Introduction to Turing’s 'The chemical basis of morphogenesis'

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Introduction

In this issue of E:CO we are reprinting the ground-breaking mathematical/chemical model of morphogenesis formulated by the remarkable English mathematician Alan Turing in the early nineteen-fifties. In parallel to John von Newman, Turing had pioneered the creation of the modern programmable computer possessing data storage capabilities. Turing’s highly innovative approach to computation and computational devices reveal his rare type of genius that could render arcane mathematical abstractions into practical “hands-on” applications. The attached classic paper from Turing is a prime example of his prodigious intelligence for it shows Turing not only uncovering deep and unprecedented insights into what was for him new disciplines (chemistry and biological morphogenesis) but along the way demonstrating how the emergence of novel order can about in complex systems.

Turing had achieved mathematical immortality for the incredible feat of leading the effort to crack the notorious Enigma code used by the German Navy (particularly U-boats) to wreak death and destruction in the North Atlantic and North Sea (see¹; and the recent film Enigma). Turing’s work on the Enigma revealed his inimitable expertise in higher level statistics, recursive functions, number theory, abstract algebra, mathematical logic and other relevant but recondite arenas of mathematical and logical abstractions.

Turing’s earlier work on computability built upon but then transcended Gödel’s 1931 incompleteness theorems and their connection to the Entscheidungsproblem (decision problem) originally posed by German mathematician David Hilbert in 1928. Hilbert’s framing of the issue and Turing’s solution of it went on to play an incalculable role in the further development of mathematical logic, number theory, and the origins of the entire field of computational complexity theory (and its famous issue of whether P = ¬P, that is whether there is a decidable procedure, i.e., an algorithmic approach, whereby every problem that is checkable by a computer in a sufficiently rapid fashion can be solved by the computer in a sufficiently rapid fashion). Turing proved that his “universal computing machine” would be capable of performing any conceivable mathematical computation if it were representable in terms of recursive functions.

But he went on to prove that there was no solution to the decision problem by first showing that the halting problem (Martin Davis’s later term) for Turing machines is undecidable, that is, it is not possible for all conceivable problems to decide algorithmically ahead of time whether a Turing machine will ever halt when given the specific problem. The artificial life researcher Vince Darley has recently shown a deep tie of the halting problem with the unpredictability of emergent phenomena.

Turing had for quite a while been interested in debunking supra-naturalistic explanations of what he felt were surely natural phenomena. Turing has been particularly taken-up in demonstrating how the morphogenesis observed during embryological development need not invoke either vitalist entelechies (e.g., see⁵) or divine creation as the argument from design for God’s existence would have it. In this project Turing was spurred-on by his friend, the chemist and philosopher Michael Polanyi, who had been invited to deliver the Gifford Lectures of 1951-52 in grand emergentist fashion like Morgan, Alexander, and Whitehead before him (also see ⁷). Polanyi, whose emergentist conceptualizations of “life’s irreducible structure” and emergent levels as constraints had promulgated an argument, based on his own interpretation of the works of Gödel and Turing, which suggested an inviolable realm for organic entities. Yet, Polanyi swerved into neo-vitalism with his declaration that an immaterial force must be at work during gastrulation in order to account for the phenomenon of a groove suddenly appearing in a perfectly symmetrical sphere of cells which then served to differentiate the head and tail ends of the embryo.

But for Turing this could be explained entirely naturalistically as a kind of symmetry-breaking. Turing had even told his student and friend Robin Gandy that what he was trying to do was nothing less than undermine the whole “argument of design” for the existence of God by demonstrating how emergent order could arise out of the internal dynamics of a system itself, what today is usually considered “self-organization”, and thus does not require an order of form outside the system by a “designer⁴ . Turing held that his mathematical perspective could demonstrate just which entirely natural circumstances were required: he demonstrated that a certain mixture of chemicals, diffusing and reacting with each other, forming into a pattern of chemical concentrations that organized cells into a novel configuration.

In our day and age, an example of such Turing pattern making can be found in⁸. These pattern formation processes are known as Turing instabilities since the stationary spatial patterns emerge through an interplay between nonlinearity in the chemical
dynamics and diffusion. Turing's genius was to see that diffusion would play the counterintuitive role of organizing the system in spite of the fact that it usually played the opposite role of smoothing out any inhomogeneity. An inspiration for Turing was D'arcy Thompson's classic *On Growth and Form* which provided mathematical explanations for many patterns found in various fauna and flora although Turing's mathematics was much more sophisticated. Turing was up against quite a difficult challenge, one which Needham had described, "[Thompson's book] was nevertheless, in spite of its mathematical profundity, less difficult in a way than the problem of finding some relation between the gross morphological forms manifested by living things and the specific molecular constitutions which they possess" (Needham's remarks were from 1951 and are quoted in [45]). Turing's mathematical approach went after just this "relation between the gross morphological form" and "the specific molecular constitutions" using variables, parameters, and the processes linking them.

**The emergence of new order**

The pioneering and solitary nature of Turing's pursuit was underscored by the fact that at this time period themes of form and pattern, even structure, were not at the forefront of scientific inquiry, e.g., the impressive achievements of Galileo, Kepler, Descartes, Newton, Faraday, and Maxwell were not directed at form or pattern. This disregard of form and pattern and structure was a factor in the general proto-emergentist distancing away from speculating about *processes* of emergence which would produce new forms.

In Darwinian evolution, morphological considerations were important to the extent that similarity of form could be a sign of common descent while discrepancy of form could be a sign of variations upon which natural selection would operate. But Darwin's theory did not directly address this last missing puzzle of embryology: exactly how did *morphogenesis* result in otherwise homogeneous cells assembling into the heterogeneous patterns found in tissues and organs so disparate in scale and form compared to the cells? Turing was very much taken-up by the beguiling question of why, from a spherically symmetric blastula, some cells formed into a head and others into a tail? Earlier conceptual frameworks such as Spencer's conjectures offered their own idiosyncratic takes on a purported tendency towards greater heterogeneity. But these conjectures remained merely speculative (as William James acerbically said about Spencer: his idea of tragedy was a fact encountering one of his theories).

What was left unaccounted for was why starfish cells "know" to settle into a five-fold symmetry or fir cones assume a Fibonacci pattern. Hodges remarked that in Turing's model, however, a certain tuning of key parameters could lead the system being modeled past a critical point toward less homogeneity and more structure. Indeed, such a sense of discontinuity in the emergence of order has been a recurring theme in emergentist thought although exactly how to interpret it has been subject to some equivocation.

Although Turing's model was hypothetical to the extent it was comprised by a mathematical treatment and not actual chemical experiments, he argued cogently and persuasively that much could be learned about real morphogenesis as his model moved between the concrete and the abstract. Thus, by carefully choosing to represent only very simple conditions in the speculated chemical brew so as to keep the mathematics tractable, Turing narrowed the field to only a few options in each case, winnowing down the possibilities for how instability and ensuing symmetry-breaking could occur. That is why he deliberately selected those conditions that could be represented by *linear* equations, what he termed his "linearity assumption", i.e., conditions that remained very close to initial homogeneity or equilibrium. Yet, he also recognized that nonlinear reaction-rate equations might be more realistic so he offered a few suggestions in that direction as to the qualitative nature of the outcomes. Nevertheless, Turing managed to avoid the much more difficult arena of nonlinear equations, at the end just mentioning they would be needed to further investigate such phenomena as phyllotaxis or the manner by which stems and leaves whorl around a central stem in a spiral pattern.

Although convention had it that the process of diffusion of chemical concentrations served more to maintain homogeneity or symmetry rather than break it (in that way displaying the usual continuity-oriented differential equation model of change), Turing's approach proposed a *diffusing instability* that brought about novel order through the *breaking of symmetries*. In particular, using sets of linear differential equations (ordinary and partial), Turing suggested how instabilities could arise as a system moved away from equilibrium: "If a rod is hanging from a point a little above its center of gravity, it will be in stable equilibrium. If, however, a mouse climbs up the rod the equilibrium eventually becomes unstable and the rod starts to swing." Similarly, an unstable condition brought about by differences in diffusion rates of the catalyzing agents would result in the system moving away from homogeneity and equilibrium, i.e., symmetrical conditions, towards inhomogeneity and nonequilibrium, i.e., symmetry-breaking which is equivalent to the onset of new order. We'll come back below to the closeness of Prigogine's lexicon and theoretical operations in his approach to the arising of order in dissipative structures.
Pointing out that while, under stable conditions, deviations from perfect symmetry would exist plentifully yet not lead to symmetry-breaking, Turing realized he had to show how conditions of instability could arise whereby the initial symmetry would be broken through an amplification of these same deviations similar to what happens in electro-magnets when rotational symmetry is broken in the presence of a magnetic or electrical field resulting in a directional alignment. Yet, Turing was also aware that instability in the form of an unstable equilibrium was not something typically entertained: “Since systems tend to leave unstable equilibria they cannot often be in them. Such equilibria can, however, occur naturally through a stable equilibrium changing into an unstable one”. Turing knew he had to confront a bias against conceiving instability as a natural occurrence and he applied his mathematical treatment to argue against this bias.

**Turing’s model and self-organization**

In her thorough and insightful account of the origin of the notion of self-organization, the celebrated scientist and science historian Evelyn Fox Keller traces one stream of the conceptualization of self-organization to Prigogine’s turn to Turing’s reaction/diffusion model. Prigogine and his student Gregoire Nicolis published a paper in 1967, “On Symmetry-Breaking Instabilities in Dissipative Systems”, the title alone revealing the strong influence of Turing’s much earlier pioneering work. Their paper translated fluid dynamics vocabulary into the language and principles of thermodynamics, in particular the so-called far-from-equilibrium condition. Initially, they didn’t explicitly link their work to nonlinearities or bifurcations in dynamical systems as the Russians had done but instead focused on, according to Keller, an attempt “to unify Turing’s reaction-diffusion patterns with spontaneous structures observed in fluid dynamics under the category of dissipative structures and to draw out some rather striking and large implications” (p. 10). Keller points out that Prigogine and Nicolis were “confident” their work on instabilities went far beyond the morphogenetic problem discussed in Turing’s earlier paper.

Keller says that to her knowledge the first time the term “self-organization” appeared in this context was on page two of this paper of Prigogine and Nicolis where it was introduced as an aside, the term being a synonym for “the spontaneous formation of dissipative structures”, or, more specifically, for the emergence of such structures in low-entropy, far-from-equilibrium systems (p. 10). But by 1974 they had incorporated the language of dynamical systems such as bifurcation and so on. Isabelle Stengers, the Belgian philosopher and protégé/coauthor of Prigogine, claims that Prigogine began talk of “self-organization” in his dissipative structures was because he frequented the company of embryologists at the University of Brussels in the early fifties and had gone to at least one of Turing’s lectures on self-organization. Although the German physicist Hermann Haken, whose School has worked in parallel to the Prigogian School, pushed for an analogy to phase transitions in the emergetics of order he studied, “dissipative structure” was used by Prigogine. However, Keller has pointed out that before Prigogine, the term was found in a paper by Gregory H. Wannier (1953), “The Threshold Law for Single Ionization of Atoms or Ions by Electrons”. But after 1967, Keller remarks the term had become so closely associated with the Prigogine school it might as well be taken as its trademark.

According to Keller, another important landmark in the history of “self-organization” was the publication in 1971 of Manfred Eigen’s extensive monograph on “Self-organization of Matter and the Evolution of Biological Macromolecules”. Eigen awarded the Nobel Prize for chemistry in 1967 for his work on high speed chemical reactions, here turned his attention to biology, specifically to the problem of the emergence of large macromolecules (like DNA) in the origin of life. He explicitly referred to the work of Prigogine and Nicolis on instabilities in the vicinity of far-from-equilibrium steady states, but he drew an important distinction: “The type of organization we need at the beginning is not so much organization in physical (i.e., geometrical) space. We need functional order among a tremendously complex variety of chemical compounds... We need organization in a different space, “which one may call information space” (Eigen was here quite prescient considering the current mania for information-based theories; p. 30).

Eigen focused directly on the recent findings of molecular biology and asked how such a complex informational molecule as DNA, and such a sophisticated relation to protein synthesis as suggested by the genetic code, might ever have arisen in the first place. Although Eigen obviously did not solve the problem, he made two crucial contributions that appeared in all subsequent discussions of the topic: first, he discovered the “error catastrophe” (i.e., the limit that the need for fidelity in replication placed on the size of nucleic acid molecules that might spontaneously evolve), and second, he developed the idea of hypercycles (referring to a doubly autocatalytic system in which the synthesis of two molecules is mutually reinforcing). This model had its difficulties but generations of future researchers were inspired to improve upon it.

Eigen’s name may not be as well known today as Prigogine’s, but his work was influential, certainly sufficient so as to draw serious scientific attention to the new context in which Prigogine had begun to use the term self-organization, whether or not the focus was the origin of life. In this context it is interesting to note that in June 1971 shortly before his papers appeared in *Naturwissenschaften*, Eigen presented his work at the Third International Conference on Theoretical Physics and Biology, held in Versailles (p. 31). Prigogine, Nicolis, and Hermann Haken were all in attendance. Keller insists that Haken would have surely recognized a connection between his own interest in cooperative phenomena in nonlinear systems and those of Eigen as well as Prigogine. But his focus was neither on the origin of biological macromolecules nor on thermodynamics; rather, he aimed to forge a new discipline linking nonlinear dynamical systems with statistical physics and, relatedly, linking what Prigogine and Nicolis had called “symmetry breaking” with phase transitions.
This approach, of course, was Haken’s “synergetics” (p. 32). In 1972 Haken organized the first of a series of workshops on synergetics (subtitled “cooperative phenomena in multicomponent systems”), and in 1975 he published an extensive review of his work, thus predating the 1977 publication of Prigogine’s and Nicolis’s *Self-Organization in Nonequilibrium Systems: From Dissipative Structures to Order through Fluctuations*. Indeed, in the same year Haken published Synergetics, *An Introduction: Nonequilibrium Phase Transitions and Self-Organization in Physics, Chemistry and Biology* Keller points out that the subject matter of both books was “strikingly similar” with the exception of Haken’s description of lasers as one of his main foci for research. In the wake of these two publications things took off quickly with self-organization, the beginning of a spike in papers using the term self-organization in 1977. Keller suspects that the explosive growth of this literature is why some have claimed a scientific revolution was in the offing around the idea of self-organization.

**Conclusion**

Although Turing’s paper came out in 1952, it did not elicit many citations until well into the nineteen seventies when the number of citations began to soar. Furthermore, evidence of Turing-type patterns in actual experiments didn’t occur until 1989.

According to the late physicist Alwyn Scott (2007), who was instrumental in advocating nonlinear science as a cornerstone for the study of complex systems, the kind of reaction/diffusion dynamics Turing demonstrated are now being observed among a wide range of collective biological phenomena including cardiac tissue, intercellular calcium waves during muscle contraction, pressure waves in the gastro-intestinal tract, slime molds, and mushroom rings.\(^6\)

David Depew and Bruce Weber (1994) point out in their history of the theory of evolution, Turing’s mathematical/chemical model of the emergence of novel order encouraged theoretical biologists to consider the possibility that the emergence of new forms need not be dependent entirely on “what natural selection has haphazardly assembled”\(^17\). Instead, novel forms could be brought about by dynamical properties applicable to any system possessing interacting components, i.e., out of the collective action of “lower” level entities.

**References**