could find a community whose general genetic make-up was such that individuals comfortably used the more sophisticated linguistic system, and children comfortably acquired it. Obviously, this allowed for the whole process to start all over again: as a result of assimilation, individuals were freed once again to make use of their cognitive plasticity, to invent and learn more linguistic innovations.

What could be genetically assimilated in our transition from stage N to stage N + 1? First, it is obvious that all the relevant aspects of general cognition were assimilated, to a certain degree at least, according to suggestions by Lieberman (1991), Donald (1991), Jablonka and Rechav (1996), Deacon (1997) and others: individuals at stage N + 1 were probably more intelligent, had better memories and better voluntary control of their sound production mechanisms, and were probably smarter social agents. We believe, however, that individuals at stage N + 1 had a cognitive constitution which was, in some minute but significant ways, more biased towards the acquisition and usage of language than the cognitive constitution of individuals at stage N. The process of genetic assimilation, which followed the long period of cultural evolution in which a community became more and more dependent on linguistic communication, and in which the survival of individuals depended to an increasing extent on their linguistic performance - must have targeted those cognitive capacities which were most useful for this specific type of behavior: some examples are the capacity of

recognizing discrete conceptual categories, of rapid processing of the speech channel, of recognizing linguistic-communicative intent, and of lexical memory. These are language-specific, and they must have been targeted by linguistically-driven genetic assimilation.

The genetic assimilation of these capacities was most likely *partial*, rather than *complete*. It could not have led to a completely innate response, because the on-going process of cultural evolution made sure that the cultural environment to which individuals were adapting was constantly changing. As we have already indicated, this state-of-affairs must have had far-reaching consequences in terms of the genetic evolution of categorization, in our case, linguistic categorization: very specific innovations, such as the meanings of specific words or specific morphological markers, were not assimilated, because they were too variable and context-dependent, and because they changed too rapidly throughout cultural evolution. The partial assimilation of the innovations, however, resulted in a cognition biased towards the common denominators of the innovations - those elements of meaning, shared by entire sets of innovations, which were less variable and less context-dependent. Effectively, this process resulted in a cognition biased towards a specific set of semantic categories. These categories did not end up completely assimilated, because cultural change still put a high premium on epistemic flexibility, but just like the partial assimilation of predator-stimuli in the monkey population we have discussed earlier, the partial assimilation of the semantic categories delineated a set of stimuli for which a dramatically smaller number of learning trials was needed. The process resulted in a cognition which was innately more attuned to a specific set of semantic categories and their linguistic marking, and was thus innately more suited for their efficient acquisition and usage.

This process of linguistically-based genetic assimilation may have actually been related in an interesting way to the general evolution of human culture and human conceptualization. As we have already indicated, genetic assimilation also targeted general intelligence. We know, after all, that there was no strong constraint on the evolution of the hominids' general intelligence: hominid brains doubled in size in 2.5 million years. As the process of cultural and linguistic evolution constantly led to an extension of the environment as perceived by the community, individuals were constantly faced with more information about the world: they could learn more, about more aspects of the world, because they could think and communicate more effectively. This created a process of positive feedback: the more individuals learned about the world, the more they could communicate about; and the more they could communicate, the more they could learn. On the one hand, individuals and the whole community were now in a position to evolve their conceptual structures - with the aid of the more complex communication tool - language. On the other hand, the evolution of conceptual structures, and general cognitive tools for learning, remembering and so on, helped the concomitant evolution of the linguistic system. The linguistic system thus spiraled together with the conceptual system (and with the motor control system, which we have not discussed in this paper). This wider spiral also included a wide variety of non-linguistic, culturally-based evolutionary processes, which interacted with each other in complex ways. The process resulted both in the expansion of hominids' conceptual capacities, and in the construction and expansion of their linguistic expressive envelope.

6. Conclusion

We started out by characterizing language as a transparent mapping-system, dedicated to the expression of a *constrained* subset of meanings by means of sound concatenation. This characterization meets the conditions set by the Neo-Darwinian mode of evolutionary explanation, as it defines language as a cognitive system which is both *functional* and *unique*. As we claimed, recent advances in linguistic research support this conception, in direct opposition to Chomsky's traditional conception of the formal, *meaning-blind* nature of grammar, as well as to the functionalists' conception of language as a *general-purpose* communication system.

We then characterized the evolution of this system – and the evolution of its social users – as the interaction between *cultural* and *genetic* evolution. We discussed the evolution of the linguistic system in *cultural* terms – as the social process of innovation, production, comprehension, transmission and propagation of linguistic conventions, in which a community isolates and foregrounds certain aspects of its epistemology, and develops social agreement about the means of their expression. This process results in a communication system which is both functional, rather than merely formal, and highly-constrained, rather than general-purpose, because it is founded on a selected subset of semantic categories. In each stage of this long and continuous process, the expressive envelope of the system expands, and the structural means of expression are sophisticated.

We then discussed the genetic evolution of the users of this system in terms of partial genetic assimilation - resulting in a linguistically-biased cognition, enabling easier and more effective language acquisition and use. As we have claimed, partial genetic assimilation does not copy linguistic specificities into brain structures, and it does not result in genes for linguistic rules. Partial genetic assimilation does construct a genetic make-up which allows for the development of a cognition biased towards the acquisition and use of linguistic knowledge - but a significant amount of learning remains mandatory. This conception captures both the fact that children seem to be innately-predisposed towards the acquisition (and, in more extreme cases, the invention) of language, and the fact that the behavioral domainspecificity of language does not seem to be explicitly manifested in innately-given patterns of the brain. This view avoids the artificial dichotomy between nature and nurture, in line with the approach suggested by Elman et al. (1996), and suggests that the question of innateness is a relative one: it is the question of how much, when and what type of learning is necessary in each stage of the evolutionary process. Moreover, our view of the continuous interaction between cultural and genetic evolution takes the dynamic nature of languages, and the attested variability between different languages, to be fundamental properties of the evolutionary process. The properties of the process lead us to expect its final products, i.e. modern-day languages, to go on changing in their social contexts, and to manifest an interesting blend of universality and variability. This, of course, is exactly what we find.

Our conception of the process renders the traditional distinction between the *syntactic* nature of present-day languages, and the supposedly *pre-syntactic* nature of the so-called 'proto-language' theoretically unnecessary. The traditional distinction is based, for example, on the development of fullfledged creole languages from rudimentary pidgins (cf. Bickerton, 1984, 1990). Pidgins are usually described as lacking in grammatical complexity, whereas creoles manifest the full range of grammatical structures characteristic of mature languages. To the extent that grammatical complexity is viewed as autonomous from meaning, this development may indeed be thought of as a qualitative leap from one type of cognitive system to another. However, to the extent that grammatical structures are thought of as semantically-determined, the rise in grammatical complexity may be thought of as the result of a parallel rise in the complexity of the expressive envelope of the language. Obviously, this rise in complexity may be a remarkable one – pidgins, after all, are very limited tools of practical communication, whereas creoles can be used for writing poetry - but it is nevertheless a rise in the complexity of the same type of cognitive system. As far as the evolution of language is concerned, then, we are entitled to think about the entire evolutionary process as a gradual and continuous one.

The framework developed in this paper reconciles the two major approaches to language evolution – the one that focuses on the evolution of language as a system of *social communication*, and the one which focuses on the evolution of the *structurally* unique properties of language. According to our conception, the formal properties of language are a reflection of meaning relations, and these, in turn, have been selected, throughout the evolution of language, on the basis of their adaptive value in terms of social communication. The formal question and the social question are thus one and the same.

A personal note

Twelve years ago John Maynard Smith invited me (E. J.) to give a lecture in Sussex on the evolutionary effects of epigenetic inheritance. This invitation was not due to John's agreement with the ideas Marion Lamb and I had been developing on the subject. On the contrary – he decidedly disagreed with many of them, even declaring at one point that dangerous Lamarckians like us should be locked in cellars (although he did compassionately concede our cellar to be a wine cellar). Nevertheless, John thought our ideas were worth a good, long argument. And we have been arguing ever since - with fun, friendship, and for me, with great profit. For, as all his friends and students know, John has an uncanny ability to stimulate thinking, and an insatiable appetite for ideas. This paper, on a subject close to John's heart - the evolution of language - is written in the same argumentative spirit as that which John has been so good at stimulating. We hope you will find it worth a good, long argument, John!

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References

- AITCHISON, J. (1996): The Seeds of Speech: Language Origin and Evolution. Cambridge University Press, Cambridge.
- ALSINA, A., BRESNAN, J. and SELLS, P. (eds) (1997): Complex Predicates. CSLI Publications.
- AVITAL, E. and JABLONKA, E. (2000): Animal Traditions: Behavioural Inheritance in Evolution. Cambridge University Press, Cambridge.
- BATALI, J. (1998): Computational simulations of the emergence of grammar. In HURFORD, J. R., SUDDERT-KENNEDY, M. and KNIGHT, C. (eds): Approaches to the Evolution of Language. Cambridge University Press, Cambridge.
- BEHERA, N. and NANJUNDIAH, V. (1995): An investigation into the role of genetic plasticity in evolution. *J. Theor. Biol.* **172**: 225–234.
- BERWICK, R. C. (1998): Language evolution and the minimalist program: The origins of syntax. In HURFORD, J. R., STUD-DERT-KENNEDY, M. and KNIGHT, C. (eds): *Approaches to the Evolution of Language*. Cambridge University Press, Cambridge.
- BICKERTON, D. (1984): The language bioprogram hypothesis. *Behav. Brain Sci.* 7:173–221.
- BICKERTON, D. (1990): *Language and Species*. University of Chicago Press, Chicago.
- BLOOM, P. (1993): Language development. In *Handbook of Psycholinguistics*. Academic Press.
- DEACON, T. (1997): The Symbolic Species: The Co-evolution of Language and the Brain. W. W. Norton, New York.
- DEAN, P. (1991): Limits to attention: A cognitive theory of island phenomena. *Cognitive Linguistics* 2:1–63.
- DONALD, M. (1991): Origins of the Modern Mind. Harvard University Press, Cambridge, MA.
- DOR, D. (1996): Representations, Attitudes and Factivity Evaluations: An Epistemically Based Analysis of Lexical Selection. Stanford University Dissertation.
- DOR, D. (2000a): Towards a semantic account of strong island constraints. Submitted to *Linguistics and Philosophy*.
- DOR, D. (2000b): From the autonomy of syntax to the autonomy of linguistic semantics: Some notes on the correspondence between the transparency problem and the relationship problem. To appear in *Pragmatics and Cognition*.
- DOR, D. (2000c): Towards a semantic account of that-deletion in English. Submitted to *Language*.
- DOR, D. and JABLONKA, E. (in press): How language changed the genes: Towards an explicit account of the evolution of

language. In TRABANT, J. (ed.): *Essays on the Origin of Language*. Mouton, Berlin.

- DOWTY, D. (1979): Word Meaning and Montague Grammar. Reidel, Dordrecht.
- DOWTY, D. (1991): Thematic proto-roles and argument selection. *Language* 67:547–619.
- DUNBAR, R. (1996): Grooming, Gossip and the Evolution of Language. Harvard University Press.
- DURHAM, W. H. (1991): Coevolution: Genes, Culture, and Human Diversity. Stanford University Press, Stanford.
- EDMUNDS, M. (1974): Defense in Animals. Longman.
- ELMAN, J. L., BATES, E. A., JOHNSON, M. H., KARMILOFF-SMITH, A., PARISI, D. and PLUNKETT, K. (1996): *Rethinking Innateness: A Connectionist Perspective on Development.* The MIT Press, Cambridge, MA.
- EWER, R. F. (1956): Imprinting in animal behaviour. *Nature* 177:227–228.
- FRAWLEY, W. (1992): *Linguistic Semantics*. Lawrence Erlbaum Associates, Publishers, Hillsdale, NJ.
- GIVON, T. (1995): *Functionalism and Grammar*. John Benjamins Publishing Company.
- GOLDBERG, A. E. (1995): Constructions: A Construction Grammar Approach to Argument Structure. University of Chicago Press, Chicago.
- HALDANE, J. B. S. (1959): Natural selection. In BELL, P. R. (ed.): *Darwin's Biological Work*. Cambridge University Press, Cambridge, pp. 101–149.
- HARDY, A. (1965): *The Living Stream: A Restatement of Evolution Theory and its Relation to the Spirit of Man.* Collins, London.
- HEESCHEN, V. (in press): The narration 'instinct'. In TRABANT, J. (ed.): *Essays on the Origin of Language*. Mouton, Berlin.
- HINTON, G. E. and NOWLAN, S. J. (1987): How learning can guide evolution. *Complex Systems* 1:495–502.
- JABLONKA, E. and RECHAV, G. (1996): The evolution of language in light of the evolution of literacy. In TRABANT, J. (ed.): *Origins of Language*. Collegium Budapest, Workshop Series No. 2, pp. 70–88.
- JACKENDOFF, R. (1983): Semantics and Cognition. The MIT Press, Cambridge, MA.
- JACKENDOFF, R. (1990): *Semantic Structures*. The MIT Press, Cambridge, MA.
- JACKENDOFF, R. (1999): Possible stages in the evolution of the language capacity. *Trends in Cognitive Sciences* 3:272–279.
- KEGL, J., SENGHAS, A. and COPPOLA, M. (1999): Creation through contact: Sign language emergence and sign language change in Nicaragua. In DEGRAFF, M. (ed.): Language Creation and Language Change. The MIT Press, Cambridge, MA.
- KIRBY, S. (1999): Learning, bottlenecks and infinity: A working model of the evolution of syntactic communication. In DAUTENHAHN, K. and NEHANIV, C. (eds): Proceedings of the AISB '99 Symposium on Imitation in Animals and Artifacts. Society for the Study of Artificial Intelligence and the Simulation of Behaviour.
- KIRBY, S. (in press, a): Syntax without natural selection: How compositionality emerges from vocabulary in a population of learners. In KNIGHT, C. (ed.): Second Book on Approaches to the Evolution of Language. Cambridge University Press.

- KIRBY, S. (in press, b): Learning, bottlenecks and the evolution of recursive syntax. In BRISCOE, T. (ed.): Linguistic Evolution through Language Acquisition: Formal and Computational Models. Cambridge University Press.
- KIRBY, S. and HURFORD, J. R. (1997): Learning, culture and evolution in the origin of linguistic constraints. In HUS-BANDS, P. and HARVEY, I. (eds): *Fourth European Conference on Artificial Life*. The MIT Press, Cambridge, MA.
- KNIGHT, C. (1998): Ritual/Speech coevolution: A solution to the problem of deception. In HURFORD, J. R., STUD- DERT-KENNEDY, M. and KNIGHT, C. (eds): *Approaches to the Evolution of Language*. Cambridge University Press.
- KRUUK, H. (1972): The Spotted Hyena. University of Chicago Press, Chicago.
- LANGACKER, R. W. (1987): Foundations of Cognitive Grammar: Theoretical Prerequisites, Vol. 1. Stanford University Press.
- LEVIN, B. (1993): *English Verb Classes and Alternations: A Preliminary Investigation*. The University of Chicago Press, Chicago and London.
- LEVIN, B. and RAPPAPORT-HOVAV, M. (1991): Wiping the slate clean: A lexical semantic exploration. *Cognition* 41:123–151.
- LEVIN, B. and RAPPAPORT-HOVAV, M. (1995): Unaccusativity: At the Syntax-Lexical Semantics Interface. The MIT Press, Cambridge, MA.
- LEWONTIN, R. (1978): Adaptation. *Scientific American* 239: 157–169.
- LIEBERMAN, P. (1991): Uniquely Human: The Evolution of Speech, Thought and Selfless Behaviour. Harvard University Press, Cambridge, MA.
- MARR, D. (1982): Vision. Freeman, San Francisco.
- MAYNARD SMITH, J. and SZATHMÁRY, E. (1995): *The Major Transitions in Evolution*. Freeman, Oxford.
- MORGAN, E. (1994): *The Descent of the Child*. Souvenir Press, London.
- NEWMEYER, F. J. (1998): On the supposed 'counterfunctionality' of universal grammar: Some evolutionary implications. In HURFORD, J. R., STUDDERT-KENNEDY, M. and KNIGHT, C. (eds): Approaches to the Evolution of Language. Cambridge University Press.
- ODLING-SMEE, F. J., LALAND, K. N. and FELDMAN, M. W. (1996): Niche construction. *Amer. Nat.* 147: 641–648.
- PINKER, S. and BLOOM, P. (1990): Natural language and natural selection. *Behav. Brain Sci.* 13:707–508.
- ROSE, S. (1993): The Making of Memory. Bantam Press.
- SAVAGE-RUMBAUGH, E. S. and LEWIN, R. (1994): *Kanzi: The Ape at the Brink of the Human Mind*. John Wiley, New York.
- SIMPSON, G. G. (1953): The Baldwin effect. *Evolution* 7: 110–117.
- SPERBER, D. (1996): Explaining Culture: A Naturalistic Approach. Blackwell, Oxford.
- SPERBER, D. and WILSON, D. (1986): *Relevance: Communication and Cognition*. Blackwell, Oxford.
- VAN VALIN, R. D. Jr. and LAPOLLA, R. J. (1997): Syntax: Structure, Meaning and Function. Cambridge University Press.
- WADDINGTON, C. H. (1953): Genetic assimilation of an acquired character. *Evolution* 7:118–126.

- WHITEN, A., GOODALL, J., MCGREW, W. C., NISHIDA, T., REYNOLDS, V., SUGIYAMA, Y., TUTIN, C. E. G., WRAN-GHAM, R. W. and BOESCH, C. (1999): Cultures in chimpanzees. *Nature* **399**:682–688.
- WIERZBICKA, A. (1988): *The Semantics of Grammar*. John Benjamins Publishing Company.