The Grammar of Inheritance

Eva Jablonka's Four Dimensions of Evolution and the Closure Framework: How Information Passes Between Levels and Becomes Conscious

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> *There is more to heredity than genes. Four inheritance systems play a role in evolution: genetic, epigenetic, behavioral, and symbolic. Each can provide variations on which natural selection can act.*
> Eva Jablonka and Marion Lamb, Evolution in Four Dimensions, 2005

> *Every finite closure generates remainder. The remainder is not noise. It is the proof that the grammar is finite.*
> CF Dietz, Consciousness, Closure, and the Cosmos, 2026

Abstract

Eva Jablonka has spent three decades expanding evolutionary biology beyond the gene-centered view. Her four inheritance systems, genetic, epigenetic, behavioral, and symbolic, describe four distinct channels through which information passes across generations at different timescales and with different degrees of plasticity. Her more recent work with Simona Ginsburg on the evolution of consciousness proposes that the transition to minimal subjective experience is marked by the emergence of unlimited associative learning: the capacity to form novel associations across any domain, to assign motivational value to new stimuli, and to use that assignment as the basis for further learning. This paper argues that Jablonka's four inheritance systems are four nested closure regimes operating at different timescales, each constituting facts at its own level while using the outputs of lower levels as its elements. The passage of information between inheritance systems is the encounter of one closure regime with the remainder generated by the one below it: the epigenetic closure uses genetic remainder as its resource, the behavioral closure uses epigenetic remainder as its resource, and the symbolic closure uses behavioral remainder as its resource. Jablonka's unlimited associative learning is the emergence of a closure regime sophisticated enough to use its own remainder as the subject of its next learning act: a closure that can learn about what it cannot yet model. That is the cognitive level where c, consciousness with content, first becomes genuinely open to M, the inexhaustible ground that exceeds every closure. Jablonka arrived at the evolutionary history of exactly what the CC-C framework describes as the architecture of conscious experience.

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1. What the Cell Remembers That the Gene Does Not

Two cells in the same organism, carrying the same DNA, can behave in fundamentally different ways. A liver cell and a neuron have identical genomes. They build different structures, perform different functions, maintain different metabolic profiles, and respond differently to the same chemical signals. The difference is not in the gene sequence. It is in which genes are expressed, how frequently, in what combination, and in response to what signals. The pattern of gene expression in a liver cell differs from the pattern in a neuron, and each cell passes its expression pattern to its daughter cells when it divides. The daughters inherit not just DNA but a pattern of gene activation that has nothing to do with the DNA sequence itself.

This is epigenetic inheritance: the transmission of cellular states that are not encoded in the DNA sequence but in the chemical marks on the DNA and its associated proteins, in the three-dimensional organization of chromosomes in the nucleus, and in the self-sustaining feedback loops of gene regulatory networks. A cell can remember, across many divisions, which genes it expresses and how, even though the memory is not stored in any sequence of bases. The memory is stored in the pattern of the closure: in the organizational state that determines how the genetic text is read.

Eva Jablonka recognized the evolutionary significance of this observation and followed where it led. If cells can inherit non-genetic information, then organisms can too. If organisms can inherit non-genetic information from their parents, then populations can change across generations through mechanisms other than the selection of random DNA mutations. The gene-centered view of evolution, which treats all heritable variation as genetic variation, is incomplete. There are other inheritance systems, each with its own rules, its own timescale, its own relationship to the environment. Evolution is not one-dimensional. It has four dimensions.

The four inheritance systems that Jablonka and Lamb describe, genetic, epigenetic, behavioral, and symbolic, are the subject of this paper. The closure framework will show that they are not four parallel channels running alongside each other but four nested levels of a single hierarchical structure: closure regimes of increasing organizational depth, each using the remainder of the one below it as its resource, each passing its own outputs to the one above it as raw material. And Jablonka's account of the evolutionary emergence of consciousness through unlimited associative learning will show where in this hierarchy the transition from mere closure to felt experience occurs.

2. Jablonka's Four Claims

Jablonka's contribution to evolutionary biology and philosophy of biology has four interconnected components.

2.1 The Four Inheritance Systems: Evolution Is Multidimensional

The genetic inheritance system is the one everyone knows: DNA sequences are copied, occasionally mutated, and transmitted to offspring through reproduction. Natural selection acts on the variation produced by mutation and recombination. This is the Modern Synthesis in its standard form.

The epigenetic inheritance system transmits cellular states that are not encoded in DNA sequences. Patterns of gene expression, chromatin structure, DNA methylation, and self-sustaining regulatory loops can all be inherited by daughter cells and, in some cases, by offspring. The epigenetic system allows cells with identical genomes to maintain different identities, allows organisms to respond to environmental conditions in ways that can be transmitted to their offspring, and allows evolution to operate on a much faster timescale than genetic mutation permits. Epigenetic inheritance is not random in the way genetic mutation is: environmental signals can specifically trigger epigenetic changes that prepare offspring for similar conditions.

The behavioral inheritance system transmits behavior through social learning, imitation, and the modification of environments by organisms. When a population of birds learns to open milk bottles, the behavior is transmitted not through genes but through observation and imitation. The behavior modifies the environment, which modifies the selection pressures acting on the population, which can eventually lead to genetic changes that support the behavior. Behavioral inheritance is faster and more plastic than epigenetic inheritance, responds more directly to environmental novelty, and can spread through populations in ways that transcend kinship lines.

The symbolic inheritance system is uniquely powerful in humans: the transmission of information through language, writing, and other symbolic media. Symbolic inheritance is not constrained by biological transmission at all: it can cross species boundaries, persist for millennia, accumulate indefinitely, and encode information about the entirely counterfactual and hypothetical. Human culture is symbolic inheritance operating at its full development.

2.2 The Systems Interact: Lower Levels Feed Higher, Higher Levels Feed Back

The four inheritance systems are not independent parallel channels. They interact in both directions. Lower-level systems provide the material that higher-level systems work with. Higher-level systems can modify the conditions that lower-level systems operate in, which can feed back into genetic and epigenetic changes.

The most important interaction is what Jablonka calls genetic assimilation: a process by which behavioral or epigenetic variation, initially transmitted non-genetically, can become encoded in the genome over evolutionary time. If a population repeatedly encounters an environment that favors a particular behavioral response, organisms that are genetically predisposed to learn that behavior quickly will be selected for. Over generations, what began as a learned behavior can become an instinct. What began as an epigenetic response to an environmental signal can become a genetic default. The higher-level inheritance systems lead the way in evolution. The genetic system plays catch-up.

This bidirectional interaction produces an evolutionary process far richer than the one-dimensional view of mutation plus selection. Organisms are not passive recipients of selection pressures acting on random mutations. They actively modify their environments, transmit behavioral solutions to offspring, respond epigenetically to environmental signals in heritable ways, and accumulate cultural knowledge that changes the selection pressures acting on their descendants. Evolution is shaped as much by what organisms do as by what happens to their genes.

2.3 Unlimited Associative Learning: The Marker of Minimal Consciousness

In The Evolution of the Sensitive Soul, co-authored with Simona Ginsburg, Jablonka extends the four-dimensional framework to the origin of consciousness itself. Their question is the one evolutionary biology has avoided: what was the transition from organisms that lacked subjective experience to organisms that had it?

Ginsburg and Jablonka propose that the evolutionary marker of minimal consciousness is a specific form of learning they call unlimited associative learning. An organism capable of unlimited associative learning can form novel associations between any stimuli across any domains, assign motivational value to novel compound stimuli that would not by themselves trigger any reflex, and use those novel associations as the basis for further learning. This is not simple conditioning, which is restricted to specific stimulus-response pairs. It is the capacity to form new relationships between any aspects of experience and to use those relationships as the starting point for more relationships.

Ginsburg and Jablonka argue that this capacity is both necessary and sufficient for minimal consciousness. It is necessary because associating across domains requires that different aspects of experience be held together in a unified experiential field: there must be something it is like to encounter the compound stimulus for the association to be formed. It is sufficient because any organism that can perform unlimited associative learning is already doing the cognitive work that consciousness makes possible. The Cambrian explosion, they argue, was driven by the emergence of unlimited associative learning in early animals: the cognitive flexibility it provided was the engine of the massive diversification of body plans and behaviors that occurred 540 million years ago.

2.4 Symbolic Inheritance as the Threshold of Rationality

The fourth and most distinctively human inheritance system, symbolic language, marks a second major transition in Jablonka's framework: the transition from minimal consciousness, the sensitive soul, to full human rationality, the rational soul. Language is not merely a more efficient behavioral inheritance system. It introduces a qualitatively different kind of information transmission: the capacity to encode and transmit information about the entirely absent, the counterfactual, and the hypothetical.

A bird can transmit the behavior of opening milk bottles through imitation. It cannot transmit the concept of milk bottle opening to birds that have never encountered a milk bottle. Language can. More importantly, language can transmit information about how to respond to situations that have never occurred and may never occur. It can encode not just what organisms do but what they could do, should do, and must not do. The symbolic inheritance system creates the possibility of cumulative cultural evolution: the accumulation of knowledge across generations that does not require each generation to rediscover everything from experience.

3. What Jablonka Needs

Jablonka's four-dimensional framework is among the most important contributions to evolutionary biology of the past three decades. It provides the conceptual vocabulary for a genuinely extended evolutionary synthesis: one that acknowledges the full range of heritable variation without reducing it to genetic variation.

There are two questions the framework raises without fully answering. The first is structural: why are there four levels of inheritance rather than three or five? What determines how many nested systems there can be, and what determines the relationship between them? Jablonka demonstrates empirically that these four systems exist and interact. She does not derive their existence from a more fundamental account of what organized information transmission must be.

The second question is more philosophical: how does the transition to unlimited associative learning produce consciousness rather than merely more sophisticated information processing? Jablonka and Ginsburg propose UAL as the marker of consciousness and argue for its evolutionary plausibility. They do not explain what it is about UAL that makes it the threshold where processing becomes experiencing. Their account describes the functional prerequisites of consciousness without explaining the relationship between those prerequisites and felt experience.

The closure framework addresses both questions. The four inheritance systems are four nested closure regimes because that is the number of qualitatively distinct levels of information storage and transmission that biological evolution has produced, each using the remainder of the one below it as its resource. The structural account of nested closure shows why the systems must be hierarchically related rather than parallel, why they interact in both directions, and why genetic assimilation is a structural necessity rather than a contingent evolutionary possibility. And the distinction between C and c, between bare conscious presence and consciousness with content, provides the philosophical account of why UAL marks the threshold of consciousness: it is the level at which the cognitive closure regime becomes sophisticated enough to take its own remainder as its next learning problem, and thereby becomes genuinely open to what exceeds it.

4. Two Concepts and the Four Levels They Explain

The closure framework is introduced here at the minimum level needed to ground Jablonka's account.

4.1 Closure Regime: What an Inheritance System Is Structurally

A closure regime is a system that stabilizes some content by drawing distinctions, establishing identity criteria, and maintaining lawful relationships among its elements. It constitutes facts within its scope and generates remainder at its boundary.

Each of Jablonka's four inheritance systems is a closure regime at a different level of organizational complexity. The genetic system is the molecular closure: it constitutes facts about protein sequences from nucleotide sequences, maintaining identity criteria across cellular divisions and reproductive cycles. The epigenetic system is the cellular closure: it constitutes facts about gene expression states from patterns of chromatin modification and regulatory network activity, maintaining identity across cell divisions without changing the underlying DNA. The behavioral system is the organismic closure: it constitutes facts about adaptive responses to environmental challenges from sensorimotor learning and social observation, maintaining behavioral repertoires across individual lifetimes and through social transmission. The symbolic system is the cultural closure: it constitutes facts about absent, counterfactual, and hypothetical situations from linguistic representations, maintaining knowledge across generations and population boundaries.

At each level, remainder plays the key role. The genetic closure constitutes the protein sequences the cell needs but generates remainder: the enormous space of possible protein configurations and regulatory interactions that no single genome can specify. The epigenetic closure uses that genetic remainder as its resource: it deploys the genome's organizational potential in context-specific ways that the genome alone cannot determine. The behavioral closure uses epigenetic remainder: the plasticity that epigenetic systems provide is the raw material for behavioral learning. The symbolic closure uses behavioral remainder: the diversity of behavioral solutions that organisms encounter but cannot fully encode in behavioral inheritance becomes the content of language and culture.

4.2 Nested Closure: Why the Systems Are Hierarchical and Bidirectional

Jablonka's observation that the inheritance systems interact bidirectionally, that higher levels modify the conditions for lower levels and lower levels constrain what higher levels can do, is a consequence of nested closure. In a nested closure hierarchy, higher levels set the boundary conditions within which lower levels operate, and lower levels generate the dynamics that higher levels integrate. This is Noble's biological relativity, Friston's nested Markov blankets, and Maturana's autopoiesis all applied to the specific hierarchy of inheritance systems that evolutionary history has produced.

Genetic assimilation is the clearest instance of this bidirectional causation. When a behavioral closure regime establishes a stable pattern of response to an environmental challenge, it modifies the selection pressures acting on the genetic closure below it. Organisms whose genetic closure generates the molecular machinery for rapid behavioral learning in the relevant domain will be favored. Over time the genetic closure updates to incorporate what the behavioral closure has established. Higher level, behavioral, modifies the boundary conditions for lower level, genetic. The modification is real, causal, and directional. Noble's downward causation, Friston's active inference, and Jablonka's genetic assimilation are three descriptions of the same structural necessity.

5. Four Claims, One Structure

The vocabulary correspondence between Jablonka's framework and the closure framework is direct and developmentally rich. What Jablonka calls an inheritance system, the closure framework calls a closure regime at a specific level of organizational complexity. What Jablonka calls epigenetic inheritance, the framework calls the cellular closure using genetic remainder as its resource. What Jablonka calls behavioral inheritance, the framework calls the organismic closure using epigenetic remainder. What Jablonka calls symbolic inheritance, the framework calls the cultural closure using behavioral remainder. What Jablonka calls the interaction between levels, the framework calls the bidirectional causation of nested closure regimes. And what Jablonka calls unlimited associative learning, the closure framework calls the emergence of a cognitive closure sophisticated enough to learn about its own remainder.

5.1 The Four Systems Are Four Nested Closures

Jablonka's four inheritance systems operate at different timescales and with different degrees of plasticity because they are closures at different levels of organizational depth. Genetic inheritance is the slowest and least plastic: the molecular closure changes primarily through random mutation and selection, which operates over many generations. Epigenetic inheritance is faster and more plastic: the cellular closure can change within an organism's lifetime in response to environmental signals, and some of those changes are heritable. Behavioral inheritance is faster still: behavioral closures can change within hours or days through individual learning and can spread through populations within a generation through social transmission. Symbolic inheritance is the fastest and most plastic: cultural closures can change within days through deliberate reasoning and can spread globally within hours through language.

The increasing speed and plasticity correspond to increasing organizational depth. Deeper closures can respond to remainder faster, using more sophisticated mechanisms for detecting mismatch and updating their identity criteria. The genetic closure updates its identity criteria over thousands of generations. The epigenetic closure updates within a lifetime. The behavioral closure updates within days. The symbolic closure updates within minutes. Each level of organizational depth brings a faster supersession cycle, a more responsive relationship with remainder, a greater capacity to adapt to what the lower level's closure cannot model.

5.2 Genetic Assimilation Is Supersession Across Levels

Jablonka's genetic assimilation, the process by which non-genetic inheritance leads to genetic change over evolutionary time, is supersession operating across levels of a nested closure hierarchy. The behavioral closure establishes a stable pattern: behavioral remainder accumulates, drives learning, and produces a new behavioral identity criterion. That new criterion modifies the selection pressures acting on the genetic closure below it. The genetic closure supersedes in response: organisms whose genomes better support the behavioral pattern are selected for. Over generations the genetic closure updates to incorporate what the behavioral closure achieved.

This cross-level supersession is the most important mechanism Jablonka has identified. It shows that evolution is not merely the selection of genetic variants by external environments. It is the continuous updating of lower-level closures in response to what higher-level closures have established. The organism as a whole, acting as an agent through its behavioral and epigenetic closures, shapes the selection pressures that modify the genetic closure beneath it. Life is not just responding to evolution. It is doing evolution, from the inside, through the accumulated effects of what organisms learn, transmit behaviorally, and encode culturally.

5.3 Unlimited Associative Learning Is Closure Learning About Itself

Jablonka and Ginsburg's unlimited associative learning is, in closure framework terms, the emergence of a cognitive closure that can take its own remainder as the subject of its next learning act. A simple conditioning organism has a closure that associates specific stimuli with specific responses. It cannot form associations between stimuli outside those specific pairings. Its remainder, the domain of possible associations it cannot form, is fixed by its organizational structure. It cannot learn about what it cannot associate.

An organism capable of unlimited associative learning can form associations across any domain. It can take the boundary of its current associative closure and treat what lies beyond it as a problem to be solved. It can learn about the limits of its own learning. This is the cognitive equivalent of a closure that uses its remainder as a resource rather than simply enduring it: the highest-order form of supersession, in which the system updates not just its responses to known stimuli but its capacity to form new response categories altogether.

This is why Jablonka and Ginsburg are right that UAL marks the threshold of consciousness. Not because UAL is sufficient to generate felt experience by itself, but because the structural condition for felt experience is a closure that is open to what exceeds it: a system organized enough to encounter its own remainder as something rather than nothing, to feel the gap between what it can model and what it opens onto. The closure framework names this structural condition C: bare conscious presence, the primitive that cannot be derived from organizational complexity but that is the condition under which organizational complexity is experienced. UAL is the functional marker for the level at which C becomes relevant: the level at which the cognitive closure is sophisticated enough for its encounter with remainder to be felt rather than merely processed.

5.4 Symbolic Language Is the Open-Ended Closure

Jablonka's symbolic inheritance system is distinctive among the four because it is the only one that can explicitly represent its own remainder. Language can say what it cannot yet say: it can mark the boundary of its current understanding with concepts like unknown, possible, hypothetical, and impossible. It can encode the absence of knowledge as a positive category. It can transmit not just what is known but what is not yet known and what might be knowable.

In closure framework terms, symbolic language is a closure that has developed the capacity to explicitly model its own boundary: to constitute facts about what it cannot yet constitute, to mark remainder as remainder rather than simply generating it unseen. This is a qualitative leap from behavioral inheritance, which can transmit solutions but cannot explicitly transmit the awareness of unsolved problems. Language creates the possibility of deliberate inquiry: the use of symbolic closure to pursue what the symbolic closure has acknowledged it does not yet know. Science, philosophy, and the entire project of systematic human inquiry are expressions of this capacity. They are the use of the symbolic closure to explore its own remainder, to push the boundary of what can be constituted toward what cannot yet be.

6. What the Encounter Produces

The encounter between Jablonka's four-dimensional framework and the closure framework has consequences for both.

For Jablonka's framework, the closure account provides the structural derivation of why the four inheritance systems must be hierarchically nested rather than parallel, why they interact bidirectionally, and why genetic assimilation is a structural necessity rather than an empirical discovery. The closure framework also provides the philosophical account of the UAL threshold that Jablonka and Ginsburg's work identifies but does not fully explain: UAL marks the level where cognitive closure becomes sophisticated enough for its encounter with remainder to be felt, where the gap between what can be modeled and what exceeds the model becomes the subject of experience rather than merely the trigger of response.

For the closure framework, Jablonka's work provides the evolutionary history of how nested closure regimes at different timescales emerged from each other in biological life. The CC-C framework describes the structure of nested closure hierarchies. Jablonka describes how that structure was built across four billion years of biological evolution, level by level, each new level using the remainder of the one below it as the resource for its emergence. Genetic closure first. Epigenetic closure building on genetic remainder. Behavioral closure building on epigenetic remainder. Symbolic closure building on behavioral remainder. And at each new level, a faster supersession cycle, a more responsive relationship with what lies beyond the current closure, a deeper opening onto M.

The connection to the Sensitive Soul work is the most significant contribution Jablonka makes to the series as a whole. Every other paper in the series has engaged thinkers who bracket consciousness or describe it from outside. Jablonka's evolutionary account of UAL as the threshold of minimal subjective experience provides the evolutionary narrative of how C, bare conscious presence, first became relevant to biological systems: not as something imposed from outside evolution but as the condition under which the most sophisticated products of four billion years of nested closure hierarchy began to experience rather than merely process what they opened onto.

7. The Grammar of Inheritance

Two cells with identical DNA, behaving differently, transmitting their differences to their daughters. That observation is where this paper began and where Jablonka's project began. It is also, the closure framework argues, where the story of how consciousness got into the world begins.

Four inheritance systems. Four nested closure regimes. Each using the remainder of the one below it as its resource for emergence. Each capable of a faster supersession cycle than the one below it. Each more responsive to what lies beyond the current closure's boundary. Genetic, transmitting the molecular organization of what to make. Epigenetic, transmitting the cellular organization of when and how to make it. Behavioral, transmitting the organismic organization of how to act in the world. Symbolic, transmitting the cultural organization of what to think about what has not yet happened.

And at the threshold of unlimited associative learning, the emergence of a cognitive closure sophisticated enough to feel what it encounters rather than merely process it. The Cambrian explosion as the moment when biological evolution first produced organisms that could experience rather than merely respond. The emergence of language as the moment when organisms began using closure to explicitly explore their own remainder.

Jablonka traced the evolutionary history of these transitions with care and precision. The closure framework names the structural logic that makes each transition possible and necessary: nested closure regimes using each other's remainder as resources, building upward through organizational depth until the closure is sophisticated enough to be felt from the inside. The grammar of inheritance is not just the grammar of how information passes between generations. It is the grammar of how organized systems of increasing depth eventually produce the felt interior of being a living thing in a world that exceeds every description of it. Jablonka followed that grammar across four billion years of evolution. The closure framework names what the grammar has always been.

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Author's Note

This paper is the eighth in a series engaging thinkers whose work converges with the closure framework developed in Consciousness, Closure, and the Cosmos. Eva Jablonka is Professor at the Cohn Institute for the History and Philosophy of Science and Ideas at Tel Aviv University. Her work with Marion Lamb on four-dimensional evolution and with Simona Ginsburg on the evolution of consciousness spans molecular biology, evolutionary theory, and philosophy of mind. This paper draws on both bodies of work because together they provide something no other paper in the series provides: the evolutionary narrative of how nested closure regimes at different timescales built the organizational depth from which conscious experience emerged. The connection between Jablonka's unlimited associative learning and the closure framework's account of C as the primitive of conscious presence is this paper's most important philosophical contribution. Jablonka found the functional threshold. The closure framework names the structural condition that the threshold marks. The author welcomes engagement from Jablonka, Ginsburg, and from evolutionary biologists, philosophers of biology, and consciousness researchers who find the connection between the four inheritance systems and nested closure either illuminating or contestable.