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

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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 & 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 an Appendix.

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 de ses idées que révèlent des documents d'archives moins connus, en particulier son projet d'article intitulé 'Outline of development of the Daisy'.

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

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 & 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 inclus en annexe.

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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,b,c, 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 4,500 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 wavelength' 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 connections between *CBM*, the lesser-known manuscripts *A diffusion reaction theory of morphogenesis in plants* (Turing and Wardlaw, 1992) and *Morphogen theory of phyllotaxis Parts I - III* (Turing, 1992d) (abbreviated to *MTP I – III*) for which coherent typescripts exist[2], and the lesser-known and far less coherent notes that start with the title *Outline of development of the Daisy* (Turing, 1992e) (abbreviated to *ODD*). Access to the original archive material for all these manuscripts is greatly facilitated by the scanned manuscript collection made available online in the form of the Turing Digital Archive (`http://www.turingarchive.org/`). A comprehensive review of the biological strands of the development of Turing's thought, concentrating in particular on phyllotaxis and *MTP I* and *MTP II*, has been given previously by Swinton (2004, 2013b). Turing's contributions in this area are set in a longer historical context in the popular science account by Ball (2009). See also the discussions by Allaerts (2003) and Sanchez Garduno (2013). In the present article I attempt to show that the mathematical demands of the model proposed in *MTP II*, and further investigated in *ODD* are far in excess of those required to understand the published paper *CBM*. Turing would certainly have seen this, and perhaps he had a growing realisation that his investigations would lead to substantially more lengthy articles for publication. Given this, it is not a surprise that this work remained unfinished, moreover, the notes that remain relating to *ODD* are nowhere near in final form: they are much more likely to be interim summaries of individual ideas that would need to be combined at a later point into a narrative that would form a coherent paper, or perhaps a set of papers, along the lines of *MTP I – III*. Supposing that the typeset manuscript pages contained in the Turing Archive at King's College, Cambridge are only sets of draft pages that may well not relate directly to each other might justify, for example, why these pages (at least as far as they have been reconstructed), despite the title of the first page, contain no direct discussion of daisies!

The second aim is to point out the development of mathematically related ideas in fluid dynamics, of which Turing appears to have been unaware. These developments, from the period 1916 – 1940 were in fact the strands that motivated work in the 1950s and after, and which tend to be cited as the original manifestations of ideas that are widely used in modern applied mathematics. It is not difficult to imagine that if the ideas in the draft pages of *ODD* had been developed into a coherent manuscript for publication, then Turing would be associated with initiating far more in applied mathematics than just the idea of diffusion-driven instability outlined in *CBM*.

1.1 The chemical basis of morphogenesis

CBM (Turing, 1952) was received for publication by the Royal Society on 9 November 1951 and appeared in print on 14 August 1952. Although *CBM* is a mathematical paper, Turing took care to write it so that it is widely scientifically accessible. He explicitly keeps the required level of mathematical preparation as low as possible, and from the first paragraph onwards is clear to point out that he makes no claim that his model contains sufficient biological detail to be at all biologically correct. However, Turing clearly has a number of specific biological examples in mind, as the list given in his letter to the physiologist J.Z. Young dated 8 February 1951[3] indicates

> At present I am not working on the problem [of the relation between the logical and physical structure of the brain] at all, but on my mathematical theory of embryology, which I think I described to you at one time. This is yielding to treatment, and it will so far as I can see, give satisfactory explanations of -
>
> (i) Gastrulation
>
> (ii) Polygonally symmetrical structures, e.g. starfish, flowers
>
> (iii) Leaf arrangement, in particular the way the Fibonacci series (0,1,1,2,3,5,8,13, ...) comes to be involved.
>
> (iv) Colour patterns on animals, e.g, stripes, spots and dappling.
>
> (v) Pattern on nearly spherical structures such as some Radiolaria, but this is more difficult and doubtful.
>
> I am really doing this now because it is yielding more easily to treatment.

Hence it is not surprising that *CBM* contains a variety of comments (in sections 11, 12 and 13) on dappled colour patterns, gastrulation and phyllotaxis problems to which the theory outlined earlier in the paper might apply. But there are hints also that Turing's plans for further work on these problems involves mathematical and numerical computation as well as more detailed study and discussion of these biological situations. For example, section 13 is headed 'Non-linear theory. Use of digital computers' and holds out the hope that one could study not just the initiation of pattern formation but also transitions between patterns of different kinds. The penultimate paragraph of *CBM* contains the words (italics in the original)

> The difficulties are, however, such that one cannot hope to have any very embracing *theory* of such processes [i.e. transitions between patterns], beyond the statement of the equations. It might be possible, however, to treat a few particular cases in detail with the aid of a digital computer. ... The essential disadvantage of [this] method is that one only gets results for particular cases. But this disadvantage is probably of comparatively little importance. Even with the ring problem, considered in this paper, for which a reasonably complete mathematical analysis was possible, the computational treatment of a particular case was most illuminating. The morphogen theory of phyllotaxis, to be described, as already mentioned, in a later paper, will be covered by this computational method. Non-linear equations will be used.

So the conclusion from *CBM* appears to be that later work will

(i) consist of numerical computation for specific examples rather than general mathematical theory,

(ii) focus on the phyllotaxis problem, and

(iii) use nonlinear equations.

To take the last of these points first, it should be pointed out that *CBM* essentially considers linear differential equations throughout. Naturally enough, Turing does begin with a model in which chemical reaction terms are nonlinear, but the analysis proceeds by assuming that the concentrations are close to equilibrium, and that only small departures from equilibrium need to be considered. The resulting equations for these small disturbances are therefore taken to be linear. This reduction to a linear problem is a central idea in modern applied mathematics: many physical phenomena arise as linear instabilities, and those that do not, such as the transition to spatiotemporal complexity in shear flows observed and reported by Reynolds (1883) (over sixty years earlier) are substantially harder to understand mathematically. Certainly Turing realised that the mathematical techniques he had available from the previous century (such as Fourier series) equipped him much better to deal with linear equations than nonlinear ones. This realisation naturally links to the first point: that numerical computation would be a better and more feasible approach to dealing with nonlinear equations should they be necessary. Moreover, given the lack of available theory, it would perhaps make sense to begin by computing, and therefore to deal only with one specific problem since the results of computational runs would be prone to delays caused by human and machine error and therefore relatively slow to arrive.

1.2 Morphogen theory of phyllotaxis

And so to point (ii) above and the phyllotaxis problem. On the phyllotaxis problem it is much clearer where Turing's work went due to the manscript *Morphogen Theory of Phyllotaxis* in three parts (*MTP I – III*), contained in the *Collected Works* (Turing, 1992c) and reprinted in the later volume (Cooper & Van Leeuwen, 2013), pages 773–826. Of these three parts, the first part (*MTP I*) is primarily concerned with geometrical relations between lattices and the spiral arrangement of leaves or florets, generally referred to as geometric phyllotaxis. In particular the selection of lattices that result in 'parastichy pairs' that are adjacent members of the Fibonacci sequence. *MTP II* changes focus, and describes in very general terms a formulation of chemical reactions for morphogens that might be able to generate phyllotactic patterns. Section 2 of *MTP II* lists three 'principal assumptions'. The last of these assumptions is that 'The only wavelengths which are significant are those which are either very long or fairly near to the optimum'[4]. It is unfortunate that there appears to be no clear statement, either in *MTP* or *ODD* as to why these two collections of wavelengths are significant and not others, or indeed not just one of these collections alone. I comment further on this below.

After subsequent simplifications and the addition of nonlinear (quadratic) terms (which, according to the second principal assumption in section 2 of *MTP II*, are are assumed to be important yet thought of only as 'perturbations' to the linear terms), Turing arrives the equations[5]

$$\frac{dU}{dt} = \phi(-\nabla^2)U + GU^2 - HUV \tag{1}$$

$$V = \psi(-\nabla^2)U^2 \tag{2}$$

This model describes the combined evolution in time of two chemical concentrations that depend on space and time: $U(\mathbf{x}, t)$ and $V(\mathbf{x}, t)$ through the processes of diffusion and reaction. However U and V play distinguished roles, quite different to the pair of chemicals imagined in *CBM*.

Section 3 of *MTP II* contains the remark:

> 'According to the point of view in which V represents the concentration of a diffusing poison, the organism is sufficiently small that the poison may be assumed to be uniformly distributed over it. The function U, on the other hand, must be a *linear combination* of diffusion eigenfunctions all with the same eigenvalue, or, in other words, waves with the same wavelength.'

(where the italics have been added for emphasis and are not present in the original).

So U in fact represents a *combination* of the two chemical substances envisaged in *CBM* that generate the pattern-forming instability, while V, completely separately, acts on long spatial scales to (in some sense) regulate the pattern, by 'poisoning' it. In *CBM* Turing described the chemical substances X and Y as 'morphogens' with the explicit idea that these corresponded to the diffusing 'evocators' proposed by Waddington (1940). As such, the chemical concentrations of X and Y were each described (in the spatially continuous setting described in section 7 of *CBM*) by a diffusion equation, i.e. a differential equation having a first order derivative in time, and a second order derivative in space. However, in the system of equations (1) - (2), the U equation has a first order derivative in time, and the complicated spatial operator $\phi(-\nabla^2)$ which, as we see later in *ODD*, Turing clearly supposes is fourth order in space, not second order (as it contains two ∇^2 terms). Moreover, the V equation has no time derivative term at all: V responds immediately to the behaviour of U rather than evolving independently. For these reasons, it is clear that U and V have distinguished roles in these equations.

It is tempting to view these distinguished roles of U and V in the light of comments in Turing's unpublished paper with the biologist C.W. Wardlaw, with the title *A diffusion reaction theory of morphogenesis in plants*[6] (Turing and Wardlaw, 1992; Wardlaw, 1953). In that paper the discussion of morphogen chemistry is couched in terms of two chemical morphogen species X and Y that are produced in autocatalytic reactions that are catalysed by a third chemical C referred to as a 'catalyst-evocator' in a nod to earlier work by Waddington (1940) referred to in sections 1 and 10 of *CBM.* The catalyst C is therefore involved in driving the linear instability from which the pattern emerges, in contrast to the role of the chemical V in (1) - (2) where V controls the amplitude of the final pattern produced, rather than controlling the parameter value at which the instability is initiated. However, there is a similarity in the way that the pattern forming process is thought of as being part of a larger set of processes, and the pattern is affected (in different ways) by the existence of interactions with additional chemical species. Clearly, the pattern formation instability, as expressed by the diffusion-reaction equations set out in *CBM*, is only one feature of the behaviour that can be generated by such chemical reactions, and Turing's thoughts range over a number of different settings in different papers.

MTP III is concerned principally with constructing solutions to equations (1) - (2) when they are posed on the surface of a sphere. *MTP III* (written with B. Richards) has in mind application of these equations to explain the form of (spherical) 'small organisms' such as Radiolaria. Hence *MTP III* is primarily concerned with the details of an expansion of the fields U and V into sums of spherical harmonics, which is specific to this problem rather than to the planar (or, more correctly, cylindrical) description of phyllotaxis. On a mathematical level, *MTP III* is concerned with finding equilibrium solutions to the equations (1) - (2) containing spherical harmonics of different degrees: these correspond to organisms whose departures from sphericity preserve different amounts of symmetry. The parts of *MTP III* that are preserved note that 'a finite number of essentially inequivalent solutions' arise, but details of the solutions that exist for different combinations of parameter values are not given, neither is the stability of these equilibria investigated.

In contrast, *'Outline of development of the Daisy'* appears to represent a continuation of the line of thought in *MPT* that proposes (1) - (2) as a model of pattern formation, and considers it in the geometrically simpler case of a planar geometry rather than a spherical one. With this geometrical simplification, Turing is able to make significantly greater mathematical progress; I now discuss the contents of *ODD* in greater detail.

2 Outline of development of the Daisy

In this section I discuss the source material for *ODD*, in terms of both the style and appearance of the manuscript and the mathematics contained in the various fragments that appear relevant. The archive of Turing's papers kept by King's College Cambridge contains two folders of draft notes that contain material relevant to morphogenesis: AMT/C/24 and AMT/C/27. The first 15 pages of folder 24 appear to be consecutive typed pages of a paper, with the title *'Outline of development of the Daisy'* given on the first page. The pages were not numbered by Turing, but in pencil additions by Robin Gandy, Turing's executor, to whom he left his collected unpublished notes and papers. As Swinton remarks in his Editorial Note that precedes his updated version of *ODD* (Turing, 2013), these 15 pages contain more material than is present in the *Collected Works* (Turing, 1992c) and this latter volume presents material in a different ordering to the pencilled numbering given by Gandy. Inspection of the material seems to indicate, firstly, that there are few clues in the text to a definitive ordering: for example the section numbers given by Turing (2013) are editorial additions, and the text does not on the whole read as a smoothly connected development of ideas as is the case in Turing's completed manuscripts. To give a number of examples:

1. The manuscript begins in abrupt fashion, stating the assumptions (which are 'by no means always satisfied' [7]) but without any reference to previous work, either *CBM* or the paper prepared with Wardlaw (Turing and Wardlaw, 1992).

2. The second section 'Considerations governing the choice of parameters' [8] makes no reference to *MTP II* which it clearly draws on.

3. The second section lists five assumptions labelled (i) to (v), but points (ii) and (v) confusingly both contain a coefficient labelled I_2; I_2 clearly has a different role in each of these cases.

4. Later, although it seems clear that the pages as numbered by Gandy and given by Turing (2013) follow on well from one to the next, page 10 [9] introduces a functional form for $\psi(\nabla^2)$ which does not immediately appear consistent with what has gone before. Further anomalies are that on page 7 [10] the typescript introduces a parameter r_{max} that is undefined, states 'with r_{max}/k_0 usually about $1/\sqrt{2}$' [11] which does not make sense on dimensional grounds (because r_{max}/k_0 has units of length squared it is not a pure number), and contains the parenthetical but unexplained comment '(This function calculated in 'Subgroup smooth')' [12].

Taking these observations together, I therefore contend that certainly by page 10 of the typed manuscript, as numbered by Gandy, the text has subsided into a more informal style than that which the opening pages sustained. Moreover, the typescript contains mathematical errors that surely Turing would have corrected before sending a final manuscript for publication. Swinton's text follows exactly the page numbering given by Gandy, and continues up to page AMT/C/24/15 (numbered as page 12 by Gandy). From consideration of the manuscript pages it does not seem possible to conclude that the ordering given by Gandy is at any point clearly incorrect. It seems hard to sustain the version given by Saunders in the *Collected Works* (Turing, 1992c) which assembles these manuscript pages in the following order: AMT/C/24/4,5,6,7,8,10,11,14,13. The omission of archive page AMT/C/24/12 is particularly curious.

Overall, the impression that the reader forms is that these notes are not the final form of a manuscript, but an intermediate set of working papers from which a coherent manuscript will be typed up at a future point. If this premise is accepted, then it becomes valid to examine the remainder of the archive material to see if additional material is available that, despite not obviously forming a continuation of the manuscript, at least forms a continuation of the thread of mathematical development that these pages begin.

The central contention of the present paper is that such material does exist further through folders AMT/C/24 and AMT/C/27, and that these notes contain new ideas which show Turing's thoughts developing along substantially more complex lines than illustrated by *CBM*.

What should be expected in any continuation of *ODD*? A clear indication is given at the end of the introductory part of the text[13] where Turing writes

> a partial differential equation will be obtained ... The choice of parameters is largely made on theoretical grounds ... but ... it is necessary to follow its behaviour by computation.

In other words, after proposing a complicated differential equation as a model, theoretical work will justify the choice of particular parameter values used in the model. Then numerical computation will show that the equation is able to generate patterned solutions of the kind required. The most obvious initial continuation is therefore the typed pages AMT/C/24/27–29 that begin with the heading 'The equation chosen for computation'. These contain slightly more general equations than are present earlier in *ODD*[14] in order that Turing can explain the choice and construction of the operators $\phi(\nabla^2)$ and $\psi(\nabla^2)$ that are supposed to take various forms earlier in the *ODD* manuscript.

This discussion also confirms that a major, but perhaps not immediately obvious, mathematical problem with the earlier equations, i.e. (1) - (2) as stated, is only a typographical error rather than a more major oversight on Turing's part. Specifically, as Turing writes on page AMT/C/24/27, 'The essential property required of the function ϕ is that it should have a maximum for some real (negative) argument...', i.e. the function ϕ ensures that U describes a patterned solution at the linear level, with the second morphogen V modifying the amplitude of U, but not directly driving the pattern forming instability. On page AMT/C/24/28, Turing combines the equations for U and V together into a single equation for U that corrects the mathematical issue present in the earlier definitions of $\phi(\nabla^2)$[15]. The resulting equation on page AMT/C/24/10 has the same linear terms as a reduced model for the problem of the onset of thermal convection in a layer of viscous fluid; although physically quite different from the chemical morphogen dynamics that motivated Turing, it is striking that developments in this area were taking place at the same time as *ODD* was being drafted. This discussion will be developed in the next section of this paper. For the moment I note that Turing's equation on page AMT/C/24/10 has a very strong resemblance to what is now called the 'Swift–Hohenberg equation' in the pattern formation literature (Swift & Hohenberg, 1977; Cross & Hohenberg, 1993; Hoyle, 2006). This resemblance is reinforced on later pages in the manuscript.

Having sifted folders AMT/C/24 and AMT/C/27 to identify material that would have formed later parts of *ODD*, two sets of consecutive pages appear to provide valuable and natural continuation. It is possible that a thorough examination of this material would yield additional material: I do not claim to have reconstructed a definitive version, only an extension of previous versions.

I have identified three sets of consecutive typed manuscript pages that are relevant to *ODD*: AMT/C/24/27–29, AMT/C/24/68–70 and AMT/C/24/72–74. I now comment briefly on these in turn since they form the bulk of the extended material that I propose for *ODD*.

The first of these sets begins with the title 'The equation chosen for computation'. These pages carry out in detail the reduction (by the introduction of new units) that is described earlier, in general terms, on page AMT/C/24/11. It is therefore easy to see these as part of the intended draft *ODD* manuscript, despite the obvious changes of notation (for example K and C_3 are used interchangeably on page AMT/C/24/27).

Pages AMT/C/24/68–70 are also typed manuscript, and begin with the statement that the case $L = 0$ will be considered. The coefficient L does not appear in pages AMT/C/24/4–15 (the version of *ODD* assembled by Swinton) but it does appear in AMT/C/24/28. Together with other indications, it seems most likely that pages 68–70 have in mind the form of the equations derived and reduced (i.e. rendered dimensionless) on pages 27–29. It is also mathematically the most natural next step: to consider whether equilibrium solutions are possible, and then to investigate their stability to small perturbations. In approach, this is extremely similar to the discussion presented in *CBM*: in *CBM* small perturbations that drive instability lead to the formation of pattern, i.e. structure, whereas here small perturbations would potentially lead to the disappearance of patterns of the form proposed (i.e. ones which have 'lattice symmetry'; here meaning hexagonal), or to the formation of even more complex patterns. This linear stability problem is derived and clearly given at the end of page AMT/C/24/70. Although only stated as a pair of differential equations, the index r runs over the integers $1 \ldots 6$, so in fact this is a set of seven coupled equations. As a result, computation of stability by hand turns out to involve significantly more lengthy algebra than *CBM*, and one can imagine that Turing made a number of attempts before finding the cleanest way to present the results of these straightforward, but longwinded, hand computations.

It is now in order to make a few more detailed remarks on the reasoning behind the ordering of the material given in the re-constituted manuscript attached as an Appendix to this paper. This ordering is the result of very careful scrutiny of the archive material, and the logic therefore involves some degree of technical understanding of the nature of the material contained in these pages. These arguments deserve perhaps a fuller treatment, so I present a summary here and leave a complete discussion of Turing's mathematics at this point to be the subject of future work.

At this point in *ODD*, pages AMT/C/27/47–50 which are handwritten (with the exception of page 49) emerge as perhaps the cleanest way to organise these computations. Certainly they follow directly, forming algebraic combinations using the notation introduced on page AMT/C/24/70 and the pen and handwriting appears to agree between pages AMT/C/24/70 and AMT/C/27/47. It is curious that out of pages AMT/C/27/47–50 only page 49 is typed. There is little text on the other pages, adding weight to the idea that these are notes rather than a final version, but notes that Turing considered to be sufficient important that the textual commentary on page 49 is typed in order to clarify the results obtained at this point.

Mathematically, the change of variables made at the top of page AMT/C/27/47 deftly divides the stability problem posed by the set of seven differential equations into two smaller problems: one with three variables that is considered completely on pages 47 and 48, and one with four variables that is considered on pages 48–50. Close examination of the archive material indicates that exploration of the stability problem continues on the typed pages AMT/C/24/30 and AMT/C/24/72–74. The archive material has been ordered in a

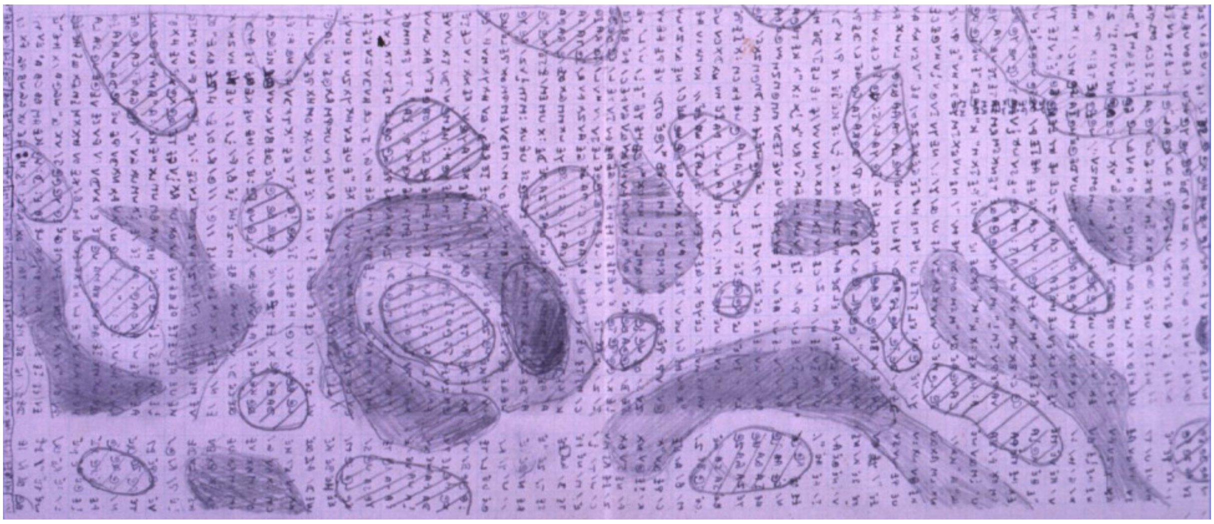


Figure 1: Detail of page AMT/K/3/8 showing a contour plot constructed and shaded by hand from the numerical solution of a model for morphogenesis. Although the pattern is a disordered snapshot and probably has not settled to equilibrium, a roughly hexagonal pattern of small hatched regions can be identified slightly to the left of the centre of the image. Copyright © W.R. Owens.

slightly unfortunate way at this point: page 74 is the continuation of page 72, and page 71 contains 'Figure X' referred to on page 73. Although there is no heading as such, the summarising tone of pages 72 and 74 invites the discussion of stability to close at this point. Other links between pages selected in this discussion are clear, for example the 'characteristic value $-\eta_1\eta_2\eta_3 \sum \frac{1}{\eta_i^2}$' on page AMT/C/24/74 is a reiteration of the result of the computation of eigenvalues and eigenvectors presented on page AMT/C/24/48, adding weight to our assertion that these pages, in the above order, form a coherent whole.

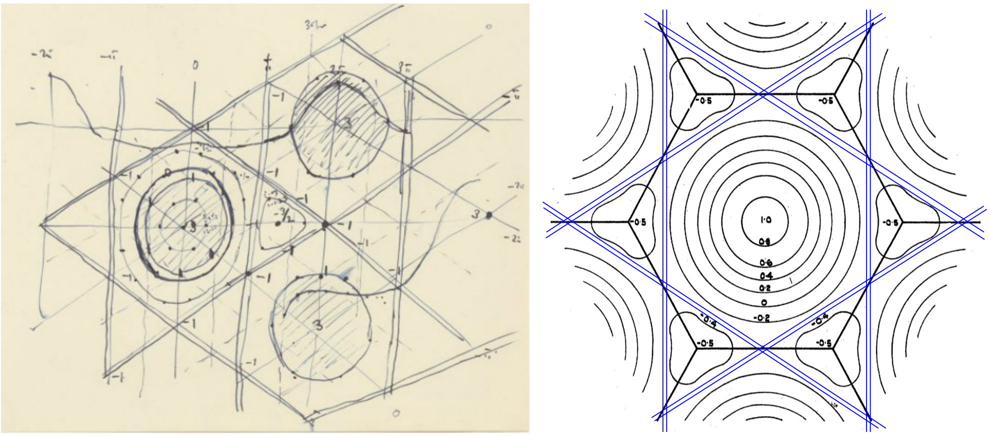
To summarise, the above reconstruction adds the contents of a further 15 pages of archive material to the contents of the 12 presented by Turing (2013). What does it say about Turing's work on morphogenesis? Put simply, it demonstrates Turing's ability to combine insight, precision and approximation. Turing would have known all along that solving the original nonlinear differential equations would not be possible analytically: either hand-computation or machine computation would always be required, and the results of such machine computations can clearly be seen in folder AMT/K/3, for example page AMT/K/3/8 shown in figure 1.

However, in order to carry out such (time-consuming) numerical solutions of his model equations, Turing would have needed to choose appropriate parameter values for the model. Calculation of the parameter values that would give the model a chance of producing the intended patterns required, in turn, analytic investigation and understanding of the different regimes of behaviour of the model. Throughout folders AMT/C/24 and AMT/C/27 there are comments that relate theory, numerical values for parameters, and computer programming, for example the comment on page AMT/C/24/25:

> Both η and σ are kept near to 1/2 so that time advance is $\frac{1}{16}$ per round (i.e. //@/ //// in YC).
> The proposed values $G = 8$ $H = 32$ also seem appropriate.

where η, σ, G and H are parameters that are clearly defined in the model equations, with the proposed parameter values being used, one supposes, in numerical computations. The rather cryptic remark in parentheses presumably refers to Turing's computer coding needed to represent the value $\frac{1}{16}$ within his computer program. The expensive nature of the computer simulations would seem a more than adequate reason to begin with pen-and-paper analysis of the nonlinear model equations, at least until those calculations became intractable.

To summarise, it seems extremely likely that *ODD* would have contained substantial mathematical exploration of model nonlinear differential equations in order to provide suitable starting points for computer-based work. This mathematical work wrestles with a different, and much more complicated problem than that presented in *CBM*. Along the way, Turing encounters and exploits various features of the model problem in



(a) (b)

Figure 2: Two sketches of hexagonal planforms for patterns. (a) Sketch by Turing, taken from AMT/C/27/19a. Copyright © W.R. Owens. (b) Figure 3 from Pellew & Southwell (1940) following Christopherson. The pairs of blue thick solid lines are added to (b) show the relation between the figure as plotted by Pellew & Southwell and the sketch in (a) by Turing.

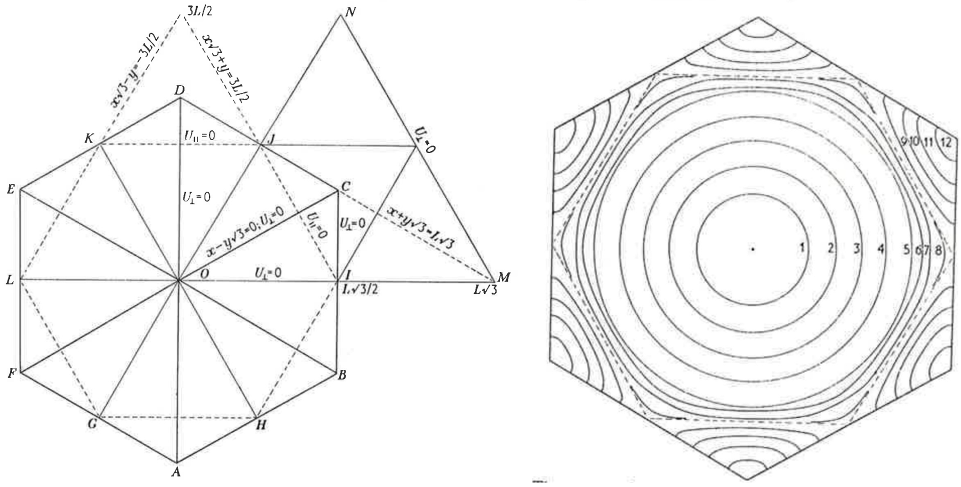
ways that indicate his detachment from other developments in British applied mathematics that are closely related. In order to provide this context, I now briefly review work on a rather different physical problem that nevertheless shares mathematical features with Turing's morphogenesis model in *ODD*.

3 Pattern formation in fluid dynamics

Motivated by the striking observations of thermal convection currents in a two-dimensional cellular array of hexagons by Bénard (1900, 1901), a succession of papers in the first half of the twentieth century made theoretical progress on the nature of the instability in which convection cells first appear as a layer of viscous fluid is heated from below. This problem of 'thermal convection' has clear geophysical and astrophysical motivation, as well as from industrial processes, building ventilation and a host of other physical situations. The first significant theoretical response to Bénard's experimental work is usually taken to be the paper by Rayleigh (1916). However, his analysis of a linear problem was observed later to be quantitatively in error, and also to say nothing about the selection of a hexagonal pattern rather than, say, stripes or squares (which are indeed observed in other, closely related, systems).

Two papers published in 1940 helped overcome some of these shortcomings: first, in a very short paper, Christopherson (1940) showed that it was entirely possible to construct a hexagonal solution to the linear problem that would describe fluid flow in a spatially periodic array of hexagonal convection cells. Second, other authors, notably Low (1929) and Pellew & Southwell (1940), revisited the linear theory proposed by Rayleigh for cases where the layer of fluid was confined by more realistic, rigid boundaries, unlike the rather idealised case considered for simplicity by Rayleigh. These advances together resulted in both better quantitative agreement between theory and experiment for the predicted value of the temperature difference at the onset of convection, and the realisation of the variety of patterns ('planforms') for convective motion that was mathematically possible. Figure 2 compares a sketch figure from Turing's archive papers with a published figure from the paper by Pellew & Southwell (1940); they contain the same information although a little care is needed in the construction and interpretation of the figure in the fluid mechanical context since the fluid flow is three dimensional and so the components of the velocity of the fluid in each direction (x, y, z) needs to be specified.

Figure 3, which shows two figures from the textbook by Chandrasekhar (1961), reinforces that in the fluid context it was, at the time, not immediately obvious that a hexagonal planform is possible. Figure 3(a) shows the geometry of the construction of hexagonal patterns, while (b) is another rendering of contours of constant vertical velocity in the hexagonal pattern, similar to figure 2(b). It should be pointed out that not



(a) (b)

Figure 3: Hexagonal planforms for thermal convection as described in Chandrasekhar's book (Chandrasekhar, 1961). Copyright © Oxford University Press. (a) Detailed construction of a hexagonal planform (page 49). (b) Contours of vertical fluid velocity within a single convection cell (page 50). This follows the earlier work by Christopherson (1940) and Pellew & Southwell (1940).

only did Chandrasekhar make substantial contributions to the theoretical analysis of thermal convection, but that his 1961 textbook (Chandrasekhar, 1961) remains a standard reference and introduction to the subject.

On the experimental side, many authors contributed to the design and analysis of more accurate experimental methods for the analysis of the onset, and dynamics, of convection. Flow visualisation was discussed extensively, and even in 1961, Chandrasekhar refers to 'a vast literature on experiments relating to thermal convection'[16]. At least some of this literature was published in the *Proceedings of the Royal Society*, for example papers by R.J. Schmidt and collaborators in 1935 and 1938, and so would presumably have been available to Turing in Cambridge and in Manchester.

Subsequent to this theoretical and experimental work on the linear problem of the onset of thermal convection, major advances were made by Malkus and Veronis (1958) and Stuart (1958). These papers were published within weeks of each other (each paper references the other, in fact) and the authors acknowledge discussions with each other during a visit made by Stuart to the Woods Hole Oceanographic Institution in the US. The central achievement of these papers is to extend the (by now well-known) linear theory to account for the most important nonlinear terms near to the onset of the convective motion. In this way one can estimate the amplitude of the pattern of convection cells that forms, and as later authors in the 1960s and 1970s (not least Friedrich Busse) realised, examine competition between different patterns to look at their relative stability.

Relevant, perhaps surprisingly so, to understanding Turing's later work is the paper by Swift & Hohenberg (1977). This paper is much cited, but essentially for a reason that is slightly peripheral to the main thrust of the work presented therein. Swift & Hohenberg attempted to understand, from a statistical mechanics perspective, the effect that thermal fluctuations ('noise') would play in describing both the onset of convection and the fluid flow that resulted just above onset. In the process of their computations they reduced the complicated Navier–Stokes equations for the fluid down to a single equation for one combination of the fluid temperature and the vertical component of its velocity. This reduced equation (perhaps most clearly shown in the Appendix to Swift & Hohenberg (1977), equation A24) has since become recognised as the simplest, and canonical, model equation that describes the process of pattern formation in many different physical contexts. It is often therefore referred to as the 'Swift–Hohenberg equation'.

The last set of mathematical developments that needs to be mentioned in connection with thermal convection is the development of a mathematical theory of bifurcations in the presence of symmetry. When applied to pattern formation on a plane, this theory organises the emergence of patterns of various kinds as a critical threshold is passed (for example, as one crosses the critical temperature for the onset of thermal convection) and the selection of one (or perhaps more than one) of these patterns to be stable equilibrium configurations for the pattern after the critical threshold has been crossed. This theory, and later work, brings together symmetry groups and their representations, the asymptotic approaches initiated by Malkus & Veronis (1958) and sets the Swift–Hohenberg theory in a solid mathematical context. Although developed by a substantial community, and applied to a number of key fluid-dynamical problems, for example Taylor–Couette flow of a viscous fluid between co-axial rotating cylinders, this theory found perhaps its most successful applications in developing our understanding of thermal convection and related problems. The most complete account of the key elements of this mathematical work is the work *Singularities and Groups in Bifurcation Theory* in two volumes: Golubitsky & Schaeffer (1984) and Golubitsky et al. (1988), respectively. By this stage the connections between Turing's work on pattern formation and the rather separate developments motivated by thermal convection were clear.

4 Discussion

In previous sections of this paper I have summarised Turing's well-known work *CBM* in which the addition of diffusion to a model for a system of chemical reactions can, counterintuitively, initiate instability of a homogeneous mixture where none existed before. I then commented on the manuscripts *MPT*, in three parts and with the appearance of being close to completion, and *ODD* for which an organised typescript for the initial sections exists, but which then degenerates into unordered pages of handwritten notes. A brief summary of the development of ideas similar to Turing's, but in the context of thermal convection, followed in order to provide a sense of the wider context in which the ideas that Turing was working on were being developed and refined.

In this discussion I will focus on three aspects of Turing's work, as presented in *ODD* and the related archive material, that reinforce perhaps the central characteristics of Turing's academic contributions overall: he was ahead of his contemporaries, and he worked in large part in isolation from them. The three aspects that I will consider, in order, are:

(i) the description of patterns in terms of modes in Fourier space and their nonlinear interactions,

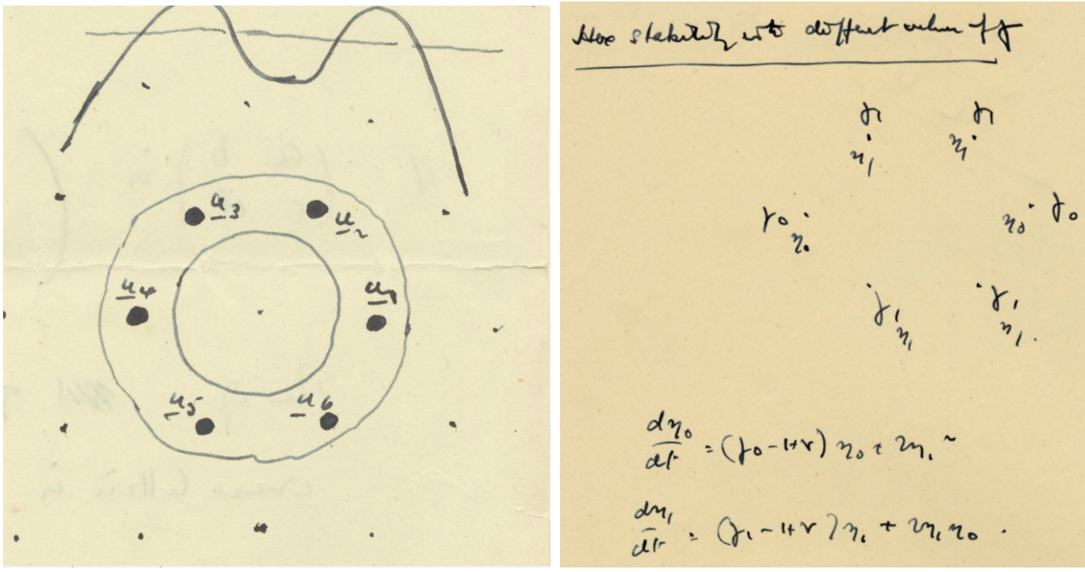
(ii) the construction of the well-known model equation usually ascribed to Swift & Hohenberg, published 23 years after Turing's death, and

(iii) the use of symmetry to organise computations of the stability of symmetrical equilibria corresponding to spatial patterns.

From the very start of *ODD*, Turing defines and uses the lattice and reciprocal lattice notation that he introduced in *MTP I*. Patterns are defined as sums of modes in Fourier space[17] and labels of the amplitudes of the relevant Fourier modes. Two examples of this are given in figure 4: in (a) the figure labels the Fourier modes around a ring of wavenumbers in Fourier space that lead to patterns. The curve at the top of the figure is almost certainly a graph plotting the growth rate of perturbations at different wavenumbers: note that the high points of the curve line up with the diameter of the ring. In figure 4(b) Turing sets up a calculation to test the stability of a hexagonal pattern to perturbations in which four perturbing modes have the same amplitude, and the other two are different, but equal. Such a calculation would test the stability of a hexagonal pattern to perturbations in the form of rectangles (another possible pattern that systems of the kind Turing investigates in *ODD* are able to form). Of course, this kind of calculation also sits in the context of Turing's quest to understand phyllotaxis, as discussed by Swinton (2004, 2013b). Although we have not developed this relationship explicitly here, it clearly deserves to be the subject of future work.

Turning to the Swift–Hohenberg equation, it is striking that so much of the discussion on pages AMT/C/24/27–29 is echoed by so much later work in the field. If the parameter L is set to zero (as Turing does in his later analysis beginning on page AMT/C/24/68) then page AMT/C/24/29 contains the simplified model equation

$$\frac{dU}{dt} = -(1+\nabla^2)^2 U + IU + U^2 - H\left(\frac{U^2}{1-\sigma^2\nabla^2}\right)U,$$



(a) (b)

Figure 4: (a) Detail of page AMT/C/27/28 showing a hexagonal lattice in Fourier space with amplitudes of the modes labelled by $\mathbf{u}_1, \ldots \mathbf{u}_6$ corresponding to points evenly spaced around an annulus. (b) Detail of page AMT/C/24/61 with the title 'Hex stability with different values of γ' showing perturbations, with amplitudes η_0 and η_1. Both parts of this figure are copyright © W.R. Owens.

which significantly differs only in the last term from the usual modern form

$$\frac{\partial U}{\partial t} \quad = \quad rU - (1+\nabla^2)^2 U + gU^2 - U^3.$$

Importantly, the first two terms on the right hand side in each case define the Swift–Hohenberg model; the linear response is the key part of this equation whereas the appropriate nonlinear terms (the last two on the right hand side in each case) vary from one physical context to another. Turing's final term is in fact very complex since it contains a (formally written) nonlocal term, i.e. implicitly this depends on an integral over the whole spatial domain that involves the function $U(\mathbf{x}, t)$. However, setting the parameter $\sigma = 0$ recovers the more usual quadratic–cubic form of the nonlinear terms.

The behaviour of this differential equation and the set of equilibrium patterned solutions has been studied in great detail over the last thirty years, and even in the last decade new results have emerged through a combination of mathematical and numerical techniques, see Dawes (2010) for a short review and Burke & Knobloch (2006); Burke & Dawes (2012) for recent mathematical papers.

The systematic construction of bifurcation theory (i.e. a precise mathematical description of the typical qualitative changes that arise in the behaviour of solutions to nonlinear differential equations) was one of the major achievements of dynamical systems theory over the course of the second half of the twentieth century. Of particular relevance to pattern formation is the extension of that theory to include an idea of what bifurcations one would typically expect to see in problems that are constrained by symmetry (for example models in which a number of identical sub-units are coupled together where their identical nature implies the system is in some sense fundamentally unchanged by relabellings of the sub-units). Pattern formation problems naturally inherit symmetries through their construction, and Turing's stability analysis of hexagonal patterns points to some of the issues that are now well-understood. For example, Turing notes on pages AMT/C/27/47–48 that two eigenvalues are found to be zero. This is a natural consequence of the symmetry of the underlying pattern formation problem. The remark 'The eigenvectors with eigenvalue 0 correspond to small shifts of origin.' on page AMT/C/27/48, as well as the deft way in which the stability calculation for hexagons is laid out, indicates that Turing certainly recognised the role of symmetry and used it to advantage.

Taken together, these observations indicate that if Turing had completed *ODD*, not only would it have been a landmark paper in its combination of biological insight, mathematical modelling, and numerical computation, but that it would have set out new ideas in applied mathematics that would have had substantial influence across the subject. In some cases these ideas would have spurred the development of parts of the subject that otherwise took several decades to be realised.

Restricting our attention to morphogenesis, Alan Turing's reputation for insight, his independence of thought, and his development of ideas ahead of his contemporaries deserves not just to rest on the single paper *The chemical basis of morphogenesis* but to be substantially further enhanced by consideration of his lesser-known material. It is apparent that this archive material indeed deserves further careful attention and that while a definitive version of *Outline of development of the Daisy* is unlikely to be agreed, further steps towards this goal should be taken.

Acknowledgements

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Notes

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

[2]The original typescripts are held at sections AMT/C/7 – AMT/C/10 in the Turing Archive in King's College, Cambridge.

[3]Typescript, archived in King's College Cambridge at AMT/K/1/78 and quoted by Hodges (1992), pp 436–437.

[4]See Turing (1992d) and archive reference AMT/C/9/6.

[5]These equations are numbered (II, 2.15) and (II, 2.14) respectively, in the original typescript, see AMT/C/9/12 and AMT/C/9/11. The equations are reproduced here as stated in the original ms. U and V are variables that describe the concentrations of two chemicals, $\phi(-\nabla^2)$ and $\psi(-\nabla^2)$ are operators describing the spatial diffusion effects, and G and H are fixed parameters.

[6]Original material archived at AMT/C/7 in King's College Cambridge.

[7]AMT/C/24/4.

[8]AMT/C/24/10, page 7 in the numbering given by R. Gandy.

[9]AMT/C/24/13.

[10]AMT/C/24/10.

[11]AMT/C/24/13.

[12]AMT/C/24/10.

[13]See AMT/C/24/9.

[14]AMT/C/24/10.

[15]Essentially, the issue with the form $\phi(\nabla^2) = I_2(1 + \nabla^2/k_0^2)$ given in assumption (ii) on page AMT/C/24/10 is that it would allow small amplitude but high-frequency spatial components of U to grow very rapidly in time. These high frequency components which oscillate rapidly in space cause huge mathematical and numerical problems; as a result the equation for U as posed on page AMT/C/24/10 is said to be ill-posed.

[16]See Chandrasekhar (1961), chapter 2, section 18, pp 61-71 and the references therein.

[17]See the displayed equation for the morphogen U on page AMT/C/24/6 and the simpler version on page AMT/C/24/68.