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ANALYTICAL NOTE ON CERTAIN RHYTHMIC RELATIONS IN ORGANIC SYSTEMS

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Periodic phenomena play an important rôle in nature, both organic and inorganic.

In chemical reactions rhythmic effects have been observed experimentally, and have also been shown, by the writer[1] and others,[2] to follow, under certain conditions, from the laws of chemical dynamics.

However, in the cases hitherto considered on the basis of chemical dynamics, the oscillations were found to be of the damped kind, and therefore, only transitory (unlike certain experimentally observed periodic reactions).   Furthermore, in a much more general investigation by the writer, covering the kinetics not only of chemical but also of biological systems, it appeared, from the nature of the solution obtained, improbable[3] that undamped, permanent oscillations would arise in the absence of geometrical, structural causes, in the very comprehensive class of systems considered.   For it seemed that the occurrence of such permanent oscillations, the occurrence of purely imaginary exponents in the exponential series solution presented, would demand peculiar and very specific relations between the characteristic constants of the systems undergoing transformation; whereas in nature these constants would, presumably, stand in random relation.

It was, therefore, with considerable surprise that the writer, on applying his method to certain special cases, found these to lead to undamped, and hence indefinitely continued, oscillations.

As the matter presents several features of interest, and illustrates certain methods and principles, it appears worth while to set forth the argument and conclusions here.

Starting out first from a broad basis, we may consider a system in the process of evolution, such a system comprising a variety of species of matter S_1, S_2....S_n of mass X_1, X_2....X_n. The species of matter S may be defined in any suitable way. Some of them may, for example, be biological species of organism, others may be components of the "inorganic environment." Or, the species of matter S may be several components of an inorganic system in the course of chemical transformation.

We may think of the state of the system at an instant of time as being defined by statement of the values of X_1, X_2....X_n; of certain parameters Q defining the character of each species (in general, variable with time); and of certain other parameters P. The parameters P will, in general, define the geometrical constraints of the system, both at the boundaries (volume, area, extension in space), and also in its interior (structure, topography, geography); they will further define such factors as temperature and climatic conditions.

For a very broad class of cases, including those commonly treated in chemical dynamics, but extending far beyond the scope of that branch of science, the course of events in such a system will be represented by a system of differential equations of the form

$$\left. \begin{array}{c} \dfrac{dX_i}{dt} = F_i(X_1, X_2....X_n; P, Q) \\ (i = 1, 2....n) \end{array} \right\} \qquad (1)$$

If we restrict ourselves to the consideration of evolution at constant P's and Q's we may write briefly

$$\frac{dX_i}{dt} = F_i(X_1, X_2....X_n). \qquad (2)$$

The writer has elsewhere[4] given a somewhat detailed discussion of the general case, in which no special assumption is made regarding the form of the functions F, that is to say, regarding the mode of physical interdependence of the several species and their environment.

We now proceed to consider a simple special case, as follows:

The system comprises

1. A species of organism S_1, a plant species, say, deriving its nourishment from a source presented in such large excess that the mass of the source may be considered constant during the period of time with which we are concerned.

2. A species S_2, for example a herbivorous animal species, feeding on S_1.

In this case we have the following obvious relations

$$\left. \begin{array}{c} \text{Rate of in-} \\ \text{crease of } X_1 \\ \text{per unit of} \\ \text{time} \end{array} \right\} = \left\{ \begin{array}{c} \text{Mass of newly} \\ \text{formed } S_1 \text{ per} \\ \text{unit of time} \end{array} \right\} - \left\{ \begin{array}{c} \text{Mass of } S_1 \\ \text{destroyed by} \\ S_2 \text{ per unit of} \\ \text{time} \end{array} \right\} - \left\{ \begin{array}{c} \text{Other dead} \\ \text{or excretory} \\ \text{matter elimi-} \\ \text{nated from } S_1 \\ \text{per unit of} \\ \text{time} \end{array} \right\} \quad (3)$$

$$\text{Rate of increase of } X_2 \text{ per unit of time} = \left\{ \begin{array}{l} \text{Mass of newly} \\ \text{formed } S_2 \text{ per} \\ \text{unit of time} \\ \text{(derived from} \\ S_1 \text{ as food in-} \\ \text{gested)} \end{array} \right\} - \left\{ \begin{array}{l} \text{Mass of } S_2 \\ \text{destroyed or} \\ \text{eliminated per} \\ \text{unit of time} \end{array} \right\} \qquad (4)$$

Or, in analytical symbols,

$$\frac{dX_1}{dt} = A'_1 X_1 - B_1 X_1 X_2 - A''_1 X_1 \qquad (5)$$

$$= (A'_1 - A''_1)X_1 - B_1 X_1 X_2 \qquad (6)$$

$$= A_1 X_1 - B_1 X_1 X_2 \qquad (7)$$

$$= X_1(A_1 - B_1 X_2) \qquad (8)$$

$$\frac{dX_2}{dt} = A_2 X_1 X_2 - B_2 X_2 \qquad (9)$$

$$= X_2(A_2 X_1 - B_2) \qquad (10)$$

The coefficients A_1, A_2, B_1, B_2 are in general functions of X_1 and X_2.

The reasons for selecting the form (5), (9) for the analytical formulation of (3), (4) require perhaps a little explanation. For small changes the rate of formation of new material of a given species of organism under given conditions is proportional to the existing mass of that species. In other words, the growth of living matter is a typically autocatakinetic[5] process. This term has, therefore, been put in the form $A' X_1$ for the species S_1. Proportionality does not hold for large changes of X_1, X_2, and this is duly provided for in that A'_1 is a function of X_1, X_2.

Similarly the mass of matter rejected per unit of time from the species S_1 is proportional to X_1, and has been put in the form $A''_1 X_1$, where A'' is in general a function of X_1, X_2.

Again, the mass of S_1 destroyed by S_2 feeding upon it will, for small changes, be proportional to X_2 and also to X_1. This term has, therefore, been set down in the form $B_1 X_1 X_2$. Here again the departures from proportionality are taken care of by the variations of B_1 with X_1 and X_2, of which variables B_1 is a function.

Similar remarks apply to the formulation (9) of (4). If there were no waste in the feeding process, and assuming that S_2 consumes no other substance than S_1, we would have $B_1 = A_2$; but in the more general case $B_1 \neq A_2$. Approaching now the analytical treatment of equations (5), (9), or their equivalents (8), (10), we note first of all that there are two ways of satisfying the condition for equilibrium, namely:

$$X_1 = X_2 = 0 \qquad (11)$$

and

$$X_1 = \frac{B_2}{A_2}; \; X_2 = \frac{A_1}{B_1} \qquad (12)$$

We shall return later to the condition (11).

Condition (12) we will employ to define a new origin. Accordingly we introduce into (8), (10) the variables:

$$x_1 = X_1 - \frac{B_2}{A_2} \tag{13}$$

$$x_2 = X_2 - \frac{A_1}{B_1} \tag{14}$$

and obtain

$$\frac{dx_1}{dt} = a_{12}x_2 + a_{112}x_1x_2$$
$$\frac{dx_2}{dt} = a_{21}x_1 + a_{212}x_1x_2 \tag{15}$$

where

$$a_{12} = -\frac{B_1B_2}{A_2} \tag{16}$$

$$a_{112} = -B_1 \tag{17}$$

$$a_{21} = \frac{A_1A_2}{B_1} \tag{18}$$

$$a_{212} = A_2 \tag{19}$$

Note the significant fact that in (15) the linear terms in the dexter diagonal are lacking. It is this circumstance which imparts an oscillatory character to the process.

For, since a_{12} and a_{21} are in general functions of x_1, x_2, let us expand them by Taylor's theorem and put

$$a_{12} = p_0 + p_1x_1 + p_2x_2 + \dots \tag{20}$$
$$a_{21} = q_0 + q_1x_1 + q_2x_2 + \dots \tag{21}$$

A general solution of the system of differential equations (15) is then

$$x_1 = P_1e^{\lambda_1 t} + P_2e^{\lambda_2 t} + P_{11}e^{2\lambda_1 t} + P_{22}e^{2\lambda_2 t} + \dots \tag{23}$$
$$x_2 = Q_1e^{\lambda_1 t} + Q_2e^{\lambda_2 t} + Q_{11}e^{2\lambda_1 t} + Q_{22}e^{2\lambda_2 t} + \dots \tag{24}$$

where λ_1, λ_2, are the roots of the determinental equation for λ

$$\begin{vmatrix} -\lambda & p_0 \\ q_0 & -\lambda \end{vmatrix} = 0 \tag{25}$$

that is to say,

$$\lambda = \pm\sqrt{p_0q_0} \tag{26}$$

Now, according to (20), (21) p_0, q_0 are the equilibrium values of a_{12}, a_{21}. Hence, if we denote by $\bar{A}_1$, $\bar{B}_2$ the equilibrium values of A_1, B_2, i.e., those values which correspond to $x_1 = x_2 = 0$, then we have, by (16), (18)

$$p_0q_0 = -\bar{A}_1\bar{B}_2 \tag{27}$$

and hence

$$\lambda = \pm\sqrt{-\bar{A}_1\bar{B}_2} \tag{28}$$

Now the coefficient B_2 is, in the nature of things, a positive number, as follows from its definition by (4), (9).

As regards the coefficient A_1, we have two possible alternatives.

If A_1 is negative for all values of X_1, X_2, then λ, as defined by (28), would be real; but this inference is nugatory. For B_1, like B_2 is, by definition (3), (5), an essentially positive quantity, and hence the equilibrium defined by (12) would in this case occur at a negative value of X_2. But this is physically impossible, since X_2 is a mass.

By referring to (5), (7) it will be seen that this case, in which A_1 is negative for all values of X_1, X_2, and in which an equilibrium of the type defined by (12) is physically impossible, corresponds to a species S_1 incapable of maintaining itself even in the absence of the tax placed upon it by the species S_2 feeding upon it. This is a case of minor interest.

If, on the contrary (12) can be satisfied by a positive value of A_1, so that an equilibrium of the type (12) is physically possible, then, evidently, by (28), λ is a pure imaginary. The solution (23), (24) then takes the form of Fourier's series; the process is an undamped oscillation continuing indefinitely.

In this connection, it is interesting to recall a passage in Spencer's "First Principles," chapter 22, paragraph 173:

"Every species of plant and animal is perpetually undergoing a rhythmical variation in number—now from abundance of food and absence of enemies rising above its average, and then by ↷ consequent scarcity of food and abundance of enemies being depressed below its average......
......amid these oscillation· produced by their conflict, lies that average number of the species at which its expansive tendency is in equilibrium with surrounding repressive tendencies. Nor can it be questioned that this balancing of the preservative and destructive forces which we see going on in every race must necessarily go on. Since increase of numbers cannot but continue until increase of mortality stops it, and decrease of numbers cannot but continue until it is either arrested by fertility or extinguishes the race entirely."

A question now arises. Do the curves representing the solution (23), (24) dip below the zero axes of X_1, X_2? This would mean that one or the other, or both, of the species S_1, S_2 would become extinct through the violence of the oscillations.

To answer this question we consider the relation:

$$\frac{dX_2}{dX_1} = \frac{X_2(A_2X_1 - B_2)}{X_1(A_1 - B_1X_2)} \qquad (29)$$

which is obtained from (8) and (10) by division. From the periodicity of x_1, x_2 (and, therefore, X_1, X_2) it follows that the curve defined in rectangular coördinates X_1, X_2 by (29) is a closed curve. Furthermore, this curve can never cross the X_1 axis, for at all points of this axis the first,

and all the higher derivatives of X_2 with regard to X_1 vanish, as can be seen from (29) directly and by successive differentiations.

Similarly it can be seen that the curve defined by (29) can never cross the X_2 axis.

Hence, if any point on any integral curve of (29) lies within the positive quadrant, the whole of that curve lies in that quadrant. Thus the oscillations can never exceed the limits of positive values X_1, X_2.

We conclude, therefore, that under the conditions of the problem as here set forth, neither the species S_1 nor the species S_2 can become extinct through severity of the oscillations alone. In practice the eventuality might arise, however, that in the course of these oscillations one or the other species might be so thinned out as to succumb to any extraneous influence that might arise such as has not been taken into account in our present considerations.

We return now briefly to the consideration of the equilibrium defined by the equation

$$X_1 = X_2 = 0 \qquad\qquad (11)$$

Applying here the criterion set forth by the author elsewhere,[6] it is seen that when A_1 is positive the determinental equation for λ has at this point two real roots of opposite sign, which is characteristic of unstable equilibrium. If, on the other hand, A_1 is negative in the neighborhood of the origin of X_1, X_2, then the equilibrium here is found to be stable, the two roots for λ being both negative.

In conclusion it may be remarked that a system of equations identical in form with (8), (10) is obtained in the discussion of certain consecutive autocatalytic chemical reactions. Here, however, the coefficients A, B are constants and the integration can be reduced to a quadrature. Aside from a certain number of periodic reactions which have been observed more or less as laboratory curiosities, a certain interest is also attached to this matter from the fact that rhythmical reactions (e.g., heartbeat, which may continue after excision), play an important rôle in physiology. We cannot, of course, say whether in such case geometrical (structural) features are the dominating factors.

[1] Lotka, A. J., *J. Phys. Chem.*, **14,** 1910 (271–274); *Zs. physik. Chem.*, **72,** 1910 (508–511); **80,** 1912 (159–164); *Phys. Rev.*, **24,** 1912 (235–238); *Proc. Amer. Acad. Arts Sci.*, **55,** 1920 (137–153).

[2] Hirniak, J., *Zs. physik. Chem.*, **75,** 1910 (675); compare also Lowry and John, *J. Chem. Soc.*, **97,** 1910 (2634–2645).

[3] Lotka, A. J., *Proc. Amer. Acad.*, loc. cit., p. 145, footnote 13.

[4] Lotka, A. J., *Science Progress*, **14,** 1920 (406–417); *Proc. Amer. Acad.*, loc. cit.

[5] Ostwald, Wo., *Über die zeitlichen Eigenschaften der Entwickelungsvorgänge*, Leipsic, 1908, p. 36.

[6] Lotka, A. J., *Proc. Amer. Acad.*, loc. cit., p. 144, et seq.