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Historia Mathematica 43 (2016) 49–64

HISTORIA MATHEMATICA

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After 1952: The later development of Alan Turing's ideas on the mathematics of pattern formation

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Available online 16 May 2015

Abstract

The paper 'The chemical basis of morphogenesis' [*Phil. Trans. R. Soc. Lond.* B **237**, 37–72 (1952)] by Alan Turing remains hugely influential in the development of mathematical biology as a field of research and was his only published work in the area. In this paper I discuss the later development of his ideas as revealed by lesser-known archive material, in particular the draft notes for a paper with the title 'Outline of development of the Daisy'.

These notes show that, in his mathematical work on pattern formation, Turing developed substantial insights that go far beyond Turing (1952). The model differential equations discussed in his notes are substantially different from those that are the subject of Turing (1952) and present a much more complex mathematical challenge. In taking on this challenge, Turing's work anticipates (i) the description of patterns in terms of modes in Fourier space and their nonlinear interactions, (ii) the construction of the well-known model equation usually ascribed to Swift and Hohenberg, published 23 years after Turing's death, and (iii) the use of symmetry to organise computations of the stability of symmetrical equilibria corresponding to spatial patterns.

This paper focuses on Turing's mathematics rather than his intended applications of his theories to phyllotaxis, gastrulation, or the unicellular marine organisms *Radiolaria*. The paper argues that this archive material shows that Turing encountered and wrestled with many issues that became key mathematical research questions in subsequent decades, showing a level of technical skill that was clearly both ahead of contemporary work, and also independent of it. His legacy in recognising that the formation of patterns can be understood through mathematical models, and that this mathematics could have wide application, could have been far greater than just the single paper of 1952.

A revised and substantially extended draft of 'Outline of development of the Daisy' is included in the Supplementary material.

Résumé

L'article unique et célèbre d'Alan Turing 'The chemical basis of morphogenesis' [*Phil. Trans. R. Soc. Lond. B* **237**, 37–72 (1952)] reste encore aujourd'hui très influent dans l'essor de la biologie mathématique. Ici, je discute les développements ultérieurs des idées de Turing révélées par des documents d'archives moins connus, en particulier son projet d'article intitulé 'Outline of development of the Daisy'.

Ces documents, replacés dans l'oeuvre mathématique de Turing sur la morphogénèse et la formation de motifs, témoignent d'avancées majeures qui vont bien au-delà de l'article de 1952. En effet, Turing aborde dans ses notes des équations différentielles sensiblement différentes de celles de 1952 qui constituent un problème de mathématique d'un abord beaucoup plus complexe.

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http://dx.doi.org/10.1016/j.hm.2015.03.003

Embrassant ce défi, Turing propose (i) une description des motifs réguliers sous la forme de modes de Fourier et de leurs intéractions non-linéaires, (ii) la construction de l'équation modèle bien connue de Swift et Hohenberg, publiée 23 ans après la mort de Turing, et enfin (iii) l'utilisation des propriétés de symétrie de ces équations d'évolution afin d'organiser et de simplifier les calculs nécessaires à l'étude de stabilité des équilibres symétriques correspondant aux motifs spatiaux.

Dans cet article, l'accent est porté sur les mathématiques de Turing et non sur les applications de ses théories à la phyllotaxie, la gastrulation, ou encore sur la morphogénèse des organismes marins unicellulaires comme les *Radiolaria*. On y montre en particulier que Turing s'est confronté à de nombreux problèmes ardus qui sont devenus dans les décennies suivantes des questions majeures en recherche mathématique, ce qui démontre une fois de plus un niveau de compétence technique hors norme qui était clairement à la fois bien en avance sur son temps, mais aussi indépendant de celui-ci. En reconnaissant que la formation de motifs peut se comprendre grâce à des modèles mathématiques, aux vastes champs d'application, il est évident que l'héritage de Turing aurait pu être beaucoup plus important que celui de son papier de 1952.

Une reproduction sensiblement révisée et complétée de son ébauche d'article 'Outline of development of the Daisy' est incluse en annexe.

MSC: 01A60; 35K57; 92C15; 92C80

Keywords: Morphogenesis; Nonlinear dynamics; Mathematical biology; Reaction–diffusion theory

1. Introduction

Alan Turing made outstanding contributions in many mathematical fields, perhaps most notably in the foundations of modern computing. His wide ranging published work, together with some lesser-known, and in some cases incomplete, manuscripts, is contained in the four volumes of his Collected Works (Turing, 1992a, 1992b, 1992c, 2001). Most biographies have, naturally, emphasised his contributions to digital computing and their origins in Turing's work at Bletchley Park during the Second World War. His work on morphogenesis (the emergence of biological structure) is less emphasised, and indeed the relevant volume (Turing, 1992c) of his Collected Works contains only a single published paper on the subject. However, this single paper (Turing, 1952), with the title *The chemical basis of morphogenesis*, and referred to below also as *CBM*, has assumed a central place in its field and has been cited over 4500 times.[1]

The key insight of *CBM* was that a model system of two reacting chemicals could generate spatial patterns when diffusion of the chemical species was allowed, under conditions in which the same two chemicals would not generate patterns if diffusion were prohibited. Thus the process of diffusion, which one might expect always led to smoother evolution of chemical concentrations, and therefore relaxation of the concentration fields to uniform values, could, in some circumstances, lead instead to an instability of this uniform state and the development of patterns. The wavelength of these patterns is given by algebraic combinations of the reaction and diffusion coefficients that describe the behaviour of the chemicals and hence the 'chemical wave-length' is an intrinsic property of the system. In spatial domains that are sufficiently large, this 'chemical wave-length' plays a key role in organising the resulting patterns and their dynamics.

This key insight has, as is evidenced by the citation count of *CBM*, driven an enormous interest and volume of research into mathematical models for mechanisms that could drive biological pattern formation.

However, not only did Turing's interest in morphogenesis continue to develop after the publication of *CBM*, but his later, lesser-known, work uses rather different mathematical models and requires substantially more computation (both algebraically by hand and numerically by computer) than that presented in *CBM*.

This article has two central aims. First, to review, from a mathematical perspective, these later developments in Turing's work on morphogenesis, and, as far as possible, trace the mathematical con-

[1] As at August 2014, according to the Thomson Reuters Web of Science citation index.