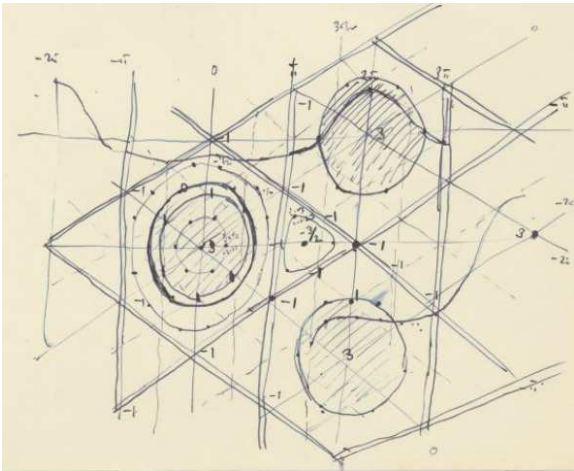


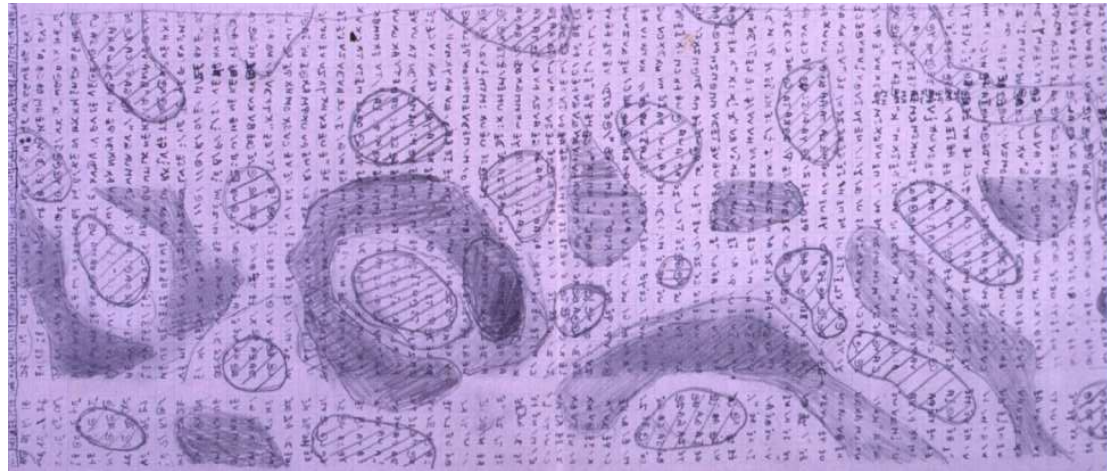
# After 1952: Alan Turing's later work on pattern formation

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AMT/C/27/19a



AMT/K/3/8

# Outline

- Part 1: Turing's life and possible influences
  - Biographical summary
  - Motivations, discussions and debates 1948 - 1951
  - *The chemical basis of morphogenesis* (1952) (CBM)
- Part 2: Turing's work 1952 – 1954
  - Archival material
  - *Morphogen Theory of Phyllotaxis I - III* (MTP)
- Part 3: *Outline of Development of the Daisy* (ODD)
  - Different mathematical situation to CBM
  - Different model equations, related to the Swift–Hohenberg eqn
  - Existence and stability of solutions
- Summary

**Unpublished writings of A.M.Turing copyright The Provost and Scholars of King's College Cambridge 2017.**

# Summary

- CBM is the 'easy version' written for a general scientific audience
- Turing's later work is mathematically much more interesting
  - 2D patterns - hexagons
  - **different, and much more complicated model equations**
  - attempts to find 'fully nonlinear' solutions
  - investigates stability of symmetric solutions

In particular

- **In 1952-54 Turing proposes the Swift–Hohenberg model (1977) ...**
- ... and began to tackle theoretical issues, e.g. the role of symmetry, and the need for a spectral gap, that remained important research questions for many years.

# Part 1: Turing's life and influences

# Turing timeline 1

- Born 23 June 1912
- Attended Sherborne School (1926 - 1931)
- Kings College Cambridge (1931-1935), elected to a Fellowship in 1935
- PhD study at Princeton with Alonso Church, 1936 - 1938

Key paper: On computable numbers, with an application to the Entscheidungsproblem *Proc. Lond. Math. Soc.* **42** (1937)

- Joined Government Code and Cypher School (GC&CS), Bletchley Park; later moved to Hanslope Park to work on electronic circuits for voice encryption, 1939 - 1945
- Joined National Physical Laboratory, Teddington, 1945

Wrote an internal report proposing the construction of an electronic computer (which would become called the ACE - automatic computing engine); analogies with the human brain

Further reading: A. Hodges, *Alan Turing: The Enigma*, Vintage Press (1983)

# Turing timeline 2

- Resumed fellowship at Kings in September 1947 (sabbatical from NPL).
- 28 May 1948: accepted post of Reader at Manchester University, and Deputy Director of the Royal Society-funded Computing Laboratory, directed by Max Newman
- 1949 - 1950: Continued to develop ideas on the relation between computing machinery and human brains
- 27 Oct 1949: Workshop *The Mind and the Computing Machine*, Manchester.

Intellectual challenge from Michael Polanyi (Chair of Physical Chemistry at Manchester 1933-1948), subsequently philosopher and social scientist

Extensive (more positive) discussions with [John Zachary Young](#) (physiologist, nervous system)

Oct 1950: wrote paper *Computing Machinery and Intelligence for Mind*.

Further reading: A. Hodges, *Alan Turing: The Enigma*, Vintage Press (1983)

# Turing timeline 3

- 8 February 1951: wrote to J.Z. Young as follows

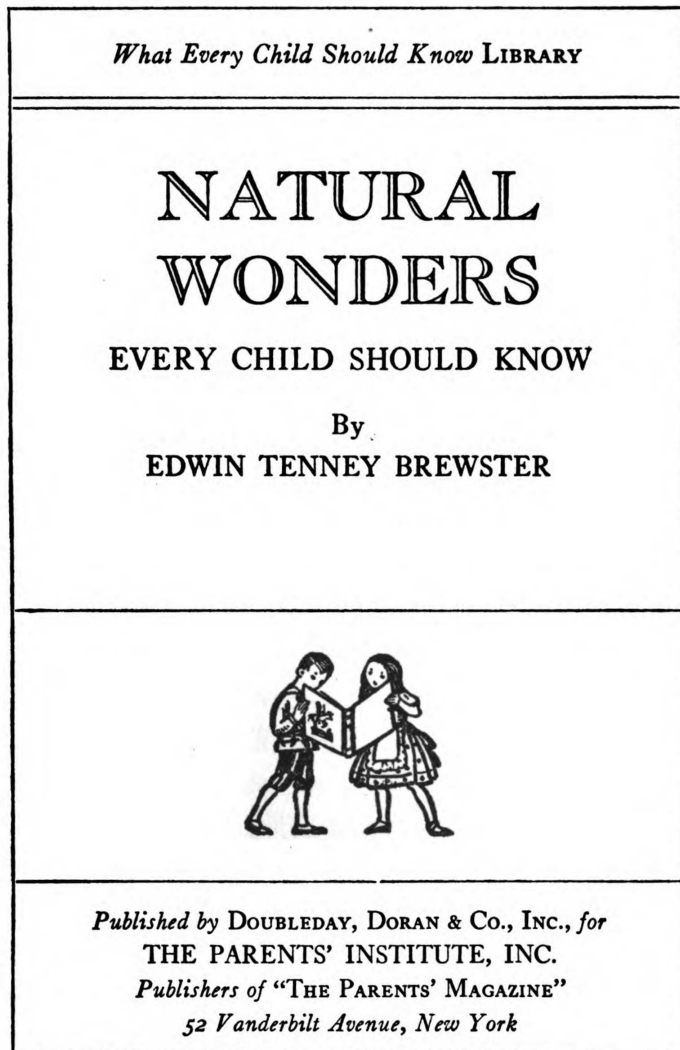
*At present I am not working on the problem [of the relation between the logical and physical structure of the brain] at all, but on my mathematical theory of embryology, which I think I described to you at one time. This is yielding to treatment, and it will so far as I can see, give satisfactory explanations 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.*

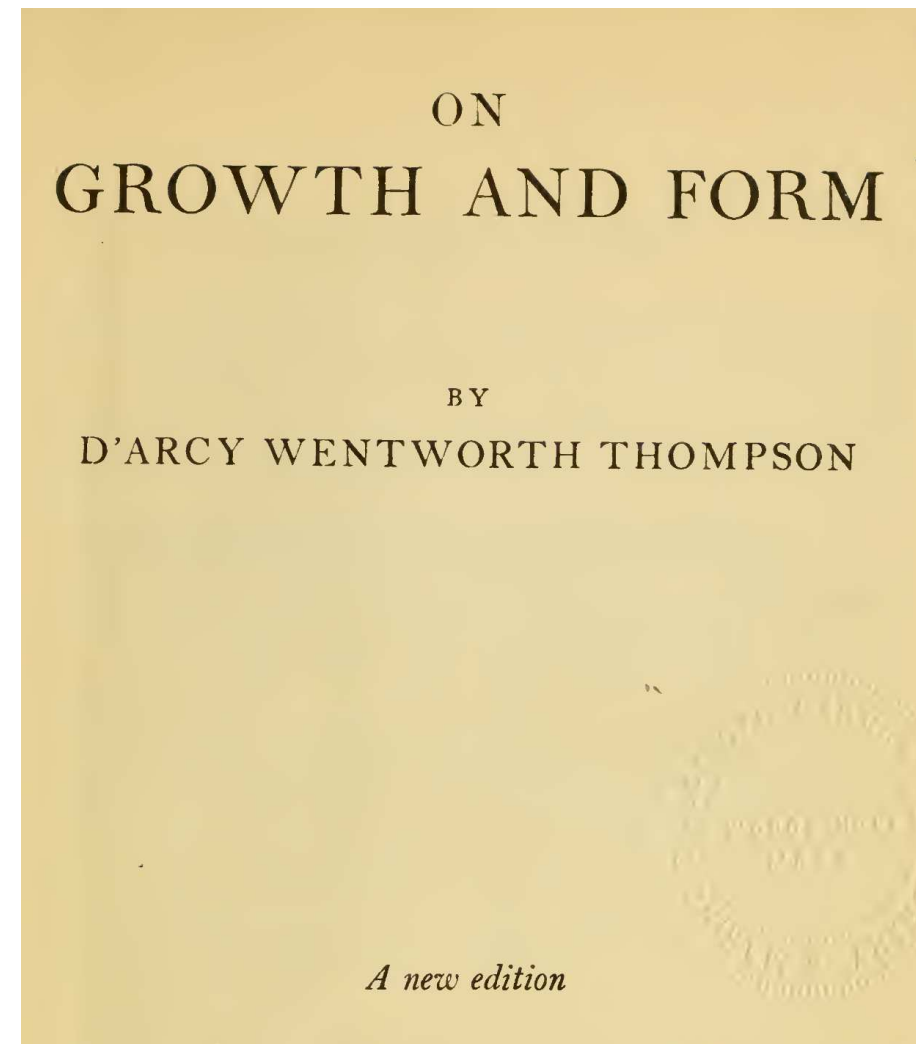
*I am really doing this now because it is yielding more easily to treatment.*

- 12 February 1951: Ferranti Mark I delivered to Manchester

# Earlier influences on Turing



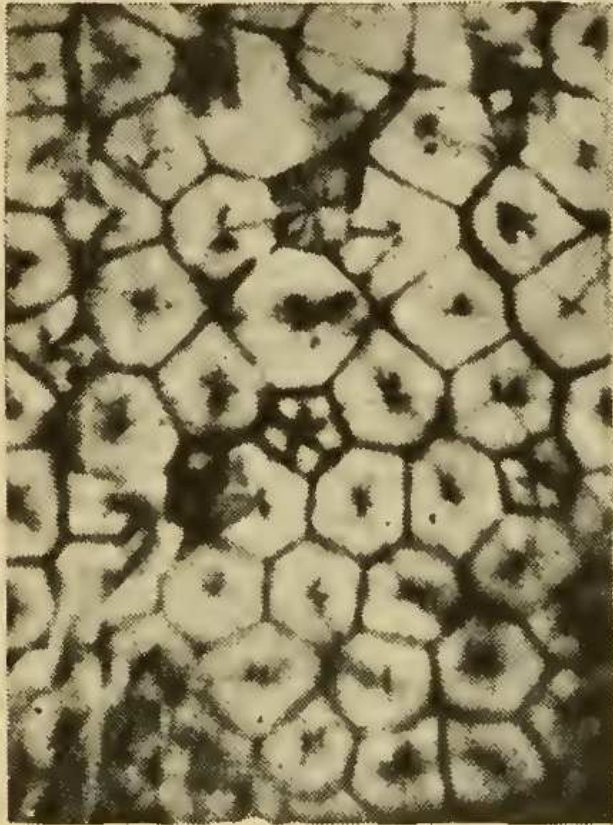
AMT's copy preserved at Sherbourne



AMT read this pre-WW2 (Hodges)



# *On Growth and Form (1917)*



A

Fig. 182. Bénard patterns in smoke:

Convection cells  
OGAF, page 520

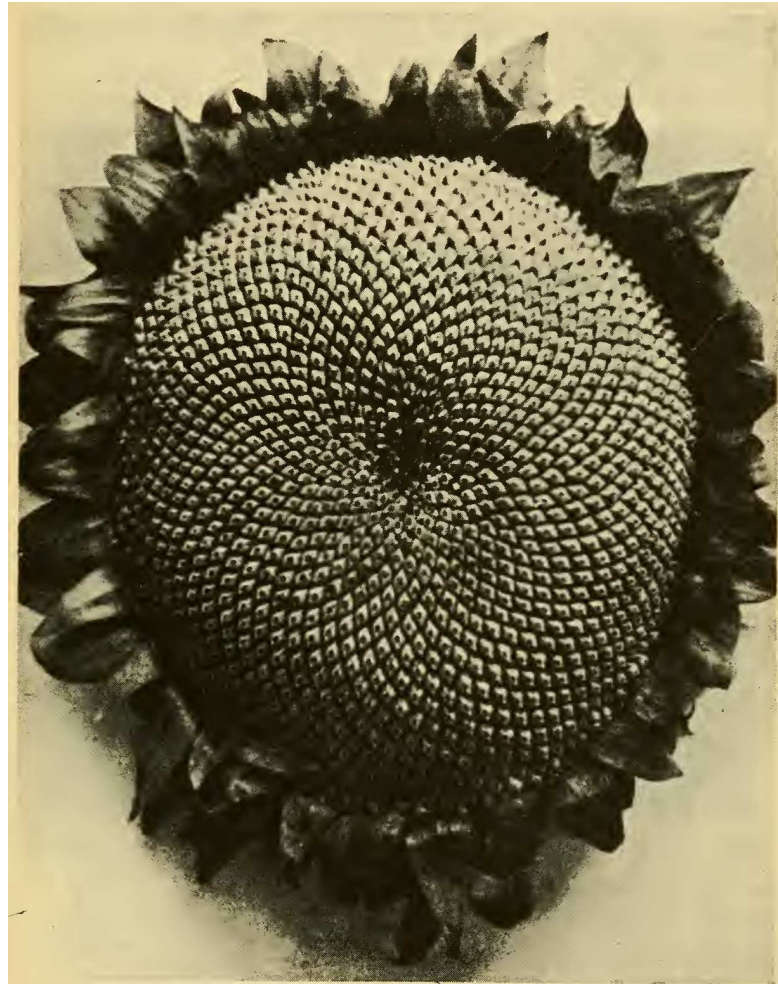


Fig. 448. A giant sunflower, *Helianthus maximus*. From H. A. Naber, after M. Brocard.

Sunflower  
OGAF, page 913

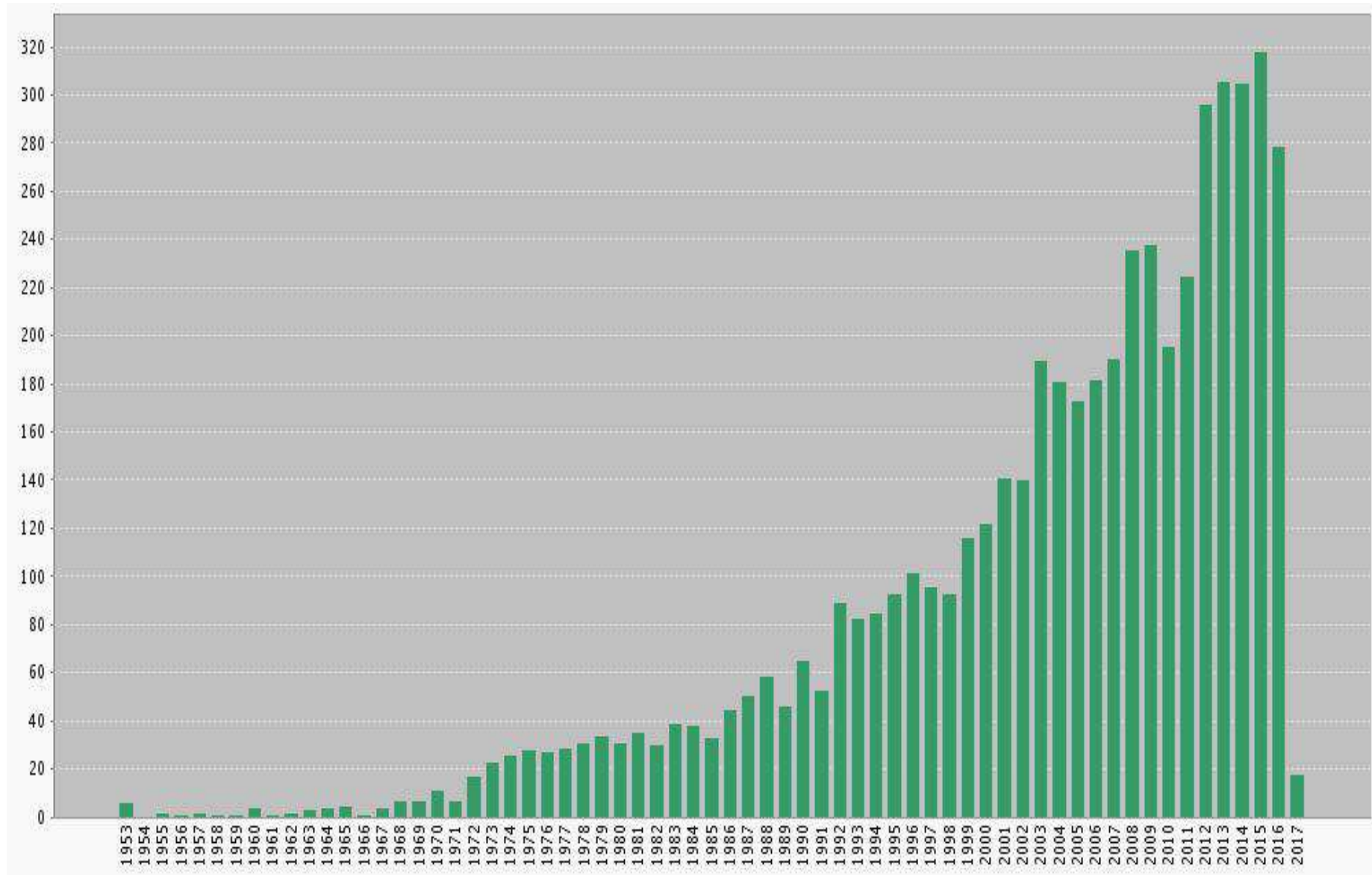
# Turing timeline 4

- 15 March 1951: Elected Fellow of the Royal Society
- 15 May 1951: BBC Radio broadcast (one of a series of 5): 'Can Digital Computers Think?'
- 9 November 1951: CBM paper submitted to *Philosophical Transactions of the Royal Society*
- 29 February 1952: completed revisions to CBM paper

2 years 3 months later ...

- 7 June 1954: died at home in Wilmslow; cyanide poisoning

# Citations for CBM, 1953 – 2017



# THE CHEMICAL BASIS OF MORPHOGENESIS

BY A. M. TURING, F.R.S. *University of Manchester*

*(Received 9 November 1951—Revised 15 March 1952)*

It is suggested that a system of chemical substances, called morphogens, reacting together and diffusing through a tissue, is adequate to account for the main phenomena of morphogenesis.

...

## 1. A MODEL OF THE EMBRYO. MORPHOGENS

In this section a mathematical model of the growing embryo will be described. This model will be a simplification and an idealization, and consequently a falsification. It is to be hoped that the features retained for discussion are those of greatest importance in the present state of knowledge.

## 2. MATHEMATICAL BACKGROUND REQUIRED

The greater part of this present paper requires only a very moderate knowledge of mathematics. What is chiefly required is an understanding of the solution of linear differential equations with constant coefficients. (This is also what is chiefly required for an understanding of mechanical and electrical oscillations.) The solution of such an equation takes the form of a sum  $\sum A e^{bt}$ , where the quantities  $A, b$  may be complex, i.e. of the form  $\alpha + i\beta$ , where  $\alpha$  and  $\beta$  are ordinary (real) numbers and  $i = \sqrt{-1}$ . It is of great importance that the physical significance of the various possible solutions of this kind should be appreciated,

...

The following relatively elementary result will be needed, but may not be known to all readers:

$$\sum_{r=1}^N \exp\left[\frac{2\pi i r s}{N}\right] = 0 \quad \text{if } 0 < s < N,$$

but

$$= N \quad \text{if } s = 0 \text{ or } s = N.$$

The first case can easily be proved when it is noticed that the left-hand side is a geometric progression. In the second case all the terms are equal to 1.

The relative degrees of difficulty of the various sections are believed to be as follows. Those who are unable to follow the points made in this section should only attempt §§ 3, 4, 11, 12, 14 and part of § 13. Those who can just understand this section should profit also from §§ 7, 8, 9. The remainder, §§ 5, 10, 13, will probably only be understood by those definitely trained as mathematicians.

Central message of the paper:

- With only two chemical concentrations, simple reactions and spatial diffusion,
- small departures from equilibrium can be enhanced over time
- leading to ‘stationary waves’
- Note the section numbering error: no section 6 !

# Example of 'stationary waves'

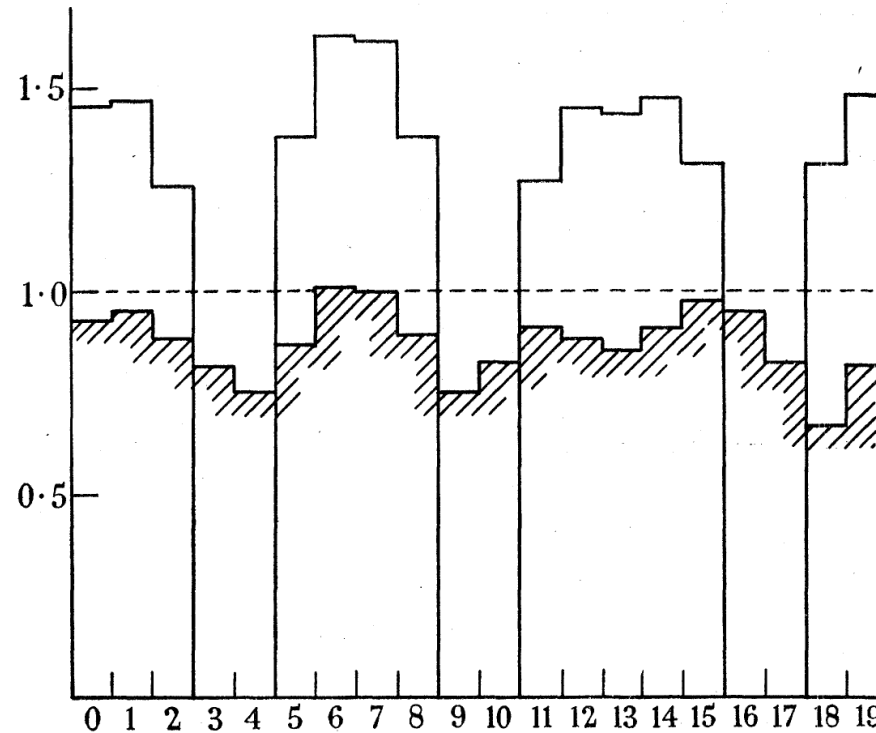


FIGURE 3. Concentrations of  $Y$  in the development of the first specimen (taken from table 1).  
----- original homogeneous equilibrium; // incipient pattern; —— final equilibrium.

'[these numerical results] were mainly obtained with the aid of the Manchester University Computer.'

- Explicit (but imagined) chemical reaction scheme proposed

# Final section of CBM

## 13. NON-LINEAR THEORY. USE OF DIGITAL COMPUTERS

The 'wave' theory which has been developed here depends essentially on the assumption that the reaction rates are linear functions of the concentrations, an assumption which is justifiable in the case of a system just beginning to leave a homogeneous condition. Such systems certainly have a special interest as giving the first appearance of a pattern, but they are the exception rather than the rule. Most of an organism, most of the time, is developing

from one pattern into another, rather than from homogeneity into a pattern. One would like to be able to follow this more general process mathematically also. The difficulties are, however, such that one cannot hope to have any very embracing *theory* of such processes, 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. This method has the advantage that it is not so necessary to make simplifying assumptions as it is when doing a more theoretical type of analysis. It might even be possible to take the mechanical aspects of the problem into account as well as the chemical, when applying this type of method. The essential disadvantage of the 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.



## Part 2: Turing's work 1952 – 1954

# Collected Works

**Collected Works Volume 4: Morphogenesis** contains

- *The chemical basis of morphogenesis* (CBM)
- *Morphogen theory of phyllotaxis Part I: Geometrical and descriptive phyllotaxis*  
(a complete draft, edited lightly by N.E. Hoskin & B. Richards)
- *Morphogen theory of phyllotaxis Part II: Chemical theory of morphogenesis*  
(unfinished, edited by N.E. Hoskin & B. Richards)
- *Morphogen theory of phyllotaxis Part III: A solution of the morphogenetical equations for the case of spherical symmetry*  
(drafted by B. Richards who worked on this problem for his MSc)
- *Outline of development of the Daisy*  
12 pages, typed with hand-drawn sketch figures.

## The Turing Digital Archive

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Abbreviations

**Alan Turing (1912-54)** is best-known for helping decipher the code created by German Enigma machines in the Second World War, and for being one of the founders of computer science and artificial intelligence.

This archive contains many of Turing's letters, talks, photographs and unpublished papers, as well as memoirs and obituaries written about him. It contains images of the original documents that are held in the Turing collection at King's College, Cambridge. For more information about this digital archive and tips on using the site see [About the archive](#).

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[AMT/D. Correspondence](#)

[AMT/E. Turing Celebration Day, Cambridge, 1 Oct. 1997](#)

[AMT/K. Material given to Kings College, Cambridge, in 1960](#)

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A diagram from Turing's notes on morphogenesis ([AMT/K/3](#))

# Archive material: 2 locations

## 1. Modern Archives, King's College, Cambridge

- digitised (by Jonathan Swinton *et al*) in 2000: [www.turingarchive.org](http://www.turingarchive.org)
- No notes or drafts of CBM survive, except an outline in an undated letter (March-Nov 1951) to Philip Hall: AMT/D/13/1-2.
- For AMT's work on morphogenesis the most interesting sections are
  - AMT/C/8-10: typescripts of MTP Parts I, II, and III
  - AMT/C/25-26: notes and drafts of MTP Parts I and II
  - AMT/C/24 (90 pages) and C/27 (116 pages):  
notes, including 12 typed pages of 'Outline of development of the Daisy'

## 2. John Rylands Library, Manchester University

- preprints of papers that AMT was reading
- notes and printouts from the Mark I Computer
- not fully catalogued, not digitised (approx 60 pages)

# CBM - letter to Philip Hall 1/2

'Waves on leopards' are rather more elementary. A leopard skin, like the spots on a leopard, is supposed to be a finite plane that is <sup>two</sup> contained chemical substances with concentrations  $U, V$ . What react and diffuse. This gives you equations of the form

$$\frac{\partial U}{\partial t} = f(U, V) + \mu \nabla^2 U$$

$$\frac{\partial V}{\partial t} = g(U, V) + \nu \nabla^2 V$$

If you take  $f$  and  $g$  to be linear (near  $U_0, V_0$ ) and the whole system to be just unstable you find

# CBM - letter to Philip Hall 2/2

AMT/D/13/2

of the anti-symmetric state equations, that  
 $U = U_0 + \alpha Z$   $V = V_0 + \beta Z$  show  $Z$  satisfies a 'wave eqn'

$$\nabla^2 Z = \frac{4i}{\lambda^2} Z$$

The wave length  $\lambda$  depending on the reaction rates  $f, g$  and diffusion rates  
 $D, \nu$ . What particular solution you get will depend on random  
disturbances just before instability started. Roughly speaking you  
get a 'random solution'. By assuming there is black there

$Z > Z_0$ , yellow for  $Z < Z_0$  you get very reasonable leopard  
skins. Certain slight variations of assumptions give you guinea fow, zebras,  
cows. Cows are dappled.

# Morphogen theory of phyllotaxis I

## Part I: Geometrical and descriptive phyllotaxis

- geometry of arrangement of primordia; relation to Fibonacci numbers.
- real-space lattice of the positions of the primordia (unroll the plant stem)

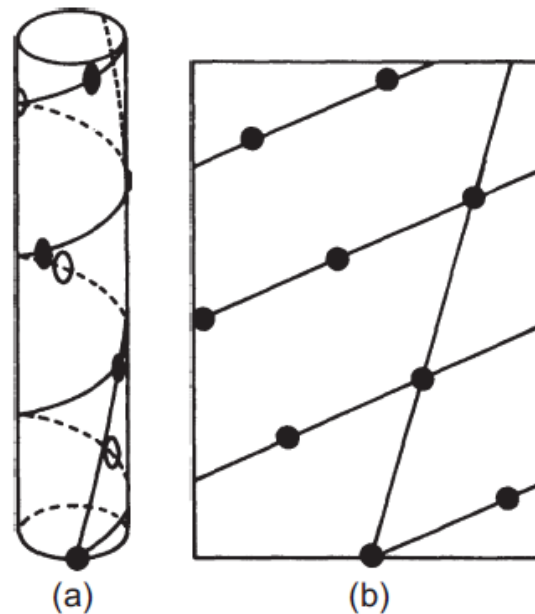


Fig. 3: (a) Side view of an idealised stem and (b) the equivalent plane lattice. The contact parastichy numbers are 1 and 2. Both the generative spiral and a parastichy of order 3 are shown.

- Flow matrices

# Morphogen theory of phyllotaxis II

## Part II: Chemical theory of morphogenesis

- Starts from a very general system of chemical reactions
  - for concentrations  $\Gamma_{mj}$  of morphogen  $m$  in cell  $j$  of volume  $v_j$
  - both in continuous tissue, and in a set of discrete coupled cells:

$$v_j \frac{d\Gamma_{mj}}{dt} = -\mu_m \sum_s g_{js} \Gamma_{ms} + v_j f_m(\Gamma_{1j}, \dots, \Gamma_{Mj})$$

- Key assumptions now made:
  - Homogeneous eqm  $\Gamma_{mj} = h_m$  for the reaction terms, satisfying ‘condition for stationary waves’ i.e. as in the usual Turing instability case (CBM)
  - Nonlinear terms are required, but are small perturbations
  - *The only wavelengths  $\alpha$  which are significant are those which are either very long ( $\alpha = 0$ ) or fairly near to the optimum ( $\alpha$  near  $2\pi/k_0$ )*



# Morphogen theory of phyllotaxis II

● Hence

$$\Gamma_{mj}(t) - h_m = W_{m\ell(0)}(0)V_j(t) + W_{m\ell(1)}(k_0^2)U_j(t)$$

eigenfunctions for deviations from homogeneous state in cell  $j$ , introducing the amplitudes  $V_j$  for the long-wavelength mode, and  $U_j$  for the finite, non-zero mode.

● Using the assumption that the important nonlinear terms are only those that are quadratic in  $U_j$  and  $V_j$ , Turing arrives at the model

$$\begin{aligned}\frac{dU_j}{dt} &= \phi(-\nabla^2)U_j + G^{(4)}V_j^2 + 2G^{(5)}V_jU_j + G^{(6)}U_j^2 \\ \frac{dV_j}{dt} &= -\psi(-\nabla^2)V_j + F^{(4)}V_j^2 + 2F^{(5)}V_jU_j + F^{(6)}U_j^2\end{aligned}$$

which are labelled as eqns (II.12.b) and (II.12.a) in MTP II.

# Morphogen theory of phyllotaxis II

- Further assumptions (projections, scalings, and that  $V_j^2$  is 'small' and rapidly evolving) leads to

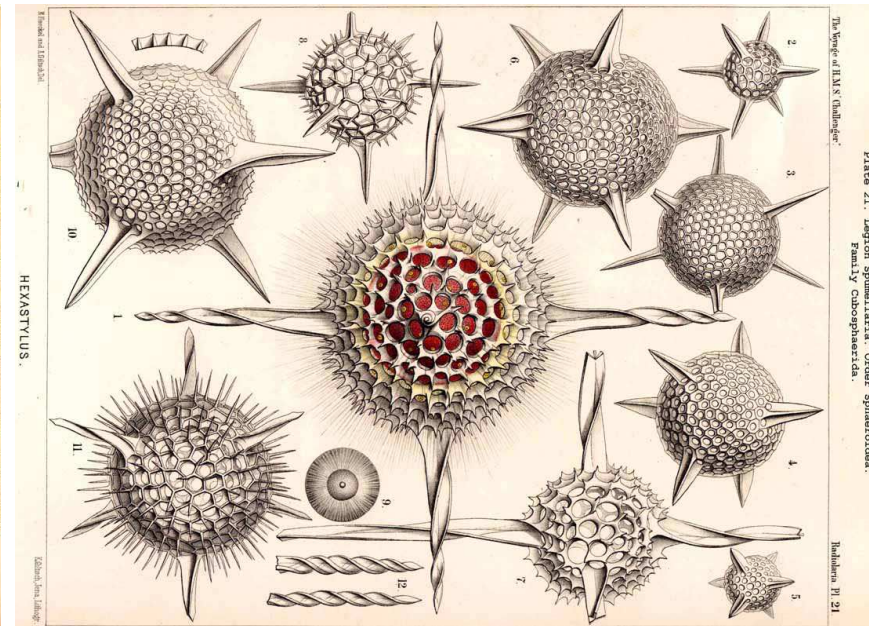
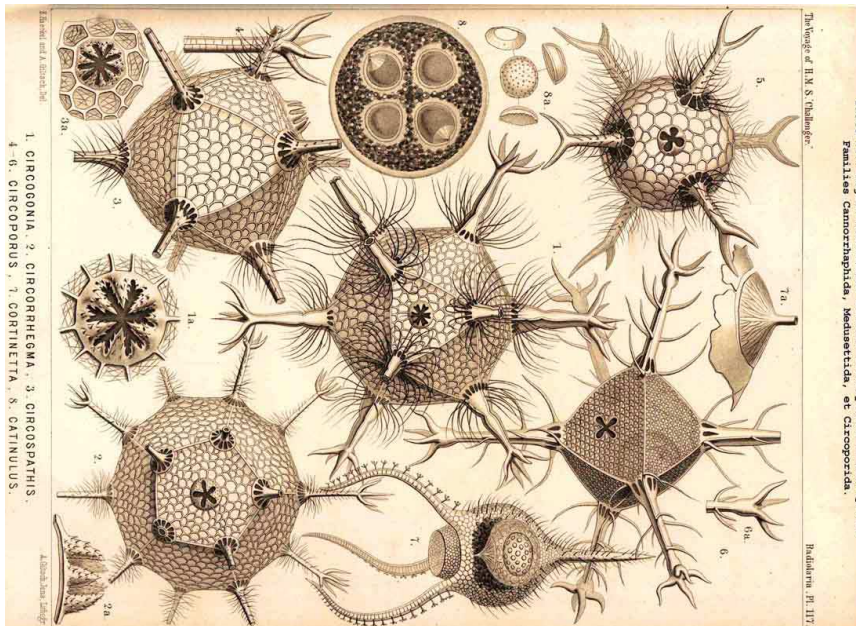
$$\begin{aligned}\frac{dU_j}{dt} &= [\phi(-\nabla^2)U]_j && - HU_jV + GU_j^2 \\ 0 &= -\psi(-\nabla^2)V && + \overline{U^2}\end{aligned}$$

- The essential point about the function  $\phi(\alpha)$  is that it has a maximum near  $\alpha = k_0^2$  . . . . An appropriate approximation for  $\phi(\alpha)$  therefore seems to be  $I(\alpha - \alpha_0)^2$ .*
- The text also implies  $\psi(\alpha)$  should have a maximum at  $\alpha = 0$ .
- The function  $U_j(t)$ , . . . , must be a linear combination of diffusion eigenfunctions all with the same eigenvalue.*
- $V$  represents the concentration of a diffusing poison, the organism is sufficiently small that the poison may be assumed to be uniformly distributed over it.*

# Morphogen theory of phyllotaxis III

Part III: A solution of the morphogenetical equations for the case of spherical symmetry.

- Begins exactly where Part II finishes
- Considers the  $(U, V)$  model above on a sphere
- Expand in spherical harmonics - solve the resulting systems of quadratic eqns
- Motivated by Radiolaria (Ernst Haeckel, 1834-1919):



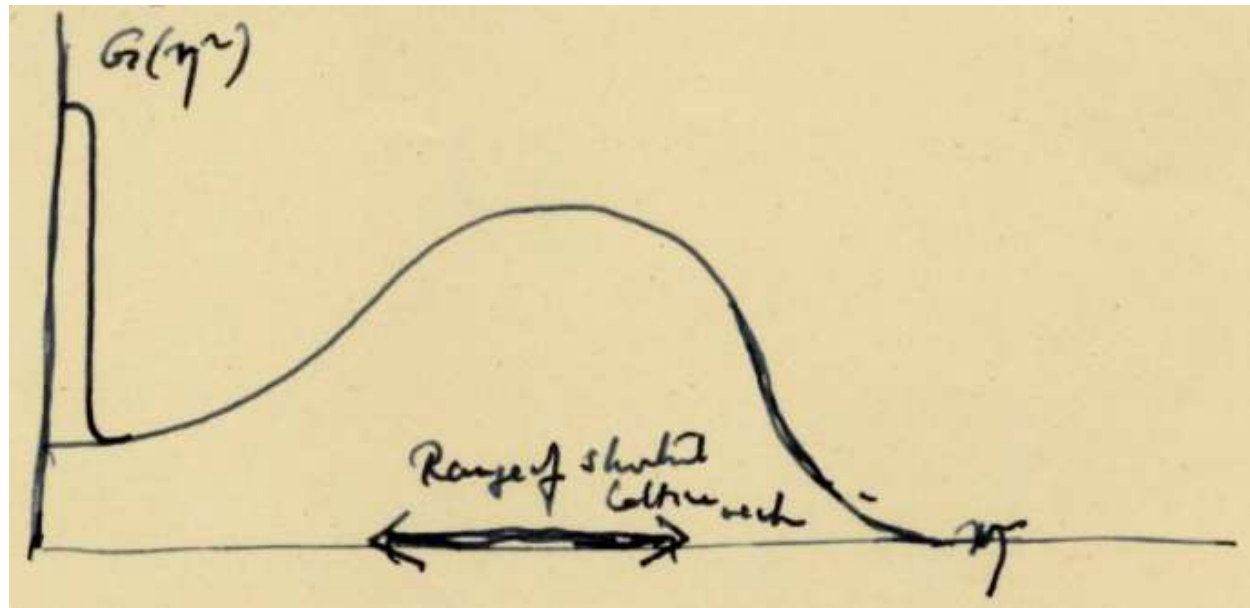
# Part 3: Outline of development of the Daisy

# Outline of development of the Daisy

The concentration of a morphogen  $U(\mathbf{x}, t)$  on an annulus  $\mathbf{x} = (\rho\theta, z)$  (where  $\rho$  is fixed) is assumed to be given by

$$U(\mathbf{x}, t) = \sum_{\eta} e^{i\eta \cdot \mathbf{x}} G(\eta^2) W(\mathbf{x})$$

where the sketch of  $G(\eta^2)$  is given (what we would call a dispersion curve):



*Annotation reads: 'Range of shortest lattice vector'*

# Outline of development of the Daisy

- Starting point: the familiar  $(U, V)$  equations from MTP II:

$$\begin{aligned}\frac{\partial U}{\partial t} &= \phi(\nabla^2)U + I(\mathbf{x}, t)U + GU^2 - HUV \\ V &= \psi(\nabla^2)U^2\end{aligned}$$

- The operator  $\phi(\nabla^2)$  is supposed to take the form

$$\phi(\nabla^2) = I_2 \left( 1 + \frac{\nabla^2}{k_0^2} \right)^2$$

- The operator  $\psi(\nabla^2)$  is supposed to take the form

$$\psi(\nabla^2) = \frac{1}{1 - \nabla^2/R^2}$$

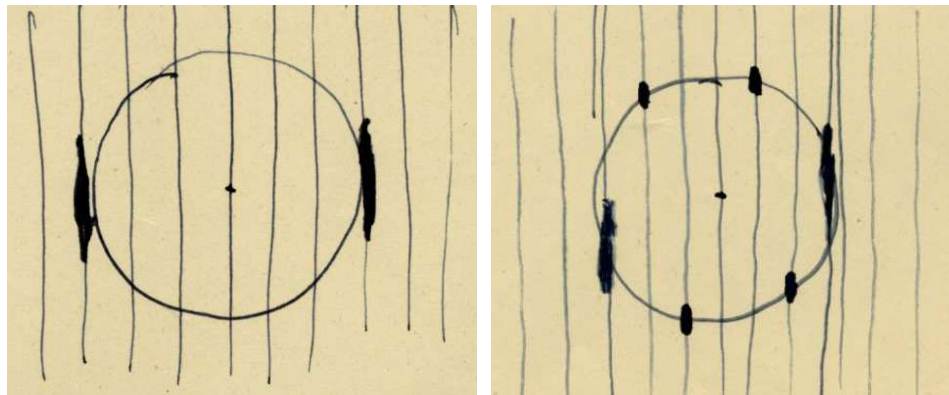
- The time derivative  $\partial U/\partial t$  is supposed to be zero (or nearly).

- $I(\mathbf{x}, t)$  is supposed given in advance, e.g.  $I(\mathbf{x}, t) = I_0 - I_2 z^2/\ell^2$

# Outline of development of the Daisy

Comments continue about the role of  $V$ :

- *The amplitude of the waves is largely controlled by the concentration  $V$  of 'poison'. If the quantity  $R$  is small, it means that the poison diffuses very fast. This reduces its power of control.*
- *... the poison, acting through the  $HUV$  term, prevents the growth of waves whose wave vectors are near to that of a strong wave train. If  $[R]$  is too small, there will be liberty for 'side bands' to develop round the strong components. These side bands will represent modulation of the patchiness.*
- *If  $R$  is allowed to become too large, ... this 'side band suppression' effect even prevents the formation of a hexagonal lattice.*



- This is roughly where the version of ODD in the *Collected Works* ends.

# ODD – new material

- Clear from (i) the end of CBM and (ii) the comments above that these results are directly informed by numerical computation.
- Page AMT/C/24/27 starts with *The equation chosen for computation*

$$\begin{aligned}\frac{dU}{dt} &= \phi(\nabla^2)U + I(\mathbf{x})U + GU^2 - HUV \\ \frac{dV}{dt} &= \psi(\nabla^2)V + KU^2\end{aligned}$$

(note a slightly different definition of  $\psi(\nabla^2)$ ).

- For the  $V$  equation a more explicit form is now proposed:

$$\frac{dV}{dt} = C_1 \nabla^2 V - C_2 V + C_3 U^2$$

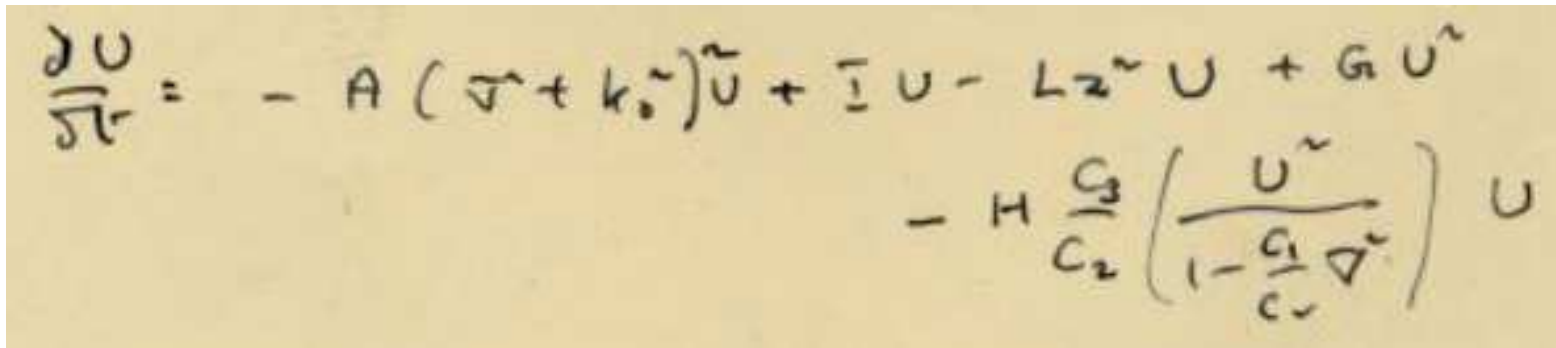
- *If the diffusion and decay occur fast by comparison with the reactions ... one may put*

$$V = \frac{C_3}{C_2} \frac{U^2}{1 - \frac{C_1}{C_2} \nabla^2}$$



# ODD – new material

- The essential property required of the function  $\phi$  is that it should have a maximum for some real (negative) argument). The most natural form for it is therefore  $-A(\nabla^2 + k_0^2)^2$ .
- After making various other assumptions *the equation may be written*



$$\frac{\partial U}{\partial t} = -A(\nabla^2 + k_0^2)^2 U + IU - Lz^2 U + G U^2 - H \frac{G_3}{C_2} \left( \frac{U^2}{1 - \frac{G_1}{C_1} \nabla^2} \right) U$$

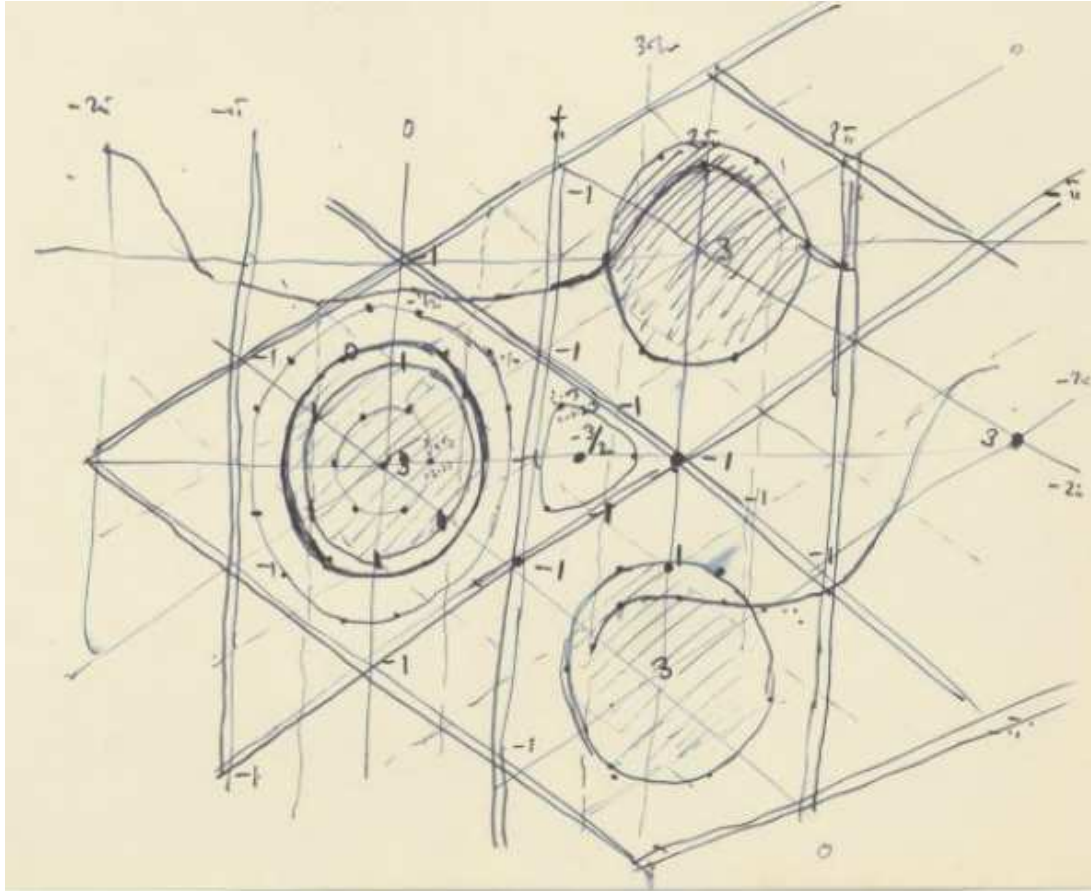
AMT/C/24/28

- Now carry out a nondimensionalisation and set  $L = 0$  to obtain

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

- and examine possible lattice solutions for  $U(\mathbf{x}, t)$ .

# ODD – computation



Sketch of desired hexagonal pattern

AMT/C/27/19a



Computer output,  
shaded by hand to  
show the pattern

AMT/K/3/8

# ODD – new material

- To find lattice solutions, specialise to a combination of 7 Fourier modes

$$U_0 = \xi + \sum_{r=1}^6 \eta_r e^{i\mathbf{k}_r \cdot \mathbf{x}}$$

where  $\mathbf{k}_{r-1} + \mathbf{k}_{r+1} = \mathbf{k}_r$  (the idea is that this is near to a hexagonal lattice)

- Derive conditions for equilibrium (ignoring higher order Fourier modes):

$$(\phi(0) - HV)\xi + V = 0$$

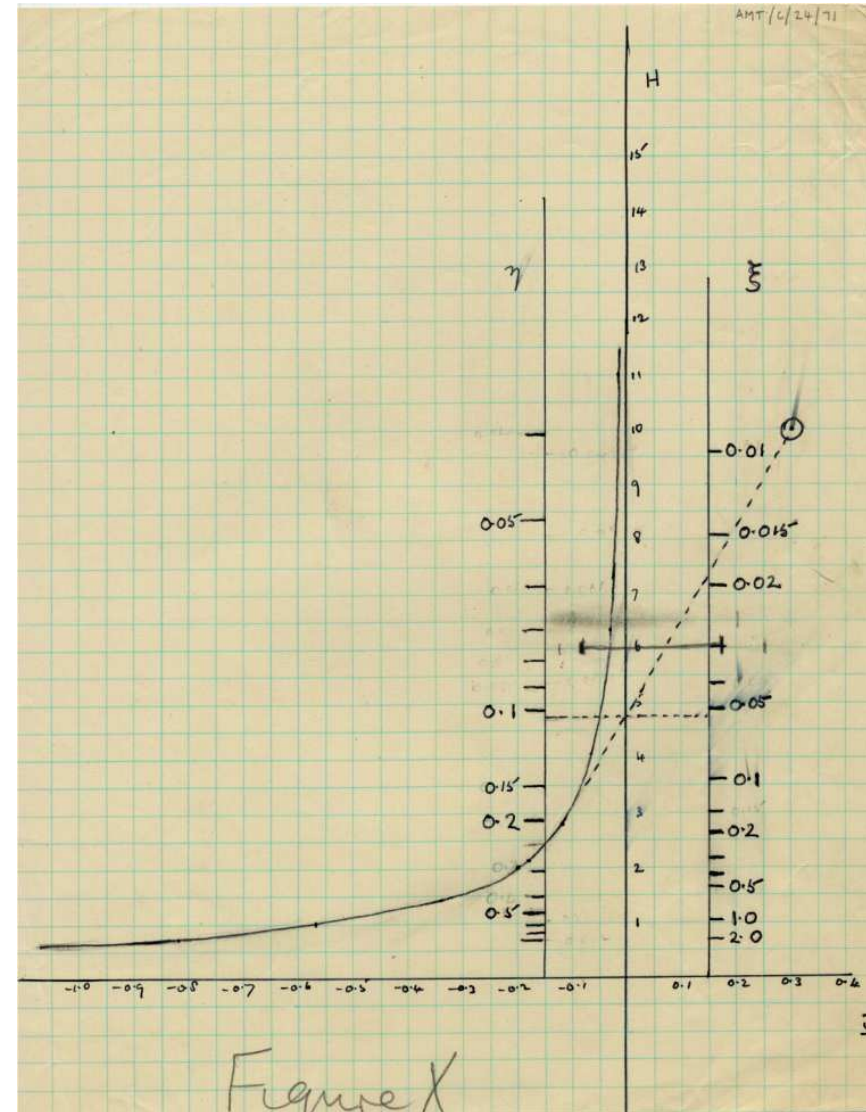
$$(\phi(-\mathbf{k}_r^2) - HV + 2\xi)\eta_r + 2\eta_{r-1}\eta_{r+1} = 0$$

- Investigate stability by writing

$$U = U_0 + \varepsilon e^{i\mathbf{x} \cdot \mathbf{x}} \left[ x + \sum_{r=1}^6 y_r e^{i\mathbf{k}_r \cdot \mathbf{x}} \right]$$

# ODD – new material

- Ends with a nomogram that identifies parameter regions in which stable hexagonal solutions exist:



AMT/C/24/71

# Summary

- New draft of ODD adds 14 more archive pages to the initial 12.
- ODD includes several completely new ideas:
  - The dynamical description of patterns in terms of modes in Fourier space and their nonlinear interactions (cf crystallography).
  - Writes down the pattern-forming equation usually called the 'Swift–Hohenberg equation' (1977). [Another example of Stigler's Law.]
  - Use of symmetry to organise stability computations.
  - Exhibits interplay between theory and computation that is now routine.
- Concepts not in Turing's work
  - activator – inhibitor
  - weakly nonlinear theory
  - bifurcation

J.H.P. Dawes, *After 1952: The later development of Alan Turing's ideas on the mathematics of pattern formation.*

*Historia Mathematica* **43**, 49–64 (2016)