A DNA ring acting as a thermal ratchet

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Abstract
Several DNA nanomotors have been recently constructed in laboratories
worldwide. These machines are, however, relatively slow and do not perform
continuous rotations. We have recently proposed a rotary DNA nanomachine
that shows a continuous rotation with a frequency of 10^2–10^4 Hz. This motor is a
closed DNA ring whose elastic features are tuned such that it can be externally
driven via e.g. periodic temperature changes. As a result, the twirling ring
propels itself through the fluid with a speed of tens of nanometres up to a few
microns per second. The current paper gives a more detailed presentation of
this motor and provides a derivation of the low- and high-frequency asymptotic
behaviour of thermal ratchets in general.

(Some figures in this article are in colour only in the electronic version)

1. Introduction

Scaling mechanical devices and machines down to the nanoscale (as popularized by
Feynman [1]) is a long lasting dream and is carried on by several visionary groups
worldwide [2]. It turns out to be crucial to use the proper material to construct such
nanomachines. Among the important material requirements are stability, self-assembly
ability, modularity, replicability, switchability and experimental tractability. One of the
most promising materials fulfilling those requirements is DNA [3]. Assemblies based on
DNA hybridization chemistry [4–14] as well as on conformational DNA transitions [15–17]
have been successfully exploited to build periodically switchable nanodevices. Despite their
beauty and conceptual originality these devices have certain limitations. The large kinetic
barriers involved in the switching process boost their switching time per cycle to $\sim 10^3$ s,
four orders of magnitude slower than their natural counterparts, the biological molecular
motors. Moreover—in contrast to their macroscopic counterparts—such motors typically
do not produce a continuous rotary motion but act as switches between two conformational
states.
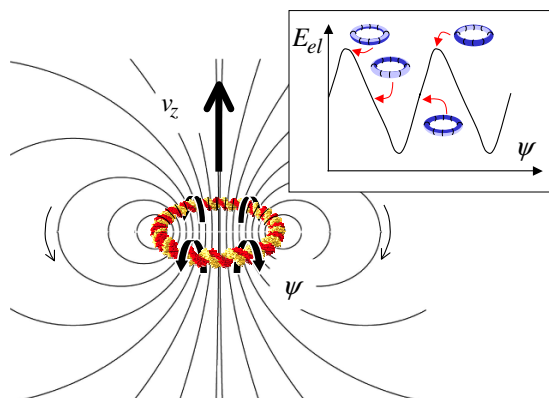
Figure 1. The twirling DNA minicircle together with its flow-field that induces its translational velocity v_z. The inset depicts the elastic energy of the ring as a function of the twirling angle ψ, that shows a ratchet shape for suitably chosen DNA sequences (cf text for details).

We have recently posed the following questions [18]: can one achieve subsecond switching times with a DNA nanomachine? Can such a motor rotate in a continuous fashion? Can such a rotating device self-propel itself through the solvent with a speed of—say—microns per second? In [18] we have indeed proposed such a DNA nanomotor that implements in a very direct way the idea of the thermal ratchet.

The present paper gives an extended presentation of this idea. In section 2 we study the elastic properties and hydrodynamics of a twirling DNA ring. In section 3 we show how temperature oscillations can be used to make this ring twirl. The final section provides conclusions. Finally, in the appendix we calculate the asymptotic time-averaged currents of thermal ratchets in general—providing the proper limits of low and high frequencies of the temperature oscillations.

2. Elasticity and hydrodynamics of a DNA ring

We have recently proposed a surprisingly simple nanomotor: a DNA miniplasmid; cf figure 1 [18]. Despite its structural simplicity this ring can be run as a motor, performing a continuous rotation with a frequency of 10^2–10^4 Hz. The relevant degree of freedom here is the Euler angle ψ (cf figure 1). It is easy to show that provided that the plasmid length is smaller than the DNA persistence length l_P all other degrees of freedom besides the ψ motion can be neglected. The main idea is to induce a directed current $\langle \dot{\psi} \rangle$—in a manner similar to the rotation of a closed rubber tube around its central circular axis. This is achieved via non-equilibrium fluctuations exploiting the ratchet effect [19, 20]; cf the inset of figure 1. As a result the twirling ring generates a hydrodynamic flow-field (also shown in figure 1) that remarkably induces a self-propulsion of the motor as detailed below.

2.1. Elasticity

The energy of an elastic deformation of a DNA ring with radius R parametrized by the arc length parameter s is in general described by three Euler angles $\theta(s)$, $\phi(s)$ and $\psi(s)$ via

$$E_{\text{el}} = \frac{1}{2} k_{\text{B}} T \int_0^{2\pi R} \sum_{i=1,2,3} l_i (\omega_i - \kappa_i)^2 \, \mathrm{d}s \tag{1}$$
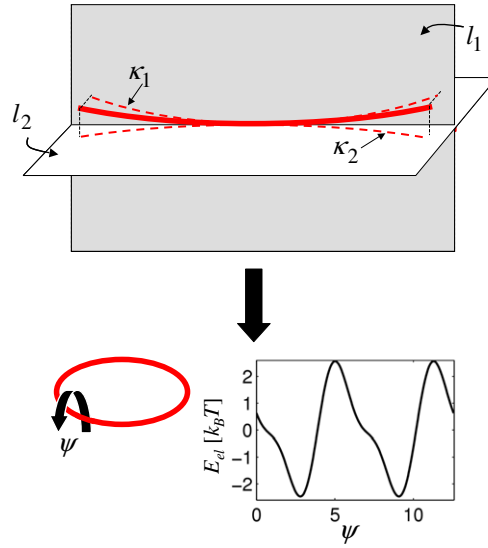
Figure 2. Closing a short piece of DNA with anisotropic bendability and bentness into a ring leads in general to ratchet-shaped bending potentials. Shown are on top the two principal bending directions with persistence lengths l_1 and l_2 and the intrinsic curvatures κ_1 and κ_2 in the corresponding perpendicular directions. The plot at the bottom gives the elastic curvature as a function of the twisting angle for a ring with the following parameters: $R = 10$ nm, $r_0 = 1$ nm (typical DNA minicircle), $l_1 = 45$ nm, $l_2 = 50$ nm, and $\kappa_1 = \kappa_2 = (200 \text{ nm})^{-1}$.

with $\omega_1 = \phi' \sin\theta \sin\psi + \theta' \cos\psi$, $\omega_2 = \phi' \sin\theta \cos\psi - \theta' \sin\psi$ and $\omega_3 = \phi' \cos\theta + \psi'$ [21]. Here l_1 and l_2 are the two principal bending persistence lengths; chains with $l_1 \neq l_2$ feature an anisotropic bendability. κ_1 and κ_2 are the intrinsic curvatures in two corresponding perpendicular directions; cf also figure 2. l_3 denotes the twist persistence length and κ_3 is the natural twist rate. All the parameters are in general functions of the arc length; here for simplicity we assume them to be independent of the arc length throughout the molecule (which is true for e.g. 10 base-pair (bp) periodic sequences). For the case of DNA minicircles of short length ($2\pi R < l_i$) and with constant κ_i and l_i fulfilling the weak bending anisotropy condition $\max\{|l_1 - l_2|/R, l_1\kappa_1, l_2\kappa_2\} \ll l_3/R$, only the conformations close to the circular untwisted state will contribute, i.e., those close to $\theta(s) = \pi/2$, $\phi(s) = s/R$ and $\psi(s) =$ constant. This leads then to the required ratchet potential as a function of ψ:

$$\frac{E_{\text{el}}(\psi)}{\pi k_{\text{B}} T} = \frac{l_1 - l_2}{2R} \cos(2\psi) + 2l_1\kappa_1 \cos\psi - 2l_2\kappa_2 \sin\psi. \tag{2}$$

Note that the twirling motion of the ring (described by ψ) does not involve any twist deformation. It is rather a sequence of bending events in different directions that is causing the rotation here.

From equation (2) we see that to generate a left–right asymmetric ratchet potential we need both nonzero bending anisotropy, $l_1 - l_2 \neq 0$, and non-vanishing intrinsic curvatures, $\kappa_{1,2} \neq 0$. The plot in figure 2 demonstrates that reasonable small values of anisotropy and intrinsic curvature can indeed induce a well defined ratchet potential.

2.2. Hydrodynamics

Next we need to calculate the hydrodynamics of a twirling ring in the limit of low Reynolds numbers. We mention that for a reasonable ring radius $R = 10$ nm (a typical miniplasmid

of ≈ 200 bp) and the DNA helix radius $r_0 = 1$ nm the slender body approximation [22] is valid with the slenderness parameter $\varepsilon = r_0/R = 0.1$. In the spirit of the slender body theory one approximates the flow-field around the twirling ring by superimposing rotlets [23] $\mathbf{u}_{\text{rot}}(\mathbf{x}; s) = \Gamma \frac{d\mathbf{c}(s)}{ds} \times (\mathbf{x} - \mathbf{c}(s))/|\mathbf{c}(s) - \mathbf{x}|^3$ placed along the ring centreline $\mathbf{c}(s)$ with arc length parameter s. The rotlet strength $\Gamma = \frac{1}{2}\omega_{\mathbf{c}} r_0^2$ is given in terms of the angular velocity $\omega_{\mathbf{c}}$ of the ring about $\mathbf{c}(s)$. The full velocity profile follows then from $\mathbf{u}(\mathbf{x}) = \int_0^{2\pi R} \mathbf{u}_{\text{rot}}(\mathbf{x}; s) \, ds$; cf. also the stream lines around the rotating ring shown in figure 1. When integrating $\mathbf{u}(\mathbf{x})$ over the DNA ring (slender torus) surface in the limit of small r_0/R one obtains a net translational velocity in the z-direction:

$$v_z(\omega_{\mathbf{c}}) = \frac{r_0^2}{2R} \left(\ln \left(8\frac{R}{r_0} \right) - \frac{1}{2} \right) \omega_{\mathbf{c}}. \tag{3}$$

Note that equation (3) coincides with the well known expression from ideal flow vortex theory [24], which is related to the fact that a rotlet $\mathbf{u}_{\text{rot}}(\mathbf{x}; s)$ is nothing else but the expression for the velocity field of an ideal point vortex. But despite this kinematic analogy between the twirling DNA and an ideal vortex ring, dynamically they are quite different. The propagation of an ideal vortex ring does not require any external forces and/or torques and is governed by conservation of kinetic energy and momentum. In contrast to this the low-Reynolds-number (Stokes) flow is governed by dissipation and thus the motion of twirling DNA ring requires the action of a torque $N_{\mathbf{c}} = 8\pi^2 x_0^2 \eta R \omega_{\mathbf{c}}$ ($\eta = 10^{-3}$ Pa s, the water viscosity) about the central axis $\mathbf{c}$. The latter expression can be verified by integrating the tangential stresses generated by $\mathbf{u}(\mathbf{x})$ over the ring surface. More generally, by virtue of the linearity of the Stokes equations we can derive a resistance matrix (M_{kl}) relating the angular velocity $\omega_{\mathbf{c}}$ (about the circular axis $\mathbf{c}$) and velocity v_z (in the z-direction) with the corresponding external torque $N_{\mathbf{c}}$ and force F_z:

$$\begin{pmatrix} F_z \\ N_{\mathbf{c}} \end{pmatrix} = 4\pi^2 \eta \begin{pmatrix} M_{11} & M_{12} \\ M_{21} & M_{22} \end{pmatrix} \begin{pmatrix} v_z \\ \omega_{\mathbf{c}} \end{pmatrix}. \tag{4}$$

Combining the previous expressions obtained for $v_z(\omega_{\mathbf{c}})$ and $N_{\mathbf{c}}(\omega_{\mathbf{c}})$ ($F_z = 0$) together with the result of Johnson and Wu [22] for the drag on a *rigid* slender Torus, we obtain entries in the leading order: $M_{11} = 2R(\ln 8/\varepsilon + 1/2)^{-1}$, $M_{22} = 2r_0^2 R$ and $M_{12} = M_{21} = r_0^2(\ln 8/\varepsilon - 1/2)(\ln 8/\varepsilon + 1/2)^{-1}$. Note that the symmetry of the resistance matrix that is a general feature of swimmers in Stokes flow [25] provides a good check for the consistency of the involved calculations. Having the mobility relation (4) one can consider different types of motion, e.g. (i) the ring is twirling freely ($N_{\mathbf{c}} = 0$) and moving under the force F_z (or at fixed v_z); (ii) the ring is prevented from rotation ($\omega_{\mathbf{c}} = 0$) and moved by the force F_z (or at fixed v_z); (iii) the ring is held in position ($v_z = 0$) by imposing a force F_z counterbalancing the action of torque $N_{\mathbf{c}}$; (iv) the DNA ring is free to move (no external force applied, $F_z = 0$) under an externally imposed torque $N_{\mathbf{c}}$ (or at given $\omega_{\mathbf{c}}$). Comparing, for instance, the velocities $v_z^{(i)}$ and $v_z^{(ii)}$ from cases (i) and (ii) one sees that $v_z^{(i)}/v_z^{(ii)} - 1 = M_{12}^2/\det M_{kl} \sim (\varepsilon/2)^2 \ln(8/\varepsilon)$; i.e., a ring with an isotropic DNA sequence (capable of twirling) settles faster than a ring with very high barriers to twirling ($\omega_{\mathbf{c}} = 0$), though in practice the difference is negligible, for instance $\sim 1\%$ for $\varepsilon = 0.1$. By comparing cases (iii) and (iv) we conclude that a ring twirling at fixed $\omega_{\mathbf{c}}$ and forced not to translate requires a slightly larger torque $N_{\mathbf{c}}^{iii}(\omega_{\mathbf{c}})$ than the unconstrained freely translating ring with $N_{\mathbf{c}}^{iv}(\omega_{\mathbf{c}})$. However the relative difference is again small and of order $O(\varepsilon^2 \ln(8/\varepsilon))$. Therefore by dropping this marginal correction to the leading order we obtain in both cases (iii) and (iv) the angular friction constant

$$\zeta = N_{\mathbf{c}}(\omega_{\mathbf{c}})/\omega_{\mathbf{c}} \approx 8\pi^2 \eta r_0^2 R \tag{5}$$

a quantity that will be important in the following. Note that the latter is the same (in our $\varepsilon \ll 1$ leading order expansion) as for a straight cylinder with radius r_0 and length $2\pi R$.

Finally, another interesting feature that can be read off equation (4) is the efficiency of the twirling ring propulsion. The latter is independent of the mechanism of twirling and can be defined as the ratio of the power $P_{\text{rigid}} = 2\pi^2 \eta M_{11} v_z^2$ dissipated by a (for simplicity) rigid ring directly moved by a force as compared to the power $P_{\text{twirl}} = \frac{1}{2} N_{\mathfrak{c}} \omega_{\mathfrak{c}}$ dissipated by twirling propulsion at the same translational speed. For a ring with $R = 10$ nm we have $P_{\text{rigid}}/P_{\text{twirl}} \approx 0.8\%$, which is comparable to the efficiency of bacterial propulsion by a rotating flagellum [25].

3. The DNA ring as a thermal ratchet

3.1. Thermal ratchets

The Fokker–Planck equation describing the time evolution of the probability density $P(\psi, t)$ of the Euler angle ψ of our twirling DNA motor is written

$$\zeta \frac{\partial P}{\partial t} = \frac{\partial}{\partial \psi} \left(\frac{\partial E_{\text{el}}}{\partial \psi} P + k_{\text{B}} T \frac{\partial P}{\partial \psi} \right) \tag{6}$$

with the twirling potential equation (2) and the angular friction constant ζ given by equation (5). To induce a directed twirling frequency

$$\omega_{\mathfrak{c}} := \langle \dot{\psi} \rangle = -\frac{1}{\zeta} \left\langle \frac{\partial E_{\text{el}}}{\partial \psi} P + k_{\text{B}} T \frac{\partial P}{\partial \psi} \right\rangle \tag{7}$$

we follow [26] by choosing a periodic time-dependent temperature variation. Specifically, we choose

$$T(t) = T_0 [1 + A_T \sin(2\pi f_T t)] \tag{8}$$

with T_0 the mean temperature, A_T the relative amplitude and f_T the frequency of the temperature oscillation.

For the case of f_T sufficiently larger than the inverse of the characteristic relaxation time $\tau_0 = 4\pi^2 \zeta /(k_{\text{B}} T_0)$ of the twirling degree of freedom (but still much smaller than the frequency of average thermal molecular kicks) an $1/f_T$ asymptotic expansion for the current $\langle \dot{\psi} \rangle$ can be employed[4]. After a long calculation—presented in detail in the appendix—we obtain from equation (A.39) (for $f_T \tau_0 \gg 1$) $\langle \dot{\psi} \rangle$ up to terms of order f_T^{-3}:

$$\langle \dot{\psi} \rangle = \frac{12\pi^3 A_T^2 (k_{\text{B}} T_0)^3 l_1 l_2 \kappa_1 \kappa_2 (l_2 - l_1)/R}{f_T^2 \zeta^3 \int_0^{2\pi} \mathrm{d}\psi \, \mathrm{e}^{-\frac{E_{\text{el}}(\psi)}{k_{\text{B}} T}} \int_0^{2\pi} \mathrm{d}\psi \, \mathrm{e}^{\frac{E_{\text{el}}(\psi)}{k_{\text{B}} T}}}. \tag{9}$$

It follows from equation (9) that for an isotropically bendable DNA sequence ($l_2 = l_1$) the directed current vanishes. The same is true if the intrinsic curvature direction coincides with one of the principal axes (i.e. if κ_1 or κ_2 vanish). Both observations are intuitive as in either case the ratchet potential, equation (2), becomes left–right symmetric and the ratchet effect disappears.

The low-frequency adiabatic limit is obtained from the asymptotic expansion of $P(\tilde{\psi}, \tilde{t})$ ($\tilde{\psi} = \psi/2\pi$, $\tilde{t} = t/\tau_0$) for small parameter $\tilde{f} = f_T \tau_0$, i.e., $P \approx P_0 + \tilde{f} P_1 + \tilde{f}^2 P_2$. As shown in the appendix (cf equation (A.18)) one has for arbitrary periodic temperature oscillations

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[4] The same expansion has been used in [20, 26] but the presented current is not invariant under time shifts; for details cf appendix.
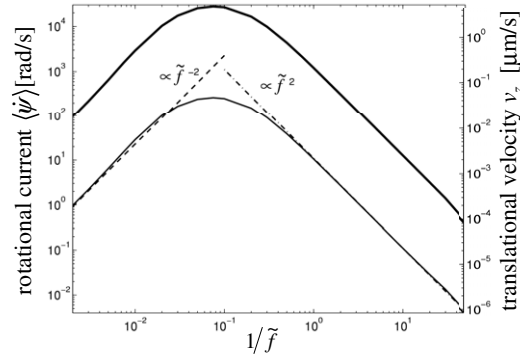
Figure 3. The rotational current $\langle \dot\psi \rangle$ and the induced translational velocity v_z as a function of the dimensionless frequency $\tilde{f}$ of the temperature (potential) oscillations. The DNA ring has the same parameters as in figure 2. Displayed are the asymptotic expressions, equation (9) (dashed line) and (10) (dashed–dotted line) together with the numerical solution of equation (6) (thin line) for a temperature ratchet with $A_T = 0.03$. The thick solid line corresponds to an oscillating potential ratchet with $A_E = 0.3$. See text for details.

$T(t) = T(t + f_T^{-1})$ (with mean temperature T_0) up to terms of order[5] f_T^3:

$$\langle \dot\psi \rangle = \frac{\tilde{f}^2}{\tau_0} \int_0^1 \mathrm{d}\tilde{t}\, \overline{\frac{1}{\overline{F}}\overrightarrow{F\partial_{\tilde{t}}\overrightarrow{P_1}}}. \tag{10}$$

Here $E(\tilde\psi, \tilde{t}) = F(\tilde\psi, \tilde{t})^{-1} = \mathrm{e}^{-E_{\mathrm{el}}(\tilde\psi)/k_{\mathrm{B}}T(\tilde{t})}$ and the abbreviations $\overrightarrow{(\ldots)}$ and $\overline{(\ldots)}$ are defined as in equation (A.12) but with the integrations with respect to $\tilde\psi$. Furthermore, the density distributions P_0 and P_1 from the upper expansion are given by $P_0 = E/\overline{E}$ (Boltzmann distribution in the adiabatic limit) and $P_1 = \frac{T_0}{T}E(\overrightarrow{Fc_1} - \frac{1}{\overline{E}}\overline{E\overrightarrow{Fc_1}})$ with $c_1 = \overrightarrow{\partial_{\tilde{t}}P_0} - \frac{1}{\overline{F}}\overline{F\partial_{\tilde{t}}P_0}$.

Equations (9) and (10) together with equations (2) and (5) allow us to get the twirling speed $\omega_{\mathbf{c}} = \langle \dot\psi \rangle$ and by virtue of equation (3) the induced translational velocity $v_z(\omega_{\mathbf{c}})$ for arbitrary DNA elastic parameters $l_{i=1,2}$ and $\kappa_{i=1,2}$.

3.2. Numbers

How fast can we operate the twirling DNA ring? Assume some realistic parameter values for a DNA minicircle, namely $R = 10$ nm, $r_0 = 1$ nm leading to $\zeta = 2 \times 10^{-7}k_{\mathrm{B}}T\mathrm{s}$ and $\tau_0 = 8 \times 10^{-6}$ s. Furthermore, we set $l_1 = 45$ nm, $l_2 = 50$ nm, $\kappa_1 = \kappa_2 = (200\,\mathrm{nm})^{-1}$, which corresponds to a rather modest anisotropy and intrinsic curvature. For the temperature variation amplitude we choose $\Delta T = \pm 10$ K, i.e., $A_T \approx 1/30$ (at room temperature $T_0 = 300$ K). Figure 3 provides a log–log plot of the rotational current and the corresponding drift speed of the ring as a function of the dimensionless frequency $\tilde{f}$ of the temperature variation. The thin solid curve gives the numerical result obtained from equation (6); the two straight lines correspond to the analytical results for the two asymptotic cases, equations (9) and (10). As can be seen from this plot the two limits show a $\tilde{f}^{-2}$ and $\tilde{f}^2$ dependence, respectively, in accordance with equations (9) and (10). The maximal rotational current is achieved in the crossover region, namely $\omega_{\mathbf{c}} \approx 200$ rad s^{-1} for $\tilde{f} \approx 10^{-1}$. Following equation (3) this implies a translational velocity of $v_z = 50$ nm s^{-1}.

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[5] Note that the $O(\tilde{f})$-term provided in [26], equation (18), *always* vanishes identically (integrated surface term, cf appendix for details) so that the second order term, equation (10), constitutes the first non-vanishing contribution to the current.

This rather modest velocity is the consequence of the small temperature oscillations that one might practically implement without melting the DNA double helix. Operating the system close to the DNA duplex melting temperature is likely to induce strong oscillations in the overall ring stiffness. This might also point towards an alternative way of driving the ratchet, namely via a periodic variation of the elastic properties of the ring[6]. The thick solid line in figure 3 shows the rotational current obtained when the elastic energy is varied as $\tilde{E}_{el}(\psi, t) = E_{el}(\psi)(1 + A_E \sin(2\pi f_E t))$, where we chose the relative amplitude $A_E = 0.3$. The fact that close to its melting temperature the DNA ring almost fully loses its stiffness renders $A_E = 0.3$ a rather conservative estimate.

As can be seen from figure 3 the maximal current of this oscillating potential ratchet occurs roughly at the same frequency as that of the thermal ratchet, but the value of ω_c is much higher, namely on the order of 2×10^4 rad s^{-1}, which implies a quite notable translational velocity of $v_z = 5 \, \mu$m s^{-1}. As a comparison a typical bacterium moves at $30 \, \mu$m s^{-1}. Our ring ratchet (with oscillating potential) with its nanoscopic size (radius 10 nm), swimming efficiency (0.8%) and speed ($5 \, \mu$m s^{-1}) resembles in several respects 'real' biological nanomotors. Note, however, that the produced forces are comparably small. In particular, the net translational force is small due to cancellation of most of the stresses, namely according to equation (4) $F_z = 4\pi^2 \eta M_{12} \omega_c \approx 0.6$ fN; stronger is the local torque $N_c = 8\pi^2 \eta r_0^2 R \omega_c \approx 0.004 k_B T$ resulting in the force $F_{loc} = N_c/r_0 = \zeta \omega_c/r_0 \approx 16$ fN acting at the DNA surface.

3.3. Experimental aspects

Effect detection. From an experimental point of view one should be aware of the fact that a ring (twirling or non-twirling) loses its initial orientation almost instantaneously due to rotational diffusion. The typical relaxation timescale of this process is on the order $\eta R^3/(k_B T)$ (up to logarithmic corrections [28]), which for a ring with $R = 10$ nm leads to 10^{-7} s. This means that a single twirling ring in solution will not perform any noticeable translational drift. A possible solution to the problem is to put the ring on a long DNA 'track', e.g. to thread it on a straightened DNA chain. Such a threading is most easily achieved by performing a sequence dependent excision, e.g. via the Cre/Lox recombination system [29]. The DNA track can be stretched out by standard single-molecule techniques and both the ring and the DNA track can be optically traced after fluorescent labelling, similarly to the DNA knot diffusion assays (cf e.g. [30]). A ring with speed $v_{max} = 5 \, \mu$m s^{-1} will then overcome dispersion due to translational diffusion after 2 s and show significant changes in the concentration profile over distances $k_B T/F_z \approx 7 \, \mu$m.

Another possible direction is to prepare semi-dilute or dense solutions of such rings and then study their response to an induced twirling. It is known that solutions of self-propelled particles show ordering as well as hydrodynamic instabilities [31], e.g. the low-Reynolds-number turbulence observed for suspensions of bacteria [32]. The presence of the ratchet effect combined with the hydrodynamic coupling between twirling rings might induce detectable corrections to their pair-correlation function.

The idea that nanomotors like the one presented here might also be of some use as mixers in nanofluidic devices (to e.g. speed up diffusion-limited reactions by enhancing the diffusion of small molecules) is however questionable. In order to achieve a significant diffusion enhancement of small (passive) tracer particles with radius r_{tr} ($<R$) would require the normals **n** of the DNA rings in the solution to be strongly correlated over distances

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[6] A possibility might be to choose a base-pair sequence where a short fraction has a predisposition to form a localized bubble that induces a flexible hinge [27]. In the presence of the bubble the ring has a teardrop shape with a reduced elastic deformation resulting in smaller oscillations in $E_{el}(\psi)$.

$l \gtrsim D_{tr}/v_{max} = \frac{k_B T}{6\pi \eta r_{tr} v_{max}}$. This gives $l \gtrsim 20$–200 μm for particles with $r_{tr} = 2$–0.2 nm (and $v_{max} = 5$ μm s^{-1}). A pure liquid crystalline interaction between rings would not be able to create such a long range coherence in **n** (because of its **n** $\rightarrow$ $-$**n** symmetry), and an efficient transport of tracers would seem unlikely on the basis of such ordering. It is currently unclear if the hydrodynamic interaction of twirling rings is in fact sufficient (or even has the right sign) to break the **n** $\rightarrow$ $-$**n** symmetry and induce the required long-range ordering.

DNA sequence. The sequence of the ring should be chosen to be elastically weakly anisotropic in order to achieve an optimal 4–6 $k_B T$ overall barrier per molecule. Both significantly higher or lower barrier heights are expected to suppress the ratchet effect and thus the selection of proper DNA sequences becomes essential. Hints for the selection principles of good sequences might be found by mimicking the design of weak nucleosome positioning sequences like 5sRNA [33, 34]. DNA, being wound within the nucleosome in a similar manner as in a tight minicircle, is believed to corkscrew within the nucleosome complex in a similar fashion as the twirling motion considered here [35]. The barriers to the corkscrew motion of nucleosomal DNA become analogous to barriers to the twirling mechanism and analogous principles of sequence design apply.

In addition, the fact that the our minicircle nanomachine is fully DNA based opens the intriguing possibility of finding the best sequences by exploiting the known methods of *in vitro* evolution (SELEX [36]). The experimental feasibility of finding the most agile DNA swimmers will strongly depend on the practical design of high-yield assays for separation of the 'good swimmer' fraction from the less mobile minicircle population.

Temperature oscillations. Fast temperature oscillations are technically feasible and might be most conveniently generated by adiabatic pressure variations, e.g. by ultrasound. Another promising method is to use the inductive heating of metal nanocrystals that are covalently attached to the DNA ring. In fact, this method has been successfully used to control the hybridization behaviour of DNA [37]. Finally, we mention the possibility of microwave adsorption in the hydration layer of DNA [38].

4. Conclusions

Whenever known principles are combined to give a new behaviour, it is worthwhile asking the question 'is there anything to wonder about?'. At first glance the ratchet effect driven twirling DNA ring reminds one of 'Baron Münchhausen lifting himself out of a swamp by pulling himself up by his bootstraps'. However both the ratchet and the propulsion effect are based on solid ground and their combination is straightforward. Of course there is always a little bit of a 'Baron Münchhausen' in every small creature swimming at low Reynolds numbers since they are seemingly defying the time reversibility of the Stokes flow. This is done by exploiting the principle of holonomy/geometric phase [39] in order to self-propel themselves through the fluid at the limit of vanishing Reynolds number. This is surely something to be wondered about in general.

The simplest among such creatures (having only one relevant degree of freedom) is a twirling torus. It was qualitatively discussed by Taylor [40] and Purcell [41]. Here we merely added the mobility matrix (4) (valid in the slender torus limit) to its more quantitative understanding.

The twirling DNA ring can be considered as the simplest toy model of a real nanomachine. Although the device extracts energy from a 'nonequilibrium channel' (e.g. an externally

oscillating scalar field), its behaviour is not fully slaved by the latter. The machine still keeps most of its relevant degrees of freedom (translational and rotational) and only its drift velocity along its axis of symmetry is affected by the energy pumping mechanism. The trick behind this 'conformational liberation' is of course related to the fact that the ratchet potential, equation (2), is here an internal property of the device rather than being embedded in the space surrounding it. This is a peculiar and possibly important difference to the nanoscaled ratchets and motors usually considered theoretically or encountered in nature. Liberating the artificial nanodevice from the 'slavery' of external potentials (while still providing it with energy) may open several routes to interesting collective self-organization effects.

Acknowledgments

Appendix. Low- and high-frequency asymptotics of the thermal ratchet

We calculate here the asymptotic current of a thermal ratchet in the limits of low and high frequencies. Consider the diffusion of a particle of friction constant ζ in a periodic potential $V(x) = V(x+L)$. The Fokker–Planck equation describing the time evolution of its probability density $P(x, t)$ is written

$$\zeta \frac{\partial}{\partial t} P = \frac{\partial}{\partial x}\left(\frac{\partial V}{\partial x}P + k_{\mathrm{B}}T(t)\frac{\partial P}{\partial x}\right) \tag{A.1}$$

with a time-dependent periodic temperature $T(t) = T(t + t_0)$. We are interested in the time-averaged current $j = -\zeta^{-1}t_0^{-1}\int_0^{t_0}(V'P + k_{\mathrm{B}}T(t)P')\,\mathrm{d}t$, which is evidently independent of the position of x, $\partial j/\partial x$, for a solution periodic in time and space, $P(x, t) \equiv P(x, t + t_0)$ and $P(x + L, t) \equiv P(x, t)$, as assumed in the following. We calculate the lowest-order non-vanishing contributions to the current in the case of small and large frequencies of the temperature oscillations, $t_0 \gg t_{\mathrm{S}}$ and $t_0 \ll t_{\mathrm{S}}$, where the Smoluchowski time $t_{\mathrm{S}} = \zeta L^2/(k_{\mathrm{B}}T_0)$ sets the typical timescale of the system (T_0: time-averaged temperature).

We rewrite the Fokker–Planck equation using dimensionless units $\xi = x/L$, $\tau = t/t_0$, $U = V/(k_{\mathrm{B}}T_0)$:

$$w\dot{P} = \frac{\partial}{\partial \xi}(U'P + \theta(\tau)P') \tag{A.2}$$

with $\theta(\tau) = T(\tau t_0)/T_0$, $w = t_{\mathrm{S}}/t_0$. The dot denotes a derivative with respect to τ and the primes derivatives with respect to ξ.

Low-frequency limit ($w \ll 1$):

We expand $P(x, t)$ in powers of w:

$$P = P_0 + wP_1 + w^2 P_2 + \cdots. \tag{A.3}$$

The aim is to find the lowest-order non-vanishing term of the time-averaged current in powers of w:

$$j = j_0 + wj_1 + w^2 j_2 + \cdots. \tag{A.4}$$

We insert the power series, equation (A.3), into (A.2). From the terms of order w^0 we recover the Boltzmann distribution

$$P_0 = \frac{\exp\left(-\frac{U(\xi)}{\theta(\tau)}\right)}{\int_0^1 \exp\left(-\frac{U(\xi)}{\theta(\tau)}\right)\mathrm{d}\xi}. \tag{A.5}$$

In the next order, w^1, we have $\dot{P}_0 = (\partial/\partial\xi)(U'P_1 + \theta(t)P_1')$, from which we find by integration

$$U'P_1 + \theta(\tau)P_1' = \int_0^\xi \dot{P}_0(\xi_1, \tau)\,\mathrm{d}\xi_1 - f_1(\tau) = g_1(\xi, \tau) \tag{A.6}$$

with $f_1(\tau)$ being an integration constant. The latter is solved by the ansatz $P_1 = c(\xi, \tau)\exp(-U(\xi)/\theta(\tau))$ with

$$c(\xi, \tau) = c_1(\tau) + \frac{1}{\theta(\tau)}\int_0^\xi \mathrm{e}^{U(\xi_1)/\theta(\tau)}g_1(\xi_1, \tau)\,\mathrm{d}\xi_1 \tag{A.7}$$

introducing another integration constant $c_1(\tau)$. $f_1(t)$ follows then directly from setting $P_1(0, \tau) = P_1(1, \tau)$ to be

$$f_1(\tau) = \frac{\int_0^1 \int_0^{\xi_1} \mathrm{e}^{U(\xi_1)/\theta(\tau)}\dot{P}_0(\xi_2, \tau)\,\mathrm{d}\xi_2\,\mathrm{d}\xi_1}{\int_0^1 \mathrm{e}^{U(\xi_1, \tau)/\theta(\tau)}\,\mathrm{d}\xi_1}. \tag{A.8}$$

The other integration constant, $c_1(\tau)$, is set by the normalization condition $\int_0^1 P_1(\xi, \tau)\,\mathrm{d}\xi = 0$:

$$c_1(\tau) = -\frac{1}{\theta(\tau)}\frac{\int_0^1 \int_0^x \mathrm{e}^{(U(\xi_1)-U(\xi))/\theta(\tau)}g_1(\xi_1, \tau)\,\mathrm{d}\xi_1\,\mathrm{d}\xi}{\int_0^1 \mathrm{e}^{-U(\xi_1, \tau)/\theta(\tau)}\,\mathrm{d}\xi_1}. \tag{A.9}$$

Summarizing, we obtain

$$P_1(\xi, \tau) = \frac{\mathrm{e}^{-\frac{U}{\theta}}}{\theta}\left[\overrightarrow{\mathrm{e}^{U/\theta}g_1} - \left(\overline{\mathrm{e}^{-U/\theta}\overrightarrow{\mathrm{e}^{U/\theta}g_1}}\right)\Big/\left(\overline{\mathrm{e}^{-U/\theta}}\right)\right] \tag{A.10}$$

with

$$g_1(\xi, \tau) = \overrightarrow{\dot{P}_0} - \frac{\overline{\mathrm{e}^{U/\theta}\overrightarrow{\dot{P}_0}}}{\left(\overline{\mathrm{e}^{U/\theta}}\right)}. \tag{A.11}$$

We have introduced in equation (A.10) a compact notation that turns out to be indispensable when dealing in the following with the rather involved expressions. For indefinite and definite integrals over the (dimensionless) length we write briefly

$$\int_0^\xi f(\xi_1)\,\mathrm{d}\xi_1 = \overrightarrow{f} \qquad \text{and} \qquad \int_0^1 f(\xi)\,\mathrm{d}\xi = \overline{f}. \tag{A.12}$$

The arrow $\overrightarrow{(\cdots)}$ points to the variable boundary, i.e., one has still a free argument (ξ above) whereas $\overline{(\cdots)}$ symbolizes that there is no (length) variable anymore. The result of $\overline{(\cdots)}$ is a constant (the average of $f(x)$) whereas $\overrightarrow{(\cdots)}$ is still a function. Similarly we will write time integrals:

$$\int_0^\tau g(\tau_1)\,\mathrm{d}\tau_1 = \underset{\rightarrow}{g} \qquad \text{and} \qquad \int_0^1 g(\tau)\,\mathrm{d}\tau = \underline{g}. \tag{A.13}$$

The actual time-averaged current (in first order) follows from equation (A.6):

$$j_1 = -\underline{g_1} = \underline{f_1} = \overline{\mathrm{e}^{U/\theta}\overrightarrow{\dot{P}_0}}\left(\overline{\mathrm{e}^{U/\theta}}\right)^{-1} \tag{A.14}$$

where we made use of the time-periodicity of P_0. Analogously, one finds the second-order term j_2 to be

$$j_2 = \overline{\mathrm{e}^{U/\theta}\overrightarrow{\dot{P}_1}}\left(\overline{\mathrm{e}^{U/\theta}}\right)^{-1} \tag{A.15}$$

with $\dot{P}_1(x_2, t)$ given by equation (A.10).

Note that j_1 is always zero. This follows from the fact that

$$\dot{P}_0(\xi, \tau) = \frac{\dot{\theta}}{\theta^2} e^{-\frac{U}{\theta}} \frac{\overline{U e^{-U/\theta}} - \overline{U} \, \overline{e^{-U/\theta}}}{\left(\overline{e^{-U/\theta}}\right)^2} \tag{A.16}$$

i.e., it $\dot{P}_0$ is of the form $\dot{P}_0 = \dot{\theta} F[\theta]$. Thus $j_1 = \int_0^1 \dot{\theta} G[\theta] \, d\tau$ vanishes identically due to the periodicity of $\theta(\tau)$.

Introducing

$$E(x, t) = e^{-U(x)/\theta(t)} \qquad \text{and} \qquad F(x, t) = e^{U(x)/\theta(t)} \tag{A.17}$$

we can rewrite the exact expressions and expansions. One has

$$j_2 = \frac{1}{\overline{F}} \overline{F \overrightarrow{P_1}} \tag{A.18}$$

with

$$P_1 = \frac{E}{\theta} \left(\overrightarrow{Fg_1} - \frac{1}{\overline{E}} \overline{E \overrightarrow{Fg_1}} \right), \quad g_1 = \overrightarrow{P_0} - \frac{1}{\overline{F}} \overline{F \overrightarrow{P_0}} \qquad \text{and} \qquad \dot{P}_0 = \frac{\dot{E} \overline{E} - E \overline{\dot{E}}}{\overline{E}^2}. \tag{A.19}$$

To introduce back dimensions, we note that $\partial P/\partial \tau = t_0 L \partial P/\partial t = -w^{-1} \partial w^2 j_2/\partial \xi = -w^{-1} L \partial w^2 j_2/\partial x$. Note that the first equality, $\partial P/\partial \tau = t_0 L \partial P/\partial t$, derives from the fact that we have assumed above that P is (also) normalized in the dimensionless units: $\overline{P} = 1$. Thus we have $j = w^2 j_2/t_S$.

High-frequency limit ($\varepsilon = w^{-1} \ll 1$).

We expand P in terms of the small parameter ε:

$$P = P_0 + \varepsilon P_1 + \varepsilon^2 P_2 + \cdots \tag{A.20}$$

with $\varepsilon = w^{-1} = t_0/t_S$. We determine the lowest-order non-vanishing term of the time-averaged current in powers of ε:

$$j = j_0 + \varepsilon j_1 + \varepsilon^2 j_2 + \cdots. \tag{A.21}$$

So we have

$$\dot{P}_0 + \varepsilon \dot{P}_1 + \varepsilon^2 \dot{P}_2 + \cdots = \varepsilon \frac{\partial}{\partial \xi} (U'(P_0 + \varepsilon P_1 + \varepsilon^2 P_2 + \cdots) + \theta(t)(P_0' + \varepsilon P_1' + \varepsilon^2 P_2')). \tag{A.22}$$

In lowest order, ε^0, we obtain $\dot{P}_0(\xi, \tau) = 0$, i.e. $P_0(\xi, \tau) = P_0(\xi)$. The next order, $O(\varepsilon^1)$, leads to

$$\dot{P}_1 = \frac{\partial}{\partial \xi} (U' P_0(\xi) + \theta(\tau) P_0'(\xi)). \tag{A.23}$$

By time integrating both sides one finds $\underline{\dot{P}_1} = 0 = \frac{\partial}{\partial \xi} (U' P_0(\xi) + P_0'(\xi))$. On the right-hand side we used that by definition $\underline{\theta} = 1$. The (time-averaged) current to order $O(\varepsilon^0)$ is thus given by $j_0 = U' P_0(\xi) + P_0'(\xi) = e^{-U} \frac{d}{d\xi} (P_0 e^U)$. Hence $P_0 = e^{-U} e^U j_0 + e^{-U} c_0$ with some constant c_0. Imposing periodicity, $P_0(0) = P_0(1)$, we get $e^{-U(0)} c_0 = e^{-U(1)} c_0 + j_0 e^{-U} \overrightarrow{e^U}$, i.e. $j_0 = 0$. From $\overline{P_0} = 1$ we obtain $c_0 \overline{e^{-U}} = 1$ and hence

$$P_0 = \frac{e^U}{(\overline{e^{-U}})}. \tag{A.24}$$

To obtain P_1 we start from equation (A.23) and integrate over time $\int_0^\tau \cdots d\tau_1$:

$$P_1(\xi, \tau) = \frac{\partial}{\partial \xi} (\tau U' P_0(\xi) + \underrightarrow{\theta(\tau)} P_0'(\xi)) + \kappa_2(\xi) \tag{A.25}$$

with $\kappa_2(\xi)$ ($= P_1(\xi, 0) = P_1(\xi, 1)$) being some function of ξ (to be determined below).

Introducing the function $\Delta(\tau) = 1 - \theta(\tau)$ and using the fact that $j_0 = U'P_0(\xi) + P_0'(\xi) = 0$ we can rewrite equation (A.25) as follows:

$$P_1(\xi, \tau) = -\underrightarrow{\Delta(\tau)} \, P_0''(\xi) + \kappa_2(\xi). \tag{A.26}$$

In order to obtain $\kappa_2(\xi)$ we need to go to order ε^2. This leads to

$$\dot{P}_2(\xi, \tau) = \frac{\partial}{\partial \xi}(U'P_1(\xi, \tau) + P_1'(\xi, \tau) - \Delta(\tau)P_1'(\xi, \tau)) \tag{A.27}$$

and—after integration over τ—to $\frac{\partial}{\partial \xi}(U'\underline{P_1} + \underline{P_1'} - \underline{\Delta P_1'}) = 0$. Inserting equation (A.26) and using $\underline{\Delta} = 0$ and $\underset{\rightarrow}{\underline{\Delta}} \, \underline{\Delta} = 0$ we arrive at

$$\frac{\partial}{\partial \xi}\left(U'\left(-\underset{\rightarrow}{\Delta}P_0'' + \kappa_2\right) - \underset{\rightarrow}{\Delta}P_0''' + \kappa_2'\right) = 0. \tag{A.28}$$

Integrating over ξ leads to $-\underset{\rightarrow}{\Delta}(U'P_0'' + P_0''') + U'\kappa_2 + \kappa_2' = j_1$ with the integration constant j_1 being the time-averaged current in $O(\varepsilon)$. Now since $\mathrm{e}^{-U}\frac{\mathrm{d}}{\mathrm{d}\xi}(\mathrm{e}^U \kappa_2) = j_1 - \underset{\rightarrow}{\Delta}(U'P_0'' + P_0''')$ we obtain

$$\kappa_2(\xi) = \mathrm{e}^{-U}\left(\overrightarrow{\mathrm{e}^U}\,j_1 - \underset{\rightarrow}{\Delta}\overrightarrow{\mathrm{e}^U(U'P_0'' + P_0''')}\right) + \kappa_2(0). \tag{A.29}$$

Recall that $\kappa_2(\xi) = P_1(\xi, 0)$ so that the normalization condition gives $\overline{\kappa_2(\xi)} = \overline{P_1(\xi, 0)} = 0$ and thus

$$\kappa_2(0) = \left(\underset{\rightarrow}{\Delta}\overline{\mathrm{e}^{-U}\overline{\mathrm{e}^U(U'P_0'' + P_0''')}} - \overline{\mathrm{e}^{-U}\overrightarrow{\mathrm{e}^U}}\,j_1\right). \tag{A.30}$$

The current j_1 follows from equation (A.29) using the periodicity of $\kappa_2(\xi) = P_1(\xi, 0)$, i.e. $\kappa_2(0) = \kappa_2(1)$:

$$j_1 = \underrightarrow{\Delta(\tau)}\frac{1}{\overline{(\mathrm{e}^U)}}\overline{\mathrm{e}^U(U'P_0'' + P_0''')} = 0 \tag{A.31}$$

where we made use of the fact that the overlined term is a boundary term (and hence vanishes due to the periodicity of U and P_0). This means that also the $O(\varepsilon)$-term of the current, j_1, is identically zero.

In the following we will need

$$\kappa_2(\xi) = P_1(\xi, 0) = \underset{\rightarrow}{\Delta}\left(\overline{\mathrm{e}^{-U}\overrightarrow{\mathrm{e}^U f}} - \mathrm{e}^{-U(\xi)}\overrightarrow{\mathrm{e}^U f}\right) \tag{A.32}$$

with $f(\xi) = U'(\xi)P_0''(\xi) + P_0'''$. Furthermore, P_2 will be of importance. Combining equations (A.26) and (A.27) we find

$$\dot{P}_2 = \frac{\partial}{\partial \xi}\left(\left(\underset{\rightarrow}{\Delta} - \underset{\rightarrow}{\Delta}\right)f(\xi) + \underset{\rightarrow}{\Delta}\,\underset{\rightarrow}{\Delta}\,P_0''' - \Delta\kappa_2'(\xi)\right) \tag{A.33}$$

and thus

$$P_2(\xi, \tau) = \underrightarrow{\underset{\rightarrow}{\Delta} - \underset{\rightarrow}{\Delta}}\,f'(\xi) + \underset{\rightarrow}{\Delta}\,\underset{\rightarrow}{\Delta}\,P_0'''' - \underset{\rightarrow}{\Delta}\kappa_2''(\xi) + \kappa_4(\xi). \tag{A.34}$$

We need next to determine the time-averaged current of order ε^2. To do so we compare terms of order ε^3: $\dot{P}_3 = \frac{\partial}{\partial \xi}(U'P_2 + P_2' - \Delta P_2')$. Time averaging leads then to

$$j_2 = U'\underline{P_2} + \underline{P_2'} - \underline{\Delta P_2'} = g(\xi) + \mathrm{e}^{-U}\frac{\mathrm{d}}{\mathrm{d}\xi}(\kappa_4 \mathrm{e}^U). \tag{A.35}$$

On the rhs of equation (A.35) we introduced $g(\xi)$; as can be seen by inspecting equation (A.34) this function is independent of κ_4, namely

$$g(\xi) = \underrightarrow{\overset{\Rightarrow}{\Delta} - \overset{\rightarrow}{\Delta}}(f'U' + f'') - \underrightarrow{\overset{\Rightarrow}{\Delta}\,\overset{\rightarrow}{\Delta}}f'' + \underrightarrow{\overset{\rightarrow}{\Delta}}(P_0''''U' + P_0''''') + \overset{\Rightarrow}{\Delta}(\kappa_2''U' + \kappa_2'''). \quad \text{(A.36)}$$

Integrating equation (A.35) over a full length interval one finds (due to the periodicity of κ_4, $\kappa_4(1) = \kappa_4(0)$) that

$$j_2 = \frac{\overline{g e^U}}{\overline{e^U}} = -\left(\underrightarrow{\overset{\Rightarrow}{\Delta}\,\overset{\rightarrow}{\Delta}}\,\overline{f''e^U}\right)\bigg/\overline{e^U} = -\frac{\left(\overset{\rightarrow}{\Delta}{}^2 - \overset{\Rightarrow}{\Delta}{}^2\right)\overline{f''e^U}}{\overline{e^U}}. \quad \text{(A.37)}$$

Here we made use of the fact that most terms of equation (A.36) lead to boundary terms that vanish due to the periodicity of the functions involved. Inserting equation (A.24) we obtain

$$j_2 = \frac{4\left(\overset{\rightarrow}{\Delta}{}^2 - \overset{\Rightarrow}{\Delta}{}^2\right)\overline{U'(U'')^2}}{\left(\overline{e^U}\,\overline{e^{-U}}\right)}. \quad \text{(A.38)}$$

Introducing back dimensions we find from $j = \varepsilon^2 j_2/t_S$

$$j_2 = \frac{4t_0^2}{\zeta^3}\left(\overset{\rightarrow}{\Delta}{}^2 - \overset{\Rightarrow}{\Delta}{}^2\right)\frac{\int_0^L V'(V'')^2\,\mathrm{d}x}{\int_0^L e^U\,\mathrm{d}x \int_0^L e^{-U}\,\mathrm{d}x}. \quad \text{(A.39)}$$

This is equal to equation (2.58) [20] if one replaces $\overset{\rightarrow}{\Delta}{}^2 - \overset{\Rightarrow}{\Delta}{}^2$ by $\overset{\rightarrow}{\Delta}{}^2$. Note that the latter expression is not invariant under time shifts.

References

[1] Feynman R P 1961 *Miniaturization* ed H D Gilbert (New York: Reinhold) pp 282–96
[2] Bissell R A, Cordova E, Kaifer A E and Stoddart J F 1994 *Nature* **369** 133
    Kelly T R, Silva H D and Silva R A 1999 *Nature* **401** 150
    Koumara N, Zijlstra R W J, van Delden R A, Harada N and Feringa B L 1999 *Nature* **401** 152
[3] Seeman N C 2004 *Sci. Am.* **290** 64
[4] Yurke B, Turberfield A J, Mills A P, Simmel F C and Neumann J L 2000 *Nature* **406** 605
[5] Simmel F C and Yurke B 2001 *Phys. Rev.* E **63** 041913
[6] Yan H, Zhang X, Shen Z and Seeman N C 2002 *Nature* **415** 62
[7] Li J J and Tan W 2002 *Nano Lett.* **2** 315
[8] Feng L, Park S H, Reif J H and Yan H 2003 *Angew. Chem. Int. Edn Engl.* **42** 4342
[9] Turberfield A J, Mitchell J C, Yurke B, Mills A P, Blakey M I and Simmel F C 2003 *Phys. Rev. Lett.* **90** 118102
[10] Liu D and Balasubramanian S 2003 *Angew. Chem. Int. Ed.* **42** 5734
[11] Sherman W B and Seeman N C 2004 *Nano Lett.* **4** 1203
[12] Chen Y and Mao C 2004 *J. Am. Chem. Soc.* **126** 8626
[13] Shin J-S and Pierce N A 2004 *J. Am. Chem. Soc.* **126** 10834
[14] Tian Y and Mao C 2004 *J. Am. Chem. Soc.* **126** 11410
[15] Mao C, Sun W, Shen Z and Seeman N C 1999 *Nature* **397** 144
[16] Alberti P and Mergny J-L 2003 *Proc. Natl Acad. Sci. USA* **100** 1569
[17] Chen Y, Lee S-H and Mao C 2004 *Angew. Chem. Int. Edn Engl.* **43** 5335
[18] Kulić I M, Thaokar R and Schiessel H 2004 *Europhys. Lett.* at press
[19] Ajdari A and Prost J 1992 *C. R. Acad. Sci., Paris* **315** 1635
    Magnasco M O 1993 *Phys. Rev. Lett.* **71** 1477
    Jülicher F, Ajdari A and Prost J 1997 *Rev. Mod. Phys.* **69** 1269
[20] Reimann P 2002 *Phys. Rep.* **361** 57

[21] Love A E 1944 *A Treatise on the Mathematical Theory of Elasticity* 4th edn (New York: Dover)
[22] Johnson R E and Wu T Y 1979 *J. Fluid Mech.* **95** 263
[23] Chwang A T and Hwang W-S 1990 *Phys. Fluids* A **2** 1309
[24] Lamb H 1993 *Hydrodynamics* 6th edn (Cambridge: Cambridge University Press)
[25] Purcell E M 1997 *Proc. Natl Acad. Sci. USA* **94** 11307
[26] Reimann P, Bartussek R, Häussler R and Hänggi P 1996 *Phys. Lett.* A **215** 26
[27] Yan J and Marko J F 2004 *Phys. Rev. Lett.* **93** 108108
[28] Paul E and Mazo R M 1969 *J. Chem. Phys.* **51** 1102
[29] Ghosh K and Van Duyne G D 2002 *Methods* **28** 374
[30] Bao X R, Lee H J and Quake S R 2003 *Phys. Rev. Lett.* **91** 265506
[31] Simha R A and Ramaswamy S 2002 *Phys. Rev. Lett.* **89** 058101
[32] Dombrowski C *et al* 2004 *Phys. Rev. Lett.* **93** 098103
[33] Satchwell S C, Drew H R and Travers A A 1986 *J. Mol. Biol.* **191** 659
     Shrader T E and Crothers D M 1989 *Proc. Natl Acad. Sci. USA* **86** 7418
     Shrader T E and Crothers D M 1989 *J. Mol. Biol.* **216** 69
     Cacchione S, Cerone M A and Savino M 1997 *FEBS Lett.* **400** 37
[34] Mattei S, Sampaolese B, De Santis P and Savino M 2002 *Biophys. Chem.* **97** 173
     Anselmi C *et al* 2000 *Biophys. J.* **79** 601
[35] Kulić I M and Schiessel H 2003 *Phys. Rev. Lett.* **91** 148103
[36] Klug S J and Famulok M 1994 *Mol. Biol. Rep.* **20** 97
[37] Hamad-Schifferli K, Schwartz J J, Santos A T, Zhang S and Jacobson J M 2002 *Nature* **415** 152
[38] Garner H R, Ohkawa T, Tuason O and Lee R L 1990 *Phys. Rev.* A **42** 7264
[39] Shapere A and Wilczek F 1989 *J. Fluid Mech.* **198** 557
[40] Taylor G 1952 *Proc. R. Soc.* A **211** 225
[41] Purcell E M 1977 *Am. J. Phys.* **45** 3–11