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Solitons in a nonlinear DNA model

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Abstract

A complete qualitative analysis of the nonlinear DNA torsional equations proposed by Yakushevich [Phys. Lett. A 136 (1989) 413] is performed. Analytical expressions for some solutions are obtained. Special attention is paid to the stability of the solutions and the range of soliton interaction in the general case. Some biological implications are suggested.

There has been a very active theoretical work on the proposal of nonlinear dynamical models for the deoxyribonucleic acid (DNA) in order to explain the origin and dynamics of open states in the double helix of this molecule [1–3], which are somehow related to the transcription or replication processes. Even though most of the models proposed are simple in the sense that not all the degrees of freedom are included, in the majority of the cases, these models predict a very rich variety of possible open states in contrast to the scarcely few experimental data related to the conformation of the open form [4–6]. Additionally, the interactions between the solitons (or open states) are variable for the different proposed models and in most cases have short range. In this paper, we study a particular model [1], which describes the torsional dynamics of the double DNA helix and we obtain the general behavior of the solutions and the range of the interaction between the solitons, which turned out to be a long range one.

Yakushevich [1] proposed the following equations for the torsional dynamics of DNA,

$$I_1\varphi_{1tt}=K_1a^2\varphi_{1zz}-k\frac{\Delta l}{l}\left[(2R^2+Rl_0)\sin\varphi_1-R^2\sin(\varphi_1+\varphi_2)\right], \quad (1a)$$

$$I_2\varphi_{2tt}=K_2a^2\varphi_{2zz}-k\frac{\Delta l}{l}\left[(2R^2+Rl_0)\sin\varphi_2-R^2\sin(\varphi_1+\varphi_2)\right], \quad (1b)$$

where

$$\frac{\Delta l}{l}=1-l_0\left[(2R+l_0-R\cos\varphi_1-R\cos\varphi_2)^2+(R\sin\varphi_1-R\sin\varphi_2)^2\right]^{-1/2}.$$

In these equations, φ_i is the torsional angle of the ith chain, I_i its moment of inertia, K_i is the rigidity of the longitudinal springs of the ith chain and k the rigidity of the transversal springs connecting both chains, R is the radius of the chains, l_0 the minimum separation between the chains and a the characteristic length of a base pair in the double helix. In Ref. [1] these equations are simplified by assuming that $l_0=0$, which leads to

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$$I_1\varphi_{1tt}-K_1a^2\varphi_{1zz}+kR^2[2\sin\varphi_1-\sin(\varphi_1+\varphi_2)]=0\,, \qquad (2a)$$

$$I_2\varphi_{2tt}-K_2a^2\varphi_{2zz}+kR^2[2\sin\varphi_2-\sin(\varphi_1+\varphi_2)]=0\,. \qquad (2b)$$

For these equations different types of solutions are proposed in order to simplify even more the set of equations. The following cases are considered as solutions of Eqs. (2): case (a) $\varphi_1=0$, $\varphi_2\neq 0$, for which Eqs. (2) are reduced to

$$I\varphi_{tt}-Ka^2\varphi_{zz}+kR^2\sin\varphi=0\,. \qquad (3)$$

This result is not quite correct since by putting $\varphi_1=0$ in Eq. (2a) then $\sin\varphi_2=0$, which leads necessarily to the solution $\varphi_2=n\pi\equiv\text{const}$ and does not correspond to a solitonic solution of Eq. (3).

On the other hand, cases (b) $\varphi_1=\varphi_2$ and (c) $\varphi_1=-\varphi_2$ lead to the equations

$$I\varphi_{tt}-Ka^2\varphi_{zz}+2kR^2\sin\varphi-kR^2\sin(2\varphi)=0\,, \qquad (4)$$

$$I\varphi_{tt}-Ka^2\varphi_{zz}+2kR^2\sin\varphi=0\,, \qquad (5)$$

respectively. These equations are only valid for symmetric chains, i.e. for $I_1=I_2\equiv I$ and $K_1=K_2\equiv K$.

Let us analyse Eq. (2) in a more general way. As usual let us introduce the travelling wave variable $\xi=z-vt$, to obtain the following system of equations,

$$W_1\varphi_1''-kR^2[2\sin\varphi_1-\sin(\varphi_1+\varphi_2)]=0\,, \qquad (6a)$$

$$W_2\varphi_2''-kR^2[2\sin\varphi_2-\sin(\varphi_1+\varphi_2)]=0\,, \qquad (6b)$$

where $W_i=K_ia^2-I_iv^2$ and the prime corresponds to the derivative with respect to ξ.

The system of Eqs. (6) can be written as

$$W_1\varphi_1''=-\frac{\partial V(\varphi_1,\varphi_2)}{\partial\varphi_1}\,, \qquad (7a)$$

$$W_2\varphi_2''=-\frac{\partial V(\varphi_1,\varphi_2)}{\partial\varphi_2}\,, \qquad (7b)$$

where

$$V(\varphi_1,\varphi_2)=kR^2[2(\cos\varphi_1+\cos\varphi_2)-\cos(\varphi_1+\varphi_2)]\,. \qquad (8)$$

$V(\varphi_1,\varphi_2)$ has local maxima at the points $\varphi_1=2n\pi$, $\varphi_2=2m\pi$, with $n=0,\pm1,\pm2,\ldots$, and $m=0,\pm1,\pm2,\ldots$. The points $\varphi_1=(2n-1)\pi$, $\varphi_2=(2n-1)\pi$ correspond to local minima while the points $\varphi_1=(2n-1)\pi$, $\varphi_2=2m\pi$; $\varphi_1=2n\pi$, $\varphi_2=(2m-1)\pi$ are saddle points. These points are shown in Fig. 1.

The local maxima have the same height so for every two contiguous local maxima there are solutions of the kink type [7,8]. For example, there are solutions with the following properties,

$$\lim_{\xi\to-\infty}\varphi_1=0,\quad \lim_{\xi\to\infty}\varphi_1=\pm2\pi\,,$$
$$\lim_{\xi\to-\infty}\varphi_2=0,\quad \lim_{\xi\to\infty}\varphi_2=0\,, \qquad (9)$$

and their symmetrical and

$$\lim_{\xi\to-\infty}\varphi_1=0,\quad \lim_{\xi\to\infty}\varphi_1=\pm2\pi\,,$$
$$\lim_{\xi\to-\infty}\varphi_2=0,\quad \lim_{\xi\to\infty}\varphi_2=\pm2\pi\,, \qquad (10)$$

and their antikink solitons, respectively.

Among these solutions only those of type (9) are stable (see the Appendix). The solutions given by (10) are unstable and decompose in two solitons of type (9), together with small amplitude travelling waves. We must also notice that the connection of the points (0, 0) and (0, 2π) cannot be done through the

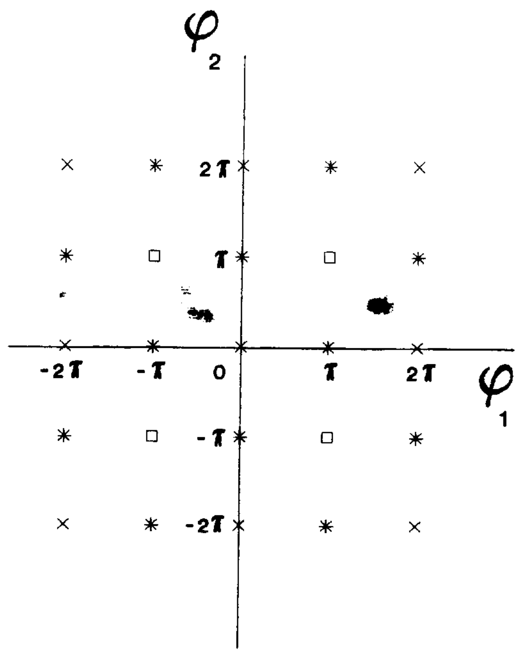

Fig. 1. Distribution of critical points for $V(\varphi_1,\varphi_2)$, where (×) are maxima, (∗) saddle and (□) minima points.

straight line at $\varphi_1=0$, which is due to the fact that $\varphi_1\equiv 0$, $\varphi_2\neq 0$ is not a solution of Eq. (3).

There are, in principle, solutions that connect saddle points, for example,

$$\lim_{\xi\to-\infty}\varphi_1=\pi,\quad \lim_{\xi\to\infty}\varphi_1=\pi\,,$$
$$\lim_{\xi\to-\infty}\varphi_2=0,\quad \lim_{\xi\to\infty}\varphi_2=2\pi\,, \tag{11}$$

but as can be readily seen, these solutions are clearly unstable.

There are different critical velocities for $K_1\neq K_2$, given by the general expression $c_i^2=K_ia^2/I_i$. We will consider first the case when the velocity of the soliton is restricted to $0<v^2<c_m^2$, with c_m the maximum critical velocity. Without any loss of generality, we can assume that $0<c_2^2\leqslant c_1^2$. In the particular case of $v=c_2$, Eq. (6b) yields a relationship between φ_1 and φ_2, given by

$$\varphi_2=\arctan\left(\frac{\sin\varphi_1}{2-\cos\varphi_1}\right), \tag{12}$$

and symmetrically when $v=c_1$. An interesting characteristic of Eq. (12) is that it displays a relationship between the two components of the solution which is qualitatively similar to the solutions of the type depicted by Eqs. (9) corresponding to any other value of the velocity. The exact solution can be obtained from Eq. (12) and the first integral of Eqs. (6) in terms of elliptical integrals. In Fig. 2, the trajectories in the plane (φ_1,φ_2) are shown for different cases.

The cases (b) and (c), represented by Eqs. (4) and (5) correspond to solutions of the type given by (10). For the last case (case (c)), we have the following exact solutions,

$$\varphi_1=-\varphi_2$$
$$=4\arctan\left[\exp\left(\frac{z-z_0-vt}{\Lambda_0(1-v^2/c^2)^{1/2}}\right)\right], \tag{13}$$

where $\Lambda_0^2=Ka^2/kR^2$, $c^2=Ka^2/I$, z_0 is the initial position of the soliton and v its translational velocity. The rest energy, i.e., the energy necessary to produce a static open state, for this solution is

$$H_0(\varphi_1=-\varphi_2)=16(2Kk)^{1/2}aR\,. \tag{14}$$

For case (b), i.e. for $\varphi_1=\varphi_2$, we have

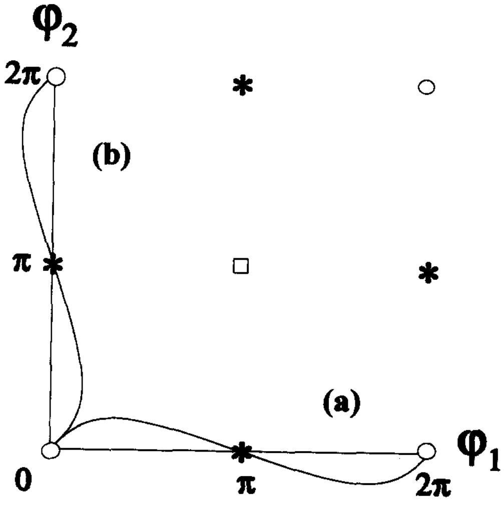

Fig. 2. Trajectories in the (φ_1,φ_2) plane for (a) $v^2=c_2^2$ and (b) $v^2=c_1^2$.

$$\varphi_1=\varphi_2=2\arctan\left(\frac{2^{1/2}}{\Lambda_0}\frac{z-vt}{(1-v^2/c^2)^{1/2}}\right)+\pi\,. \tag{15}$$

For this case, the rest energy is given by

$$H_0(\varphi_1=\varphi_2)=4\pi(2Kk)^{1/2}aR\,. \tag{16}$$

Note that in Eq. (15), there is no exponential in the argument of the function arctan. The type of solution described by Eq. (13) will be called asymmetric, while solution (15) will be called symmetric. Both types of solutions are shown in Fig. 3 and the distances between base pairs are shown in Fig. 4. For the type of solution described in Eq. (9), the rest energy can be written approximately as

$$H_0=8(Kk)^{1/2}aR\,. \tag{17}$$

By comparing the energies for the unstable states (asymmetric and symmetric), given by Eqs. (14) and (16), respectively, with the energy of the stable soliton, Eq. (17), it is possible in principle to calculate the energy radiated through the generation of small amplitude travelling waves.

The system described by Eqs. (7) can be written as an autonomous dynamical system,

$$\varphi_1'=\theta_1,\quad \theta_1'=\frac{kR^2}{W_1}\,[2\sin\varphi_1-\sin(\varphi_1+\varphi_2)]\,,$$
$$\varphi_2'=\theta_2,\quad \theta_2'=\frac{kR^2}{W_2}\,[2\sin\varphi_2-\sin(\varphi_1+\varphi_2)]\,. \tag{18}$$

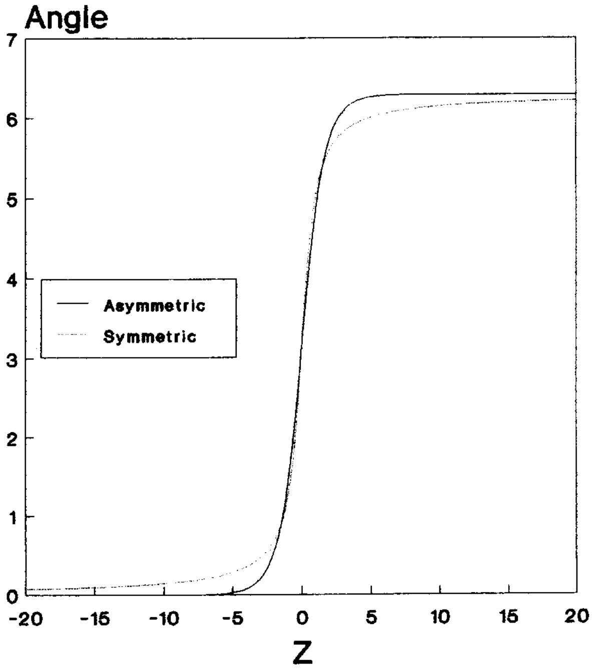

Fig. 3. Comparison of the shape of the asymmetric and symmetric solitons in the case of $l_0=0$.

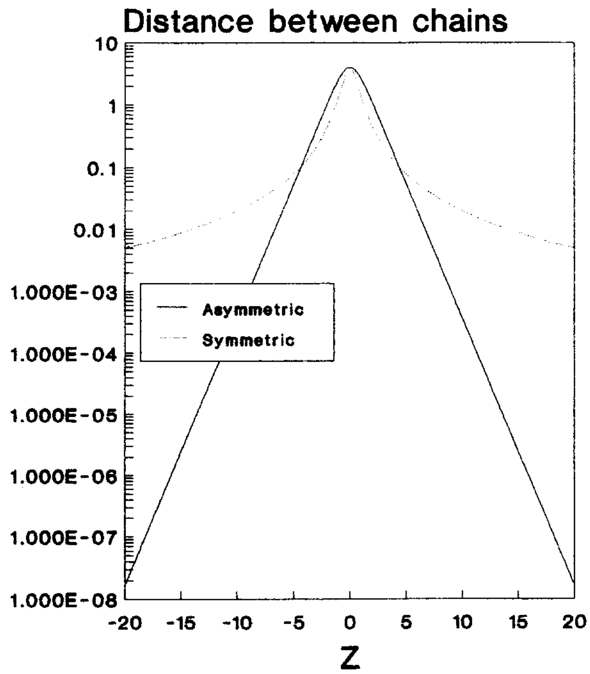

Fig. 4. Opening distances for the asymmetric and symmetric solitons in the case of $l_0=0$.

The eigenvalues of the Jacobi matrix at the critical points $\varphi_1=2n\pi$, $\varphi_2=2m\pi$, are

$$\lambda_{1,2}^2=0\,, \tag{19}$$

$$\lambda_{3,4}^2=\frac{kR^2}{W_1}+\frac{kR^2}{W_2}\,. \tag{20}$$

The eigenvalues equal to zero, Eq. (19), reflect that there is some degeneracy at the critical points and also there is some anisotropy at these points reflected by the fact that the behavior of the solitons produced along the line $\varphi_1=\varphi_2$ is different from that along $\varphi_1=-\varphi_2$. This difference in behavior can be seen for the solutions given by Eqs. (13) and (15). For the former one there is a fast exponential behavior at the tails of the soliton when $\xi\to\pm\infty$, while for the second type, the behavior is somewhat slower. Recalling that

$$\varphi'=[2\arctan(B\xi)+\pi]'=\frac{2B}{1+(B\xi)^2}\,,$$

i.e. $\varphi'\sim 1/\xi^2$ and $\varphi\sim 1/\xi$ when $\xi\to\pm\infty$. This result is important for the type of interaction between solitons and will be discussed later in this work.

If we consider the case $v^2>c_1^2\geqslant c_2^2$, then we obtain solutions that correspond to supersonic or takhionic solitons. In the case $W_1=W_2=W$ and since $W<0$, we have

$$\varphi_1''=-\frac{\partial U(\varphi_1,\varphi_2)}{\partial\varphi_1}\,, \tag{21a}$$

$$\varphi_2''=-\frac{\partial U(\varphi_1,\varphi_2)}{\partial\varphi_2}\,, \tag{21b}$$

where $U(\varphi_1,\varphi_2)=-V(\varphi_1,\varphi_2)$ and in the plane (φ_1, φ_2) the maxima and minima are interchanged so the solutions can only join the points $(\pm n\pi, \pm m\pi)$.

Let us suppose that $\varphi_1=-\varphi_2$ and identical critical velocities. Eqs. (21) reduce to a system of uncoupled sine-Gordon equations with the exact solution

$$\varphi_1=-\varphi_2 =4\arctan\left[\exp\left(\frac{\sqrt{2}\,(z-z_0-vt)}{\Lambda_0(v^2/c^2-1)^{1/2}}\right)\right]-\pi\,, \tag{22}$$

which corresponds to a totally open state with a streamly narrow closed region. The solution for $\varphi_1=\varphi_2$ is more complex analytically and can be obtained by the elliptic integral,

$$\int_0^{\varphi} \frac{d\varphi'}{(3+2\cos\varphi' - \cos^2\varphi')^{1/2}} = \frac{\sqrt{2}\,(z - z_0 - vt)}{A_0(v^2/c^2 - 1)^{1/2}}, \tag{23}$$

which again corresponds to a totally open state as the asymmetrical case.

Let us now study the general system given by Eqs. (1) with $l_0 \neq 0$. In this case the solitons of the system

$$W_1 \varphi_1'' = -\frac{\partial V(\varphi_1, \varphi_2)}{\partial \varphi_1},$$

$$W_2 \varphi_2'' = -\frac{\partial V(\varphi_1, \varphi_2)}{\partial \varphi_2}, \tag{24}$$

where

$$V(\varphi_1, \varphi_2) = -\tfrac{1}{2}kR^2\{[(2 + l_0/R - \cos\varphi_1 - \cos\varphi_2)^2 + (\sin\varphi_1 - \sin\varphi_2)^2]^{1/2} - l_0/R\}^2 \tag{25}$$

and the first integral is

$$\tfrac{1}{2}W_1\varphi_1'^2 + \tfrac{1}{2}W_2\varphi_2'^2 + V(\varphi_1, \varphi_2) = \text{const}. \tag{26}$$

From a qualitative point of view, the potential energy $V(\varphi_1, \varphi_2)$ for the exact system is not different from the one described in Fig. 1, i.e., the solitonic solutions connect the same critical points. However, there is a quantitative difference between both situations.

The eigenvalues of the Jacobi matrix at the points $\varphi_1 = 2n\pi$, $\varphi_2 = 2m\pi$ for system (24) are all equal to zero. This result means that there is no optical branch in the vibrational spectrum for the general system (24), in opposition to what is claimed in Ref. [1].

In the neighborhood of the points $\varphi_1 = 2n\pi$ and $\varphi_2 = 2m\pi$, the function $V(\varphi_1, \varphi_2)$ has the following behavior,

$$V(\varphi_1, \varphi_2) = -\tfrac{1}{2}kR^2\Big[\tfrac{1}{4}(1 + 1/\epsilon)^2(\varphi_1^4 + \varphi_2^4) - \frac{1}{\epsilon}(1 + 1/\epsilon)(\varphi_1^3\varphi_2 + \varphi_1\varphi_2^3) + \Big(\frac{3}{2\epsilon^2} + \frac{1}{\epsilon} + \frac{1}{2}\Big)\varphi_1^2\varphi_2^2\Big], \tag{27}$$

where $\epsilon = l_0/R$.

These points are completely degenerate and in their neighborhood, Eqs. (24) do not show linear terms. According to (24), the terms different from zero in the expansion of $V(\varphi_1, \varphi_2)$ are of fourth order. This dependence is of particular importance for the properties of solitons, its dynamics and interactions [9]. Firstly, as it was shown by Eqs. (15), the asymptotical behavior of the solitons at the critical points is as $\varphi \sim 1/\xi$, which means that the interaction between the solitons is of long range type.

Exact solutions in the general case can be obtained by choosing appropriate trajectories in the (φ_1, φ_2) plane, in particular, for $\varphi_1 = -\varphi_2$, the exact solution can be obtained from

$$\int_0^{\varphi} \frac{d\varphi'}{[\epsilon^2 + 4(2+\epsilon)(1 - \cos\varphi')]^{1/2} - \epsilon} = \frac{z - z_0 - vt}{\sqrt{2}\,A_0(1 - v^2/c^2)^{1/2}}. \tag{28}$$

When $\varphi_1 = \varphi_2$, it can be readily seen that $V(\varphi_1, \varphi_2)$ is independent of ϵ, and so the solution is identical to the one given by Eq. (15) for the case $l_0 = 0$.

It can be demonstrated that all solutions in the general case have an asymptotical behavior which is smoother than the classical kink type soliton of the sine-Gordon equation. We can express the sine-Gordon equation solution as

$$\xi \sim \int_0^{\varphi} \frac{d\varphi'}{(1 - \cos\varphi')^{1/2}}. \tag{29}$$

The function given by Eq. (29) is the inverse of the φ solution. An exponential behavior of φ near the critical points ($\varphi = 0$, $\varphi = 2\pi$) corresponds to a logarithmic behavior of $\xi(\varphi)$ near the points 0 or 2π, more explicitly,

$$\frac{d\xi}{d\varphi} \sim \frac{1}{(1 - \cos\varphi)^{1/2}} \sim \frac{1}{\varphi}. \tag{30}$$

For the solution given by Eq. (15), valid for the case $\varphi_1 = \varphi_2$ and any value of l_0, we obtain

$$\frac{d\xi}{d\varphi} \sim \frac{1}{1 - \cos\varphi} \sim \frac{1}{\varphi^2}, \tag{31}$$

which corresponds to a nonexponential behavior for the φ solution. For Eq. (28), we have

$$\frac{d\xi}{d\varphi} \sim \frac{1}{[\epsilon^2+4(2+\epsilon)(1-\cos\varphi)]^{1/2}-\epsilon}$$

$$\sim \frac{\epsilon}{(2+\epsilon)\varphi^2}\,. \qquad (32)$$

As it can be seen in Eqs. (31) and (32), in the case $\epsilon \neq 0$, the solutions have an asymptotical behavior different to those for $\epsilon = 0$.

The qualitative shapes of the solitons are shown in Figs. 5 and 6 for the asymmetric and symmetric types, respectively, with the asymmetrical mode more opened than the symmetrical one. In Ref. [9], it was demonstrated that if the local behavior for the potential at the critical points is as φ^{2n}, $n > 1$, then the interaction force between the solitons decreases with the distance r as

$$F \sim r^{2n/(1-n)}\,. \qquad (33)$$

The interaction force for the solitons of system (1) with $l_0 \neq 0$ decreases with the distance as

$$F \sim r^{-4}\,. \qquad (34)$$

This could be of particular importance in the regulation of biological processes, such as DNA transcription, since the existence of an open state somewhere in the chain could affect the dynamics and formation of distant open states, modulating the opening and transcription processes. Also, the region of the chain

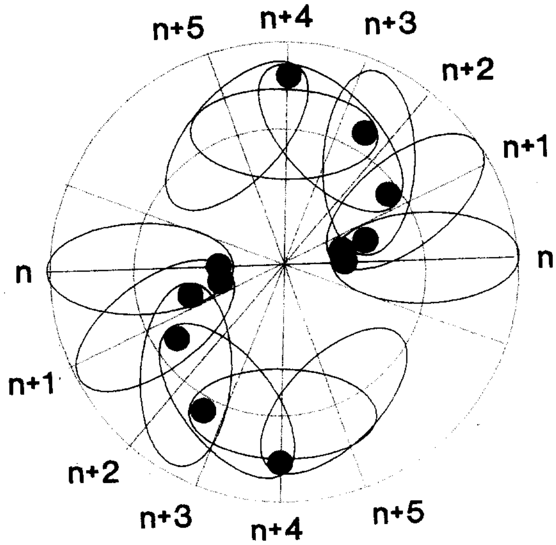

Fig. 5. Asymmetric soliton.

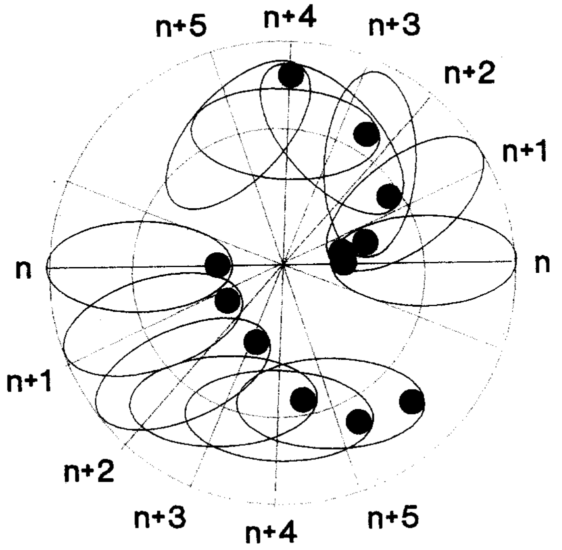

Fig. 6. Symmetric soliton.

where there is a maximum opening is larger for the general case, since the asymptotical behavior for the kink type solitons is smoother than the one corresponding to the solutions in the particular case ($l_0 = 0$) giving the possibility of an enzyme to take charge for the opening of the chain. Of particular importance are the supersonic solutions, since they represent states which are totally open and could contribute significantly to the fusion of the DNA strand to the enzymatic activity. Also, in general, the presence of a propagating soliton along the chain could contribute to its opening through the interaction among different types of open states, thus playing an important role in the transcription process. In a further work, the effect of damping and external forces will be included.

Appendix

For Eqs. (2) with $I_1 = I_2 = I$ and $K_1 = K_2 = K$ we will consider perturbed solutions of the form

$$\varphi_1 = \varphi_{1k} + \psi_1\,, \qquad (A.1a)$$

$$\varphi_2 = \varphi_{2k} + \psi_2\,, \qquad (A.1b)$$

where φ_{1k} and φ_{2k} are solitonic solutions of Eqs. (2) and $|\psi_1| \ll |\varphi_{1k}|$, $|\psi_2| \ll |\varphi_{2k}|$. The linear equations obtained for the functions ψ_1 and ψ_2 are

$$\frac{1}{c^2}\psi_{1tt}-\psi_{1zz}+\frac{1}{\Lambda_0^2}[2\cos(\varphi_{1k})\psi_1 -\cos(\varphi_{1k}+\varphi_{2k})(\psi_1+\psi_2)]=0\,, \qquad \text{(A.2a)}$$

$$\frac{1}{c^2}\psi_{2tt}-\psi_{2zz}+\frac{1}{\Lambda_0^2}[2\cos(\varphi_{2k})\psi_2 -\cos(\varphi_{1k}+\varphi_{2k})(\psi_1+\psi_2)]=0\,. \qquad \text{(A.2b)}$$

The solutions can be written as $f_i(z)\exp(\lambda t)$, so we get the following eigenvalue problem,

$$-f_{1zz}+\frac{1}{\Lambda_0^2}[2\cos(\varphi_{1k})f_1 -\cos(\varphi_{1k}+\varphi_{2k})(f_1+f_2)]=\Gamma f_1\,, \qquad \text{(A.3a)}$$

$$-f_{2zz}+\frac{1}{\Lambda_0^2}[2\cos(\varphi_{2k})f_2 -\cos(\varphi_{1k}+\varphi_{2k})(f_1+f_2)]=\Gamma f_2\,, \qquad \text{(A.3b)}$$

where $\Gamma=-\lambda^2/c^2$.

If we obtain solutions to Eqs. (A.3) such that their eigenvalues λ are negative, then these solutions are stable, otherwise they are unstable. For the particular solution $\varphi_{1k}=-\varphi_{2k}$, then

$$-f_{1zz}+\frac{1}{\Lambda_0^2}[2\cos(\varphi_k)f_1-f_1-f_2] =-\frac{\lambda^2}{c^2}f_1\,, \qquad \text{(A.4a)}$$

$$-f_{2zz}+\frac{1}{\Lambda_0^2}[2\cos(\varphi_k)f_2-f_1-f_2] =-\frac{\lambda^2}{c^2}f_2\,. \qquad \text{(A.4b)}$$

There are two eigenvalues corresponding to the discrete spectrum. The solution for the eigenvalue $\lambda=0$ (translational mode) is

$$f_1=\frac{d\varphi_k}{dz}=\frac{4\sqrt{2}}{\Lambda_0\cosh(\sqrt{2}\,z/\Lambda_0)}\,, \qquad \text{(A.5a)}$$

$$f_2=-\frac{d\varphi_k}{dz}=-\frac{4\sqrt{2}}{\Lambda_0\cosh(\sqrt{2}\,z/\Lambda_0)}\,. \qquad \text{(A.5b)}$$

Nevertheless, we have a positive eigenvalue, $\lambda=\sqrt{2}\,c/\Lambda_0$ with the solution

$$f_1=f_2=\frac{4\sqrt{2}}{\Lambda_0\cosh(\sqrt{2}\,z/\Lambda_0)}\,. \qquad \text{(A.6)}$$

The remaining eigenvalues are imaginary and correspond to the continuous spectrum. For the solution of the type given by Eq. (9), the system (A.2) is topologically equivalent to

$$\frac{1}{c^2}\psi_{1tt}-\psi_{1zz}+\frac{1}{\Lambda_0^2}[\cos(\varphi_{1k})\psi_1]=0\,, \qquad \text{(A.7a)}$$

$$\frac{1}{c^2}\psi_{2tt}-\psi_{2zz}+\frac{2}{\Lambda_0^2}\psi_2=0\,, \qquad \text{(A.7b)}$$

which contains the classical kink type solution of the sine-Gordon equation and just one eigenvalue corresponding to the discrete spectrum ($\lambda=0$). These solutions are stable.

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