## Restrictions on biological adaptation in language evolution

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Language acquisition and processing are governed by genetic constraints. A crucial unresolved question is how far these genetic constraints have coevolved with language, perhaps resulting in a highly specialized and species-specific language "module," and how much language acquisition and processing redeploy preexisting cognitive machinery. In the present work, we explored the circumstances under which genes encoding language-specific properties could have coevolved with language itself. We present a theoretical model, implemented in computer simulations, of key aspects of the interaction of genes and language. Our results show that genes for language could have coevolved only with highly stable aspects of the linguistic environment; a rapidly changing linguistic environment does not provide a stable target for natural selection. Thus, a biological endowment could not coevolve with properties of language that began as learned cultural conventions, because cultural conventions change much more rapidly than genes. We argue that this rules out the possibility that arbitrary properties of language, including abstract syntactic principles governing phrase structure, case marking, and agreement, have been built into a "language module" by natural selection. The genetic basis of human language acquisition and processing did not coevolve with language, but primarily predates the emergence of language. As suggested by Darwin, the fit between language and its underlying mechanisms arose because language has evolved to fit the human brain, rather than the reverse.

Baldwin effect | coevolution | cultural evolution | language acquisition

The mechanisms involved in the acquisition and processing of language are closely intertwined with the structure of language itself. Children routinely acquire language with little intentional tutoring by their parents and as adults use language with minimal effort. Indeed, our unique and nearly universal capacity to acquire and use language has even been cited as one of eight key transitions in the evolution of life (1). These features of species specificity and species universality, combined with the intimate fit between language structure and the mechanisms by which language is acquired and used, point to substantial genetic constraints. The nature and origin of the genetic basis for language remain the focus of much debate, however (2–4).

An influential line of thinking in the cognitive sciences suggests that the genes involved in language predetermine a highly specialized and species-specific language "module" (5), "instinct" (6), or "organ" (7). This module has been assumed to specify a number of domain-specific linguistic properties, including case marking, agreement, and conformity to highly abstract syntactic constraints, such as X-bar theory (8). Although some have argued that the genes encoding a language module arose through a sudden "catastrophic" genetic change (9), and others have remained agnostic on this point (10), "the default prediction from a Darwinian perspective on human psychological abilities" (ref. 11; p. 16) is the adaptationist view, that genes for language coevolved with human language itself for the purpose of communication (1, 8, 12–18).

A challenge for the adaptationists is to pinpoint an evolutionary mechanism by which a language module could become genetically encoded (19). The problem is that many of the linguistic properties purported to be included in the language module are highly abstract and have no obvious functional basis-they cannot be explained in terms of communicative effectiveness or cognitive constraints-and have even been suggested to hinder communication (20). By analogy with the conventions of communication protocols between computers, it has been suggested that even completely arbitrary linguistic properties can have an adaptive value, if the same conventions are adopted by all members of a speech community (12). That is, although any number of equally effective communicative "protocols" may serve equally well for communication, what matters is that everyone adopts the same set of culturally mediated conventions.

The subsequent shift from initially learned linguistic conventions to genetically encoded principles necessary to evolve a language module may appear to require Lamarckian inheritance. The Baldwin effect (21, 22) provides a possible Darwinian solution to this challenge, however. Baldwin proposed that characteristics that are initially learned or developed over the lifespan can become gradually encoded in the genome over many generations, because organisms with a stronger predisposition to acquire a trait have a selective advantage. Over generations, the amount of environmental exposure required to develop the trait decreases, and eventually no environmental exposure may be needed-the trait is genetically encoded. A frequently cited example of the Baldwin effect is the development of calluses on the keels and sterna of ostriches (22). The proposal is that calluses were initially developed in response to abrasion where the keel and sterna touch the ground during sitting. Natural selection then favored individuals that could develop calluses more rapidly, until callus development became triggered within the embryo and could occur without environmental stimulation. We investigated the circumstances under which a similar evolutionary mechanism could genetically assimilate properties of language in a domain-specific module (1, 12, 13).

**Simulation 1: Establishing the Baldwin Effect.** We first specified a model of the mutual influence of language and language genes. To provide the best chance for the Baldwin effect to operate, we chose the simplest possible relationship between language and genes (23). We considered a language governed by *n* principles,  $P_1, \ldots, P_i, \ldots, P_n$ , which potentially may be encoded in *n* genes. Each principle has two variants,  $+_L$  and  $-_L$ . The corresponding genes,  $G_1, \ldots, G_i, \ldots, G_n$ , have three alleles,  $+_G$ ,  $-_G$ , and  $?_G$ , two

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