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Twirling DNA rings —Swimming nanomotors ready for a kickstart

I. M. Kulić[1,2], R. Thaokar[1,3] and H. Schiessel[1,4]

[1] *Max-Planck-Institute for Polymer Research, Theory Group*
P.O. Box 3148, D 55021 Mainz, Germany
[2] *Department of Physics and Astronomy, University of Pennsylvania*
Philadelphia, PA 19104, USA
[3] *Department of Chemical Engineering, Indian Institute of Technology*
Bombay, Mumbai, 400076, India
[4] *Instituut-Lorentz, Universiteit Leiden - Postbus 9506*
2300 RA Leiden, The Netherlands

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Abstract. – We propose a rotary DNA nanomachine that shows a continuous rotation with a frequency of around 100 Hz. This motor consists of a DNA ring whose elastic features are tuned such that it can be externally driven via a periodic temperature change. As a result, the ring propels itself through the fluid with a speed up to tens of nanometers per second.

The long-lasting dream of scaling mechanical devices and machines down to the nanoscale (as popularized by Feynman [1] and carried on by several visionary groups worldwide [2]) continues to fire the imagination of researchers —now in the third generation. Among many experimental difficulties that appear in this context, choosing the proper material for the assembly of a nanodevice turns out to be crucial. Important material requirements are: stability, self-assembly ability, modularity, replicability, switchability, experimental tractability. Presently, one of the most promising materials fulfilling those requirements is DNA [3]. Assemblies based on DNA hybridisation chemistry [4–7] as well as conformational DNA transitions [8] were successfully exploited to generate periodically switchable nanodevices. However, despite their beauty and conceptual originality all of these devices suffer one major problem: 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 (biological molecular motors). A natural question arises then: Can one achieve *subsecond* switching times with a DNA nanodevice? Can such a device be operated in some manner to *swim directionally*? In this letter we show theoretically the principal feasibility of such DNA nanomachines.

Let us in the following propose a surprisingly simple nanomotor: a DNA miniplasmid, cf. fig. 1(a). We will show that despite its structural simplicity a miniplasmid can be turned into a nanomachine able to produce fN forces and self-propelling at speeds of tens of nanometers per second through the fluid. In order to run the plasmid as a motor we use here the Euler-angle ψ (cf. fig. 1(a)) as the relevant degree of freedom [9]. The main idea now is to induce a

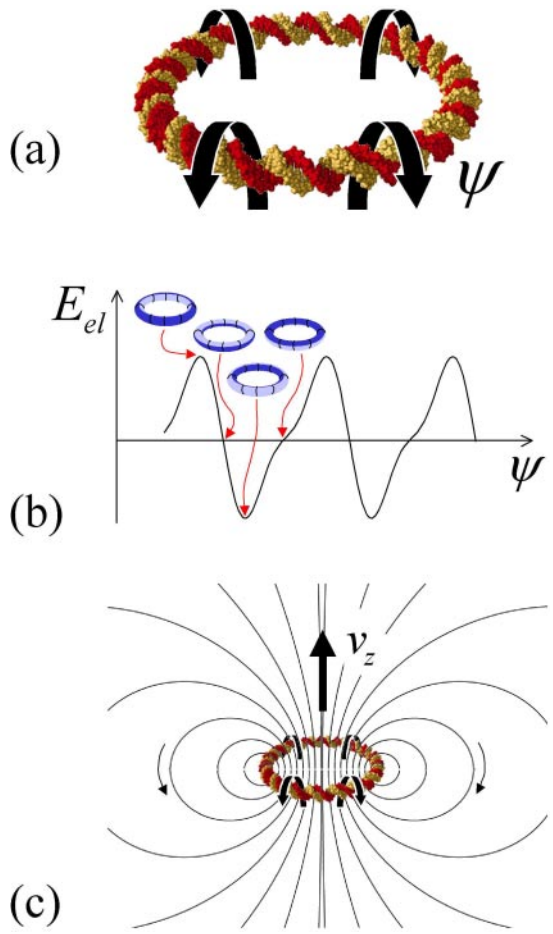

Fig. 1 – The operation principle of the DNA-minicircle propeller: (a) the twirling degree of freedom; (b) the elastic energy as a ratchet potential; (c) the flow-field around the twirling ring induces its translational velocity v_z.

directed current $\langle\dot{\psi}\rangle$ —in a manner similar to the rotation of a closed rubber tube around its central circular axis— via non-equilibrium fluctuations and the ratchet effect [10, 11], cf. fig. 1(b). As a result, the twirling ring generates a hydrodynamic flow-field (shown in fig. 1(c)) that remarkably induces an efficient self-propulsion of the motor as detailed below.

The DNA nanomotor is formed by closing a DNA chain of length $2\pi R$ into a circle. Crucial is to use a chain with an anisotropic bendability and bendedness —characterized by two principal bending persistence lengths, l_1 and l_2, and intrinsic curvatures, κ_1 and κ_2, in two corresponding perpendicular directions. For simplicity, we assume these parameters to be independent of the arc-length throughout the chain [12]. The elastic distortion energy of the chain parametrized by the arc length parameter s is then described by three Euler angles $\theta(s)$, $\phi(s)$ and $\psi(s)$ via $E_{el} = \frac{1}{2}k_BT\int_0^{2\pi R}\sum_{i=1,2,3} l_i\left(\omega_i - \kappa_i\right)^2 \mathrm{d}s$ with $\omega_1 = \phi'\sin\theta\sin\psi + \theta'\cos\psi$, $\omega_2 = \phi'\sin\theta\cos\psi - \theta'\sin\psi$ and $\omega_3 = \phi'\cos\theta + \psi'$ [16]. l_3 denotes the twist persistence length and —for simplicity— we choose $\kappa_3 = 0$. Assume now the chain being closed into an untwisted ring [17]. For the case of DNA minicircles of short length ($2\pi R \lesssim l_i$) and with constant κ_i

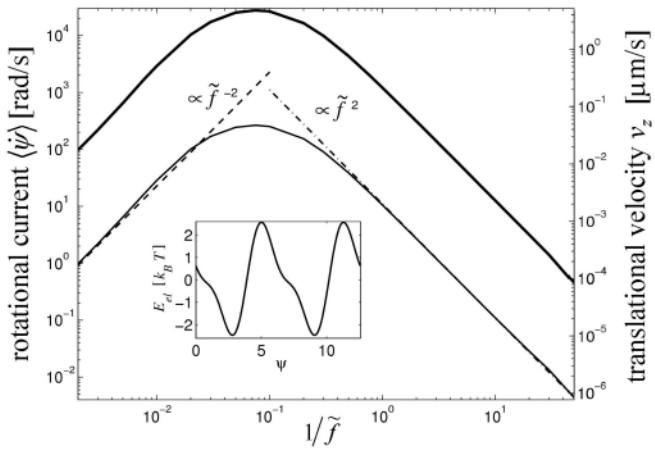

Fig. 2 – The rotational current $\langle\dot{\psi}\rangle$ and the induced translational velocity v_z as a function of the dimensionless frequency $\tilde{f}$ of the temperature (potential) oscillations. The DNA ring has the following parameters: $R = 10\,\mathrm{nm}$, $r_0 = 1\,\mathrm{nm}$ (typical DNA minicircle), $l_1 = 45\,\mathrm{nm}$, $l_2 = 50\,\mathrm{nm}$, $\kappa_1 = \kappa_2 = (200\,\mathrm{nm})^{-1}$ leading to the ratchet potential displayed in the inset. Displayed are the asymptotic expressions, eqs. (5) (dashed line) and (6) (dash-dotted line) together with the numerical solution of eq. (2) (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.

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 $\psi(s) = \mathrm{const}$. This leads then to the required ratchet potential acting on ψ:

$$\frac{E_{el}(\psi)}{\pi k_B T} = \frac{l_1 - l_2}{2R}\cos(2\psi) + 2l_1\kappa_1\cos\psi - 2l_2\kappa_2\sin\psi. \tag{1}$$

From eq. (1) we see that for generating a ratchet potential we need both non-zero bending anisotropy, $l_1 - l_2 \neq 0$, as well as non-vanishing intrinsic curvatures, $\kappa_{1,2} \neq 0$. The inset in fig. 2 demonstrates that reasonable small values of anisotropy and intrinsic curvature can induce a well-defined ratchet potential.

The Fokker-Planck equation describing the time evolution of the probability density $P(\psi, t)$ of the Euler angle ψ writes

$$\zeta\frac{\partial P}{\partial t} = \frac{\partial}{\partial\psi}\left(\frac{\partial E_{el}}{\partial\psi}P + k_B T\frac{\partial P}{\partial\psi}\right) \tag{2}$$

with the friction constant ζ that we will compute below. As a source of non-equilibrium we will choose here a time-dependent variation of temperature $T(t)$, cf. ref. [19].

Before we compute the friction constant ζ we need to shed some light on the low Reynolds-number hydrodynamics of the twirling DNA ring. The latter turns out to be peculiarly related to the inviscid (ideal) fluid vortices (rings of smoke) and as a matter of fact both of them propagate in analogous manner. To see this, we first remark that for a reasonable ring radius $R = 10\,\mathrm{nm}$ (a typical miniplasmid of $\approx 200\,\mathrm{bp}$) and the DNA helix radius $r_0 = 1\,\mathrm{nm}$ the slender-body approximation [20] is valid with the slenderness paramenter $\varepsilon = r_0/R = 0.1$. In the spirit of the slender-body theory one approximates the flow-field around the twirling ring by superimposing rotlets [21] $\boldsymbol{u}_{rot}(\boldsymbol{x}; s) = \Gamma\frac{\mathrm{d}\boldsymbol{c}(s)}{\mathrm{d}s} \times (\boldsymbol{x} - \boldsymbol{c}(s))/|\boldsymbol{c}(s) - \boldsymbol{x}|^3$ placed along

the ring centerline $\boldsymbol{c}(s)$ with arclength parameter s. The rotlet strength $\Gamma = \frac{1}{2}\omega_{\boldsymbol{c}} r_0^2$ is given in terms of the angular velocity $\omega_{\boldsymbol{c}}$ of the ring about $\boldsymbol{c}(s)$. The full velocity profile is then given by $\boldsymbol{u}(\boldsymbol{x}) = \int_0^{2\pi R} \boldsymbol{u}_{rot}(\boldsymbol{x}; s)\,\mathrm{d}s$; cf. also the stream lines around the rotating ring shown in fig. 1(c). When integrating $\boldsymbol{u}(\boldsymbol{x})$ 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:

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

The fact that eq. (3) coincides with the well-known expression from ideal flow vortex theory [22] should not surprise if we recall that a rotlet $\boldsymbol{u}_{rot}(\boldsymbol{x}; s)$ 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/torques and is governed by conservation of kinetic energy and momentum. In sharp contrast to that the low Reynolds-number (Stokes) flow is governed by dissipation and the motion of twirling DNA ring requires the action of a torque $N_{\boldsymbol{c}} = 8\pi^2 x_0^2 \eta R \omega_{\boldsymbol{c}}$ ($\eta = 10^{-3}$ Pa s, the water viscosity) about the central axis $\boldsymbol{c}$. The latter expression can be verified by integrating the tangential stresses generated by $\boldsymbol{u}(\boldsymbol{x})$ 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 $\omega_{\boldsymbol{c}}$ (about the circular axis $\boldsymbol{c}$) and velocity v_z (in the z-direction) with the corresponding external torque $N_{\boldsymbol{c}}$ and force F_z:

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

Combining the previous expressions obtained for $v_z(\omega_{\boldsymbol{c}})$ and $N_{\boldsymbol{c}}(\omega_{\boldsymbol{c}})$ ($F_z = 0$) together with the result of Johnson and Wu [20] for the drag on a *rigid* slender torus we obtain entries in the leading order: $M_{11} = 2R\left(\ln 8/\varepsilon + 1/2\right)^{-1}$, $M_{22} = 2r_0^2 R$ and $M_{12} = M_{21} = r_0^2\left(\ln 8/\varepsilon - 1/2\right)\left(\ln 8/\varepsilon + 1/2\right)^{-1}$. Note that the symmetry of the resistance matrix being a general feature of swimmers in the Stokes flow [23] provides a good check for the consistency of the involved calculations. From eq. (4) we obtain the angular friction constant (entering eq. (2) above) in leading order $\zeta = N_{\boldsymbol{c}}(\omega_{\boldsymbol{c}})/\omega_{\boldsymbol{c}} \approx 8\pi^2\eta r_0^2 R$. 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 $2\pi R$.

Having determined the friction constant ζ we return to the ratchet dynamics given by eq. (2) with the twirling potential eq. (1). To obtain the directed twirling frequency $\omega_{\boldsymbol{c}} := \langle\dot{\psi}\rangle = -\frac{1}{\zeta}\langle\frac{\partial E_{el}}{\partial\psi}P + k_B T\frac{\partial P}{\partial\psi}\rangle$ we follow [19] by choosing a periodic time-dependent temperature variation as follows: $T(t) = T_0\left[1 + A_T\sin(2\pi f_T t)\right]$ 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 $\tau_0 = 4\pi^2\zeta/(k_B T_0)$ 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 [24]. After a long calculation we obtain (for $f_T > f_{res}$) $\langle\dot{\psi}\rangle$ up to terms of order $\mathrm{O}\left(f_T^{-3}\right)$:

$$\left\langle\dot{\psi}\right\rangle = \frac{12\pi^3 A_T^2\left(k_B T_0\right)^3 l_1 l_2 \kappa_1 \kappa_2\left(l_2 - l_1\right)/R}{f_T^2\zeta^3\int_0^{2\pi}\mathrm{d}\psi e^{-\frac{E_{el}(\psi)}{k_B T}}\int_0^{2\pi}\mathrm{d}\psi e^{\frac{E_{el}(\psi)}{k_B T}}}. \tag{5}$$

From eq. (5) we see 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, eq. (1), 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.*, $P\approx P_0+\tilde{f}P_1+\tilde{f}^2P_2$. Rather involved calculations lead to [25]

$$\left\langle\dot{\psi}\right\rangle=-\frac{\tilde{f}^2}{\tau_0}\int_0^1 \mathrm{d}\tilde{t}\,\frac{1}{\overline{E}}\overrightarrow{F\overline{\partial_{\tilde{t}}P_1}} \tag{6}$$

with $E(\tilde{\psi},\tilde{t})=F(\tilde{\psi},\tilde{t})^{-1}=e^{-E_{el}(\tilde{\psi})/k_BT(\tilde{t})}$ and the abbreviations $\overrightarrow{(...)}$ and $\overline{(...)}$ defined as in [24] 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 $P_1=\frac{T_0}{T}E\left(\overrightarrow{Fc_1}-\frac{1}{\overline{E}}\overline{E\overrightarrow{Fc_1}}\right)$ with $c_1=\overrightarrow{\partial_{\tilde{t}}P_0}-\frac{1}{\overline{F}}\overline{F\overrightarrow{\partial_{\tilde{t}}P_0}}$.

Equations (5) and (6) together with eq. (1) and $\zeta=8\pi^2\eta r_0^2R$ allows us to get the twirling speed $\omega_{\boldsymbol{c}}=\langle\dot{\psi}\rangle$ and by virtue of eq. (3) the induced translational velocity $v_z(\omega_{\boldsymbol{c}})$ for arbitrary DNA elastic parameters $l_{i=1,2}$ and $\kappa_{i=1,2}$.

Numbers and experimental aspects. How fast can we operate the twirling ring machine? We shall assume some realistic parameter values for the DNA ring: $R=10\,\mathrm{nm}$, $r_0=1\,\mathrm{nm}$ (typical DNA minicircle) leading to $\zeta=2\cdot10^{-7}k_BT\,\mathrm{s}$. Furthermore, we set $l_1=45\,\mathrm{nm}$, $l_2=50\,\mathrm{nm}$, $\kappa_1=\kappa_2=(200\,\mathrm{nm})^{-1}$ which corresponds to a rather modest anisotropy and intrinsic curvature. Values like these are readily found in nature, *e.g.*, in weak nucleosome positioning sequences like 5sRNA [13, 14]. 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 [15]. The barriers to the corkscrew motion of nucleosomal DNA become analogous to barriers to the twirling mechanism and analogous principles of sequence design apply.

For the temperature variation amplitude we choose $\Delta T=\pm10\,\mathrm{K}$, *i.e.*, $A_T\approx1/30$ (at room temperature $T_0=300\,\mathrm{K}$). Figure 2 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 eq. (2), the two straight lines correspond to the analytical results for the two asymptotic cases, eqs. (5) and (6). As can be seen from this plot the two limits show a $\tilde{f}^{-2}$- and $\tilde{f}^2$-dependence, respectively, in accordance with eqs. (5) and (6). The maximal rotational current is achieved in the crossover region, namely $\omega_{\boldsymbol{c}}\approx200\,\mathrm{rad/s}$ for $\tilde{f}\approx10^{-1}$. Following eq. (3), this implies a translational velocity of $v_z=50\,\mathrm{nm/s}$.

Such fast temperature oscillations are technically feasible and might be generated by adiabatic pressure variations via ultrasound, *e.g.* as nowadays employed in the field of sonochemistry and sonoluminescence [26]. However, despite potentially large temperature oscillations (up to 3000 K on short time scales) achievable by this method, the shearing forces might pose a problem for the DNA molecule integrity. Another more promising method is to exploit the broad electromagnetic absorption spectrum of the DNA molecule (and its ordered water shell) ranging from UV to microwave frequencies and to heat the molecule selectively with short light pulses. The covalent modification of the DNA backbone with artificial fluorophores [27] and nanoncrystals [28] can expand the range of frequencies for electromagnetic heating. In fact, inductively heated gold nanoparticles attached to the DNA backbone have been successfully used to control the melting of DNA [29].

This might also point towards an alternative way of driving the ratchet, namely via a periodic variation of the elastic properties of the ring. Operating the system close to the DNA duplex melting temperature is likely to induce strong oscillations in the overall ring stiffness. Above the melting temperature of 50–70 °C [30] the DNA molecule dissociates into two single strands with negligible bending stiffness [31]. Therefore it is not unreasonable to assume

that the oscillation of the bending potential amplitude becomes the major effect then varying by a factor of $\sim$ O(1) (in the vicinity of the melting temperature). The thick solid line in fig. 2 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 $A_E = 0.3$. As can be seen from fig. 2, the maximal current of this oscillating potential ratchet occurs roughly at the same frequency as that of the thermal ratchet but the value of $\omega_{\boldsymbol{c}}$ is much higher, namely on the order of 2×10^4 rad/s which implies a quite notable translational velocity of $v_z = 5\,\mu$m/s. As a comparison, a typical bacterium moves at $30\,\mu$m/s. Our ring ratchet (with oscillating potential) resembles in many respects "real" biological nanomotors. Besides its nanoscopic size (radius 10 nm), swimming efficiency (0.8%) and speed ($4\,\mu$m/s) it can generate forces and torques close to that of biomolecular motors. Although the net translational force resulting from eq. (4) $F_z = 4\pi^2 \eta M_{12} \omega_{\boldsymbol{c}} \approx 0.6$ fN is comparably small (due to cancelling of most of the stresses), the local torque $N_{\boldsymbol{c}} = 8\pi^2 \eta r_0^2 R \omega_{\boldsymbol{c}} \approx 0.004 k_B T$ and the force acting at the DNA surface $F_{loc} = N_{\boldsymbol{c}}/r_0 = \zeta \omega_{\boldsymbol{c}}/r_0 \approx 16$ fN are significant if we consider the simplicity of the mechanism behind.

From an experimental point of view one should be aware of the fact that a ring (twirling or non-twirling) looses its initial orientation almost instantaneously due to rotational diffusion. The typical relaxation time scale of this process is on the order $\eta R^3/(k_B T)$ (up to logarithmic corrections [32]) which for a ring with $R = 10$ nm leads to 10^{-7} s. That 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 "track", *e.g.* to thread it on a straight DNA chain. A ring with speed $5\,\mu$m/s will then overcome dispersion due to translational diffusion after 2 seconds. Another promising 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 such solutions of self-propelled particles show hydrodynamic instabilities [33], *e.g.* the low-Reynolds number turbulence observed for suspensions of bacteria [34]. Nanomotors like the one presented here might be used as mixer in nanofluidic devices (to, *e.g.*, speed up diffusion-limited reactions) or to drive a solvent flow through a nanochannel.

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