Symmetry breaking in solitary solutions to the Hodgkin–Huxley model

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Abstract This paper presents necessary and sufficient conditions for the existence of bright/dark solitary solutions in the Hodgkin–Huxley model. The second-order analytic solitary solutions are derived using the generalized differential operator technique. It is shown that the heteroclinic bifurcation in the Hodgkin–Huxley model yields a symmetry breaking effect. Trajectories of solitary solutions before the bifurcation lie on manifolds of one of the saddle points and the separatrix between periodic and non-periodic solutions. A new separatrix emerges after the heteroclinic bifurcation—but solitary solutions do not lie on this trajectory. This symmetry breaking effect is demonstrated using analytic and computational experiments.

Keywords Solitary solution · Hodgkin–Huxley model · Generalized differential operator · Heteroclinic bifurcation

Mathematics Subject Classification 35B32 · 35C08

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1 Introduction and motivation

Since it was first published in 1952, the Hodgkin–Huxley model [7] remains one of the cornerstones of modern neuroscience. Though originally it was developed to model the propagation of action potentials in the squid giant axon, in more recent years the model has been applied to various fields of research including information representation [13], pattern recognition [28], noise-induced synchronization [23] and small-world networks modeling [9].

In this paper, the following Hodgkin–Huxley model is considered:

$$u_t = u_{\xi\xi} + u\,(u-k)\,(u-1)\,; \quad k \in \mathbb{R}. \tag{1}$$

This version of the Hodgkin–Huxley model is also sometimes referred to as the FitzHugh–Nagumo model [2,15].

Although there have been extensive numerical studies of the Hodgkin–Huxley model [1,4,6,16], construction of analytical solitary wave solutions remains an essential step toward fully understanding the physical meanings of nonlinear processes occurring in Hodgkin–Huxley models. Since Hodgkin–Huxley system models the propagation of neural impulses, the derivation of dark/bright solitary solutions to this system would support the hypotheses that nerve impulses propagate via solitary waves [5,12] and enable the further investigation of such propagation phenomena.

There are a number of papers dealing with solitary solutions to (1) [3,24,29]; however, explicit conditions of the existence of solitary solutions in the space of the equation parameters and the space of initial conditions are not given. In this paper, the following techniques are utilized for the construction of analytical solitary solutions: Inverse balancing is used to determine necessary existence conditions; the generalized differential operator technique enables the derivation of sufficient existence conditions of solitary solutions; linear recurring sequences transform the series solutions generated by the generalized differential operator technique into a closed form.

The construction of analytical solitary solutions enables the analysis of phase plane phenomena occurring in the Hodgkin–Huxley model. One of the parameters of the system is designated as the control parameter. The main objective of this paper is to demonstrate that the heteroclinic bifurcation in the Hodgkin–Huxley model yields a symmetry breaking effect of bright/dark solitary solutions.

2 Preliminaries

A short overview of the techniques that are required to construct analytical dark/bright solitary solutions to (1) is given in this section. Firstly, the Hodgkin–Huxley model is transformed into an ordinary differential equation (ODE) via the wave variable substitution. However, it will be shown that the construction of solitary solutions to the transformed equation is not directly possible. Thus, a narrowed equation (which is an equation that yields the transformed Hodgkin–Huxley equation when differentiated) must be considered. After these transformations, the generalized differential operator technique and linear recurring sequences can be used to construct closed-form analytical solitary solutions to (1). These techniques are described in Sects. 2.2 and 2.3.

2.1 The transformation of the Hodgkin–Huxley equation

Equation (1) can be transformed into an ordinary differential equation using the wave variable transformation $x := \omega\xi + vt$; $\omega, v \in \mathbb{R}$ [10,20]:

$$-vy'_x + \omega^2 y''_{xx} + y\left(y-k\right)\left(y-1\right) = 0, \tag{2}$$

where $y = y(x)$.

It is convenient to rename the coefficients of (2) and state the Hodgkin–Huxley equation in a more general form:

$$y''_{xx} + by'_x = a_0 + a_1 y + a_2 y^2 + a_3 y^3; \quad b, a_k \in \mathbb{R}. \tag{3}$$

Initial conditions on (3) read:

$$y\left(c\right) = u; \quad y'_x\bigg|_{x=c} = v; \quad c, u, v \in \mathbb{R}. \tag{4}$$

In the remainder of this paper, solitary solutions to the Cauchy initial value problem (3), (4) are considered.

2.2 Extended and narrowed differential equations

Consider two initial problems on differential equations of different orders:

$$z'_x = Q\left(x, z\right); \quad z(c) = u; \tag{5}$$

and

$$w''_{xx} = R\left(x, w, w'_x\right); \quad w(c) = u; \quad w'_x\bigg|_{x=c} = v. \tag{6}$$

It is proven in [19] that if (6) is obtained by differentiating both sides of (5), then the solutions to (5) and (6) are connected by the relationship:

$$z(x; c, u) = w\left(x; c, u, Q(c, u)\right). \tag{7}$$

Thus, the solution to (5) also satisfies (6) for initial conditions that are on the curve $v = Q(c, u)$.

2.3 The construction of closed-form solutions

2.3.1 Solitary solutions

Let us consider solitary solutions of the following form [26]:

$$y = \sigma \frac{\prod_{k=1}^{m}\left(\exp\left(\eta\left(x-c\right)\right) - y_k\right)}{\prod_{k=1}^{m}\left(\exp\left(\eta\left(x-c\right)\right) - x_k\right)}, \tag{8}$$

where $\sigma, \eta \in \mathbb{R}$ are constants and y_k, x_k; $k = 1, \ldots, m$, may depend on initial conditions u, v.

The analytical expression (8) can be simplified by the following substitution:

$$\widehat{x} := \exp\left(\eta x\right); \quad \widehat{c} := \exp\left(\eta c\right). \tag{9}$$

Using (9) on (8) yields:

$$\widehat{y} = \widehat{y}\left(\widehat{x}\right) = y\left(x\right) = \sigma \frac{Y\left(\frac{\widehat{x}}{c}\right)}{X\left(\frac{\widehat{x}}{c}\right)}, \tag{10}$$

where

$$X\left(\xi\right) := \prod_{k=1}^{m}\left(\xi - x_k\right); \quad Y\left(\xi\right) := \prod_{k=1}^{m}\left(\xi - y_k\right). \tag{11}$$

2.3.2 The generalized differential operator technique

Let us consider a general nth-order ODE of the following form:

$$w_x^{(n)} = P\left(x, w, w_x', \ldots, w_x^{(n-1)}\right). \tag{12}$$

Initial conditions on (12) read:

$$\left. w_x^{(k)} \right|_{x=c} = u_k; \quad k = 0, \ldots, n-1. \tag{13}$$

The generalized differential operator corresponding to the Cauchy problem (12), (13) reads [17]:

$$\begin{aligned} \mathbf{D} := \mathbf{D}_c + u_1\mathbf{D}_{u_0} + \cdots u_{n-1}\mathbf{D}_{u_{n-2}} \\ + P\left(c, u_0, \ldots, u_{n-1}\right)\mathbf{D}_{u_{n-1}}. \end{aligned} \tag{14}$$

Operators $\mathbf{D}_\alpha$ correspond to partial differentiation with respect to the index variable.

The general series solution to (12), (13) can be written using (14) [17]:

$$w = w\left(x; c, u_0, \ldots, u_{n-1}\right) = \sum_{j=0}^{+\infty} \frac{(x-c)^j}{j!}\mathbf{D}^j u_0. \tag{15}$$

2.3.3 Linear recurring sequences and closed-form solutions

Equation (15) generates a solution in power series form. Closed-form solitary solutions can be obtained from (15) if the sequence of coefficients $p_j := \frac{1}{j!}\mathbf{D}^j u_0$, $j = 0, 1, \ldots$, forms a linear recurring sequence [18].

In order to determine the existence of the closed-form solitary solutions, a sequence of Hankel matrix determinants is formed:

$$d_k := \det\left[p_{j+l-2}\right]_{1 \le j, l \le k+1}. \tag{16}$$

Since $p_j = p_j\left(c, u_0, \ldots, u_{n-1}\right)$ are functions of initial conditions (13), determinants d_k also depend on $c, u_0, \ldots, u_{n-1}$.

If for any $c, u_0, \ldots, u_{n-1}$ and some $m \in \mathbb{N}$, the condition $d_m \neq 0$, $d_{m+j} = 0$, $j = 0, 1, \ldots$, holds true, the sequence $\left(p_j;\ j = 0, 1, \ldots\right)$ is a linear recurring sequence with the following characteristic polynomial [11]:

$$\begin{vmatrix} p_0 & p_1 & \cdots & p_m \\ p_1 & p_2 & \cdots & p_{m+1} \\ \vdots & \vdots & \ddots & \vdots \\ p_m & p_{m+1} & \cdots & p_{2m} \\ 1 & \rho & \cdots & \rho^m \end{vmatrix} = 0. \tag{17}$$

Consider that the roots $\rho_1, \ldots, \rho_m$ of (17) are distinct. Then, elements of $\left(p_j;\ j = 0, 1, \ldots\right)$ take the following form:

$$p_j = \sum_{k=1}^{m} \lambda_k \rho_k^j, \tag{18}$$

where $\lambda_1, \ldots, \lambda_m$ are coefficients determined from a linear system that is obtained by setting $j = 0, \ldots, m-1$ in (18).

As shown in [18], if the following relations hold true:

$$\mathbf{D}\lambda_k = \lambda_k\rho_k; \quad \mathbf{D}\rho_k = \rho_k^2, \tag{19}$$

then inserting (18) into series solution (15) yields the rational closed-form solution:

$$\begin{aligned} w &= \sum_{j=0}^{+\infty}(x-c)^j p_j = \sum_{k=1}^{m}\lambda_k \sum_{j=0}^{+\infty}\left(\rho_k\left(x-c\right)\right)^j \\ &= \sum_{k=1}^{m}\frac{\lambda_k}{1-\rho_k\left(x-c\right)}. \end{aligned} \tag{20}$$

If the polynomial (17) has one repeated root $\rho_0 := \rho_l = \rho_s$, while the rest are distinct, then the sequence $\left(p_j;\ j \in \mathbb{Z}_0\right)$ has the following form:

$$p_j = \lambda_0\rho_0^j + \lambda_{01} j \rho_0^{j-1} + \sum_{\substack{k=1 \\ k \neq l,s}}^{m} \lambda_k \rho_k^j. \tag{21}$$

It is demonstrated in [18] that if conditions (19) hold for roots ρ_k; $k \neq l, s$ and $\rho_0, \lambda_{00}, \lambda_{01}$ satisfy:

$$\mathbf{D}\rho_0 = \rho_0^2; \quad \mathbf{D}\lambda_0 = \lambda_0\rho_0 + \lambda_{01}; \quad \mathbf{D}\lambda_{01} = 3\lambda_{01}\rho_0, \tag{22}$$

then the general series solution can be written in the following closed form:

$$w = \sum_{j=0}^{+\infty} (x-c)^j p_j = \frac{\lambda_{01}(x-c)}{\left(1-\rho_0(x-c)\right)^2} + \sum_{\substack{k=0 \\ k\neq l,s}}^{m} \frac{\lambda_k}{1-\rho_k(x-c)}. \tag{23}$$

2.4 Inverse balancing technique

In order to construct solitary solutions to nonlinear differential equations, it is essential to determine the maximum possible order of such solutions. The inverse balancing technique [21] is used to determine the maximum order and necessary existence conditions of solitary solutions with respect to system parameters.

The main idea of the inverse balancing technique is to express the differential equation parameters in terms of the solution parameters. Inserting the solitary solution as an ansatz into the differential equation results in a system of linear equations with respect to the parameters of the differential equation. If this system is degenerate, the solitary solution of respective order cannot exist. However, if the linear system is solvable with some conditions imposed on the solution parameters, solitary solutions exist and the imposed conditions coincide with existence criteria for the considered solution [21].

The inverse balancing technique described above is applied in Sect. 3 to the Hodgkin–Huxley equation in order to determine the maximum possible order solitary solutions that the model admits.

3 The maximum possible order of solitary solutions to the Hodgkin–Huxley model

The first step of the inverse balancing technique for the Hodgkin–Huxley model is the application of transformation (9) to (3):

$$\eta^2\widehat{x}^2\widehat{y}''_{\widehat{x}\widehat{x}} + \left(\eta^2+\eta b\right)\widehat{x}\widehat{y}'_{\widehat{x}} = a_0 + a_1\widehat{y} + a_2\widehat{y}^2 + a_3\widehat{y}^3, \tag{24}$$

where $\widehat{y}(\widehat{x}) = y(x)$. Dividing both sides of (24) by η^2 transforms (24) into:

$$\widehat{x}^2\widehat{y}''_{\widehat{x}\widehat{x}} + \widehat{b}\widehat{x}\widehat{y}'_{\widehat{x}} = \widehat{a}_0 + \widehat{a}_1\widehat{y} + \widehat{a}_2\widehat{y}^2 + \widehat{a}_3\widehat{y}^3, \tag{25}$$

where $\widehat{b} := 1 + \frac{b}{\eta}, \widehat{a}_k := \frac{a_k}{\eta^2}; k = 0,\dots,3.$

Next, the solitary solution (10) is inserted into (25), which, after simplification, results in the following polynomial of $\widehat{x}$:

$$\begin{aligned}\sigma\frac{\widehat{x}^2}{\widehat{c}^2}\widetilde{Y}_2\left(\frac{\widehat{x}}{\widehat{c}}\right) + \sigma\frac{\widehat{x}}{\widehat{c}}\widehat{b}\widetilde{Y}_1\left(\frac{\widehat{x}}{\widehat{c}}\right)X\left(\frac{\widehat{x}}{\widehat{c}}\right) \\ = \widehat{a}_0X^3\left(\frac{\widehat{x}}{\widehat{c}}\right) + \sigma\widehat{a}_1X^2\left(\frac{\widehat{x}}{\widehat{c}}\right)Y\left(\frac{\widehat{x}}{\widehat{c}}\right) \\ + \sigma^2\widehat{a}_2X\left(\frac{\widehat{x}}{\widehat{c}}\right)Y^2\left(\frac{\widehat{x}}{\widehat{c}}\right) + \sigma^3\widehat{a}_3Y^3\left(\frac{\widehat{x}}{\widehat{c}}\right),\end{aligned} \tag{26}$$

where

$$\widetilde{Y}_1 := \widehat{c}\left(Y'_{\widehat{x}}X - X'_{\widehat{x}}Y\right); \tag{27}$$

$$\widetilde{Y}_2 := \widehat{c}^2\left(Y''_{\widehat{x}\widehat{x}}X^2 - X''_{\widehat{x}\widehat{x}}YX - 2Y'_{\widehat{x}}X + 2X'_{\widehat{x}}Y\right). \tag{28}$$

Subtracting the left- and right-hand sides of (26) yields a $3m$th degree polynomial in $\frac{\widehat{x}}{\widehat{c}}$. Equating the coefficients of this polynomial to zero results in $3m+1$ linear equations—if the obtained linear system is not degenerate (either in general or under some conditions for the parameters of X, Y), the considered equation admits solitary solutions of the respective order.

Note that the Hodgkin–Huxley model can admit first-order kink solitary solutions ($m = 1$) [20]. However, the main objective of this paper is to investigate transient dynamics of the Hodgkin–Huxley model by considering higher-order solitary solutions that are obtained in cases $m \geq 2$. Since kink solitary solutions (case $m = 1$) are monotonous and do not exhibit transient dynamics leading to complex effects, such solutions fall out of the scope of this study.

3.1 Bright/dark solitary solutions to (3)

Let the solitary solution order $m = 2$. Then collecting terms of like powers of $\widehat{x}$ yields a system of seven linear equations with respect to the system parameters $b, \widehat{a}_0, \dots, \widehat{a}_3$. The solution to this linear system is given in Appendix A. Note that there are five parameters and seven equations; thus, to ensure the consistency of the linear system, the following conditions must be imposed on the parameters of the solitary solution:

$$\frac{Y(x_2)}{Y(x_1)} = \frac{x_2}{x_1}; \tag{29}$$

$$\sigma^3 y_1{}^3 y_2{}^3 a_3 + \sigma^2 x_1 x_2 y_1{}^2 y_2{}^2 a_2 + \sigma x_1{}^2 x_2{}^2 y_1 y_2 a_1 + x_1{}^3 x_2{}^3 a_0 = 0. \tag{30}$$

It can be observed that (29)–(30) hold true in the following two cases:

Case 1

$$x_1 x_2 = y_1 y_2. \tag{31}$$

Inserting (31) into the results of the inverse balancing technique leads to $b = 0$.

Case 2

$$x_1 = x_2 = \frac{2y_1 y_2}{y_1 + y_2}. \tag{32}$$

Analogously, this case leads to $a_3 = 0$. However, this case reduces the order of the nonlinearity of Eq. (3) which results in the model not equivalent to the Hodgkin–Huxley model. Thus, this case is not investigated further in this paper.

Note that the balancing equations are also satisfied when $x_1 = y_1, x_1 = y_2$ or $x_1 + x_2 = y_1 + y_2 = 0$; however, these conditions result in kink solitary solutions (since terms in the numerator and denominator of (8) cancel) that, as mentioned previously, due to the straightforward nature of their transient dynamics, are out of scope of this study.

3.2 Higher-order solitary solutions

Consider third-order solitary solutions that are obtained by setting $m = 3$ in (8). Note that solving the balancing Eq. (26) results in the following conditions on the solution parameters:

$$x_{j_1} = y_{k_1}; \tag{33}$$

$$x_{j_2} x_{j_3} = y_{k_2} y_{k_3}, \tag{34}$$

where j_s; k_s, $s = 1, 2, 3$, are distinct triples of numbers from the set $\{1, 2, 3\}$.

It can be observed that condition (33) leads to a bright/dark solitary solution, which has been already discussed in the previous section.

4 Bright/dark solitary solutions to the Hodgkin–Huxley model

Without loss of generality, (3) is transformed into a different form:

$$y''_{xx} = a_3 \left(y - h_1\right)\left(y - h_2\right)\left(y - h_3\right), \tag{35}$$

where h_1, h_2, h_3 are roots of the polynomial $a_3 y^3 + a_2 y^2 + a_1 y + a_0$.

4.1 Narrowed equations of the Hodgkin–Huxley equation with $b = 0$

It can be demonstrated that solutions to (3) with $b = 0$ are obtained from a first-order differential equation of the form:

$$z'_x = \sqrt{A_0 + A_1 z + A_2 z^2 + A_3 z^3 + A_4 z^4}; \quad A_4 \neq 0; \tag{36}$$

$$z(c) = u. \tag{37}$$

Denoting $P(z) := A_0 + A_1 z + A_2 z^2 + A_3 z^3 + A_4 z^4$ and applying the extension procedure detailed in Sect. 2.2 to (36) yield:

$$z''_{xx} = \frac{P'_z}{2\sqrt{P(z)}} z'_x = \frac{1}{2}\left(A_1 + 2A_2 z + 3A_3 z^2 + 4A_4 z^3\right). \tag{38}$$

Renaming the function z to y yields the Hodgkin–Huxley equation with $b = 0$:

$$y''_{xx} = a_0 + a_1 y + a_2 y^2 + a_3 y^3, \tag{39}$$

where $a_k := \frac{k+1}{2} A_{k+1}$, $k = 0, \ldots, 3$.

Let us consider initial conditions on (39) of the form (4). Then, the solution to (36) is also a solution to (39) with initial conditions (4) if and only if $v = \sqrt{P(u)}$. Thus, the following relation holds true:

$$y\left(x; c, u, \sqrt{P(u)}\right) = z(x; c, u). \tag{40}$$

Note that the parameter A_0 appears in (36), but not in the coefficients of (39). This leads to the conclusion that there is an infinite set of equations (36) (obtained as A_0 varies from $-\infty$ to $+\infty$) that lead to the same Hodgkin–Huxley equation (39). Thus, for a fixed equation (39) and fixed initial conditions u, v, the algebraic equation $v = \sqrt{P(u; A_0)}$ can be solved with respect to A_0, which leads to a narrowed equation (36) corresponding to the considered Hodgkin–Huxley equation and its initial conditions. Furthermore, phase trajectories of solutions to (39) have the form $y'_x = \sqrt{P(y)}$.

4.2 Solitary solutions to the Hodgkin–Huxley equation with $b = 0$

Applying the inverse balancing technique to (36) yields that it admits solitary solutions only when it has the following form:

$$z'_x = A\,(z - z_1)\sqrt{(z - z_2)\,(z - z_3)}; \quad A \neq 0, \tag{41}$$

where z_1 is double root of $P(z)$ and z_2, z_3 are single roots of $P(z)$. The relationship between parameters of (40) and (35) reads:

$$a_3 = 2A^2; \tag{42}$$

$$h_1 = z_1; \tag{43}$$

$$h_2 + h_3 = \frac{1}{4}\,(2z_1 + 3z_2 + 3z_3)\,; \tag{44}$$

$$h_2 h_3 = \frac{1}{4}\,(z_1 z_2 + z_1 z_3 + 2z_2 z_3)\,. \tag{45}$$

The generalized differential operator technique described in Sects. 2.3.2 and 2.3.3 is applied to derive solitary solutions to (41) (and, in turn, (3) when initial conditions satisfy the relation $v = A\,(u - z_1)\sqrt{(u - z_2)\,(u - z_3)}$). The detailed explanation of the construction of solitary solutions to (41) is provided in Appendix B.

5 The symmetry breaking effect

5.1 Solitary solutions to the Hodgkin–Huxley model

Let us consider the following Hodgkin–Huxley equation:

$$y''_{xx} = 62 + 12y - 42y^2 + 8y^3; \tag{46}$$

$$y\,(c) = u; \quad y'_x\Big|_{x=c} = v; \quad c, u, v \in \mathbb{R}. \tag{47}$$

Since $b = 0$, the above equation admits a solitary solution that satisfies the narrowed equation:

$$z'_x = \pm 2\,(z + 1)\sqrt{(z - 4)\,\left(z - 5\right)}; \tag{48}$$

$$z(c) = s. \tag{49}$$

The parameters of the narrowed equation are computed using relations (42) – (45). Note that the solution to (48) satisfies (46) only if initial conditions (47) satisfy relation $v = 2\,(u + 1)\sqrt{(u - 4)\,\left(u - 5\right)}$). The solitary solutions to (46) are shown in Fig. 1. It is important to note that there are two distinct types of solitary solutions. Figure 1a corresponds to a bright solitary solution (that does not have singularities), while Fig. 1b depicts a solitary solution with two singularities.

5.2 The heteroclinic bifurcation

Equation (46) can be rewritten in the following form:

$$y'' = 8\left(y - h_1\right)\left(y - h_2\right)\left(y - h_3\right), \tag{50}$$

where $h_1 = -1, h_2 = \frac{1}{8}\left(25 - \sqrt{129}\right), h_3 = \frac{1}{8}\left(25 + \sqrt{129}\right)$. The phase plane that corresponds to these parameter values is given in Fig. 2a. Note that the solitary solutions only exist on the curve $v = 2\,(u + 1)\sqrt{(u - 4)\,\left(u - 5\right)}$. Trajectories of the solitary solutions lie on the stable and unstable manifolds of one of the model's saddle points. Also, the non-singular solution is a separatrix that separates periodic and non-periodic solution trajectories.

Let h_2 be the control parameter. Note that in Fig. 2a, $h_2 < \frac{h_1+h_3}{2}$. As h_2 approaches the midpoint between h_1 and h_3, the distance between the trajectories denoted by thick gray and black lines in Fig. 2a decreases and these trajectories merge at $h_2 = \frac{h_1+h_3}{2}$, forming a heteroclinic orbit (see Fig. 2b).

The case $h_2 = \frac{h_1+h_3}{2}$ produces a kink solitary solution. (This can also be noted from conditions (42)–(45) which give $z_2 = z_3$ and result in a Riccati nar-

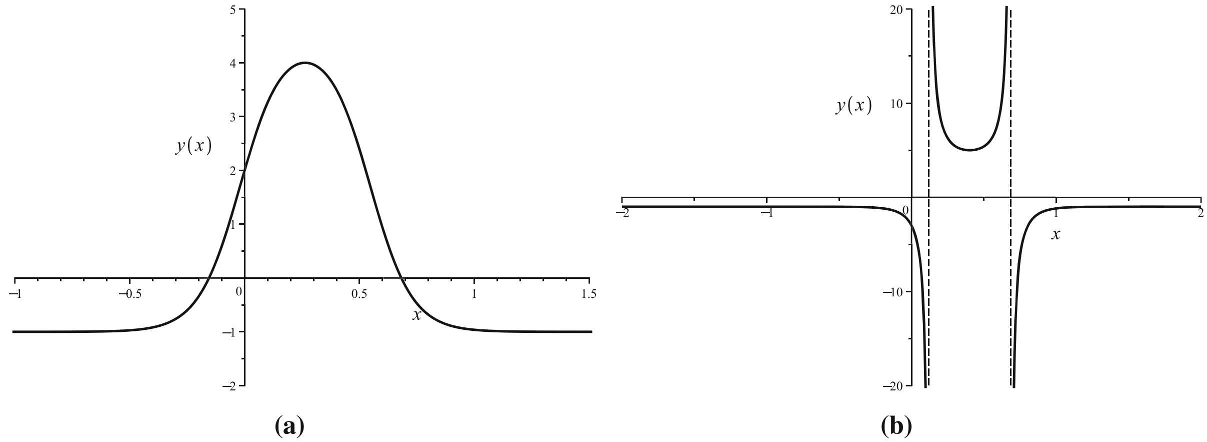

Fig. 1 Solitary solutions to Hodgkin–Huxley model (46) with initial conditions $c = 0$, $u = 2$, $v = 6\sqrt{6}$ (in **a**); $c = 0$, $u = -3$, $v = -8\sqrt{14}$ (in **b**). Dashed lines denote singularity points of the solitary solutions that occur at $x = \frac{1}{2\sqrt{30}} \log \frac{(\sqrt{14}\pm 1)\sqrt{30}+15}{(\sqrt{14}\pm 1)\sqrt{30}-15}$

rowed equation.) The kink solution corresponds to heteroclinic trajectories (thick gray lines in Fig. 2b). In addition to the kink solution, two solitons with one singularity are observed in the system (thick black lines in Fig. 2b). An equivalent effect is observed in the Duffing equation—kink solitary solutions also form a heteroclinic orbit [22].

The case $h_2 > \frac{h_1+h_3}{2}$ does not produce results that are symmetric with respect to solitary solutions to the ones presented in Fig. 2a. Selecting $h_2 = \frac{\sqrt{129}}{4} - 1$ (a point that has the same distance from $\frac{h_1+h_3}{2}$ as the value of h_2 used to generate Fig. 2a) yields the phase plane depicted in Fig. 2c. Solitary solutions satisfying the narrowed equation of the form (41) still exist in this system, but they do not correspond to the separatrix between periodic and non-periodic solutions (thick gray and black lines in Fig. 2b). However, the separatrix trajectory still exists in a symmetrical manner to Fig. 2a, but the solutions that correspond to it do not come from (41). Furthermore, the derivations presented in Sect. 3.1 indicate that solitary solutions satisfying the Hodgkin–Huxley model (50) must satisfy the condition $x_1 x_2 = y_1 y_2$, which leads to the conclusion that the separatrix of the phase plane shown in Fig. 2c does not correspond to a solitary solution.

Phase plane symmetry breaking effect with respect to solitary solutions is demonstrated in Hodgkin–Huxley model. First, the solitary solutions form a separatrix between periodic and non-periodic solution trajectories. When the control parameter reaches the critical value resulting into the heteroclinic bifurcation, the orbit connecting two saddle points transforms into the kink solitary solution. When the control parameter exceeds the critical value, the phase plane topology remains analogous to the case before the bifurcation—however, trajectories of dark and bright solitary solution do no longer correspond to the separatrix.

6 Discussion

As mentioned in “Introduction,” the paradigmatic conductance-based Hodgkin–Huxley model describes the dynamics of action potentials in neurons. Different variations of the Hodgkin–Huxley model (including generic phase oscillators) have been used to model the time evolution of neuronal dynamics by associating the equations of the system with the dynamics of the dendrite and the phase dynamics of the axon, respectively [8]. The incorporation of the dendritic dynamics into a model of a generic phase oscillator significantly changes the dynamics of the network of neurons. Two stable regimes can coexist: the quiet regime where all neurons stop firing and the oscillatory synchronized regime, where the stimulation only alters the firing rates of neurons [14].

The coexistence of two different states (attractors) of a dendritic neuron makes possible to design different desynchronization techniques based on neuron phase resetting pulses [27]. These control techniques are typically based on short pulses which shift the evolution

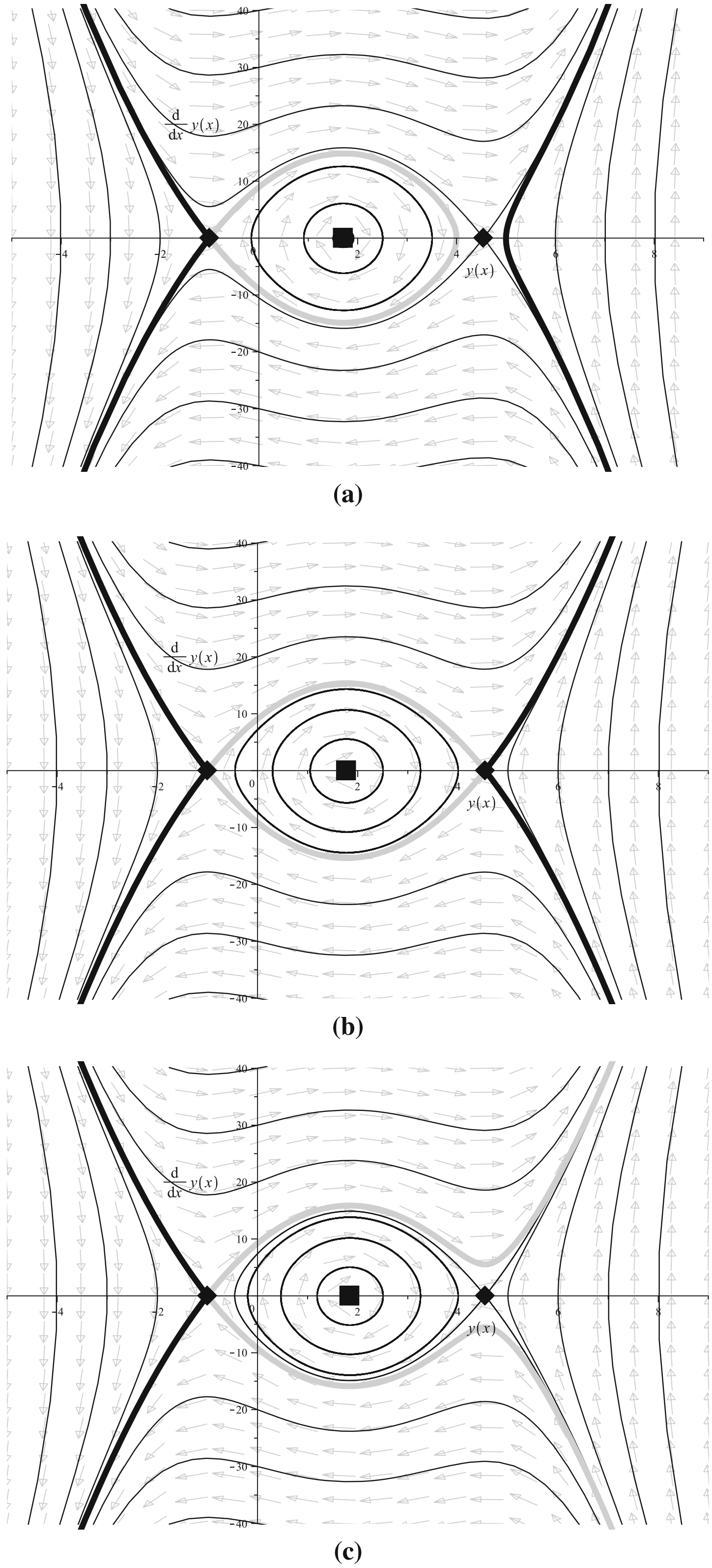

Fig. 2 Symmetry breaking effect in the Hodgkin–Huxley model for $h_2 < \frac{h_1+h_3}{2}$ (**a**), $h_2 = \frac{h_1+h_3}{2}$ (**b**) and $h_2 > \frac{h_1+h_3}{2}$ (**c**). Thin black lines in both parts correspond to solution trajectories. Diamonds at $(h_1, 0)$ and $(h_3, 0)$ denote saddle points; the square at $(h_2, 0)$ corresponds to a center equilibrium point. The thick gray and black lines in **a** correspond to the dark/bright solitary solutions depicted in Fig. 1a, b respectively. In **b**, thick gray lines denote kink solitary solution trajectories; thick black lines denote trajectories of solitary solutions with one singularity. In **c**, thick gray and black lines denote trajectories that correspond to solitary solutions with one singularity. These solution are neither dark/bright nor kink-type solutions

of the neuron dynamics from the basin boundary representing the firing neuron to another basin boundary representing the quiet neuron [25].

It appears that the derived solitary solutions to our model do define the separatrix between different basin boundaries in our model before the emergence of the symmetry breaking effect. In other words, the analytic expression of solitary solutions could be beneficial for the accurate selection of the magnitude of the control pulse. The zone bounded by thick gray lines in Fig. 2a corresponds to the quiet neuron. However, thick gray lines do open after the emergence of the symmetry breaking effect (Fig. 2c) and do not bound a finite area in the phase plane. The analytic expression of solitary solutions would not be helpful for the selection of the magnitude of the control pulse if $h_2 > \frac{h_1+h_3}{2}$.

As mentioned previously, generic phase oscillators are commonly used for the description of the dynamics of dendritic neurons. One of the classical techniques used for the control of such models of neurons is based on small control pulses which bring the evolution of the neuron from one basin boundary to another basin boundary. Our results demonstrate that analytic solitary solutions do not determine a separatrix between different basin boundaries after the emergence of the symmetry breaking effect. This is an interesting result which can be beneficial for the design of control techniques applicable to different models of dendritic neurons.

7 Conclusion

Necessary and sufficient existence conditions for second-order solitary solutions to the Hodgkin–Huxley model have been obtained using the inverse balancing and generalized differential operator techniques. Analytical dark/bright solitary solutions have been constructed which enables the consideration of the symmetry breaking effect occurring in the Hodgkin–Huxley model. Using one root of the right-hand side polynomial of the Hodgkin–Huxley model as a control parameter reveals three distinct topological structures of the phase plane.

First, the dark/bright solitary solution trajectories form a separatrix between periodic and non-periodic solutions. A heteroclinic orbit composed of the trajectories of two kink solitary solutions appears when the control parameter reaches the critical value. As the control parameter exceeds the critical value, the heteroclinic orbit is replaced by a new separatrix with a different orientation. However, this new separatrix is not composed of solitary solutions. Therefore, the Hodgkin–Huxley system exhibits symmetry breaking behavior of solitary solutions in the phase plane. Such a complete analytical study of the solitary solutions to the Hodgkin–Huxley equation provides deeper insight into the nonlinear dynamics of this seminal model.

Compliance with ethical standards

Conflicts of interest The authors declare no conflict of interest.

Apppendix A: Details of the application of the inverse balancing technique to the Hodgkin–Huxley equation

Setting the solitary solution order to $m = 2$ transforms (26) into:

$$\begin{aligned}
&\eta\sigma b\frac{\widehat{x}}{\widehat{c}}X\left(\frac{\widehat{x}}{\widehat{c}}\right)\left(X\left(\frac{\widehat{x}}{\widehat{c}}\right)\left(2\frac{\widehat{x}}{\widehat{c}}-y_2-y_1\right)\right.\\
&\quad\left.-Y\left(\frac{\widehat{x}}{\widehat{c}}\right)\left(2\frac{\widehat{x}}{\widehat{c}}-x_2-x_1\right)\right)\\
&\quad+2\eta^2\sigma\frac{\widehat{x}^2}{\widehat{c}^2}\left(\left(X\left(\frac{\widehat{x}}{\widehat{c}}\right)\right)^2-X\left(\frac{\widehat{x}}{\widehat{c}}\right)Y\left(\frac{\widehat{x}}{\widehat{c}}\right)\right.\\
&\quad-X\left(\frac{\widehat{x}}{\widehat{c}}\right)\left(2\frac{\widehat{x}}{\widehat{c}}-y_2-y_1\right)\\
&\quad\left.\times\left(2\frac{\widehat{x}}{\widehat{c}}-x_2-x_1\right)+Y\left(\frac{\widehat{x}}{\widehat{c}}\right)\left(2\frac{\widehat{x}}{\widehat{c}}-x_2-x_1\right)^2\right)\\
&=\widehat{a}_3\sigma^3\left(Y\left(\frac{\widehat{x}}{\widehat{c}}\right)\right)^3+\widehat{a}_2\sigma^2\left(Y\left(\frac{\widehat{x}}{\widehat{c}}\right)\right)^2X\left(\frac{\widehat{x}}{\widehat{c}}\right)\\
&\quad+\widehat{a}_1\sigma Y\left(\frac{\widehat{x}}{\widehat{c}}\right)\left(X\left(\frac{\widehat{x}}{\widehat{c}}\right)\right)^2+\widehat{a}_0\left(X\left(\frac{\widehat{x}}{\widehat{c}}\right)\right)^3.
\end{aligned}\tag{51}$$

Taking $\widehat{x} = \widehat{c}x_1$, $\widehat{x} = \widehat{c}x_2$, $\widehat{x} = \widehat{c}y_1$, $\widehat{x} = \widehat{c}y_2$, $\widehat{x} = \widehat{c}(x_1 + x_2)/2$,$\widehat{x} = \widehat{c}(y_1 + y_2)/2$ and $\widehat{x} = 0$ results in seven linear equations. The solutions to these equations with respect to $b, \widehat{a}_0, \ldots, \widehat{a}_3$ are given as follows:

$$\widehat{a}_3 = 2\left(\frac{\eta x_1(x_1-x_2)}{\sigma Y(x_1)}\right)^2; \tag{52}$$

$$\widehat{a}_0 = -\frac{2y_1y_2\sigma\eta^2(\Theta_1+\Theta_2)}{\Omega_1},$$

$$b=-\eta+\frac{2\left(y_2X\left(y_1\right)\Theta_2-y_1X\left(y_2\right)\Theta_1\right)}{\left(y_2-y_1\right)\Omega_1},\qquad(53)$$

where

$$\begin{aligned}\Theta_1&:=y_1X\left(y_2\right)\left(\left(y_2-y_1\right)\left(x_1+x_2-2y_2\right)-X\left(y_1\right)\right);\\ \Theta_2&:=y_2X\left(y_1\right)\left(\left(y_1-y_2\right)\left(x_1+x_2-2y_1\right)-X\left(y_2\right)\right);\\ \Omega_1&:=X\left(y_1\right)X\left(y_2\right)\left(y_2X\left(y_1\right)+y_1X\left(y_2\right)\right).\end{aligned}\qquad(54)$$

$$\begin{aligned}\widehat{a}_1=&\frac{1}{\Omega_2}\Big(\Lambda_{10}\widehat{a}_0+\Lambda_{13}\widehat{a}_3+\Lambda_3\left(2\tau_xX\left(\tau_x\right)Y\left(\tau_y\right)\right.\\&\left.-2\tau_yY^2\left(\tau_x\right)\right)\left(\eta^2+\eta b\right)+\sigma\eta^2X\left(\tau_x\right)\\&\times\Big(Y\left(\tau_y\right)\Phi_1-Y\left(\tau_x\right)\Big(\Phi_2+2\tau_x^2X\left(\tau_y\right)Y^2\left(\tau_y\right)\\&+2\tau_y^2Y\left(\tau_x\right)X^2\left(\tau_y\right)\Big)\Big)\Big);\\ \widehat{a}_2=&\frac{1}{\sigma\Omega_2}\Big(-\Lambda_{20}\widehat{a}_0-\Lambda_{23}\widehat{a}_3-\Lambda_3X\left(\tau_x\right)\left(2\tau_xX\left(\tau_y\right)\right.\\&\left.-2\tau_yY\left(\tau_x\right)\right)\left(\eta^2+\eta b\right)+\sigma\eta^2X\left(\tau_x\right)\\&\times\Big(Y\left(\tau_x\right)X\left(\tau_y\right)\Phi_1+X^2\left(\tau_x\right)\\&\Big(\Phi_2+2\tau_y^2X^2\left(\tau_y\right)Y\left(\tau_x\right)\\&-2\tau_x^2X^2\left(\tau_y\right)Y\left(\tau_y\right)\Big)\Big)\Big),\end{aligned}\qquad(55)$$

where

$$\begin{aligned}\tau_x&:=\frac{x_1+x_2}{2},\quad\tau_y:=\frac{y_1+y_2}{2},\\ \Phi_1&:=2\tau_x^2X\left(\tau_y\right)X\left(\tau_x\right)Y\left(\tau_y\right);\\ \Phi_2&:=2\tau_y^2Y\left(\tau_x\right)Y\left(\tau_y\right)\left(4\left(\tau_x-\tau_y\right)^2-X\left(\tau_y\right)\right);\\ \Lambda_{10}&:=X\left(\tau_x\right)Y^2\left(\tau_x\right)X^3\left(\tau_y\right)\\&\quad-X\left(\tau_y\right)Y^2\left(\tau_y\right)X^3\left(\tau_x\right);\\ \Lambda_{13}&:=\sigma^3\left(X\left(\tau_x\right)Y^2\left(\tau_x\right)Y^3\left(\tau_y\right)\right.\\&\quad\left.-X\left(\tau_y\right)Y^2\left(\tau_y\right)Y^3\left(\tau_x\right)\right);\\ \Lambda_{20}&:=Y\left(\tau_y\right)X^2\left(\tau_y\right)X^3\left(\tau_x\right)\\&\quad-Y\left(\tau_x\right)X^2\left(\tau_y\right)X^3\left(\tau_y\right);\\ \Lambda_{23}&:=\sigma^3\left(Y\left(\tau_y\right)X^2\left(\tau_y\right)Y^3\left(\tau_x\right)\right.\\&\quad\left.-Y\left(\tau_y\right)X^2\left(\tau_x\right)Y^3\left(\tau_y\right)\right);\\ \Lambda_3&:=2\sigma\eta X\left(\tau_y\right)X\left(\tau_x\right)Y\left(\tau_y\right)\left(\tau_x-\tau_y\right);\\ \Omega_2&:=\sigma X\left(\tau_x\right)X\left(\tau_y\right)Y\left(\tau_x\right)Y\left(\tau_y\right)\\&\quad\left(Y\left(\tau_y\right)X\left(\tau_x\right)-Y\left(\tau_x\right)X\left(\tau_y\right)\right).\end{aligned}$$

Appendix B: Construction of solitary solutions to (41)

An independent variable transformation (9) is applied to (41):

$$\eta\widehat{x}\,\widehat{z}'_{\widehat{z}}=A(\widehat{z}-z_1)\sqrt{(\widehat{z}-z_2)(\widehat{z}-z_3)}.\qquad(56)$$

Initial conditions (37) are transformed to:

$$\widehat{z}\left(\widehat{c}\right)=u.\qquad(57)$$

The generalized differential operator with respect to (56) reads:

$$\mathbf{D}:=\mathbf{D}_{\widehat{c}}+\frac{1}{\eta\widehat{c}}A\left(u-z_1\right)\sqrt{\left(u-z_2\right)\left(u-z_3\right)}\mathbf{D}_u.\qquad(58)$$

Computing Hankel determinants (16) for the sequence $\widehat{p}_j:=\frac{1}{j!}\mathbf{D}^ju;\ j=0,1,\ldots$, yields the following relation:

$$d_4=\frac{1}{\eta^{12}\widehat{c}^{12}}\left(\eta^2-A^2\left(z_1-z_2\right)\left(z_1-z_3\right)\right)f\left(\eta,u\right),\qquad(59)$$

where $f\left(\eta,u\right)$ is a polynomial in η,u. The above equation yields that $d_4=0$ only if:

$$\eta=\pm A\sqrt{\left(z_1-z_2\right)\left(z_1-z_3\right)}.\qquad(60)$$

Equation (56) can admit closed-form solutions only if conditions (19) hold true. To verify (19), the characteristic roots $\widehat{\rho}_k,k=1,2,3$, are computed from the characteristic polynomial:

$$\begin{vmatrix}\widehat{p}_0&\widehat{p}_1&\widehat{p}_2&\widehat{p}_3\\ \widehat{p}_1&\widehat{p}_2&\widehat{p}_3&\widehat{p}_4\\ \widehat{p}_2&\widehat{p}_3&\widehat{p}_4&\widehat{p}_5\\ 1&\widehat{\rho}&\widehat{\rho}^2&\widehat{\rho}^3\end{vmatrix}=0.\qquad(61)$$

Solution to (61) reads:

$$\widehat{\rho}_1=0;\qquad(62)$$

$$\begin{aligned}\widehat{\rho}_2=&\frac{1}{2\widehat{c}\left(z_1-z_3\right)\left(z_1-z_2\right)}\\&\Big(\Big(\pm\sqrt{\left(u-z_2\right)\left(u-z_3\right)}+u-z_1\Big)\\&\times\sqrt{\left(z_1-z_2\right)\left(z_1-z_3\right)}-\left(z_1-z_2\right)\left(z_1-z_3\right)\Big);\end{aligned}\qquad(63)$$

$$\begin{aligned}\widehat{\rho}_3=&\frac{1}{2\widehat{c}\left(z_1-z_3\right)\left(z_1-z_2\right)}\\&\Big(\Big(\pm\sqrt{\left(u-z_2\right)\left(u-z_3\right)}-u+z_1\Big)\end{aligned}$$

$$\times \sqrt{(z_1 - z_2)(z_1 - z_3)} - (z_1 - z_2)(z_1 - z_3)\Big). \tag{64}$$

Formula (18) together with (62)–(64) yields:

$$\widehat{p}_j = \lambda_1 0^j + \lambda_2 \widehat{\rho}_1^j + \lambda_3 \widehat{\rho}_2^j. \tag{65}$$

Note that $0^0 := 1$. Definition of the generalized differential operator $\mathbf{D}$ and sequence $\widehat{p}_j$ for $j = 0, 1, 2$ results in:

$$\lambda_1 = z_1; \tag{66}$$

$$\lambda_2 = \frac{\widehat{p}_1 \widehat{\rho}_2 - \widehat{p}_2}{\widehat{\rho}_1 \left(\widehat{\rho}_2 - \widehat{\rho}_1\right)}; \tag{67}$$

$$\lambda_3 = \frac{\widehat{p}_1 \widehat{\rho}_1 - \widehat{p}_2}{\widehat{\rho}_2 \left(\widehat{\rho}_1 - \widehat{\rho}_2\right)}. \tag{68}$$

Using (62)–(64) and (66)–(68), it is verified that conditions (19) hold true; thus, the solution to (56) reads:

$$\widehat{z} = z_1 + \frac{\lambda_2}{1 - \widehat{\rho}_2 (\widehat{x} - \widehat{c})} + \frac{\lambda_3}{1 - \widehat{\rho}_3 (\widehat{x} - \widehat{c})}. \tag{69}$$

Using the inverse of transformation (9) yields the solution to (41):

$$z = \frac{z_1 \left(\exp\left(\eta (x - c)\right) - \alpha_1\right)\left(\exp\left(\eta (x - c)\right) - \alpha_2\right)}{\left(\exp\left(\eta (x - c)\right) - 1 - \frac{1}{\rho_2}\right)\left(\exp\left(\eta (x - c)\right) - 1 - \frac{1}{\rho_3}\right)}, \tag{70}$$

where

$$\rho_k = \rho_k(u) = \widehat{c}\widehat{\rho}_k; \quad k = 2, 3; \tag{71}$$

and

$$\alpha_2 = \frac{1}{2z_1}\left(-K + \sqrt{K^2 - 4z_1 L}\right);$$

$$\alpha_3 = -\frac{1}{2z_1}\left(K + \sqrt{K^2 - 4z_1 L}\right). \tag{72}$$

The functions $K(u)$, $L(u)$ have the following expressions:

$$K = -\left(z_1 \left(2 + \frac{1}{\rho_2} + \frac{1}{\rho_3}\right) + \frac{\mu_2}{\rho_2} + \frac{\mu_3}{\rho_3}\right); \tag{73}$$

$$L = z_1 \left(1 + \frac{1}{\rho_2}\right)\left(1 + \frac{1}{\rho_3}\right) + \frac{\mu_2}{\rho_2}\left(1 + \frac{1}{\rho_3}\right) + \frac{\mu_3}{\rho_3}\left(1 + \frac{1}{\rho_2}\right). \tag{74}$$

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