

This is an abbreviated version of a forthcoming chapter on the so-called Extended Evolutionary Synthesis. I have cut out some of the more ‘insider baseball’ arguments to give you a sense of the whole.

Hypertextuality of an hyperextended synthesis: on the interpretation of theories by means of selective quotation

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“Or we may say: this egg is older than that fowl (the fowl having been produced from it); and on the contrary; this fowl existed before that egg (which she has laid). And this is the round that makes the race of the common fowl eternal; now pullet, now egg, the series is continued in perpetuity; from frail and perishing individuals an immortal species engendered. ... And whether we say, or do not say, that the vital principle (*anima*) inheres in the egg, it still plainly appears, from the circuit indicated, that there must be some principle influencing this revolution from the fowl to the egg and from the egg back to the fowl, which gives them perpetuity.” William Harvey (1651/1847, p. 285)

A specter is haunting biology—the specter of final causes. Fear of this specter—teleophobia—stifles speech. Thou shalt not ask why. We wander without direction. Our time is out of joint. We hear strident calls for revolution and a return to past certainties. Partisans man the barricades. The forces of reaction mobilize to crush dissent. Things fall apart. The center cannot hold. The best lack all conviction, while the worst are full of passionate intensity. Is something rotten in the state of Darwinism?

From Darwin to Derrida (Haig 2020) is an extended argument about the origins of meaning and purpose. It is a defense of the use of teleological language in biology and an attempted reconciliation of biology and the humanities. Central to its argument is the concept of an interpreter, an entity that has evolved or been designed to use information in choice. The action chosen is the *meaning* of the information for the interpreter. This is a definition not a discovery. *Texts* are a subset of meanings: interpretations *intended* to be interpreted; outputs chosen to be *used* as inputs to future interpretations. Other terms, from *environment* to *phenotype* to *gene*, are also given non-standard definitions. The book’s readers will judge whether this reconfiguration of terms is a hyperextended synthesis that stretches common sense beyond its limits, causing injury and pain, or a chiropractic adjustment that restores flexibility to an immobile joint.

For a man with a hammer, every problem looks like a nail. For a peasant with a sickle, every problem looks like a head of wheat. My favorite hammer fits snugly in my hand: effects can be causes of causes when

causes recur. Two truths universally acknowledged are that one should not confuse cause and effect, and that a cause cannot come after its effect. These truths justify the rejection of final causes: the end (*telos*) of a process is an effect of the process and cannot be its cause. These truths deceive. Teleological language is justified in biology because natural selection confounds common understandings of cause and effect.

Exclusivity of cause and effect is unproblematic in statements about individual things: a particular egg is either laid by a particular chicken (the chicken is a cause of the egg) or develops into that chicken (the egg is a cause of the chicken), but it cannot be both (for completeness, one should add that an egg is neither cause nor effect of an unrelated chicken). However, what is true of relations among individual things (token-causation) need not be true of relations among kinds of things (type-causation), especially when kinds are related by reproductive recursion. An egg is both an effect of a chicken-that-was and a cause of a chicken-to-be. Eggs (considered as kinds) are both causes and effects of chickens (considered as kinds). Scientific laws are statements about kinds, meant to have general validity.

The hammer strikes. What is true of chickens and eggs is true of genotypes and phenotypes. Genotypes determine phenotypes by developmental processes. Phenotypes determine genotypes via natural selection. A protein is a cause of its DNA sequence, the central dogma of molecular biology notwithstanding. Past phenotypes explain present genotypes. Effects reinforce their causes. Genes exist *for the sake of* their functions. Adaptations are final causes. The differential beating of hearts has shaped cardiac development via rhythmic effects on differential survival of bodies and replication of genes. Projecting nails can cause injury if they are not hammered home.

Purpose, goal, and direction

Ever since Aristotle, the notion of *telos* (final cause or end) has encompassed two somewhat different, but related, concepts. One is the usefulness of a thing, the other is the goal toward which a thing moves or develops: driving-in nails is the *telos* of a hammer; a chicken is the *telos* of an egg. The concepts are related because a carpenter has a goal in mind when she purposefully uses a hammer. For Aristotle, *telos* was internal to organisms: the potential chicken within the egg was actualized in development. The living thing held its end within itself (*entelechia*).

In simplistic terms, Christianity replaced Aristotle's intrinsic *telos* with an extrinsic *telos*. Entelechies yielded to a creator. Thomas of Aquinas offered five arguments for the existence of God of which

“The fifth way is based on the guidedness of nature. Goal-directed behaviour is observed in all bodies obeying natural laws, even when they lack awareness. Their behaviour hardly ever varies and practically always turns out well, showing that they truly tend to goals and do not merely hit them by accident. But nothing lacking awareness can tend to a goal except it be directed by someone with awareness and understanding; the arrow, for example, requires an archer. Everything in nature, therefore is directed to its goal by someone with understanding, and this we call God.”

His was a teleological universe. Obedience to natural laws was evidence of guidedness and hence of a guiding hand. Without what we call God, all would be chaos. The antithesis of a lawful universe of *directed* events was a lawless universe of *random* events. The primary adjectival sense of random in the *Oxford English Dictionary* is “Having no definite aim or purpose; not sent or guided in a particular direction; made, done, occurring, etc., without method or conscious choice; haphazard.”

The scientific revolution of the seventeenth century led to a general acceptance among natural philosophers that one could have physical law without a legislator, order without orders, direction without a director. For hard-minded physicalists this meant the exclusion of final causes from science. Teleology became anathema. For some, God played a role in setting the mechanism in motion but then the universe unfolded without further intrusion. Natural theologians used the appearance of order and purposefulness in nature, especially in living things, as evidences of a creator. Their argument from design combined both purpose and goal. Organisms possess purposeful parts. Purposes require minds with goals. Therefore, the purposive features of organisms prove the existence of a divine mind who has a goal (including for us).

The exclusion of final causes bore abundant fruit in physical science, but the exquisite order of living things, their goal-directedness, and occasional disobedience, did not fit easily within a purposeless but lawful universe. Despite these appearances, many nineteenth-century biologists came to see living things as subject to physical law and therefore bereft of final causes. Vitalists demurred that there was something special about living things, some kind of internal drive or life-force. Into this mix, was thrown the theory of natural selection. Darwin (1859) gave a naturalistic account of contrivance in nature that dispensed with a mind or a goal. Two major interpretations of Darwin’s import for final causes can be distinguished: the first, that natural selection *eliminates* purposes and goals; the second, that natural selection *explains* purposes without pre-existing goals.

Karl Ernst von Baer and *Zielstrebigkeit* (goal-directedness)

The eminent embryologist Karl von Baer addressed purpose (*Zweck*) and goal (*Ziel*) in a paper on paedogenesis (1866a, p. 126). Many natural scientists condemned reference to goals. He felt called upon to justify his preference for teleological language against “this fear in front of purposes, or better goals—this teleophobia, as one might call it” („*diese Furcht vor Zwecken, oder besser Zielen—diese Telephobie, wie man sie nennen könnte*”). *Zweck* and *Ziel* could be used as synonyms, but von Baer preferred *Ziel*. He coined another term *Zielstrebigkeit* to designate the goal-directedness of living things. This term possesses strong connotations of inner initiative (German *streben* and English *strive* are orthologous).

That same year, Ernst Haeckel’s (1866) *Generelle Morphologie der Organismen* presented its author’s monistic, materialist synthesis of the science of organic form in which he stridently and uncompromisingly rejected all appeal to final causes in favor of efficient causes alone (p. 98). Teleology had no place in scientific explanation. He called instead for a science of rudimentary organs, what one might call a theory of inaptitude (*Unzweckmässigkeitslehre*) or dysteleology (*Dysteleologie*). For Haeckel, Darwin had banished forever the ghost of final causes: “*In Darwin’s discovery of natural selection in the struggle for existence, we see the most*

striking proof of the exclusive validity of mechanically acting causes in the entire field of biology; we see in it the definitive death of all teleological and vitalistic judgments of organisms” (p. 100).

von Baer responded in an address delivered in December 1866 in which he derided Haeckel's materialism and defended his own teleological views (*Über den Zweck in den Vorgängen der Natur*, republished in Baer 1876). In this address, von Baer explained his preference for *Ziel* and *Zielstrebigkeit* over *Zweck* and *Zweckmäßigkeit*: *Zweck* implied conscious intent, and was properly restricted to human affairs or to nature as a whole (*die Gesamtheit der Natur*) (*ibid*, p. 74); *Ziel* was more inclusive than *Zweck* because it did not presuppose consciousness but could include conscious *Zwecke* (*ibid*, p. 82). von Baer employed a familiar metaphor for *Zielstrebigkeit*: when I desire to shoot an arrow into a target, the purpose is mine and stays with me, but the arrow moves with absolute necessity to *its* goal without knowing the purpose (*ibid*, p. 86). It is in this sense that the goal of an egg is the development of a new chicken (*Das Ziel des Eies ... ist die Entwicklung eines neuen Hühnchens*) (*ibid*, p. 83). Haeckel, not Darwin, was the target of von Baer's opening fusillade. For Haeckel, according to von Baer, everything occurred in the world from absolute necessity (*absolute Nothwendigkeit*), leaving no room for chance (*Zufall*), purpose in nature (*Zweck in der Natur*), or free will (*freier Wille*). von Baer found absurd Haeckel's argument that physical necessity was incompatible with purpose and was incredulous at Haeckel's denial of a role for chance (*ibid*, p. 68ff).

von Baer shifted aim when he turned his rhetorical fire to the Darwinian hypothesis (*Zum Darwins Lehre* in Baer 1876). Haeckel had been targeted, in part, because his insistence on absolute necessity left no room for chance (*Zufall*) but the Darwinian hypothesis, as von Baer had come to understand it, ascribed too great a role to chance. Chance was not creative. It had no goals. It could not create complex things. Darwinists, he argued, wanted to replace explanation by *Ziel* with explanation by *Zufall*. His embryological studies had convinced him of the cardinal importance of *Ziel*. *Zielstrebigkeit* acted from within, like Aristotle's *entelechy* (*ibid*, p. 458, including footnote), rather than from without like Darwin's material causes. When he came to address the transmutation of species, von Baer wrote:

“But we must especially fight against Darwin's view of the entire history of organisms only as a result of material effects, and not as a development. It seems to us unmistakable that the gradual formation of organisms into higher forms and finally to man was a development, a progress towards a goal, which one may conceive as more relative than absolute.”

(Baer 1876, p. 425; translation by Nyhart 1995, p. 118)

Ay, there's the rub. Few Darwinists, then or now, would dispute that embryonic development is goal-directed, but extrapolation of the goal-directedness of development to evolutionary change aroused, and continues to arouse, Darwinian teleophobia. For von Baer, organisms had goals but not purposes; the evolutionary process was goal-directed; nature as a whole, not its parts, had a purpose. For Darwin, organisms evolved with goals and purposes, but natural selection had neither goals nor purposes.

Emil Du-Bois Reymond (1876, p. 23), on the other hand, believed that Darwin had shown how Nature could continually throw doubles even with unloaded dice. In physiology, teleology could be used as a heuristic principle (“*der Teleologie als heuristischen Principes uns zu bedienen*”). Because of the theory of

natural selection, the anthropomorphic name ‘*Zweckmässigkeit*’ no longer had anything uncanny (*Unheimlich*) about it. He saw no need for exchanging the older term for the name ‘*Zielstrebigkeit*’ as suggested by von Baer.

Directedness

“According to Teleology, each organism is like a rifle bullet fired straight at a mark; according to Darwin, organisms are like grapes of which one hits something and the rest fall wide.” (TH Huxley 1864)

For many of von Baer’s contemporaries, the principal explanatory antithesis divided directed lawfulness (*Zielstrebigkeit*) from random lawlessness (*Zufälligkeit*). When Darwinists derived purposiveness (*Zweckmäßigkeit*) from undirected variation, it was easy to interpret them as claiming the wonders of the living world had been assembled by chance. The implausibility of the creation of complex beings by repeated throws of dice remains one of the principal arguments of creationists against Darwinists, and has been expressed to me privately by eminent biochemists and molecular biologists. Those unconvinced by Darwinism often desire a more *directed* process. But their argument from design is mistaken. Under the Darwinian hypothesis, natural selection, not mutation, is the creator of order and source of organismic direction.

Nineteenth-century diatribes are echoed in twenty-first century tirades. Proponents of an EES ascribe an evolutionary role to directed variation that adds *zielstrebig*e leaven to the *zufällige* dough. Orthodox Darwinists insist that mutational variation is undirected. What would it mean for variation to be *directed*? The noun *direction* comes from the verb *direct* whose oldest sense in the *Oxford English Dictionary* is “To write (something) directly or specially *to* a person, or for his special perusal”. The meanings of words evolve. Compare the modern sense of direction in ‘He proceeded in a northerly direction’ with the sense in ‘She has five students working under her direction.’ The adjective *directed* can be used in a passive sense of *has a direction* or an instructive sense of *was directed*. There are sufficient degrees of freedom of interpretation for authors to mean different things by ‘directed variation’ and to yell at each other.

Every random variable has a mean and deviations from that mean. When an archer shoots at a target, she does not release the arrow in a random direction but, when she shoots repeatedly at the same target, the scatter of her shots are undirected deviations from her intended mark. If the target is moved, then she changes aim and releases her arrows in a new direction. Her shots will now exhibit random scatter around a new center. If she attempts to hit a moving target, then she must anticipate where the target will be when the arrow arrives. Her shots will show random variation around the spot where she aims but may show systematic deviation from the shifting goal if she poorly anticipates its future positions.

In the standard Darwinian account, archers are products of evolution by natural selection, but natural selection is not an archer. If the adaptive target has been stationary for a prolonged period then most genetic shots will be ‘on target’ with random scatter due to the slings and arrows of outrageous fortune. The evolutionary history of the mean is non-random but variation around the mean is random. If the target

moves, then shots previously on target will miss the mark and mutant shots that ‘by chance’ were closer to the new target will increase in frequency and be surrounded by a new halo of off-target variation. Past changes of utility, as judged by natural selection, determine the non-random location of the ‘mean’ but mutational variants are ‘random’ with respect to current or future utility. Natural selection accounts for evolutionary responses that track a shifting target, but most Darwinists would reject suggestions that mutation anticipates the direction of change that is needed. The adaptive fit of organisms to their environments remains ‘on target’ by negative selection and ‘shifts target’ by positive selection.

Although most Darwinists reject evolutionary goals, most are comfortable with organismic goals: actions taken *for the sake of an end* (purpose) proceed *toward an end* (goal). The directedness of development is explicable in terms of reproductive recursion. Development toward a goal is purposive because adult forms have transmitted genetic differences responsible for their distinctive development. Differences of development are the phenotypic effects of developmental genes. For each genetic difference, the factors that are the same are its developmental niche. Variation in development is winnowed by the constraints of this developmental niche. Adaptationists are also comfortable with contingent goal-directed behavior, with the twists and turns of a cheetah as it pursues a fleeing gazelle. The same is true of contingent goal-directed development. Adaptationists feel no discomfort when a branch grows toward the light. Adaptive phenotypic plasticity allows adjustment of aim by feedback from targets.

The poetry of life

‘Phenotype determines genotype’ is a picaresque and quixotic epic of discursive difference-making. The varied effects of allelic variants, of *p*’s and *q*’s, in a complex world determine which variants become invariant. The judgment of nature in a single generation, whether a variant is ‘Copied’ or ‘Not Copied’, may rest on a single difference made at a moment of crisis or many differences of different nature made over the course of a lifetime. Similar judgments of nature must be repeated, generation after generation in which variants make many differences (never precisely repeated), before one genetic variant replaces another. A variant’s fate is determined by its overall effects relative to the alternatives. It is not a simple story, and a story unknowable for most details that made a difference, but it is the cause of why organisms do the things that they do, rather than something different. ‘Genotype determines phenotype’ is a much simpler tale of molecular mechanisms. It dominates research and funding, but there is much that it leaves unexplained.

All parts work together in a well-crafted sentence. The combination of meiotic randomization with repeated trials has similarities to back-propagation methods used to assign ‘credit’ in the training of the deep-learning networks of artificial intelligence. Under back-propagation, the adjustment of nodal strength is achieved by linear estimation of a node’s contribution to successful performance as assessed by the training mechanism. A detailed knowledge of the connections of every node in a network gives little insight into how the network achieves what it does. Functionalities cannot readily be ascribed to individual nodes or localized parts but are distributed across the network. Natural selection similarly rewards additive contributions to fitness of the genetic parts of highly non-additive networks. How these networks perform their adaptive

functions and how individual parts contribute to organismal performance are likely to be difficult to understand, even with complete knowledge of the connections.

Artificial intelligence teaches difficult lessons. Deep-learning performs impressive feats of interpretation by transparent mechanisms for obscure reasons. The opacity of how these networks achieve what they do is a cautionary tale for systems biologists who want to make sense of a cell by describing all the connections and interactions of its genetic and biochemical networks. And it is also a cautionary tale for adaptationists who want to understand the genetic substrate of adaptive features. A difference of coat color may be readily assigned to a genetic difference in a pigmentation pathway but the genetic contributors to more complex adaptations are probably broadly distributed across gene regulatory networks and participate in many other complex adaptations. Knowing the network may provide less understanding than is hoped or hyped.

The training of artificial intelligences involves recursive adjustment of connections of ready-formed networks, comparable in some respects to learning in a single lifetime. Organisms, on the other hand, form by developmental recursion. Form is generated anew each new generation. There must be an hereditary record of past choices of nature or all would be lost. This is the role of genes. They are the persistent presence of what worked in the past. Genes are *formal causes* of what makes organic materials one kind of organism rather than another. The environmental contingencies that wrote the genetic record of past successes are an organism's *final causes*. They determine what an organism is good at doing.

Purposeless processes of formless materials produce purposeful material forms as specified by the textual record of past choices of nature. Genes are the texts of nature that give form to the phenotypic performances of living things. This is not the strawman of genetic determinism: not all that goes into a successful performance of *Hamlet* can be found in Shakespeare's text. Genetic texts are neither sacred nor unchangeable. DNA synthesis is non-selective quotation with occasional misquotation. Negative selection removes corruptions of meaning by mutational misquotation, but the precise wording drifts with unintended slips of the pen, and meaning evolves by positive selection as rare slips of the pen are tested and found good in the changing environment of critical reception of the text (Haig 2020).

Many arguments in evolutionary theory are disagreements about how to interpret what others have written. The underlying arguments can be difficult to follow beneath the blizzard of words. Hard-minded experimentalists say theoreticians are not doing real science, but experimentalists' interpretations of the outcomes of their experiments are often shaped by unquestioned philosophical commitments. The modern debate between advocates of EES and SET reveals unresolved tensions in biology. This essay evolved as I grappled with texts from more than a century of debate, some in a language I know poorly: Why does Kevin Laland deny functions are causes but favor directed variation? Why did Karl von Baer warn against teleophobia but oppose Darwinism? As a man with a hammer, I have pounded these puzzling protrusions by asking what they reveal about the authors' underlying teleological commitments. Each reader will judge whether I have hit these nails on the head. Every workman prefers her own tools.

The hypertextuality of evolutionary debates is no coincidence. We have evolved from a world of matter in motion—of material and efficient causes obeying physical laws—to a living world of information, meaning, and purpose; a world of goal-directed beings that obey the letter of physical law but not in spirit. Biology cannot

do without concepts of purpose and goal, although some biologists twist their prose into knots to deny what they do in practice. The meaningful features of life are difficult to quantify: attempts to mathematize meaning are often changing the question. One of the final metaphors of *From Darwin to Derrida* identifies natural selection as a poet who means many things at once. An organism and a long non-coding RNA make sense in many ways. The poet tries the mutations finding words that work.

Telos—the reciprocal relation of purpose and goal, of *Zweck* and *Ziel*—is the distinctive feature of life, grounded in the recursive relations of phenotypes and genotypes and of chickens and eggs. Making sense of the poetry of life will not be easy. “Hypothesizing about adaptive rationales is easy to do badly, and difficult to do well” (Welch 2017). This is hard science. It is time we cured our teleophobia and worked together to develop and evolve a predictive and explanatory teleology of life. We should interpret each other’s arguments kindly. We have a choice of hammers.