In previous work [1], I derived by biological reasoning and mathematical reduction the following system, attributable to G. I. Bell:

\[
\begin{align*}
(1a) \quad & \frac{du}{ds} = u[\lambda_1 + k\lambda_1 u - k(\alpha_1 - \lambda_1)v + kn\lambda_1 w], \\
(1b) \quad & \frac{dv}{ds} = \beta[v[-\lambda_2 - k(\alpha_2 + \lambda_2)u - k\lambda_2 v - kn\lambda_2 w] + k\gamma uvw], \\
(1c) \quad & \frac{dw}{ds} = w[-\lambda_3 + k(\alpha_3 - \lambda_3)u - k\lambda_3 v - kn\lambda_3 w - (k\alpha_3/\beta)uvw].
\end{align*}
\]

Equations (1) simulate the immune response of an organism to antigen invasion. The dependent variables \(u, v, w\) are, respectively the concentrations of antigens, antibodies, and antibody-producing cells. The meanings of all parameters and constants are found in [1, pp. 93—96].

Equations (1) have two nontrivial rest points. The one nearest the origin, \((u_p, v_p, w_p)\), is stable or unstable according to whether \(\beta > \beta_c\) or \(\beta < \beta_c\), where \(\beta_c > 0\) is a critical value of the parameter \(\beta\) in equation (1b). It is shown [1, Theorem 1] that at \(\beta = \beta_c\), a continuous family of periodic solutions bifurcates from \((u_f, v_f, w_f)\). I was able to obtain a direction of bifurcation formula only in the special case where \(\lambda_3 = 0\). Namely, periodic solutions bifurcate to the left (right) of \(\beta_c\), and are stable (unstable) if

\[
(2) \quad \beta_c > (\alpha_1 - \lambda_1)\lambda_1/((\alpha_1 - \lambda_1)(\alpha_2 + \lambda_2) + 2\lambda_1\lambda_2), \quad (<).
\]

Herein I announce the development of a general formula for direction of bifurcation in equations (1), which approaches condition (2) as \(\lambda_3 \to 0\). An analytic direction of bifurcation formula will be important in developing the global theory of these bifurcated families of periodic solutions, and in ascribing possible biomedical implications. I describe the new formula.

First we substitute \(u = u_f + u^0, v = v_f + v^0, w = w_f + w^0\) into equations (1), and thus obtain equations centered at \((u_f, v_f, w_f)\). Then we let \(A_{\beta_c}\) be the matrix of the linear part of these centered DE's, with \(\beta = \beta_c\). The matrix \(A_{\beta_c}\) has the three linearly independent eigenvectors represented symbolically as

\[
(3) \quad (\xi_1, \eta_1, \xi_1), \quad (\overline{\xi}_1, \overline{\eta}_1, \overline{\xi}_1), \quad (\xi, \eta, \xi).
\]
Equations (1) also have an invariant surface passing through \((\mu, \nu, \omega)\), represented as follows:

\[
(4) \quad z = \phi(x, y) = a_{20}x^2 + a_{11}xy + a_{02}y^2 + o(x^2 + y^2),
\]

where \(x, y, z\) are new dependent variables obtained from \((\mu^0, \nu^0, \omega^0)\) through a principal axis transformation.

We must define the following quantities:

\[
\begin{align*}
C &= \imath \delta_{12}^\top \beta_2 \lambda_2, \quad D = \imath \delta_{12}^\top \beta_2 (\alpha_2 + \lambda_2) + \imath \delta_{11}^\top (\alpha_1 - \lambda_1), \\
E &= \imath \delta_{12}^\top \beta_2 \lambda_2 n + \imath \delta_{11}^\top \lambda_3, \\
F &= -\imath \delta_{12}^\top \beta_2 \gamma - \imath \delta_{11}^\top \lambda_1 n - \imath \delta_{13}^\top (\alpha_3 - \lambda_3 - (2 \alpha_3/\theta)\omega), \\
G &= -\imath \delta_{11}^\top \lambda_1, \quad H = \imath \delta_{13}^\top (n \lambda_3 + (\alpha_3/\theta)\nu), \quad I = \imath \delta_{13}^\top \alpha_3/\theta,
\end{align*}
\]

where

\[
\begin{align*}
s_{11}^{-1} &= \frac{\delta \eta_1 - \delta \xi_1 \eta}{\Delta}, \\
s_{12}^{-1} &= \frac{-\delta \xi_1 + \delta \eta_1 \xi}{\Delta}, \\
s_{13}^{-1} &= \frac{\eta_1 \delta \xi_1 - \xi_1 \delta \eta_1}{\Delta}
\end{align*}
\]

with

\[
\Delta = 2 \imath [\delta \xi \imath (\eta_1 \delta \xi_1) - \eta \imath (\xi_1 \delta \eta_1) + \xi_1 \imath (\xi_1 \delta \eta_1)].
\]

We make the realistic assumption that \(\alpha_1 > \lambda_1, \alpha_3 > \lambda_3\).

Also we need the constant \(l = \sqrt{\text{trace} A_{\beta_c}}\) where \(A_{\beta_c}\) is the first compound of the matrix \(A_{\beta_c}\).

Using the constants defined in (4), I put forward the following direction of bifurcation criterion: Define

\[
\kappa = \frac{1}{l} \Re \left\{ \imath [(a_{20} - a_{02}) + i a_{11}] [2 \eta \bar{\eta}_1 C + (\xi \bar{\eta}_1 + \eta \bar{\xi}_1) D + (\eta \bar{\xi}_1 + \xi \bar{\eta}_1) E \\
+ (\xi \bar{\xi}_1 + \eta \bar{\eta}_1) F + 2 \xi \bar{\xi}_1 G + 2 \xi \bar{\xi}_1 H] \\
+ 2 \imath [a_{20} + a_{02}] [2 \eta \bar{\eta}_1 C + (\xi \bar{\eta}_1 + \eta \bar{\xi}_1) D + (\eta \bar{\xi}_1 + \xi \bar{\eta}_1) E \\
+ (\xi \bar{\xi}_1 + \eta \bar{\eta}_1) F + 2 \xi \bar{\xi}_1 G + 2 \xi \bar{\xi}_1 H] \\
+ \imath \xi \bar{\xi}_1 \delta I + 2 \imath \xi_1 [\xi_1 \delta] \}
\]

\[
+ \frac{2}{l^2} \Re \left\{ -[(l/2)^2 [2 \eta \bar{\eta}_1 \delta \bar{C} + (\xi \bar{\eta}_1 + \bar{\xi}_1 \eta_1) D + (\eta \bar{\xi}_1 + \xi \bar{\eta}_1) E \\
+ (\xi_1 \bar{\xi}_1 + \bar{\xi}_1 \xi_1) \bar{F} + 2 \xi_1 \delta \bar{G} + 2 \xi_1 \delta \bar{H}] \\
\times [\eta_1 \bar{C} + \bar{\xi}_1 \xi_1 \bar{D} + \bar{\eta}_1 \bar{F} + \bar{\xi}_1 \bar{G} + \bar{\xi}_1 \bar{H}].\right\}
\]

The criterion is as follows: If \(\kappa\) is negative (positive), then the bifurcation periodic solutions of equations (1) exist in a left (right) neighborhood of \(\beta = \beta_c\), and are stable (unstable).
As can be seen in (5), the quantities $C, D, E, F$ are linear in the critical value $\beta_c$. Therefore formula (6) gives a representation that is a quadratic function of $\beta_c$. Moreover it turns out that the quadratic equation $\kappa = 0$ has a largest positive root when $\lambda_3 \geq 0$. We call this root $\beta_{cc}$.

Then the criterion for direction of bifurcation can be interpreted as follows: If $\beta_c > \beta_{cc}$, the bifurcated periodic solutions emanating from $\beta = \beta_c$ exist in a left (right) interval of $\beta_c$ and are stable (unstable).

The quantity on the right in inequality (2) is, in fact, the greatest positive root of $\kappa = 0$ when $\lambda_3 = 0$.

The proof utilizes the focal point-saddle point type of analysis that goes back to Poincaré [2, pp. 167–181].

REFERENCES


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