present at the time of program execution. If none of this is right, the program is totally useless and does not run at all.

Similarly, the DNA macromolecule only becomes information when there is the interpretive machinery that can act upon it. Otherwise, it is a totally dead piece of matter. Just like a computer program, the interpreting process integrates the environment. So in that sense, the genetic system is not just the replicating DNA; it necessarily requires and includes the epigenetic system. Likewise, aspects of a situation in the world or of the behavior of another individual only become informative after an enormously complex process of perception and context-sensitive interpretation has been able to make sense of what is going on. A collection of speech sounds only becomes a carrier of information if there is somebody that can parse and interpret it in a specific context.

The cultural transmission scenario assumes that enough information is present in the perception of behaviors or in language sentences so that the system needed to interpret and reuse them can be copied by imitation from one individual to another. Here lies the difficulty. The imitator/learner must have a sense of what aspects of reality are relevant and what the underlying intentions are before he or she can imitate. The real world is infinitely complex. Without an interpretive capacity in place, the imitator cannot know what exactly needs to be retained in his or her own behavior and when it is appropriate. For example, the tones of a vowel are very relevant in Chinese but are irrelevant in English, so an English speaker trying to imitate Chinese will not properly pay attention to the tonal distinctions, let alone be capable to replicate them.

This is the fundamental paradox for all models of behavioral or symbolic inheritance that rely on imitation or observational learning – to imitate, you must know what counts as information and what is the intention of the producer. So the behavioral or cultural transfer of the interpretive capacity must already have taken place before the imitative act. This is in contrast to the copying mechanism underlying genetic inheritance, which does not need to know anything about what it is copying. This paradox explains why attempts to operationalize imitation in artificial systems have failed, despite a lot of effort (Dautenhahn & Nehaniv 2002). Models of cultural evolution based on imitation appear to assume what they try to explain.

So what is the alternative? Perhaps it is not such a good idea to make the analogy between different forms of inheritance so strong. Szathmáry (2006) draws our attention to a distinction between replicators and reproducers that may be helpful here: Replicators multiply with heredity plus variation, so that selection can act on the population of variants. However, replicators cannot replicate on their own. To copy them, a reproducer is needed – an entity that can do the replication. Genes are replicators but not reproducers; the cell is the reproducer. But because the cell can perform replication of genes, which can then reproduce another cell given the right additional (epigenetic) context, they can also be regarded as replicators. Viruses, in contrast, are replicators but not reproducers themselves, because they need another living cell to reproduce.

This indicates the following analogies and differences between genetic inheritance and symbolic or behavioral inheritance (Steels 2004): Utterances or features of utterances can be viewed as replicators (as in Croft 2000). Every time the same sort of utterance (or feature of an utterance) is produced, it is a replication, unavoidably, with some variation. The reproducer is the speaker's total language system, which might have had to be expanded to achieve the speaker's communicative goals for that utterance. When the utterance is interpreted by the hearer, he or she will have to exercise his or her own total language system, possibly expanding or adjusting it as well. Within this scenario, language systems are not transferred by imitation or observational learning but are actively constructed by speakers and hearers and are aligned to maximize success in communication. With enough interactions, the language system of a speaker will seem to have been transmitted to the hearer; but in fact, the transmission does not at all take place by copying, the way it does for DNA.

The missing chapter: The interaction between behavioral and symbolic inheritance

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Abstract: A strength of Jablonka & Lamb's (J&L's) book lies in its accessible as well as thorough treatment of genetic and epigenetic inheritance. The authors also provide a stimulating framework integrating evolutionary research across disciplines. A weakness is its unsystematic treatment of the interaction between behavioral and symbolic inheritance, particularly in their discussion of language.

In *Evolution in Four Dimensions*, Jablonka & Lamb (J&L, 2005) provide a coherent, unifying evolutionary framework that does not compromise complexity but, instead, embraces it. From our perspective, the meatiest chapters of this book are those on genetic and epigenetic inheritance systems and their interaction. The authors' rich discussion of epigenetic inheritance is fascinating, and their criticism of pure selfish-gene theory compelling. Despite these positive impressions, we found J&L's discussion of behavioral and symbolic inheritance to be less thorough than their comprehensive coverage of genetics and epigenetics, from which we learned so much. Our primary concern is the lack of focus on the interaction between behavioral and symbolic inheritance. This limitation is surprising, given that gene–behavior and gene–language interactions are provided special attention. The relationship between genes and language may be more controversial than that between behavioral and symbolic inheritance. Nevertheless, we argue that behavioral–symbolic interactions are crucial for understanding symbolic language. A discussion of this interaction would have made J&L's four-dimensional framework more complete. In short, there is a chapter missing from this book. In what space we have, we propose some of the material such a chapter could contain.

First, inheritance through behavior-influencing substances may have an analogue in the prenatal auditory experience infants receive in the womb. Research by Shi and colleagues (Shi et al. 1999) suggests that very early auditory perceptual abilities may contribute to grammatical development. Shi et al. studied 1- to 3-days-old infants' responses to two separate classes of words: function words (short, unstressed words such as *will* and *for*) and content words, such as nouns and verbs. Infants detected a change when different words were presented auditorily, but only when the change happened across these classes. Other experiments have demonstrated perceptual sensitivity to the difference between the mother's voice and a stranger's voice in utero (Kisilevsky et al. 2003). J&L argue that maternal diet has chemical consequences that bias a child's early culinary sensitivities. Similarly, one may argue that maternal language has perceptual consequences that bias early linguistic sensitivities. Some may debate the functional significance of this phenomenon, but it is a reasonable possibility that it provides an advantage for children whose prenatal auditory experiences permit early preferences to the mother's language (DeCasper & Fifer 1980; DeCasper & Prescott 1984).

J&L's second behavioral inheritance system, non-imitative social learning, seems also to have a role in early language learning. Some developmental psychologists have argued that socially mediated environmental contingencies promote vocal and social learning that is crucial for later language skill. Watson's (1966; 1985) early work on infants' contingency perception offered a possible basis for emerging social skill. More recently, Goldstein and colleagues (Goldstein et al. 2003) showed that, during early stages of vocal development, social contingencies can affect characteristics of vocalization, including the quality and quantity

of vowel sounds. These contingencies likely emerge in the language-learning environment while the caregiver naturally attends to vocalization by the child (see also Goldstein & West 1999).

Imitation, J&L's third type of behavioral inheritance, likely has some role in language development as well. In fact, numerous authors have argued for an intimate link between imitation and language (e.g., Meltzoff 1988; Tomasello 2003). A great number of studies have suggested a variety of imitative behaviors by young children. Although debate continues about certain studies and their relevance, researchers have reported imitation of basic facial expressions and gestures early in infancy (Meltzoff & Moore 1977), sound productions that reflect the ambient language environment (de Boysson-Bardies & Vihman 1991), and reproduction of novel words modeled by adults (Tomasello & Barton 1994). These imitative actions may be foundational for aspects of language acquisition, including gesture, phonology, and word learning.

As children progress from early word learning to more advanced stages of language use, they seem to rely increasingly on symbolic inheritance to further their language skills. In formal education and informal learning alike, children and adults can learn the meanings of new words through multi-word definitions coming from direct instruction or even reference books. Thus, language knowledge is a product of both behavioral and symbolic inheritance (with the symbolic feeding back onto itself).

As J&L argue, there is a reasonable basis for distinguishing symbolic and behavioral inheritance. We urge, however, that this distinction can be subtle and deserves more attention, particularly when considering language and its acquisition. For example, is language learning transmitted mostly through symbolic inheritance, or through behavioral inheritance? At the early stages of learning, when the most fundamental linguistic conventions are developing, behavioral inheritance seems more relevant than symbolic inheritance. In fact, many have found it challenging to draw a cutoff where a child's language becomes symbolic. Language itself may be symbolic to varying degrees, depending on factors such as the extent to which a lexical item is generalized across environmental contexts, and the extent to which a phrase is conventionalized (Bates et al. 1979; Bybee 2006; Tomasello 2003).

We should note that, scattered throughout J&L's book, one can find reflections similar to those presented here. For instance, the authors discuss Chomskyan and functionalist theories about the role of input in language acquisition; they also suggest genetic adaptations in cognitive faculties that promote language learning. However, they rarely relate these reflections to their behavioral inheritance dimension. A formal discussion of behavioral–symbolic interaction would be useful for multiple reasons. First, behavioral inheritance underlies our ability to transmit symbolic information. Second, symbolic information presumably affects what is transmitted through behavioral inheritance. Finally, behavioral inheritance may be one route through which the genetic and symbolic dimensions interact.

Authors' Response

Bridging the gap: The developmental aspects of evolution

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Abstract: The commentaries on *Evolution in Four Dimensions* reflect views ranging from total adherence to gene-centered neo-Darwinism, to the acceptance of non-genetic and Lamarckian processes in evolution. We maintain that genetic, epigenetic, behavioral, and cultural variations have all been significant, and that the developmental aspects of heredity and evolution are an important bridge that can unite seemingly conflicting research programs and different disciplines.

When writing *Evolution in Four Dimensions* (Jablonka & Lamb 2005; henceforth *E4D*), we often thought about our future readers and tried to engage in a dialogue with them, a dialogue that is reflected in some parts of our discussions with the fictional Ifcha Mistabra, our devil's advocate, which are found at the end of each chapter. We hoped that the book would be read not only by professional biologists, but also by non-biologists, such as psychologists, social scientists, and scholars of culture, who either directly or indirectly draw on evolutionary theory. The commentaries in *BBS* now give us a welcome opportunity to participate in a real cross-disciplinary discussion. As anticipated, most commentators have focused on the relations among heredity, evolution, and development at the behavioral and cultural level. Some doubt that our challenge to neo-Darwinism is necessary, and question the productivity of the Lamarckian perspective and the importance of epigenetic inheritance in evolution; others feel that we did not go far enough. The commentators also refer to our scant discussion of the evolution of cognitive plasticity, question the nature of cultural and behavioral inheritance and their interrelations, highlight the ambiguous and evasive nature of the notion of symbol-based evolution, and present different views about semantic information and the evolution of language. They made us think about areas that we did not explore or did not explore fully, and we are grateful to them.

The two topics that gave us most difficulty when writing *E4D* were finding a satisfactory way of clarifying the notion of semantic biological information, which is a unifying concept in the book, and elucidating the nature of symbols and of symbol-based evolution. Both issues were picked up by several commentators, and we are glad to have the opportunity of saying more about them. But before we do so, we briefly address the more general issues that were raised in the commentaries, which are (1) the relation between developmental plasticity and heredity, (2) our position vis-à-vis terms like neo-Darwinism and Lamarckism, and (3) the evolutionary importance and scope of non-genetic inheritance systems.

R1. The developmental aspects of heredity and evolution

In *E4D* we emphasized developmental aspects of heredity, but our focus and starting point was heredity, not development. We discussed developmental plasticity and environmentally induced variations as they contribute to heredity, concentrating on what can be thought of as temporally extended, intergenerational, developmental plasticity – on the inheritance of environmentally influenced changes. The evolution of plastic responses that are limited to a single generation was not a major topic in the book, although we did discuss (p. 312) the conditions under which plasticity in the classical sense would evolve. It was