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THEMATIC ISSUE ARTICLE: LADISLAV KOVÁČ AND THE ORIGINS OF COGNITIVE BIOLOGY

Fundamental Principles of Cognitive Biology 2.0

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Abstract

Cognitive biology, as a scientific program-in-waiting, is the direct (if unacknowledged) offspring of the 20th century revolution in molecular biology, which revealed for the first time the deep, nonmetaphorical parallels between the activities of biological components and processes and the knowledge-generating capabilities characteristic of cognition. The article examines cognitive biology's parentage—Brian C. Goodwin and Ladislav Kováč—and the context which gave birth to it, twice. Special reference is made to Kováč, without whose work, which is honored in this special issue, cognitive biology as such could have perished. Putting to one side Kováč's own continuing work in the area, cognitive biology developed in the 21st century both in ways he and Goodwin (who died in 2009) would recognize and in ways they would not. One of the paths taken within their lineage is my own, which has travelled under different labels (the biogenic approach to cognition, basal cognition) and developed, also independently, from unorthodox beginnings. It is important to emphasize that cognitive biology is not simply the "biologizing" of the study of cognition. In a very real sense, cognitive biology is not about cognition—as a biological function of whole organisms—at all. It is a recognition that biological processes, what normally passes for mere physiology and development, have properties traditionally associated with cognitive capacities in animals, properties that are inadequately captured by a generic (usually poorly specified) notion of "information processing." Cognitive biology is related to the search for the biological basis of cognition, and does much to illuminate that search, but was never motivated by that search. It was motivated entirely by the search for a more general biological theory. Inspired by Kováč's seminal "Fundamental Principles of Cognitive Biology," a considerably expanded set of principles is gathered here for the first time from multiple sources. Together they show how cognitive biology reunites the sciences of life and cognition on a foundation that is gratifyingly substantial, and which may point the way to a future science.

Keywords Basal cognition · Biogenic approach to cognition · Cognitive biology · Cognitive science · Evolution of cognition

Prologue

In the closing three decades of the 20th century, *cognitive biology* was proposed as a new theoretical framework for the conduct of the life sciences based on mounting evidence that biological processes rely on embodied as well as acquired knowledge about the world to function, and that this has profound implications for how these processes are to be explained and understood. Knowledge in this context is not a metaphor, or an anthropomorphism; it is a description (according to this view) of how things work in living systems in the only terms that make sense. Biological processes that rely on information to function not only reflect but also embody regularities of the world in which the organisms they constitute have evolved to make a living. Regularities must be "known" in some fashion before they can be embodied in the genome or developmental processes. How this happens is very poorly understood. The origin and early evolution of developmental plasticity, currently the only serious candidate for explaining how such processes continue to adapt and change to meet changing circumstances, are also very poorly understood.

What all these processes seem to have in common—at multiple scales, from molecules to whole organisms—is

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that they somehow *acquire, evaluate and use information about the environment and the current internal state to select actions furthering existential goals*. "Evaluate" means the capacity to determine whether a state of affairs or a behavior is advantageous—in the first instance, whether it is useful or correct in terms of past history—or is harmful or incorrect (Lyon and Kuchling 2021, p. 123). All known organisms, even the simplest, as well as their constituent processes, demonstrate the capacity to select among alternatives (genomic, developmental, behavioral) to ensure existential goals are met when the default choice is unavailable or thwarted (Lyon 2006a, 2015a; Levin 2023). For William James (1890) this "pursuance of future ends," whatever they might be, "and the choice of means for their attainment" constitutes "*the mark and criterion of the presence of mentality* in a phenomenon" (p. 8; author's italics). All organisms and most (all?) processes that constitute them display what looks very like cognition so defined. This is what living by information entails, however unpalatable that has been to many in the life sciences for the past 400 years, centuries before "information" entered scientific discourse, and may still be. Cognitive biology recognizes this fact. It is not alone in doing so. However, it is the only proposal to explicitly include that recognition in the label by which its practitioners elect to be known.

It is important not to conflate cognitive biology with research into the biological basis of cognition, which generally runs on a different track and typically is motivated differently. As we will see, in a very real sense cognitive biology is not about cognition—as a biological function of whole organisms—at all. It is a recognition that biological processes, what normally passes for ordinary physiology and development, have properties traditionally associated with cognitive capacities in animals, properties which are inadequately captured by a generic (usually poorly specified) notion of "information processing." How such processes came to have these properties surely will occupy scientists, computational modelers, and philosophers for decades to come. Cognitive biology is related to the search for the biological basis of cognition, and does much to illuminate that search,[1] but was never motivated by that search. It was motivated by the search for a more general theory of molecular biological processes.

Cognitive biology is a multidisciplinary endeavor with two parents, who independently gave birth to it. The first is Brian Goodwin (1976, 1978, 2009), visionary Canadian mathematician-biologist and co-founder of complexity science. The second is Ladislav Kováč (1982, 2000, 1986, 1995), biochemist, "biopedagogue," peripatetic thinker, survivor of four decades of communist rule, and the first Minister for Education of post-communist Slovakia, whose work this special issue honors. A promising young experimental physiologist and early convert to the emerging mathematical biology, Goodwin (1978) developed his "cognitive view of biological processes" in an intellectual environment at the cutting edge of molecular and theoretical biology, thanks to his close association with British developmental biologist Conrad H. Waddington, who helped lay the foundations for systems biology, epigenetics, and evolutionary developmental biology. Goodwin had everything going for him, at a time when resonant ideas were developing in diverse quarters (Pattee 1969; Maturana 1970; Popper 1972; Waddington 1972; Campbell 1974). Yet Goodwin's cognitive biology, as proposed, failed. Few cited the work. Even those developing similar ideas (e.g., Howard Pattee) did not adopt Goodwin's radically cognitive stance or terminology. Kováč would reinvent the idea some years later in a very different milieu, in a time of rapid political change, with vanishingly few resources and little support, in the latter stages of a career spent under authoritarian rule. Yet Kováč's cognitive biology arguably is making headway, and that success has revived interest in Goodwin's remarkable foundational work.

The past dozen or so years have seen several excursions into "cognitive biology" from different quarters, notably animal behavior and neurobiology (Tommasi et al. 2009; Fitch 2013, 2014), but also information science (Auletta 2011). None were influenced by Goodwin or Kovač, or their insights concerning the cognitive nature of basic biological processes. All are concerned with the biological basis of cognition and hug close to well-known terrain occupied by nervous systems, which runs counter to both incarnations of the original idea. Two contemporary approaches grew directly out of contact with Kovač's work, however. The first is research by neuroscientist Isabella Sarto-Jackson, who encountered Kovač's research through mutual connections at the Konrad Lorenz Institute for Evolution and Cognition Research (KLI) (Altenberg, Austria), where Kovač produced his "Fundamental Principles of Cognitive Biology" (Kováč 2000). The second approach is my own, which has substantial historical antecedents in the late 19th and early 20th centuries.

This second approach, which began with a highly unorthodox PhD project (Lyon 2006a) with an entirely different motivation, has travelled under different names: the biogenic approach to cognition (Lyon 2004, 2006b, 2015a, 2017) and basal cognition (Manicka and Levin 2019; Lyon 2020; Lyon et al. 2021a; Levin et al. 2021; Lyon 2021; Lyon and Kuchling 2021; Lyon and Cheng 2023), the latter of which has benefited greatly from the mind-bending work

[1] The study of the biological basis of natural cognition, on the other hand, does not straightforwardly illuminate the cognitive nature of biological processes, the target of cognitive biology. The relation is asymmetrical.

of developmental computational biologist and natural philosopher Michael Levin, whose output is too prolific to cite (but see in particular Levin 2022, 2023). The stated aim of basal cognition is to connect such evolutionary dots as may exist, and identify important discontinuities, between the cognitive capacities found in animals with nervous systems and those found not only in unicellular organisms, plants, fungi, and sponges but also processes that constitute organisms (Levin et al. 2021; Lyon et al. 2021b). The belief is that only with such an approach will it be possible to understand the origin and evolution of natural cognition on this planet, including, importantly, human cognition. While arrived at independently and from a different starting point, the principles of cognitive biology set out by Kováč and which can be inferred from Goodwin's work have in a very real sense made the project of connecting the dots in the evolution of cognition much more biologically comprehensible.

The article aims to show how cognitive biology provides a framework that directly reunites the sciences of life and cognition by reconceptualizing living systems as constituted by processes intrinsically dependent on knowledge about aspects of the world in which these organisms make a living. Such knowledge, which makes use of information about the external and internal milieux, is embodied in modes of physiological interaction and reaction that involves sensing, recognizing, remembering, evaluating, selecting actions among alternative possibilities, and learning—phenomena normally regarded as cognitive (Lyon et al. 2021a).

The article consists of four sections. The first part briefly outlines the Zeitgeist at the time cognitive biology was first proposed, which was shaped by information theory arising from communication, electrical, and computing engineering during and immediately following World War II. The second part describes key elements of Goodwin's cognitive biology, which failed to thrive despite his growing scientific profile. The third describes Kováč's independent development of cognitive biology less than a decade after Goodwin, in the wake of the fall of the Soviet Union. Kováč's "fundamental principles" are combined with principles extrapolated from Goodwin's work. The foundation for a science begins to take shape. The fourth part describes how cognitive biology developed in this century, specifically in my work. This provides another set of principles relevant to cognitive biology.

In the Beginning was Information

Although unacknowledged, cognitive biology is demonstrably the child of molecular biology, the multidisciplinary enterprise that began in the 1920s and 1930s with research into the mechanisms of genetic inheritance and became firmly established in leading universities and other research institutions in the 1950s and 1960s. Cognitive biology depended entirely upon empirical discoveries made possible by molecular biology—in cellular physiology and multicellular development as well as genetic expression—which effectively were invisible before. Molecular biology profoundly altered the life sciences and attracted several eminent physicists (e.g., Max Delbrück, Erwin Schrödinger, Walter Elsasser, David Bohm), who offered not only increasingly sophisticated techniques for investigation, such as x-ray crystallography, but also a firm belief in the role of theory for the proper conduct of a science. To some of these physicists, the life sciences seemed overly preoccupied with accumulating phenomenological facts, an endless enterprise, rather than drawing general principles from these facts (Pattee 1969), such that novel findings (at best) could be predicted and (at least) better understood.

Cognitive biology arose from the concern to develop a robust, coherent theoretical biology, a goal still awaiting realization. An emerging trend in molecular biology promised a hook to a new body of theory: the growing realization that many (all?) of the processes that sustain and replicate life are fundamentally dependent on *information* (Baetu et al. 2024). Definition of that elusive something in the context of biological organization proved somewhat tortuous, however, and arguably remains incomplete. The historical context in which information arose to become the ubiquitous biological concept it became is therefore necessary to understand how cognitive biology came to be at all. This is not a simple or a straightforward story. In some respects, it defies logic. A more detailed treatment is necessary. For now, however unsatisfactory it may be, the following brief summary must suffice.

As is well known, the concept of information and the theory supporting it entered the life sciences during and after World War II from an alien context: the communication of signals via electromagnetic means—telephonic, televisual, radio, radar, etc.—and, given the emerging field of computer science, their digital instantiation. A powerful mathematical theory of information, which quickly rose to prominence, was advanced in the immediate postwar period by Claude E. Shannon (Shannon and Weaver 1949), a mathematician at Bell Telephone Laboratories. Shannon defined information in terms of uncertainty. Effective information transmission reduced uncertainty in the receiver, yet a message containing a high degree of unpredictable content (e.g., a series of random numbers) was said to carry a large amount of information (Cornelius 2002). As Warren Weaver, Shannon's co-author, stressed: "The word *information*, in this theory, is used in a special sense that must not be confused with its ordinary usage" (Shannon and Weaver 1949, p. 99). Computer scientist, mathematician, and philosopher Norbert

Wiener (1948) advanced his own measure of information in the context of cybernetic control and communication in machines and animals, but failed to provide a functional account or definition of what is being measured (Corning 2001). Shannon's "technical definition" became the default.

Communication involves three problems: the technical problem (efficient transmission); the semantic problem (meaning); and "the effectiveness problem," relating to a change in behavior of the receiver. Shannon information theory[2] addressed only the technical problem. In ordinary usage, meaning is critical to understanding information, but Shannon emphatically denied meaning is necessary to his concept. Communication engineers "are not at all interested in semantics or the meaning implications of information," Shannon declared. "Information for the communication engineer is something he transmits from one point to another…and it may not have any meaning at all" (Shannon 1951, p. 123). An alternative, biologically plausible mathematical theory of information existed in which meaning played a central role; it was proposed and developed by Scottish mathematician and physicist Donald MacKay (1951, 1969, 1983), who worked on radar systems for the British Admiralty at the end of WWII. Although MacKay was recognized as a leading light in the field, and his information theory much published and discussed, Shannon's overshadowed all. This had unfortunate consequences for the use of the concept of information in biology generally and developmental biology particularly.

The irrelevance to biology of Shannon information as a theoretical construct has been noted repeatedly over the decades by researchers in different disciplines (Lorenz 1969; Oyama 1985; Sarkar 1996; Mahner and Bunge 1997; Cornelius 2002; Capurro and Hjørland 2003; Kauffman et al. 2008). Although Shannon's mathematics became a valuable tool in some areas of the life sciences, his concept of information had a very uneven reception. Even those who seemed to embrace Shannon's concept were forced to develop their own definitions for use in the biological context of their work (e.g., Crick 1958). Waddington (1957) was among the first to note the importance of information to biology but also the first to declare Shannon's technical theory "not merely useless" in that context but also "a dangerous snare" (Waddington 1968, p. 4) because it could not connect with a key biological phenomenon: development of an embryo to adult form. The role of information in biological processes thus became a central issue in "Towards a Theoretical Biology," a series of conferences organized by Waddington at Bellagio on Lake Como, Italy, in 1965–68.

Waddington was already concerned with the epistemological implications of developmental processes (Hall and Laubichler 2009), which unfold sequentially in multicellular contexts (where every cell contains the same genetic material) and often self-correct in the face of perturbation. Among the participants at Bellagio was a young US physicist, Howard H. Pattee, who made a substantial impression on Waddington. Pattee's two contributions to the conferences built on a language metaphor he first advanced in *How Does a Molecule Become a Message?* (Pattee 1969). According to Pattee, biological processes constrained by other processes that appear to be governed by rules seem to reflect human language learning and use. In his final address at the last Bellagio conference, Waddington advanced the "language metaphor" as a theoretical ordering principle for biology (Waddington 1972). Cognitive biology developed from the language metaphor.

Cognitive Biology: Brian C. Goodwin

The theoretical and experimental contributions of Canadian physiologist and mathematician Brian Goodwin to biological theory and experiment, as well as to the sciences of complexity which he co-founded, are substantial and of continuing utility and relevance (Lambert et al. 2013). If cognitive biology has a father, Goodwin's name is on the birth certificate. He gave it life, named it, and developed its implications in extensive physiological and molecular detail in *Analytical Physiology in Cells and Developing Organisms* (Goodwin 1976). *Analytical Physiology*, and the cognitive biology introduced in its final chapter, are the direct products of two influences: Waddington and Bellagio. Goodwin attended all four conferences. Waddington, who died the year before the book was published, was Goodwin's PhD supervisor at Edinburgh University, mentor, and advocate. *Analytical Physiology* is dedicated to him. As Goodwin says admiringly in his preface, Waddington was "always reaching beyond accepted ideas and involved a constant flirtation with the heretical," a balance between knowledge and vision that made "this play with heterodox fire" possible only because it "was firmly based upon a deep familiarity with the detailed behavior of organisms" (Goodwin 1976, p. vii).

At the time of the first Bellagio conference in 1968, Goodwin already had a growing reputation as a brilliant young experimental physiologist and mathematician, known for his discovery of a basic mechanism contributing to the temporal dimension of cellular physiology (Goodwin 1963). Goodwin showed mathematically how the dynamics of enzymatic regulation, using feedback inhibition, can generate biochemical oscillations, which in turn can be coupled

[2] Weaver was keenly interested in and wrote on the semantic and effectiveness problems. Hence, I call it Shannon information theory although Shannon-Weaver is the typical default.

to do more work. Coupling generated "simple" global structures of activity based on increasingly complex physiology at the molecular level. Biological clocks (circadian, ultradian), which enable biological processes to be temporally partitioned and are now known to be ubiquitous, are a prime example. Goodwin's work on oscillators became "a core model for a large class of biological systems" (Gonze and Ruoff 2021, p. 857).

Goodwin shared his mentor's concerns with the epistemological and meaning-associated implications of developmental processes and his support for Pattee's contributions. Goodwin later saw additional support for the language metaphor in Chomsky's theories about language competence (Chomsky 1957), which relied on cognitive capacities for generating syntax, presumed to be largely innate and which emerge during early development. Molecular physiology is full of rules and constraints that direct (and correct) biological activity and order sequences of interaction, which manifest in the (mostly) reliable unfolding of development. As Goodwin observes: "All 'statements' in developmental language, are commands or algorithms" to do something specific in a particular context (Goodwin 1976, p. 223). The operation of commands and algorithms relies on knowledge. Knowledge (as understood then and now) is impossible without an interpreter of meaning, a notion intrinsic to the concept of cognition. Cognitive biology was born.

From Language to Knowledge, and Knowledge to Cognition[3]

The central tenet of cognitive biology is that not only organisms but also the biological processes constituting them are dependent upon knowledge of the world in which they operate. Goodwin describes knowledge in terms of "the development of internal models or representations of aspects" of that world (Goodwin 2009, p. 122). The purpose of this modeling and/or representational activity is "to reach more stable states of relationship" with elements of the world with which the organism is compelled to interact and can be predictable and unpredictable (2009, p. 122). Knowledge thus is defined as "a useful description of some aspect of the world, giving the possessor the competence to behave in a manner which contributes to survival and reproduction," which are internally generated goals (Goodwin 1978, p. 120). "The fact that we are dealing with a description means that there is some code or set of codes which relate to that which is described" (Goodwin 1976, p. 191); there is a shorthand enabling action of some sort.

Knowledge thus is not information. To Goodwin knowledge differs from information because it involves two capacities: the capacity to select among alternative possibilities and the capacity to act, based on that selection, to fulfil a task or goal. Knowledge-using biological processes thus have meaning, purpose, or direction, due to "the property of appropriateness relative to an internally defined goal" (Goodwin 1978, p. 123). Knowledge acquisition, use, consolidation, and modification is the signature of cognition; it is part of the concept's definition in ordinary meaning in the English language as well as in its scientific deployments, sometimes explicitly, sometimes implicitly. Goodwin (1976) defines "a cognitive system" as "one which operates on the basis of knowledge of itself and its environment" (p. 191).

An example of a cognitive system is the *lac* operon, by which the bacterium *Escherichia coli* metabolizes lactose in the absence of more easily utilized sugars (e.g., glucose) through internal changes in cellular form and function. The *lac* operon consists of three genes. One (*lacZ*) produces an enzyme that cleaves lactose into glucose and galactose, sugars better suited to biosynthetic tasks. The second gene (*lacY*) expresses a membrane protein that facilitates lactose transport into the cell. The third (*lacA*) is an enzyme that transfers an acetyl group from an enzymatic source to lactose, for reasons still poorly understood but presumably to ensure galactoside is safely metabolized. Lactose is a backup nutrient. Its utilization is much more energetically costly than glucose metabolism, so when the preferred sugar is available, the lac operon is blocked. When glucose is depleted and lactose is available, the block is lifted and the operon is transcribed. Production is ratcheted up of the membrane protein that admits lactose into the cell and the cleaving and chemical-transporting enzymes enabling its metabolism. When glucose is once more available, the *lac* operon is blocked again. The process is more complex and much leakier than this sounds, but that is the general picture in brief.

> The various encodings, transmissions, decodings and interaction rules which make up the entire functional *lac* operation in *E. coli* constitute a useful description of an aspect of the world, which in this case is the fact that lactose is a molecule which can be converted into simpler molecules with a concomitant release of energy. This knowledge is implicit in the causal relationships between the elements which make up the lactose control circuit…and it becomes manifest when lactose is present and dominant sugars such as glucose are absent from the environment. (Goodwin 1976, p. 192)

[3] This section is based on three sources: Goodwin 1976; Goodwin 1978; and Goodwin 2009; originally published in 1982. Only direct quotations are referenced.

Goodwin's definition of a cognitive system not only applies to physiological systems as well as to whole organisms, it often applies *more* to physiological systems than it does to whole organisms, whose overt behavior may not be as sophisticated as the biological processes implementing it. "[A] prominent feature of organisms," Goodwin observes, is that complex collective dynamics among molecular "units" often give rise to "simple, ordered behavior" (Goodwin 1976, p. 203). An operon, for example, is a cluster of genes under the control of a single promotor, a protein that activates or inhibits transcription, which allows the cluster to function as a single unit of DNA. Behavioral capacities at the organism level thus may be simpler and appear to be less intelligent—certainly less complicated—than the underlying dynamics.

Crucially for Goodwin, knowledge is expressed in biological processes "in the form of rules or constraints" which give rise to biological form and pattern by generating "behavior useful to the organism or the species for survival, reproduction and evolution" (Goodwin 1978, p. 117). These rules "are biological, not physical," although they do not violate physical and chemical laws (1978, pp. 117–118). But they also are not laws of nature because they are contingent: the rules "have been arrived at by the evolutionary process as a solution to a problem of reliably and repeatedly generating particular types of form" (Goodwin 1978, p. 119). The contingent manner of their evolution and development means that biological rules are "to some extent arbitrary" (Goodwin 1976, p. 192). Realization of a function, the accomplishment of a goal, may take different physiological paths in different organisms (sometimes even within a single organism).

> Thus a yeast cell is also able to catabolize lactose and has a control circuit whose net behavior is similar to that which operates in *E. coli*. However, the details of the encoding, transmission, decodings, interaction and assembly rules are different. (Goodwin 1976, p. 192)

The element of arbitrariness in historically contingent solutions to existential challenge supports Goodwin's cognitive view of biological processes in two ways.[4] First, it provides an empirical proof of concept in physiological terms of "a basic characteristic of knowledge, that there are many different ways in which it can be expressed" (Goodwin 1976, p. 192). Second, these solutions—usually involving sequences of coordinated steps in activity—suggest a kind of learning, in organisms and in evolution. "[T]he system has to 'learn' by trial and error which assembly rules or interactions of proteins with membranes and cytoplasmic elements give the desired result" (Goodwin 1976, p. 191). Operons, regulons, biological clocks, stress responses, and countless other biological packages of coordinated processes, large and small—including overt behavior—all arose through trial-and-error problem solving, according to Goodwin, because genetic mutation is insufficient to explain the existence of coordinated developmental processes. Knowledge in biological processes thus is inextricably linked to finding better ways to do things, to maintain organizational robustness and stability in an energetically economical fashion, as well as finding solutions to challenges arising in the search for matter and energy, reproduction, and threats to survival. This kind of problem solving—meeting and overcoming obstacles to the fulfilment of existential goals—never stops, because perturbation and challenge, as well as the presentation of new opportunities, are predictably unpredictable.

Cognitive Biology: Failure to Thrive

Following publication of *Analytical Physiology*, Goodwin pursued his cognitive view of biological processes in two publications outside the biological domain. The first was a paper in a Belgian university-published volume of the International Workshop on the Cognitive Viewpoint, published as "Cognitive Biology" (Goodwin 1977) in the now-defunct, interdisciplinary journal *Communication & Cognition.* The second, Goodwin's best-known statement of cognitive biology, is "The Cognitive View of Biological Processes" (Goodwin 1978), published in the *Journal of Social and Biological Structures.*

These efforts attracted an influential advocate, Margaret Boden, a pioneer in the philosophical wing of cognitive science and artificial intelligence at the University of Sussex, where Goodwin also worked (from 1965 to 1983) and cognitive biology was gestating. Based primarily on Goodwin's 1978 article, Boden put the positive case for a cognitive biology (Boden and Khin Zaw 1980), thereby providing an entree into mainstream philosophy of science and cognitive science. She cited several advantages of applying cognitive concepts to biology, chief among them the capacity to focus enquiry on "proper experimental questions":

> …not "what is the molecular biology of this substance, and how does it combine with other molecules?" but, rather, "what function is this substance performing for the organism: what information is it passing…what instruction is it embodying?" (Boden and Khin Zaw 1980, pp. 42–43)

[4] On the other hand, the contingency of biological rules presents an obstacle to another kind of knowledge: "discovering general laws of biological organization, which must transcend all particular realizations" (Goodwin 1976, p. 193). Power laws are an exception.

Boden's sympathy for cognitive biology was strictly limited to its instrumental utility in theoretical practice, however. Cognitive terminology deployed in biological description and explanation should under no circumstances be mistaken for cognition, she warns; the referent is not an underlying reality reflecting the ordinary use of the noun or its adjectival form. Conceptualization for theoretical purposes must not be mistaken for how things are.[5]

Goodwin's last hurrah in the field he created appears to be a paper in a French journal situating cognitive biology in the context of Piaget's genetic epistemology and constructionist biology, published in 1982 and rescued from obscurity via reprint in this journal (Goodwin 2009). Here Goodwin expresses his feeling that the case for cognitive biology had been "considerably strengthened" in the preceding eight years (Goodwin 2009, p. 123), the period during which he developed the framework. There followed silence. Neither Goodwin's nor Boden's work in cognitive biology were particularly influential.

How to explain cognitive biology's failure to thrive, especially given Goodwin's growing reputation in developmental biology, his deep understanding of molecular physiology, and his creativity in mathematical modelling? Goodwin (2009) himself saw this work as caught between two "seductive polarities which have brought shipwreck to so much biological thought" (Goodwin 2009, p. 115). These he called "the Scylla of neo-Darwinism and molecular biology (simplistic reductionism)"— which in another context he paired with the Cartesian view of living systems as machine-like (Goodwin 1978) —"and the Charybdis of idealist holism (vitalism)" (Goodwin 2009, p. 115). The consequences for the work of Goodwin and others of the clash of these "seductive polarities," which affected even the career of an eminence such as Waddington, is beyond the scope of this article but deserves a detailed treatment elsewhere.

Nevertheless, cognitive biology's rescue arrived at the turn of the century, in the work of a relatively obscure biochemist from a country out of the mainstream of scientific endeavor who independently arrived at conclusions similar, but not identical, to Goodwin's through his own careful molecular research in yeast.

Cognitive Biology, Slovakian Style: Ladislav Kováč

If Goodwin was the father of cognitive biology, then Ladislav Kováč is its mother: giver of life, gentle nurturer, and unfailing support. Fully immersed in the informatic paradigm developing as the theoretical backbone of the molecular biological revolution, Kováč independently developed his own account of cognitive biology based on the knowledge-using and knowledge-acquiring nature of biological processes he encountered in his own molecular research into the bioenergetics of yeast (Kováč 1982, 1986). From his initial intuitions he developed a form of science education, biopedagogy (Kováč 1995), a set of philosophical principles of cognitive biology (Kováč 2000), and continued to explore the implications of this work in numerous publications in the context of contemporary issues—scientific, philosophical, and social—until, finally, he arrived at a worldview, an "ultimate optimism" (Kováč 2023) based on the creativity inherent in the cognitive view of biology.

Kováč's theoretical contribution to cognitive biology arguably cannot be understood apart from the dominant political facts of his history: World War II and four decades of communist rule. He was born into a country (Czechoslovakia), formerly a part of the Austro-Hungarian Empire, that had been an independent country not even for two decades before ceasing to exist, reemerging (with bits missing) after World War II, falling under the orbit of the Soviet Union, and finally splitting in two (the Czech Republic and Slovakia) in 1992 after the fall of the Soviet Union. This is a man for whom abstract notions such as nationhood and political regimes were not dependable realities, despite liberal humanitarian sympathies which would cost him dearly, in terms of academic employment, following the Prague Spring of 1968. This period of protest, cultural efflorescence, and political and social democratization was suppressed violently by the Soviet-led Warsaw Pact of which Czechoslovakia was a member. The intellectual legacy of European culture and developments in science, philosophy, logic, and pedagogy such as came his way in materially impoverished, extremely limiting circumstances, and to which Kováč was able to contribute remarkably, remained his guiding lights even as they delivered his great disappointment. As a measure of the high regard in which he was later held as a scientist and thinker, Kováč served as Minister for Education for the Slovak Republic within the federation (1989–1990) and as the last Czechoslovakian ambassador to UNESCO (1990–1992).

Precisely how and when Kováč came to think in terms of cognitive biology under that label is unclear, even to him. He compares tracing the genealogy of cognitive biology to similar exercises for molecular biology: impossible to capture the phenomenon and invariably leaving people out.[6] Whereas Goodwin was at the very heart of research in the emerging molecular biology, Kováč was not so fortunate. As a freshly minted biochemist in Czechoslovakia, recruited *upon graduation* to establish a new program in molecular

[5] Boden's position is superficially similar to Daniel Dennett's "intentional stance."

[6] Personal communication, 29 March 2024.

biology in his native Slovakia, his main interest was understanding the energetics of the cell, centered on mitochondria. Baker's yeast (*Saccharomyces cerevisiae*), cheap and plentiful, became his model organism. This program of basic research, carried out in a group trained in Kovač's intellectually peripatetic, big-picture approach, proceeded extraordinarily well. The first summit-topping result of this effort was a publication in *Science* (Kováč et al. 1967), on "the usefulness of mutants in the unraveling of complex, highly organized, membrane-bound processes such as oxidative phosphorylation" (p. 1564). Oxidative phosphorylation is a fundamental cellular process that leads to the creation of high-energy phosphate bonds in the form of adenosine triphosphate (ATP), a universal energetic currency. Kovač's group had found a single recessive gene mutation that abolished the efficiency of oxidative phosphorylation, both in vitro and in vivo, without impairing electron transfer, a highly unexpected finding. This work led to a collaboration with researchers at Cornell University, another fundamental discovery, and another major publication, in *Proceedings of the National Academy of Sciences USA* (Groot et al. 1971): the demonstration that mitochondrial energy transfer can occur in the absence of an oxygen-based respiratory chain. Then came the widespread suppression of the Prague Spring, and Kováč's exile to a remote posting at a psychiatric hospital, where he tested drugs on the behavior of the fruit fly *Drosophila melanogaster* (Kováč et al. 1978).

Six years after his exile, a Central Party decision to (re)develop a national competence in molecular biology brought "rehabilitation"; he had the knowledge and skills they needed. Kováč's re-embrace of his first love—bioenergetics—at an institute for farm animal research led to more ground-breaking work, much of it published in a series of papers on bioenergetics in *Biochimica et Biophysica*, the first journal established in biochemistry and biophysics in 1947. Kováč's series of articles began after the *Science* paper and continued into the early 1980s.

At each stage of his molecular research it would have been possible for Kováč to make his own observations about the informatic, knowledge-using, cognitive nature of living systems. What cannot be stressed enough, in my view, is the difficulty of the conditions under which he labored and his ideas took shape, which included not only strenuous challenges in acquiring the material resources to do the work, under more or less constant surveillance, but also in accessing the latest science, most of it published in English, in an environment actively hostile to the language and the ideologies that its expression purportedly represented.

Kováč does not cite Goodwin's work, which he credits (glancingly and nonspecifically) for providing "some pioneering ideas" until his own "Fundamental Principles of Cognitive Biology" (Kováč 2000, p. 3). The citation is of Goodwin's 1976 book, which came to Kováč in Russian translation years after its publication in English.[7] Boden is not cited in the agenda-setting paper. In my view, this suggests Kováč was unaware of Boden's work and came very late to Goodwin's, well after his own ideas about cognitive biology were starting to be expressed (Kováč 1982) and possibly after he was already using the phrase in pedagogical contexts (Kováč 1986, 1995). Given his geographical location within the Soviet sphere and his marginal employment post-Prague Spring, this would not be surprising.

The only influence Kováč cites as key in the development of his thought is the gifted Swiss biochemist Hans Kuhn. In particular, Kováč cites two articles by Kuhn: the first on self-organizing molecular systems and the evolution of the genetic apparatus (Kuhn 1972), and a more wide-ranging theoretical piece some years later on the origin of life and its effect on physics through the development of complexity (Kuhn 1988). Here Kuhn muses on how biological structures came to carry information and accumulate knowledge and thereby modified biological structures by becoming more complex, which in turn altered the interplay of physical-chemical forces within them. By that time, however, Kováč had already published a (non-English language) introduction to cognitive biology (Kováč 1986). When his manifesto was published in 2000, Kováč had been working in the area he called cognitive biology for 14 years and was director of the first Center for Cognitive Biology in the Faculty of Sciences at Comenius University in Bratislava, where he also continued to head the research group into bioenergetics.

Principles of Cognitive Biology

Of cognitive biology's two progenitors, only Kováč (2000) was explicit about the fundamental principles he considered necessary to its proper practice. Goodwin was not explicit in this way. Such principles as he articulated had to be excavated from the last chapter of *Analytical Physiology of Cells and Developing Organisms* and "A Cognitive View of Biological Processes." Because the overlap between the two sets of principles is nontrivial, their content has been synthesized in Table 1. The wording of headings and text, as well as the order in which they appear, are mine. Therefore, the errors are also mine. Both Goodwin and Kováč included observations not directly germane (in my view) to the practice of cognitive biology but useful to know. For Goodwin, knowledge use is the signature of the animate. For Kováč, the proper conduct of cognitive biology requires a "principle of minimal prejudice," an axiom for keeping an open mind. The human tendency to maximal prejudice (disbelief, outrage, retaliation) when faced with the unexpected,

[7] Personal communication, 29 March 2024.

Table 1 Combined principles of cognitive biology: Goodwin (1976, 1978) and Kováč (2000)*.

1. **The principle of goal-directed agency**. The activity of organisms, and the organized processes that comprise them, is directed toward fulfilment of internally generated goals (e.g., persistence, growth, reproduction).
a) Goals arise from the **needs of the system to maintain its organization and behavior**. **Interaction with the environment** is required to do that.
b) Internal goal specification (at all levels of biological organization) **determines the appropriateness** of the activity undertaken to accomplish a task or goal.
c) Goal-directed activity requires **means of detecting errors** in accomplishing goals, at all levels of biological process.
2. The knowledge principle. Organisms and the organized processes that comprise them embody (represent) existentially useful aspects of the world in which they evolved to make a living. They are knowledge-using systems. This makes them cognitive.
a) The embodiment and acquisition of knowledge enables development of **a more stable relationship** between the system and the milieu in which it makes a living.
b) **Knowledge enables capacity**, the behavioral competence to fulfil goals.
c) **Information ≠ knowledge.** Information contained in an object, signal, behavior, or event **requires interpretation** by a structure or process evolved to do so. (Goodwin 1976)
d) Living systems acquire information through **sensory modalities** and respond to that information. Sensed features are **valued positively**, **negatively**, **or not at all** relative to the organism's organization, which is a product of its history, within the lifespan and through evolution. Knowledge acquired through an organism's cognitive capacities thus is **inherently incomplete.** (Kováč 2000)
3. The learning principle. Organisms, and the processes comprising them, develop rules (procedures) that govern activity for accomplishing goals. These rules are acquired through a process usually conceived in terms of trial-and-error learning.
a) The **rules governing biological activity** do not violate physical and chemical laws but are different from them because they are acquired and have evolved within lineages.
b) Because they are acquired and evolved, these rules are **contingent and to some extent arbitrary**. The physiological pathway to instantiating the same function or achieving the same goal may be quite different in different organisms, for example. (Goodwin 1976)
b) Development and evolution of such rules require developmental plasticity (degrees of freedom) as well as the capacity to transfer knowledge from one generation to the next by means not solely restricted to the contents of the genome and their random alteration. The generation of rules that govern biological processes rely substantially on **epigenetic mechanisms.** (Goodwin 1976)
c) Learning processes instantiated at the levels of whole organisms and of their constituent processes **may be similar but also may be very different**. (Goodwin 1976)
d) Any new development **necessarily builds upon previous developments**, a tendency toward rearrangement or recombination of existing elements to meet new needs that Françoise Jacob called bricolage and others evolutionary "tinkering." (Kováč 2000)
4. The principle of increasing complexity. Except in circumstances of symbiotic mutualism or parasitism, organisms and the biological processes that comprise them tend to be knowledge-maximizing. This becomes a source of complexity as new knowledge is embedded (ultimately through evolution) into the genome, development, metabolism and behavior.
a) The generation of greater complexity through knowledge acquisition and via innovation within constraints, in the continual process to escape thermodynamic equilibrium, is **inherently creative.**
b) Traits, properties, and processes are more productively studied in systems of **lesser—even minimal—complexity**, on the basis that constructions that work (over time) are refined, multiplied, and retooled, as well as new constructions developed. (Kováč 2000)
5. The principle of simplicity from complexity. Any organismic activity reflects a **complex underlying space of functions** at the molecular/physiological level. What emerges from the complexity of collective underlying phenomena is relatively **simple**, **ordered behavior.** (Goodwin 1976)
a) Much of the knowledge embedded in biological processes and behaviors represent the shortest distance or number of steps possible to accomplish tasks or meet goals. Much complexity built into living systems consists of such **minimal trajectories.** (Kováč 2000)
6. The principle of minimization of suffering. A substantial amount of biological process and behavior is devoted to minimization of the organism's suffering through specialized, knowledge-saturated responses to perceived threats to continued persistence. (Stress responses, ubiquitous in living systems, are biological evidence of this.) (Kováč 2000)

* Most principles contained in this chart are a synthesis of material found in the work of both Goodwin and Kováč. Principles that contain a reference were contributed by that author alone.

unwanted, or seemingly outrageous (according to some framework) is strong; it requires moderation if we are to properly understand nature.

21st Century Developments in Cognitive Biology

In the first two decades of this century, cognitive biology emerged as a label in several quarters, but not in the sense it was introduced by Goodwin or Kováč, that is, relating to the cognitive nature of molecular processes. Rather, cognitive biology was deployed in relation to the biological basis of cognition, with which it is easily conflated. An edited book—*Cognitive Biology*, *Evolutionary and Developmental Perspectives on Mind*, *Brain and Behavior* (Tommasi et al. 2009)—expanded the pool of neural invertebrates for the study of cognition. Another book bearing the label—*Cognitive Biology*, *Dealing with Information from Bacteria to Minds* (Auletta 2011)—addresses the role of information processing in living systems situated firmly in the still-dominant engineering paradigm of cognitive science and thus focused principally on neural organisms, despite the title. Finally, a Department of Cognitive Biology was established at the University of Vienna in 2009, under the direction of W. Tecumseh Fitch, who made an interesting argument for intentionality—the capacity to "be about" or "directed toward" something—in neurons and other eukaryotic cells as "a necessary building block for cognition and high-order intentionality" (Fitch 2008, p. 157). Rebranded the Department of Behavioral and Cognitive Biology, research focuses principally on neural animals.

Isabella Sarto-Jackson

If Kováč's successor could be ordered from a catalogue, it would certainly be Sarto-Jackson, editor of this special issue honoring his work. A highly respected neurobiologist, Sarto-Jackson's work began in the chemistry of the brain and has ranged from the molecular to the applied. She is the executive manager of the KLI near Vienna, the place where Kováč's principles coalesced over two years' residency, and past president of the Austrian Neuroscience Association. As does Kováč, she has a fondness for pedagogy and chaired the education committee of the International Society for the History, Philosophy and Social Science of Biology (ISHPSSB). Most enduringly important, she shares Kováč's deep concerns for the minimization of suffering. This is evident both in a ground-breaking book—*The Making and Breaking of Minds: How Social Interactions Shape the Human Mind* (Sarto-Jackson 2022)—and her work in recent years to develop and provide opportunities for children at risk so they may reach their full cognitive potential.

Sarto-Jackson contributed two papers to cognitive biology. The first, "How to Bake a Brain: Yeast as a Model Neuron" (Sarto-Jackson and Tomaska 2016), does for the single-celled eukaryote *S. cerevisiae* (Kováč's model organism) what Koshland (1980) attempted to do for bacterial cells 36 years earlier: to bring to the attention of neurobiologists (and others) the advantage of a single-celled model organism for getting a better grip on understanding the properties of the neuron. Sarto-Jackson and Tomaska's argument has the great advantage of nearly three decades of close molecular work with advanced techniques on the yeast model proposed, the extensive detail of which she and her co-author know well. The second paper, "Converging Concepts of Evolutionary Epistemology and Cognitive Biology Within a Framework of the Extended Evolutionary Synthesis"(Sarto-Jackson 2021), provides a highly original theoretical linkage between cognitive biology (the knowledge-based view of biological processes), evolutionary epistemology (based on biological trial-and-error problem solving), and the extended evolutionary synthesis (Laland et al. 2015), a cornerstone of which is the role of developmental plasticity and epigenetic inheritance in generating phenotypes. While Goodwin was explicit about the importance to cognitive biology of developmental plasticity (although he didn't yet have that term), as well as the need for epigenetic modes of inheritance, Kováč does not address these issues.

On Finding No Cognition in Cognitive Science

I came to Kováč's cognitive biology after finishing an unorthodox PhD in 2006 at the Australian National University (Lyon 2006a). Unorthodox, how? First, it was a thesis on the biology of cognition in a Faculty of Asian Studies. Second, it advanced an approach to cognitive phenomena based explicitly on the facts of biology (Lyon 2006b), and presented a logic of how cognition arises from the facts of biology. Third, it applied the framework to an unorthodox model system: bacteria (Lyon 2015b). Finally, it began life in a project in comparative philosophy that required describing the views of cognition in Tibetan Buddhism and modern science. On the Buddhist side was a describable, phenomenologically based view of the processes by which experience is generated, conceived, and known. Buddhist scholars and meditators had been working successfully with this framework, and developing powerful, transformative states of mind and body, for more than 2,500 years. Cognitive science, by contrast, provided nothing nearly so coherent and certainly nothing as pragmatically useful. This statement may well seem to many exaggerated, uncharitable, and probably false. I am talking here solely about my experience upon encountering cognitive science as a PhD student with a particular project to discharge. That project relied critically on providing a defensible consensus concept of mind/cognition in two traditions, Tibetan Buddhism and contemporary science, neither of which is monolithic.

Regardless of the Buddhist tradition, broad agreement exists about the conventional phenomenal characteristics of mind (clear, knowing awareness), what mind does, and how it works. A vast Buddhist literature exists on how to observe and work with mind. Relying on these written and oral instructions over many years of arduous practice, highly experienced meditators can train their minds to do astonishing things, things science cannot yet explain (e.g., Benson et al. 1982; Lott et al. 2021). I was not prepared for how confused and confusing the material would prove to be on the Western philosophical/scientific side when I began doing my research in September 2000. "The mind is the brain" is an ontological statement, not a functional characterization, and the brain does a whole lot more than being a mind. While the demarcation between putatively mental and putatively physical processes seemed widely assumed to be sharp and "intuitive," I could find no solid arguments for that assumption. "Cognition is information processing" seemed to me almost vacuous; information processing for what? "The mind is a computer" explains nothing about what natural cognition is and how it works, but cognitive science did not appear to be as interested in coming to an understanding of those things as it was in making machines that could think, plan, and play games. I did not have to look far to find confirmation of my deep suspicion that, unlike the Tibetan tradition, the cognitive sciences could provide no account of what cognition is and what it does, although they were chipping away at how it works in the absence of any firm understanding of the first two (Bechtel et al. 1998).

I was a child of science, I believed in science, but the modern side of the equation featured, in addition to a mind-numbing mountain of data, ideological assertions about ontology that moved the explanatory dial not at all, endless debate about fundamental principles, and very few useful definitions. I would later learn this situation had bedeviled James (1892), long before there was an ocean of data, and has persisted more or less to this day (Henriques 2022). Primatologist Frans de Waal's observations about the psychological and social scientific literature he encountered sums up to the letter the situation in which I found myself relative to the study of cognition more generally:

> Looking…as a relative outsider, I see thousands of ideas that are barely interconnected. One could argue that they do not need to interconnect, yet this amounts to an admission that every area within the discipline is free to come up with its own explanations. This approach results in *a serious lack of mooring to the thinking in psychology*, a lack of an overarching scheme within which everything makes sense. (de Waal 2002, p. 187; my italics.)

In the corner of the scientific world de Waal occupied, evolution provided the overarching scheme that canalizes and constrains explanation. Evolutionary thinking was conspicuously absent in cognitive science when I was hitting the wall in 2000, however. (See Lyon and Cheng 2023 for a fuller account.) Biology and animal behavior were mainly instrumentally useful domains from which one might pluck empirical ballast to support personal intuition. There were notable exceptions, but most were marginal. Consensus criteria for identifying "genuine" cognition in the natural world did not exist, if a human or language were not involved. How had cognitive science brought us here? How to get out of this mess? What, in short, was the road to a scientific understanding of cognition that could do work? This became the subject of my PhD. Comparative philosophical analysis was out; there was no comparator. Buddhist views could not help me. It was clear I should steer clear of the label "mind"; "cognition" was safer (Miller 2003).

The Biogenic Approach to Cognition

Despite assurances that I would find nothing satisfying there, in the microbiological literature I found an incredible, ever-surprising world I have yet to leave. The signal transduction literature had it all: sensorimotor coupling, computational complexity, memory, valence, decision making, behavioral complexity through collective activity enabled by communication, nonassociative learning via habituation and sensitization—all uncontroversially considered cognitive in mammals, including humans—and more degrees of freedom than I had been led to expect. What I found in the micro-world convinced me that evolution and biology were the correct path to a stable and robust scientific account of cognition. What I needed next was to ascertain the explanatory principles of biology that might shape and constrain a concept of cognition and identify the extant work in this domain. This involved a lot of reading.

From this excursion I extracted two broad families of approaches to the living state: *self-organizing complex systems* (SOCS) (exemplifed by Bertalanffy 1968; Schrödinger 1944/1967; Elsasser 1975; Rosen 1985a; Kauffman 1993, 2000) and *autopoiesis* (Maturana 1970; Maturana and Varela 1980). Of these scientists, only Maturana and Varela drew an explicit connection between biological organization and cognition, however. Kauffman (2000) skirted close in his meditation on agency but stopped well short. As Goodwin knew well, making the life–cognition connection was perilous business because this was a key indicator of "vitalism," an amorphous label applied to anyone claiming reductionism and mechanism alone were insufficient to explain biological phenomena, development chief among them (Gilbert and Sarkar 2000; Donohue and Wolfe 2023). As had Waddington, an organicist who attempted to thread a "third way" between mechanism and vitalism, Ludwig von Bertalanffy and Walter Elsasser were both tarred with the vitalist brush. General systems theorist Bertalanffy was called out by no less a personage than Nobel laureate Monod (1972) in his immensely popular book, *Chance and Necessity*, while another Nobel Prize winner, Crick (1966), took aim at physicist Elsasser, who strenuously denied the possibility of reducing biology to physics and chemistry (Peterson 2023). Autopoiesis as a concept saved Maturana and Varela's work, but the cognitive implications of their theory of biological organization remain relatively obscure in biology even today.

In the end I identified 18 species of cognitive explanation, which I called "biogenic," 13 influenced by or grounded in the SOCS approach and 5 in autopoeisis.[8] All were marginal. The upshot of the biogenic approach is quite simple, but it cannot be understood except in contrast to its opposite, an artefact of the 17th century and Descartes's legacy: "assume human cognition as the paradigm"—not simply another instantiation of a phenomenon, however complex—"and work 'down' to a more general explanatory concept."

> The biogenic approach, on the other hand, starts with the facts of biology as the basis for theorizing and works "up" to the human case by asking psychological questions as though they were biological questions. (Lyon 2006b, p. 11)

While the biogenic approach is a methodological stance, the approach does contain principles meant to guide investigation, to both assist and constrain explanation. These principles, synthesized from the literature, set (very) hard constraints on speculation about cognition. This convinced me I was on to something. They appeared to provide the kind of "mooring" de Waal was talking about, considerably more solid than simply evolution. They also made sense of what I considered to be a signature characteristic of organisms and cognition: agency, the ability to act to further internally generated goals.[9] Cognitive science typifies the contrast case, the anthropogenic approach. However it developed over time, cognitive science from its beginnings was grounded in the human capacities for language, computing numbers and other high-level mental abilities then assumed to be exclusive to *Homo sapiens*, which is why the first salvos in what would become the embodied cognition movement (Gibson 1979; Maturana and Varela 1980; Winograd and Flores 1986; Beer 1990; Brooks 1991) seemed so radical and took some time to catch on (Lyon and Cheng 2023). For an account of the principles governing the anthropogenic approach to cognition, see Lyon (2006b).

Ladislav Kováč's "fundamental principles" entered my life after graduation and the search for a postdoc to continue the work. I came to Goodwin's work much later and read him closely only for this review article. What a relief it was to read Kováč's manifesto! There was a name for what I was doing: cognitive biology. There were even principles, some of which I had already intuited. Others were thinking these things, seeing what I saw. In my excavation of the microbial literature I repeatedly found in suborganismal molecular phenomena what Kováč and Goodwin identified: molecular interactions that seemed to rely on capacities typically considered cognitive (e.g., sensing, memory, evaluation, learning, anticipation, decision making, error correction). I knew, too, that dangers lay here: a description of work I was doing to a philosophical colleague whose opinion I valued had already elicited the V-word (vitalism). What I didn't know then was that a reductionist agenda had been attempting to "expunge function, purpose, teleology and vitalism from biology" since the 1930s (Lane 2024), and had succeeded to an extent barely creditable today.

I put a proposal to Jon Opie, a philosopher–cognitive scientist at the University of Adelaide. We put together a successful proposal for an international collaboration entitled "Foundations for a Cognitive Biology," set up a website, and hosted a workshop in 2009 with heavyweight participants from Australia, the US, and Europe. The project ultimately failed, but connections were made, seeds planted, and some continued to grow. These came to fruition in June 2018 at a KLI workshop entitled "The Ground Floor of Cognition: From Microbes to Plants and Animals," co-organized with my longtime friend and colleague Fred Keijzer, with indispensable help from Eva Jablonka. This should have been a celebration of cognitive biology. However, I had been discouraged by recent developments in cognitive biology (described above) which were antithetical to our emphasis on empirical and experimental work in aneural organisms (e.g., single-celled organisms, plants, sponges); organisms with very simple nervous systems (e.g., planaria,

[8] Alvaro Moreno's autonomy school at the University of the Basque Country should have been on that list, but I hadn't engaged that work at the time of Lyon (2006a). I was aware of it obliquely but by then was exhausted.

[9] *The Agent in the Organism: Toward a Biogenic Theory of Cognition* was the title of my PhD thesis. Chapter 4, entitled "the agentive framework," presents three syllogisms based on biological premises that produce a working definition of cognition, the initial iteration of a still-developing characterization. Gratifyingly, agency as a biological concept has undergone substantial rehabilitation in the past dozen years. When this was written, it was still philosophically suspect.

Hydra); and research into the origin and early evolution of nervous systems, including choanoflagellates (e.g., Göhde et al. 2021; Ros-Rocher and Brunet 2023). Like "evolutionary psychology," the idea of cognitive biology had come to mean something much narrower than originally intended (de Waal 2002). At the workshop, however, it became clear we needed a label of some kind. I proposed "basal cognition," which I regret.

Why regret? Because it stuck, and because—as I have stated elsewhere (Lyon 2020)—in my opinion it's all cognition, a biological function that operates to the same ends in different organisms: enabling familiarity with and evaluation of features of environments in relation to internal states for the purpose of action to further existential goals. "Basal" is a weasel word to make a nontraditional class of proposed models in the sciences of cognition acceptable through the suggestion of earlier evolution. However, determining actual evolutionary relationship requires ascertainment of homology (a more fraught concept is hard to find) and genomic phylostratigraphic investigation, not only phylum by phylum, but by proteins considered diagnostic. Try identifying the purported evolutionary origin of *Bacillus subtilis.* Not easy. Why? Because proteins encoded by more recently acquired genes, which may play a key role in current phyletic identity, "tend not to be expressed under standard experimental conditions and are probably triggered in specific conditions that led to their inclusion in the genome, i.e., specific stress conditions or environmental challenges" (Ravikumar et al. 2018, p. 6). The modifier "basal" was emphatically never meant to refer to a kind of cognition. If deep evolutionary relationship is not realistic, that removes the warrant for the modifier.

Basal cognition, as I and others have practiced it (particularly Michael Levin), effectively grew from the soil of cognitive biology,[10] that is, research into molecular processes. It *is* cognitive biology, and has moved cognitive biology forward. The principal methodological desideratum—*start simple*, *extract principles*, *scale up and test*—is Kováč's principle of minimal complexity, arrived at by different means. At the time they were extracted, the biogenic principles were assumed (and asserted by me) to relate to cognition in whole organisms, not component processes. No longer. It is now abundantly clear that most of these principles readily apply to component processes. Table 2 presents the combined principles of the biogenic approach and basal cognition, which add to the principles of cognitive biology.

[10] These three articles provide a reasonable overview of the work I have done in basal cognition: Lyon 2021, Lyon et al. 2021a; Lyon and Cheng 2023.

Conclusion

Cognitive biology was proposed in the 1970s at a time when the life sciences were undergoing seismic change. The behavior of molecular biological entities, particularly in the context of development, was unexpected, surprising, and hard to fathom. The concept of information was enlisted to explain these phenomena but the dominant information theory was ultimately unfit to do so. In 1976 Goodwin proposed a cognitive view of biological processes as knowledge-using systems that reflect aspects of the world in which they function and evolve. Those capacities are somehow learned, across generations and through evolutionary time, and thereby become embedded in biological structure, physiology, and behavior. This proposal did not gain significant traction, but it was an idea whose time had nevertheless come. From within the Soviet bloc, a few years after Goodwin published his ideas in a language inaccessible to him, Kováč made similar observations about the molecular phenomena he had long studied in yeast. In 1982, Kováč began advancing (in a language inaccessible to the rest of the world) his own conception of cognitive biology, which powerfully resonated with Goodwin's but was arrived at independently, justified differently, and reflected Kováč's unique philosophical and pedagogical concerns. These ideas entered the mainstream in 2000. In that year, on the other side of the world, a PhD project began in Australia that would independently arrive at an approach for studying cognition grounded in biology at the level of both organisms and molecules. The Australian approach, which began in the search for the biological basis of cognition, is firmly in the tradition of cognitive biology envisioned by both Goodwin and Kováč.

This article aimed to clarify the history of cognitive biology, to gather principles from these three frameworks and thereby demonstrate the robustness of cognitive biology as a plausible partial foundation for an overarching theory of the sciences of life and cognition. It is partial because such a theory requires an account of biological organization, which autopoiesis provides, and a theory of evolution, which the extended evolutionary synthesis and "third way" tradition provides. These have not been discussed. Clearly, a much longer argument is required, of which this review is but the opening gambit.

The longer argument will require two related explorations. The first will focus on how information entered biological discourse in the 1950s—and was much needed—but how the dominant concept was utterly unfit for guiding investigation of basic biological processes. This led to other proposals, such as Goodwin's cognitive biology and Waddington's language metaphor, which both failed to gain adherents who could make productive use of the ideas contained within

Table 2 Combined principles* of the biogenic approach to cognition (Lyon 2006a, b) and basal cognition (Lyon et al. 2021a).

1. **Function**. The function of cognition, as for any other biological function, is to contribute to the existential goals of persistence (survival), growth and reproduction.
2. Cognitive capacities can be described ***functionally*** *(what they do for the organism) and* ***mechanistically*** *(how they are instantiated). A complete explanation requires both.*
3. **Continuity (evolution).** Complex cognitive capacities have evolved from simpler forms of cognition. There is a continuous line of meaningful descent. Continuity does not rule out the emergence of novel capacities with increasing complexity.
4. **Control**. Cognition directly or indirectly modulates the processes that constitute an organism.
5. **Interaction**. Cognition facilitates the establishment of reciprocal causal relations with features of the environment, leading to exchanges of matter and energy that are essential to the organism's persistence, growth, or reproduction.
6. **Normativity**. Cognition relates to the (more or less) continuous assessments of system needs relative to prevailing circumstances, the potential for interaction, and whether the current interaction is working or not. Error correction depends on norms.
7. **Memory.** Cognition requires information be retained for a period of time greater than zero.
8. **Discrimination (selectivity).** Because an organism is capable of interacting profitably with some, but not all, properties of the environment, cognition involves the differentiation of some states of affairs from other states of affairs.
9. **Valence.** Relative to the organism's needs and/or history, different properties of the environment will be invested with different degrees of force or salience, both positive (advantageous) and negative (harmful).
10. **Context sensitivity**. Whether a stimulus is treated as advantageous or harmful depends upon the total state of the organism, the priority of its needs and the nature of stimuli currently impinging on its senses. Valence is often relative.
11. **Learning.** The capacity to adapt behavior to salient stimuli according to past experience by altering the threshold for or the nature of the response. (Experience-modulated behavior change.)
12. **Anticipation.** Cognition is intrinsically future-oriented (what happens next?) and is thus predictive.
13. Cognition is comprised of a ***toolkit of capacities****. These capacities include (so far): orienting response (attention), sensing/perception, discrimination, memory, valence, decision making, interactive behavior, problem solving, error detection, motivation (via existential goals), learning, anticipation, and communication. (See* Table 1 *in* Lyon et al. (2021a).*)*
*14.***Common mechanisms** *known to instantiate cognitive processes in animals with nervous systems and in aneural organisms include: intracellular signal transduction; extracellular cell-cell signaling (by autocrine, paracrine, justacrine, "endocrine" and "neuroendocrine" mechanisms); oscillations (intra- and intercellular); networks and circuits (intra- and intercellular); ion channel-mediated bioelectricity; cell-cell adhesion (intercellular); local, regional, and global regulatory responses (intra- and intercellular; volume chemical transmission; and extracellular vesicles. (See* Table 2 *in* Lyon et al. (2021a).*)*
*15.***Fundamental insights** *into processes that explain cognitive capacities in animals will come from* ***organisms too simple to have nervous systems*** *(single-celled prokaryotes and eukaryotes); multicellular organisms, including animals, which do not possess nervous systems (plants, fungi, sponges, placozoa); and animals with very simple nervous systems (cnidarians and ctenophores). The methodological corollary of this is* ***start simple, extract principles, scale up, and test.***
16. **Randomness reduction.** Cognition is an important mechanism by which biological systems reduce and modulate the influence of random perturbations on their functioning, making them increasingly robust to perturbation.
17. **Stress.** A critical function of cognition is to enable the organism to cope with threats to its continued persistence. Coevolution of cognitive systems and immune/defensive systems is likely.
18. **Interdependence.** The biochemical pathways subserving cognition are intimately linked to those of other biological functions, making delineation difficult and largely a function of explanatory goals. (The map is not the territory.)

* Biogenic principles are in regular font. Basal cognition principles are in italic.

these proposals. An alternative information theory existed, much better suited to biology and foreshadowing many of the phenomena cognitive biology addressed, but it, too, failed to gain significant traction, despite influential advocates. This leads us to the second exploration, the hypothesized cause of that failure: biology's embrace of Newtonian reductionism coupled with the Cartesian machine metaphor, a centuries-old ideology rather than a specific model that views living systems as "machines" comprised of particles acted on by forces described by physics and chemistry, just like rocks, rivers, and watches (Rosen 1985b; Lewontin 2001; Henning and Scarfe 2013).[11] Reductionism, against which Waddington labored his entire career and Goodwin (perhaps unwisely) deliberately pitted cognitive biology, also suppressed nascent attempts to establish a science of epigenetics (Peterson 2016), upon which Goodwin's cognitive biology firmly rests. Today epigenetics is transforming our understanding not only of the mechanisms of inheritance but also of what kinds of information (knowledge of the world) can be transmitted.

Recognition that biological phenomena are intrinsically cognitive—that they function at the level of physiological processes as well as whole organisms in ways that employ (nonmetaphorically) a substantial portion of the toolkit of capacities that underlie cognition as we know it—has the potential to change much in the sciences of life and cognition by providing new conceptual tools for asking questions, designing experiments, and interpreting data. The shift in perspective, above all, will be in the direction of understanding reality, how things are, which is what science is for.

[11] The routine search for mechanisms in biology—how things work—does not necessarily entail that living systems *are* machines.

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