Journal of Molecular Evolution (2024) 92:258–265
https://doi.org/10.1007/s00239-024-10169-w

ORIGINAL ARTICLE

A Concept of Complementarity Between Complexity and Redundancy can Account for Kant's Biological Teleology and Unify Mechanistic and Finalistic Biology

Rama S. Singh[1]

Received: 26 October 2023 / Accepted: 28 March 2024 / Published online: 25 April 2024

Abstract

Over 160 years after Darwin and 70 years after the discovery of DNA, two fundamental questions of biology remain unanswered: *What differentiates the living from the nonliving? How can mechanistic and finalistic or holistic biology be unified?* Niels Bohr introduced a concept of complementarity in quantum physics and based on the paradox of light as a simultaneous wave and particle, conjectured that a similar concept might exist in biology that would solve the paradox of life originating from the nonliving. Bohr proposed that two mutually exclusive-independent observations may be necessary to explain a phenomenon and provided support to Immanuel Kant's idea that the "purposive" behaviour of organisms could only be explained in teleological terms and that mechanical and teleological approaches were necessary and complementary to explain biology. We present a concept of complementarity whereby *biochemical pathways or cellular channels for the flow of information are simultaneously complex and redundant and complexity and redundancy complement each other.* The postulates of biological complementarity are that (1) it was an essential condition in the origin of life; (2) it provided physiological flexibility that allowed organisms to mount *self-protection response* and complexity to evolve in the face of deleterious mutations before the evolution of bi-parental sex; (3) it laid the foundation for the evolution of a *choice of response* when confronted with threat; and (4) it applies to all levels of biological organizations and, thus, can serve as a basis for the unification of mechanistic and holistic biology. It is proposed that teleology is simultaneously *constitutive* and *heuristic*: constitutive because organisms' "purposive" behaviours are adaptive and are grounded in mechanism (complexity and redundancy), and heuristic because with our finite cognition and our goal-oriented (humans alone are aware of "tomorrow") and anthropomorphic pre-disposition, teleology will remain useful as a guide to our making sense of the world, even how to ask a meaningful question.

Keywords Complexity · Redundancy · Complementarity · Mechanistic · Finalistic · Holistic · Teleology

Introduction

The mechanisms behind the origin of life and the rules of development connecting molecules to morphology remain unanswered areas of biology. From Aristotle to Darwin and from Mendelian genetics to genomics, the determination of the properties of matter and laws of nature that gave rise to the origin of life has long been a topic of discussion in science. Niels Bohr formulated the principle of complementarity, which holds that two mutually exclusive paradoxical observations or theories can complement each other toward the understanding of a phenomenon (Bohr 1958). Bohr used the paradox of light as a simultaneous wave and particle to explain his principle and conjectured that a similar concept of complementarity could explain the paradox of biology, namely the origin of the living from the nonliving. This vision became the basis of Max Delbrück's quest for complementarity in biology (Strauss 2017). Delbruck chose to work with virus replication and helped to found the field of molecular biology; however, the concept of biological complementarity defied him (Strauss 2017). No laws or

Handling editor: **Cara Weisman**.

✉ Rama S. Singh
singh@mcmaster.ca

1 Professor Emeritus, Department of Biology, McMaster University, 1280 Main St West, Hamilton, ON L8S 4K1, Canada

principles like the light paradox have yet been discovered in biology.

The question of complementarity in biology is relevant not only to our understanding of the origin of life but also for the long-held mechanistic vs. finalistic dichotomy in biology (Mazzocchi 2010). The Newtonian mechanistic explanation of biology was frustrated by the "teleological features" of organisms, which were described as "self-causation", "self-preservation" and "self-generation". While Darwin refuted Aristotle's "finalistic teleology" and William Paley's theological argument from "Design", teleological reasoning continued to persist in biology (Haig 2023). Life was considered an "emergent property" of organized matter that could not be connected to its material causes. This "emergent view of life" led to the opinion that although the cellular operations of organisms could be explained in mechanical terms, their teleological behaviours required another explanation. Biology became a paradox because it was not analyzable at the level of atomic physics (Bohr 1958), and because no laws were evident that could explain the "goal-seeking" or "purposive" behaviour of an organism.

After the discovery of DNA, the mechanistic-finalistic debate had taken on new forms and is currently presented as reductionist vs. holistic biology or evolutionary vs. functional biology (Mayr 1961), which signify the analysis level or evolutionary perspective, respectively. The micro and macro-levels are considered connected through their bottom-up and top-down cellular communication and information flow (Mazzocchi 2010). Molecular biological phenomena such as epigenetics, pleiotropy and genetic redundancy are often treated as different levels of organization as opposed to parts of the mechanistic or genomic program. While some complex traits can be explained by gene–gene and gene-environment interactions, even the simplest behavioural traits may require *context-dependent* actions as a result of phenotype–environment interactions. In contrast, complex behavioural traits, especially "purposive" behaviours, would require "choice-based" actions and would be considered *emergent properties* of the organism. It is emergent, because there is no known mechanism that *directly links* the purposive behaviours of animals and their genomes. In this article, we provide one such mechanism.

This study first briefly reviews the vision of Niels Bohr and the quest for complementarity in biology of Max Delbrück, and then provides a concept of complementarity between *complexity* and *redundancy* using the following arguments regarding biological complementarity: (1) it was an essential condition in the origin of life by making the process of "natural selection" possible; (2) it provided physiological flexibility that allowed organisms to mount *self-protection response* and complexity to evolve in the face of deleterious mutations before the evolution of bi-parental sex; (3) it laid the foundation for the evolution of a "purposive" *choice of response* when confronted with threat; and (4) it applies to all levels of biological organizations and thus can serve as a basis for the unification of mechanistic and holistic biology. Biological complementarity provides a mechanism for the evolution of "purposive" behaviours and serves as the basis for reconciling mechanism and teleology.

Niels Bohr's Vision of Complementarity in Biology

Bohr presented a lecture on "Light and Life" to a congress on light therapy in Copenhagen in 1932 (Bohr 1933) and used the light paradox of atomic physics, in which light is simultaneously a wave and a particle and proposed that a similar paradox may exist in biology. He stated that "the spatial continuity of our picture of light propagation and the atomicity of the light effects are complementary aspects in the sense that they account for equally important features of the light phenomenon which can never be brought into direct contradiction with one another since their closer analysis in mechanical terms demands mutually exclusive experimental arrangements". (Bohr 2010, p. 5). Later Bohr abandoned the case of light as an example of complementarity in favour of that between kinematic vs. dynamical systems (https://plato.stanford.edu/archives/win2019/entries/qm-copenhagen/). The concept of complementarity applies to the relation between mutually exclusive experimental descriptions of atomic phenomena rather than to worldly, description-independent properties. Bohr held that complementarity was a general feature of science and the accumulation of knowledge and declared that "just as the general theory of relativity expresses the essential dependence of any phenomenon on the frame of reference for its coordination in space and time, the notion of complementarity serves to symbolize the fundamental limitation, met with in atomic physics, of the objective existence of a phenomenon independent of the means of their observation". (Bohr 2010, p. 7). Bohr saw complementarity as a generalization of the ideal of causality and saw it applicable to biology.

Bohr used two lines of arguments for complementarity in biology based on two different senses. First, using the example of atomic structure, he likened the "essential non-analyzability of atomic stability in mechanical terms" to the "impossibility of a physical or chemical explanation of the peculiar functions [sic] characteristic of life". (Bohr 2010, p.9). He remarked, "if we were able to push the analysis of the mechanism of living organisms as far as that of atomic phenomena, we should scarcely expect to find any features differing from the properties of inorganic matter" and "we should doubtless kill an animal if we tried to carry the investigation of its organs in vital functions so far that we could describe the role played by single atoms in vital functions". Bohr argued that "on this view, the existence of *life in biology must be considered as an elementary fact* [emphasis added], just as in atomic physics the existence of the quantum of action has to be taken as a basic fact that cannot be derived from ordinary mechanical physics" (Ibid, p. 9). Bohr deemed that *teleology and mechanistic description were mutually exclusive but necessary for the understanding of life*; teleology could not be reduced to physics and chemistry (McKaughan 2005) and the role of natural selection had not been factored in.

Second, citing the exclusive features of "self-preservation" and "self-generation" of organisms and the fact that external biological environments cannot be controlled to the same extent as those of atomic physics, Bohr indicated the limitations of applying the analogy from atomic physics to biological sciences. Thus, he considered the exclusivity, or "non-susceptibility" to further analysis, of life traits such as self-preservation and self-generation as complementary to the subdivision or reductionist approach for any physical analysis. Bohr supported the concept of purpose and stated that "teleological argumentation may be regarded as a legitimate feature of physiological description which takes the due regard to the characteristics of life in a way analogous to the recognition of the quantum of action in the correspondence argument of atomic physics" (Bohr 2010, p. 10).

Bohr's argument for a "teleo-mechanical" complementary approach to the life sciences corroborated the Kantian philosophy of human knowledge, which held that there was a limit to requiring mechanical explanations for all aspects of organisms (Roll-Hansen 2000; McKaughan 2005). Immanuel Kant identified a paradox in biology which held that while human understanding required mechanistic explanations, the "purposive" behaviours of organisms could only be explained in teleological terms and there were limits to using mechanical explanations for human understanding. Kant believed that complementary mechanical and teleological approaches were required in biology, but he treated the latter to have only a regulative heuristic role and not a genuine explanation.

Bohr was interested in solving the problem of how life originated. In the pre-DNA era, a reductionist approach to biology that would explain the origin of life was difficult to imagine. At that time, little thought was given to the idea that complementarity in biology, if it did exist, may not necessarily operate in the same manner as that of atomic physics and that the same molecular processes that allowed evolution of life could also explain evolution of organism's "purposive" behaviour.

Max Delbrück's Quest for Complementarity in Biology

Delbrück moved from the physical sciences to biology and decided to pursue self-generation (replication) using bacteriophages as a possible source of complementarity in biology because he believed that *self-replication* marked the main boundary between animate and inanimate matter. Initially, Delbrück did not believe that biology was an autonomous science, and he was attempting to find new physical laws that would explain biological phenomena (Roll-Hansen 2000; McKaughan 2005); he did not believe that biology had any special laws of its own. In his 1949 lecture "A physicist looks at biology", Delbrück recounted the prevailing view of physicists and chemists that "…. by virtue of two great generalizations- that living matter is made up of the same elements as those of the inanimate world, and that conservation of energy is valid for processes occurring in living matter, just as it is for processes in the inanimate world.… it seemed clear that the processes of living matter must be essentially the same as those of the inorganic world and that *there could not possibly exist a biological science ruled by its own laws* [emphasis added]." (Delbrück 1949).

Delbruck was open to the idea that the laws of atomic physics may not be sufficient to explain biological phenomena. He became convinced of the enormity of the cellular complexity and stated that "The meanest little cell becomes a magic puzzle box full of elaborate and changing molecules, and far outstrips all chemical laboratories of man in the skill of organic synthesis performed with ease, expedition, and good judgement of balance.…*any living cell carries with it the experiences of a billion years of experimentation by its ancestors*". (Delbrück 1949, emphasis added).

Delbrück remarked that the idea of complementarity "puts the relationship between physics and biology on a new footing. Instead of aiming from the molecular physics end at the whole of the phenomena exhibited by the living cell, we now expect to find natural limits to this approach, and thereby implicitly new virgin territories on which laws may hold which involve new concepts and which are only loosely related to those of physics, by virtue of the fact that they apply to phenomena whose appearance is conditioned on not making observations of the type needed for a consistent interpretation in terms of atomic physics" (Delbrück 1949). Delbruck remarked that biology was not yet at a point "where we are presented with clear paradoxes, and this will not happen until the analysis of the behaviour of living cells has been carried into far greater detail" (Delbrück 1949).

Delbruck's atomic physics approach looking for biological complementarity was paralleled by Schrodinger's thermodynamic approach which looked at living systems in terms of thermodynamics and order and disorder of matter (Schrodinger [1944] 2010). Schrodinger contrasted the origin of "order from disorder", which explains physical laws based on the entropy-principle, with "order from order" which we see in mechanical clocks, and which, he held, maintains living systems. He saw organisms as maintaining order by feeding on "negative entropy" from their environment (through literally feeding on "ordered" organic matter) and the hereditary material as being protected from disorder presumably by natural selection.

With the arrival of genomics biology, we have reached the point which Delbruck was envisioning of, and which can allow investigation of cells in greater detail to shed light on the origin and evolution of life in terms of both information and order or complexity.

A Concept of Complementarity in Biology

To recap, there are two aspects of complementarity: Light's wave- particle complementarity as "special complementarity", and its use as a principle of science and accumulation of knowledge as "general complementarity". Special complementarity is limited to observations of an object or phenomenon within the same level of organization, while general complementarity would apply to observations both within and between levels of organizations. Almost all discussions of complementarity in biology in the past have been limited to observations *between* levels of organizations, for example, contrasting mechanistic and holistic biology (Mazzochi 2010). This is probably because once it became obvious that life was not an inherent property of matter or it did not originate as a sudden event, interest in special complementarity died out. Different types of complementarities have been proposed in biology (see Theise and Kafatos 2013 and references there in) and while they may not be contradictory to each other, a concept of complementarity that applies to all levels of biology is still lacking.

The question of complementarity in biology cannot be entertained independently of evolution and the essential conditions for the origin of life. While origin of life research has traditionally used a bottom-up approach, genomics is allowing scientists to utilize a top-down approach to the evolution of informational molecules. Genomics bears the same relationship to Mendelian genetics today as quantum mechanics did to the classical physics a hundred years ago. Genomics is the quantum physics of biology. Bohr believed that *complexity* was the source of biological complementarity and others have made the same point (Thesie and Kafatos 2013). A joint concept of complexity and redundancy has been previously presented which argued that redundancy is a prerequisite to the evolution of complexity (Singh and Gupta 2020; Singh 2021, 2023). Complexity, at the molecular level, is defined as the total number of gene–gene interactions and biochemical pathways necessary for a given molecular function, trait, or an organism (Singh and Gupta 2020). Redundancy is defined as the presence of alternate biochemical pathways for a given function, trait, or organism (Singh 2021). Redundancy is characteristic of life at all levels of organization, including within the genetic code, in relation to the physiological flexibility of biochemical pathways, and in the exercise of choice by humans and certain animals. The interaction and mutual *interdependence* of complexity and redundancy as a concept of complementarity can be stated as follows:

> *Biochemical pathways or the cellular channels of information flow between genotypes and phenotypes are simultaneously complex and redundant, and complexity and redundancy complement each other.*

This concept of biological complementarity bears close similarity to that in atomic physics; however, unlike the latter which involves mutually exclusive descriptions of quantum phenomena, the former involves *interdependent and essential* descriptions of properties of the evolutionary system. Thus, complexity and redundancy are two aspects of the gene–gene interacting networks in the same way as the complex criss-crossing and alternate passages are two aspects of the road grid of a big city. We cannot have complexity without redundancy in living systems.

Biological complementarity, as defined here is proposed to have four features: (a) it was an essential condition in the origin of life by making the process of "natural selection" possible; (2) it provided physiological flexibility that allowed organisms to mount *self-protection responses* and complexities to evolve in the face of drift fixing deleterious mutations (Lynch 2010) and before the evolution of bi-parental sex; (3) it laid the foundation for the evolution of a "purposive" *choice of response* when confronted with threat; and (4) it applies to all levels of biological organizations and thus can serve as a basis for the unification of mechanistic and holistic biology. Genomics is unravelling molecular complexities across the ladder of life, and, for an example, redundancy is a major feature of prokaryotes evolution as similar cellular functions are coded by different genes (Koonin 2003). In the following we discuss how complementarity between complexity and redundancy may have aided in the origin of life and natural selection and how it can serve as a basis for reconciling mechanism and teleology and for unifying mechanistic and holistic biology.

Biological Complementarity as an Essential Condition for the Origin of Life

Biology has dual causation that come from both inside and outside of the field. Knowledge from various sources, including chemistry (Morowitz and Smith 2007), physics (Kaufmann 2009) and genomics (Zhang et al. 2010), has revealed that the path to the origin of life must fulfil three basic and essential conditions, one of which is the need for a *source of energy*. While geochemical sources of energy may have driven the initial steps in the origin of life forms, the sun provides the main source of energy for the evolution of all life forms. The second condition for the origin of life was the *choice of material that could serve for coding "biological information"*. The material for coding information turned out to be judiciously "chosen" (Kuhn and Wasser 1983) as it had the ability for self-replication (complementary pairing of DNA). Equally important was the *imperfection* of DNA replication, which became a perpetual source of variation for adaptation and evolution. The third condition for the origin of life, as described below, was the *birth of natural selection.*

Research on the origin of life has struggled with the discordant concepts of life as the outcome of a single sudden event or a result of a long process of evolutionary change. The main origin of life theories are categorized into two groups: "metabolism first" and "RNA first" (Kamminga 1988; Orgel 2008; Preiner et al. 2020; Papastavrou et al. 2024). "Metabolism first" theories assert that molecules or polymers arose from molecular interactions which were catalysed by each other and once this system was encapsulated inside the protocell, it became encrypted as a message in the DNA/RNA and subject to evolutionary change. According to this theory, a zone of "unknowns" exists in the mutual molecular catalysis which is involved in the evolution of order from disorder. The "replication first" theory or "RNA world hypothesis" attests that genetic information materialized first, and the remaining essential steps, including replication and translation, may have followed a deterministic manner and not necessarily in a single place. Regardless of which process came first, the essential molecules must have emerged contemporaneously to be encapsulated inside the protocell (Preiner et al. 2020). Our intention is not to propose a theory of the origin of life, but to show how the birth of natural selection, regardless of which process came first, would have complemented physical and chemical conditions, and allowed for the evolution of the complementarity of complexity and redundancy which made origin and evolution of life possible.

"First phenotype" and the Birth of Natural Selection

Origin of life research contains much discussion regarding the source of information and how it was derived (Walker and Davies 2013; Cartwright et al. 2016). Some have suggested that life could have evolved without Darwinian selection. The argument given here is that since life did not arise in a singular event (which is the consensus) but rather *evolved*, natural selection was an essential condition along with, of course, a source of energy and a choice of suitable material.

Selection acts on phenotype; the origin of natural selection would have required a phenotypic base. The origin of life can be conceived as the emergence of a molecule which had the rudimentary property of self-replication, and which could improve its "survival" or persistence by using variations produced by imperfections in the replication process. *Production of a "molecular phenotype" that was affected by certain aspects of the environment was the key to the initiation of natural selection.* We use a DNA molecule as an example to demonstrate how natural selection could have originated.

Phenotypic variations may have occurred that linked DNA replication and certain aspects of its phenotypes, such as *DNA fragment length and its stability*, to certain aspects of the environment including heat (e.g. temperature-dependent DNA fragment enlargement); therefore, DNA fragment length could have been *the first phenotype to initiate the action of "natural selection"*. If higher stability of DNA molecules can lead to longer DNA fragments, natural selection would have acted to increase DNA fragment length. DNA has the unique property of complementary pairing and self-replication (reproduction). If we accept the evolution of DNA fragment length as a selectable trait, then DNA fragment variants can be considered both *genotypes and phenotypes*. Considering DNA replication as the "first phenotype" in the origin of life provides the advantage of enrichment of genetic material. This simple preliminary model does not ignore the fact that efficient replication of DNA would have required evolution of specific proteins, which would have required natural selection.

Natural selection in terms of molecular stability and enrichment by non-diffusion could have occurred similarly with other biomolecules. Selection and evolution must have originated with the synthesis and enrichment of various individual biomolecules, if variation (copying error) and inheritance (copying mechanism) were occurring, as was the case with DNA (Eigen 1971; Szathmary and Maynard Smith 1997). Thus, natural selection could have been involved in the evolution of each component of life forms, both concurrently and independently as an enrichment and improvement process before it was combined into the protocell (Biebricher et al. 1986; Sharma and Annila 2007; Vasas et al. 2010; Markovitch and Lancet 2012; Frenkel-Pinter et al. 2019; Preiner et al. 2020).

These transactions must consider *how genetic information arises*. DNA fragment length and stability is suggested to have become temperature-dependent; however, before this stage, the DNA molecule was simply a chain of nucleotides. The hypothetical temperature dependency of DNA stability allows the molecule to become "informational" by linking "genotype" (DNA fragment length and pairing) to "phenotype" (stability) and creating condition for the action of natural selection. When a feature or property of a biomolecule is linked with an aspect of the environment that increases the survival and reproduction of the molecule, that feature becomes genetic information. Thus, genetic information is not a collection of pieces or an instruction which is devoid of a "molecule/organism-environment" interaction. *All genetic information in the DNA must come from organism-environment interaction.* This is what Erwin Schrodinger meant when he said organism maintains high levels of orderliness by "continually sucking orderliness from its environment" (Schrodinger [1944] 2010, p. 73). Complementarity of complexity and redundancy not only enabled life to evolve but organisms to "keep going" (ibid, p. 69) and keep producing evermore complex organisms.

Biological Complementarity can Explain Kant's "purposive" Teleology

Living organisms are endowed with properties promoting self-generation and self-protection which often appear "intentional" and cannot be explained by Newtonian mechanics and call for additional causes, laws, and principles. Kant proposed that all aspects of life cannot be reduced to mechanical causes and that the function and purposive behaviour of organisms should be considered as arising from independent and *self-explanatory causes.* Kant replaced the metaphysical reasons for organisms with "natural teleology" and argued that Newtonian mechanistic causes were insufficient explanations. He believed that organisms have "natural ends" because they follow the principles of "self-causation", "self-preservation" and "self-propagation or self-replication" that are driven by "organized matter", which he conceived as arising from inanimate matter. Although Kant noted that teleology is partly a product of our cognitive faculty (i.e. our ability to see order in nature), he warned against not accepting teleology as a *constitutive causality* of living things. Despite these warnings and explanations, teleology became the main theory of the organism's "purposive" behaviour, not only in terms of regulation as Kant suggested, but also as constitutive causal agent generally. This tied the hands of biologists, as they were unable to provide a "biological" explanation, as well as physicists, who were unable to offer a mechanistic explanation within the physical–chemical framework. Therefore, Niels Bohr's concept of complementarity in biology was founded on the framework of Kant's biological teleology (Roll-Hansen 2000; McKaughan 2005; Bohr 2010). Bohr generalized the concept of complementarity to support Kant's theory that the mechanistic and finalistic descriptions of organisms are complementary and necessary.

We can ask why Bohr was supporting Kant's position 50 years after Darwin had swept away Aristotelian finalism. This may be because it was 30 years before the discovery of DNA and Bohr, like other physicists of his time, may have ben imagining origin of life as an event separate from evolution by natural selection. Evolution of organismic diversity could be understood but origin of organism could not. It was to be taken as given. Our intention here is not to discuss pro and con of biological teleology or the role of natural selection; there is no need for the teleology hypothesis to explain origin of life (the reader is referred to Dretske 1995, and Millikan 1995). Our intention is to ask why 160 years after Darwin and 70 years after DNA, biological teleology continues to play a significant role in the shaping of our cognition and our look at the world? We show that biology has advanced and can provide answers.

Biology has advanced in many ways. First, we do not have to take "life as given", as Bohr declared; rather, we need to accept that life, which has been defined as a self-causing, self-maintaining and self-generating entity, *evolved* by successive molecules following physical–chemical laws. Second, purposive behaviours of organisms can be considered phenotypic expressions that were derived from the same evolutionary processes that endowed organisms with "non-goal-seeking" adaptations. Both goal-seeking and non-goal-seeking adaptations have the same result, that of self-survival. Ervin Schrödinger made the same point when he stated that humans, and to a great extent animals, behave similarly when faced with comparable environmental challenges: " If…fire suddenly breaks out on the road in front of a rider or an unexpected gulf opens before him, the beast he is riding shrinks back in fear just as he does himself, and this is only one example of thousands which could be listed" (Schrödinger 1964, p. 91–92).

Third, just as physical laws are predicated on the initial conditions present at the point of the origin of the universe, biological laws can depend on the initial conditions present at the origin of life. Finally, since organisms drive their evolution through organism-environment interactions and are not passive participants, any laws of biology must be the result of "self-causation" and must also come from the evolutionary process itself. The "purposiveness" of nature or the "goal-seeking" behaviours of organisms can be explained by *molecular-mechanistic redundancy*, which gives organisms a *choice of response or freedom of action.* Redundancy in choice and freedoms of thought is the foundation of reason and judgement. Complementarity predicts that more complex organisms will display more purposive behaviour which is the case.Teleological arguments need not be construed in religious context; they can be construed in evolutionary context (Mossio and Bich 2014).

Biological Complementarity and the Unification of Mechanistic and Finalistic Biology

Despite the claims of earlier physicists that a biological science ruled by its own laws was not possible (see Delbruck 1949), biologists have maintained that biology is a complex autonomous science. Mayr (2004) argued this concept using the following points: a dual causation exists that consists of physio-chemical laws, as well as laws, principles and concepts that are unique to biology; evolutionary and functional biology are distinct, with the latter presenting more commonalities with physical sciences than the former; concepts are more important in biological theories than laws (downplaying the role of laws in evolutionary biology theory); and no universal laws of biology can exist because of the importance of variation in evolution.

Evolutionary worldviews apply to both biological and nonbiological systems (Lewontin 1968; see Wong et al. 2023 for a recent "universal concept of selection") but there are essential differences between them. Physical systems may evolve and go under transformation of material, but they are closed and subject to the second law of thermodynamics. Biological systems, on the contrary, are not only open but unique in allowing *for self-replication and retention of lineage-specific organismic information*. This happens because, as Max Delbruck put it, living cells carry "memory" of their past experiences and they build on it (Delbruck 1949). Nonbiological systems do not. Uniqueness of biology is that *any law of biology must also be an outcome of evolution; causes and effects are not always separate and are often interdependent and mutually reinforcing*. Complexity and redundancy are such laws.

Complementarity is relevant to all fields of biology some of which have been presented elsewhere (Singh 2021, 2023). Here we briefly point out an application of complementarity to developmental biology. The problem of developmental biology can be broken down into two steps: transition from *genes to genotypes* and transition from *genotypes to phenotypes*. Genotypes are more than combinations of genes. Genes are the raw material from which genotypes, i.e. genetic information, is created. All combinations of genes and genetic variants do not become part of usable genetic information at any given time. And those that do become part of the usable genetic information will change over time because due to redundancy alone some genetic information will get modified, less often used, or even lost as evolution proceeds over time.

Similarly, just as only selected gene combinations become part of usable genetic information, only selected genotype–phenotype transitions become critical developmental landmarks in the ontogeny of the organisms. For example, "self-organization" and "emergent" properties would be evolved landmark developmental features of the organism. In contrast to physics and chemistry where emergent properties can arise (water is nothing like its individual elements, oxygen, and hydrogen), the dictates of biological processes themselves do not provide for "emergent" properties in organisms. What we deem "emergent" can only arise from genetic information, meaning genetic variation and gene regulation in response to changes in the environment. Redundancy provides mechanisms for the same gene not only to affect different traits but act at different stages of development and provide opportunity for "emergence".

In summary, complexity imposes limits on what can be computed, and redundancy implies loss of information. Redundancy takes away genes' functional autonomy and replaces it with multitude of options for collective response to environmental challenges. Redundancy of molecules and morphology including complex behaviours of organisms provide organisms with continuous evolvability and is the invisible link connecting mechanistic and finalistic biology. Redundancy allows for the evolution of an entity that is greater than the sum of its parts and can explain an origin that appears emergent.

Conclusions

The present study proposed that the physicist's concept of "complementarity in biology" is untenable; any concept of complementarity in biology must be based on evolution by natural selection. The concept of complementarity between complexity and redundancy presented here ensures that as gene–gene interaction networks increase, biochemical pathways (i.e. the cellular channels of information flow between genotypes and phenotypes) multiply and become redundant and remain open to the evolution of novel functions and to further evolution of complexity. It is further proposed that biological complementarity was an essential condition for the origin of life and explains the evolution and emergence of freedom of choice and other "goal-seeking" behaviours in complex animals. Biological complementarity applies to all levels of biological organization which can serve as the basis for the unification of mechanistic and finalistic biology (Mossio and Bich 2014; Desmond and Huneman 2020). Biological complementarity can also explain teleology. It is proposed that teleology is simultaneously *constitutive* and *heuristic*: constitutive because organisms' "purposive" behaviours are adaptive and are grounded in mechanism (complexity and redundancy); and heuristic because with our finite cognition and our goal-oriented (humans alone are aware of "tomorrow") and anthropomorphic pre-disposition, teleology will remain useful as a guide to our making sense of the world, even how to ask a meaningful question.

Acknowledgements We acknowledge and thank David Haig, Paul Higgs, and Ellen Larsen for their valuable comments on this manuscript. This research was supported by Faculty of Science, McMaster University.

Declarations

Conflict of interest Author declares no conflict of interests.

References

Biebricher CK, Eigen M, Luce R (1986) Template-free synthesis by Qβ replicase. Nature 321:89–91

Bohr N (1933) Light and life. Nature. 133:4213-423 (pt. 1)-457-459 (pt. 2)

Bohr N (1958) Atomic physics and human knowledge. Wiley, New York

Bohr N (2010) Atomic physics and human knowledge. Dover publications, New York

Cartwright JHE, Giannerini S, González DL (2016) DNA as information: at the crossroads between biology, mathematics, physics, and chemistry. Philos Trans A Math Phys Eng Sci. https://doi.org/10.1098/rsta.2015.0071

Delbruck M (1949) A physicist looks at biology. Trans Conn Acad Arts Sci 38:173–190

Dretske F (1995) Naturalizing the mind. MIT Press, Cambridge

Eigen M (1971) Self-organization of matter and the evolution of biological macromolecules. Naturwiss 58:465–523

Frenkel-Pinter M, Haynes JW, Martin C, Petrov AS et al (2019) Selective incorporation of proteinaceous over non proteinaceous cationic amino acids in model prebiotic oligomerization reactions. Proc Natl Acad Sci USA 116:16338–16346

Haig D (2023) Femmes finales: natural selection, physiology, and the return of the repressed. Qeios. https://doi.org/10.32388/467BMX

Kamminga H (1988) Historical perspective: the problem of the origin of life in the context of developments in biology. Origins Life Evol Biosph 18:1–11

Kaufmann M (2009) On the free energy that drove primordial anabolism. Int J Mol Sci 10:1853–1871

Koonin EV (2003) Comparative genomics, minimal gene-sets and the last universal common ancestor. Nat Rev Microbiol 1:127–136

Kuhn H, Wasser J (1983) Molecular self-organization and genesis of life. Experientia 39:834–841

Lewontin RC (1968) The concept of evolution. Int Encycl Social Sci V18:202–210

Lynch M (2010) Evolution of the mutation rate. Trends Genet 26(8):345–352

Markovitch O, Lancet D (2012) Excess mutual catalysis is required for effective evolvability. Artif Life 18:243–266

Mayr E (1961) Causes and effect in biology. Science 134:1501–1506

Mayr E (2004) What Makes Biology Unique? Cambridge University Press, Cambridge

Mazzocchi F (2010) Complementarity in biology. EMBO Rep 11(5):339–344

McKaughan DJ (2005) The influence of Neils Bohr on Max Delbruck: revisiting the hopes inspires by "Light and Life." Isis 96:507–529

Millikan RG (1995) White queen psychology and other essays for Alice. MIT Press, Cambridge

Morowitz H, Smith E (2007) Energy flow and the organization of life. Complexity 13:51–59

Mossio M, Bich L (2014) What makes biological organization teleological? Synthese 194:1089–1114

Orgel LE (2008) The implausibility of metabolic cycles on the prebiotic Earth. PLoS Biol 6:e18

Papastavrou N, Horning DP, Joyce GF (2024) RNA-catalyzed evolution of catalytic RNA. Proc Natl Acad Sci USA. https://doi.org/10.1073/pnas.2321592121

Preiner M, Asche S, Recker S et al (2020) The future of origin of life research: bridging decades-old divisions. Life. https://doi.org/10.3390/life10030020

Roll-Hansen N (2000) The application of complementarity to biology: from Niels Bohr to Max Delbruck. Hist Stud Phys Biol Sci 30(2):417–442

Schrodinger E ([1944] 2010) What is Life? with Mind and Matter. Cambridge University Press, Cambridge, p 1992

Schrödinger E (1964) My View of the World. Cambridge University Press, Cambridge

Sharma V, Annila A (2007) Natural process–Natural selection. Biophys Chem 127:123–128

Singh RS (2021) Decoding unnecessary complexity: a law of complexity and a concept of hidden variation behind "missing heritability" in precision medicine. J Mol Evol 89(8):513–526. https://doi.org/10.1007/s00239-021-10023-3

Singh RS (2023) A law of redundancy compounds the problem of cancer and precision medicine. J Mol Evol. https://doi.org/10.1007/s00239-023-10131-2

Singh RS, Gupta BP (2020) Genes and genomes and unnecessary complexity in precision medicine. npj Genomic Med 5:21

Strauss BS (2017) A physicist's quest in biology: Max Delbruck and "complementarity." Genetics 206:641–650

Szathmary E, Maynard SJ (1997) From replicators to reproducers: the first major transitions leading to life. J Theor Biol 187(4):555–571

Theise ND, Kafatos MC (2013) Complementarity in biological systems: a complexity view. Wiley Online Library 18(6):11–20

Vasas V, Szathmáry E, Santos M (2010) Lack of evolvability in self-sustaining autocatalytic networks constraints metabolism-first scenarios for the origin of life. Proc Natl Acad Sci USA 107:1470–1475

Walker SI, Davies PCW (2013) The algorithmic origins of life. J R Soc Interface 10:20120869

Wong ML, Cleland CE, Arend D Jr, Barlett S, Cleaves HJ II et al (2023) On the role of function and selection in evolving systems. Proc Natl Acad Sci USA. https://doi.org/10.1073/pnas.2310223120

Zhang W, Li F, Nie L (2010) Integrating multiple "omics" analysis for microbial biology: application and methodologies. Microbiology 156:287–301