Motor-free contractility in active gels

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Animal cells form contractile structures to promote various functions, from cell motility to cell division. Force generation in these structures is often due to molecular motors such as myosin that require polar substrates for their function. Here, we propose a motor-free mechanism that can generate contraction in biopolymer networks without the need for polarity. This mechanism is based on active binding/unbinding of crosslinkers that breaks the principle of detailed balance, together with the asymmetric force-extension response of semiflexible biopolymers. We find that these two ingredients can generate steady state contraction via a non-thermal, ratchet-like process. We calculate the resulting force-velocity relation using both minimal and microscopic models.

In living cells, most force generation is due to molecular motors that move in a directed manner, such as linearly along a substrate. In animal cells, for instance, myosin motors moving along polar actin filaments can drive large scale contraction and force generation [1, 2]. While this is especially apparent in the case of muscle cells with ordered arrays of actin and myosin, a similar mechanism is at play in a wide range of cellular processes in non-muscle cells, including cell migration, the establishment of cell polarity and even developmental processes at the multi-cellular level [3]. At the molecular scale, such motor activity fundamentally depends on a combination of broken time and spatial symmetries. Motors such as myosin undergo a directed cycle of transitions among conformational states [4] that violates the principle of detailed balance [5–8]. Such a cyclical reaction manifests a directionality in time and is only possible in steady-state with the consumption and dissipation of energy, e.g., in the turnover of adenosine triphosphate (ATP) or other metabolic components [1]. But, even an energy consuming reaction is insufficient to generate directed motion or force. For this, a spatial symmetry must also be broken. This is usually due to the polarity of the substrate such as actin, with well-defined plus and minus ends, to which a motor such as myosin couples. The resulting rectification of the motor’s conformational transitions to generate linear motion and do useful work is reminiscent of the Smoluchowski-Feynman thermal ratchet [6, 9–11].

Here, we propose a mechanism for motor-free contractility that depends on non-equilibrium activity but without polarity or broken spatial symmetry of the substrate. The fundamentally contractile nature of this mechanism manifests the broken time-reversal symmetry and violation of detailed balance. But, contractility can occur even with apolar filaments such as intermediate filaments (IF) or in unpolarized arrays or disordered networks of filaments. As we show, contractility is a natural consequence of the asymmetric force-extension of semiflexible filaments such as actin or IFs in the cytoskeleton, which effectively rectifies the stochastic binding and unbinding and breaks the spatial symmetry, with the direction of motion always being in the ‘contractile’ direction. This can happen, provided that the transient (un)binding is active, e.g., depends on metabolic components such as ATP. This model may provide a basis for understanding recently reports myosin-independent contractility in cells [12, 13].

In our minimal model, we consider a substrate such as an unpolarized, disordered network of filaments, to which a particular semiflexible filament can bind. For simplicity, we treat each segment between crosslinks as a filament that can bind (unbind) to (from) a continuum viscoelastic substrate [see Fig. 1(a)]. In the binding state, the polymer exerts tension on the gel, \(\tau(\ell) = dU_p(\ell)/d\ell\), resulting in an average contractile force

\[
\langle F_\tau \rangle_\ell = \int P_{on}(\ell)\tau(\ell)\,d\ell. \tag{1}
\]

Here \(\ell\) is the end-to-end length of the polymer, \(U_p\) is the potential of mean-force (PMF) of the polymer, and \(P_{on}\) is the probability of the polymer to have a given end-to-end distance \(\ell\) in the bound state. If the (un)binding is passive, then \(P_{on}(\ell)\) must be governed by a Boltzmann distribution, detailed balance must be satisfied and the contractile force must vanish. However, when the binding and/or unbinding process are active, e.g., due to consumption or catalysis of a metabolic component such as ATP, \(P_{on}\) is generally not a Boltzmann distribution. This, together with an asymmetric PMF, can lead to a net contractile force.

The force-extension relation for a semi-flexible polymer is [see Fig. 1(b)] [14–18]:

\[
\ell(\tau) - \ell_0 = \left(\frac{\Delta \ell}{\Delta \ell}\right)^{\frac{\tau}{\tau_0}} + \epsilon \left[\frac{\tau}{\tau_0} \left(1 + \frac{\tau}{\mu}\right)\right],
\]

where \(\tau_0 \equiv \pi^2 k_B T / 6(\Delta \ell)\) is a characteristic tension, \(\langle \Delta \ell \rangle \simeq \ell_0^2 / (6\ell_p)\) is the mean end-to-end thermal contraction of a stiff polymer of rest length \(\ell_0\) and persistence length \(\ell_p\). Here, \(\mu\) is the enthalpic stretch modulus, \(k_B\) is the Boltzmann constant, \(T\) is the temperature and \(\epsilon(\phi) = 1 - 3\pi(\sqrt{\phi - \cosh(\pi(\sqrt{\phi})^{(-2)})})^{-1}\) [18]. Equation (2) shows strong asymmetry: the polymers are hard to stretch and easy to compress. Although this particular form of the force-extension relation
FIG. 1. (a) Illustration of the minimal model. One polymer segment from a disordered network undergo binding/unbinding process attaining a steady-state length distribution, $P_{\text{on}}$. The bound and unbound states are denoted by dark and light purple, respectively. (b) Force-extension relation for inextensible semiflexible polymer ($\tau(\ell)/\mu \to 0$ in Eq. (2)) and the two-spring potential with $K_1 = 2\tau_0/3(\Delta \ell)$ and $K_2 = 10K_1$. (c) Schematic plot of the equilibrium distribution of a semiflexible polymer end-to-end length with $\ell_0$ being the rest-length.

is valid for contour lengths less than $\ell_p$, as is appropriate for cytoskeletal filaments, a qualitatively similar asymmetric relation holds in the opposite limit of semiflexibility, such as for DNA with small persistence length [19]. As we show, such an asymmetry is sufficient to generate contraction, even for a symmetric substrate binding potential. To demonstrate the sufficiency of this condition, we first consider a simplified and analytically tractable asymmetric two-spring force-extension relation

$$\tau(\ell) = \begin{cases} K_1(\ell - \ell_0) & (\ell < \ell_0) \\ K_2(\ell - \ell_0) & (\ell \geq \ell_0) \end{cases},$$

where $K_1 < K_2$ are different spring constants for compression and stretching, respectively.

In the following, we consider the substrate to be isotropic with a characteristic spacing $d$ between binding sites. The binding rate can then be written as $\omega_{\text{on}} P_b(\ell_b)$, where $\omega_{\text{on}}$ defines the average time spent in the unbound state and $P_b(\ell_b)$ is the probability to bind at an initial end-to-end polymer length $\ell_b$. We divide the process into four steps: (i) in the unbound state we assume the polymer quickly relaxes to an equilibrium distribution with rest length $\ell_0$ (see Fig. 1(c)), (ii) the polymer binds to the substrate at rate $\omega_{\text{on}}$ and initial end-to-end length $\ell_b$ with probability $P_b(\ell_b)$, (iii) once the polymer binds, it contracts the gel due to its PMF, $U_s$, and (iv) the polymer actively unbind at constant rate $\omega_{\text{off}}$. Here, we neglect thermal aspects of unbinding that we assume to be dominated by active processes.

In our model, in addition to $d$, another key length scale is the width $d\ell$, of the thermal distribution of the filament end-to-end distance, $\ell$. We begin by considering a simplified limit in which this width is narrow compared with $d$, i.e., $d\ell \ll d$. Since we are interested in non-motor crosslinkers, these do not introduce any asymmetry in the binding potential. Together with the network isotropy this implies that the binding probability, $P_b(\ell_b)$, must be symmetric around $\ell_b = \ell_0$ (see [20] for details). We consider the simplest symmetric form for this probability distribution, characterized by just a width $d$ that represents the typical spacing of binding sites:

$$P_b(\ell_b) = \frac{1}{d} \quad \text{for} \quad \ell_0 - \frac{d}{2} < \ell_b < \ell_0 + \frac{d}{2},$$

and $P_b = 0$ otherwise.

The steady-state distribution for constant on/off rates is $P_{\text{on}}(\ell) = \omega_{\text{on}} \int d\ell_0 P_b(\ell_b) \langle P(\ell, \ell_b; t) \rangle$, where $\omega_{\text{on}} = \omega_{\text{off}}/(\omega_{\text{on}} + \omega_{\text{off}})$ is the fraction of time spent in the bound state, and $\langle P(\ell, \ell_b; t) \rangle$ is the time-averaged length distribution of the polymer just before it unbinds. Here we define $P(\ell, \ell_b; t)$ as the probability distribution of the polymer length $\ell$, for a single binding event starting from $\ell = \ell_0$ and time $t = 0$, with unbinding rate $\omega_{\text{off}}$. For a rigid substrate, $\langle P(\ell, \ell_b; t) \rangle = \delta(\ell - \ell_b)$, and $P_{\text{on}}(\ell) = \omega_{\text{on}} P_b(\ell_b)$, which leads to a contractile force $\langle F_s \rangle t = d\omega_{\text{on}}(K_2 - K_1)/8$. In fact, any symmetric distribution $P_b$ generates a net contractile force. For a compliant substrate such as a viscoelastic gel that resists deformation, this force will drive contraction. We consider two limiting behaviors of such a gel: a viscous liquid and an elastic solid.

For a viscous substrate response, with an effective drag coefficient $\gamma$, the polymer length in the binding state is a dynamic variable obeying

$$\frac{d\ell_f(t)}{dt} = -\gamma(\ell_f - F),$$

where $F$ is an external load and $\ell_f(t = 0) = \ell_b$. For constant off rate, $P(\ell, \ell_b; t) = \delta(\ell - \ell_f) \exp(-\omega_{\text{off}} t)$. The average contractile velocity is then given by $v = \langle [F_s] \rangle / \gamma$. For the simple, two spring force extension in Eq. (3), the contractile velocity for vanishing load is [20],

$$v = \frac{d\gamma \omega_{\text{on}} \omega_{\text{off}}^2 (K_2 - K_1)}{8(K_1 + \gamma \omega_{\text{off}})(K_2 + \gamma \omega_{\text{off}})}.$$

The analytical expression for a finite load can be found in [20]. In the elastic limit, $\langle F_s \rangle t$ has the same form as Eq. (6) with $\gamma \omega_{\text{off}} \to K_s$, an effective spring constant (see [20]).

For $d \ll \delta \ell$, one can calculate the binding probability distribution $P_b(\ell_b)$ perturbatively, since it reduces to the equilibrium end-to-end distribution $P_{\text{eq}}$ (Fig. 1(c)) in the limit
For an analytic force-extension relation $\tau(\ell)$, a possible asymmetry will appear to lowest order as an anharmonic second derivative $\tau''$. Thus, the expected scaling of the net/average force from Eq. (1) is given by $(F_s) \sim \tau'' d^2$, leading to $v \sim d^2$ [20]. Therefore, a crossover from a quadratic to linear dependence on $d$ is expected. To find the velocity for general $d$, we developed a numerical simulation that takes into account both thermal fluctuations in $P_b(\ell_t)$ and a thermal Langevin noise in Eq. (5) (see [20]). The length in the unbound state is then sampled from its equilibrium distribution $P_b$ (Eq. (1(b)), and $P_b$ of Eq. (4) is assumed to be distributed symmetrically about this sampled length, over a width of order $d$. The contractile velocity for the two-spring (Eq. (3)) and the semiflexible polymer (Eq. (2)) PMFs are similar in both the small and large $d$ limits, as can be seen in Fig. 2(a). For $d \ll \delta \ell$, our numerical simulation verifies the expected $v \sim d^2$ for both PMFs [20].

For larger $d$, due to the sampling of the extremes in the semiflexible PMF, the stretch modulus $\mu$ begins to dominate and the system becomes well-described by the two-spring potential with $K_2 \to \mu/\delta\ell_0$ and $K_1 \to 0$, which represents a rope-like limit [20]. Here, we observe both the predicted linear dependence of Eq. (6) (red line in Fig. 2(a)), as well as the expected coincidence of the two models for the parameters chosen. Importantly, our results for the two-spring potential do not depend qualitatively on $K_1$ or $K_2$ as long as these spring constants are not equal.

In Fig. 2(b)-(c) we plot force-velocity curves for the small and large $d$ limits, respectively. In Fig. 2(b) we use the two-spring potential, while in Fig. 2(c) we use the semiflexible polymer PMF. In both cases, the velocity is reduced by an applied load, in a way similar to molecular motors [21]. For small $F$, we find that decreasing $\tilde{\gamma}$ results in lower velocities and correspondingly lower stall forces. This is the result of the increased compliance and stress relaxation of the substrate due to the decreased substrate friction. Under increasing load $F$, the increasingly negative velocity for increasing $\tilde{\gamma}$ are also due to substrate compliance under the large external force.

Having demonstrated the conceptual mechanism for contraction, we introduce a microscopic model for a single binding/unbinding event of an active crosslink to illustrate the broken spatial symmetry for an initially symmetric binding potential. As sketched in Fig. 3(a), we consider a 1D model of a semiflexible segment whose two ends, $A$ and $B$, bind and unbind to a substrate with rates $\omega_{on}$ and $\omega_{off}$, respectively. The substrate has multiple binding sites separated by an average distance, $d$. Each of the binding sites is assumed to have a symmetric binding potential $U_s$, as appropriate for a substrate consisting of apolar filaments or a disordered network.

Specifically, we use a periodic triangular potential with depth $\Delta E$ and period $d$, although periodicity is not essential. The PMF of the polymer is $U_r(x_B - x_A)$, where $x_A$ and $x_B$ are the positions of $A$ and $B$, respectively.

Consider a binding event in which the polymer end $B$ binds to the substrate at site $S_B$, while the other polymer end, $A$, remains bound at $S_A$ (see Fig. 3(a)). The positions of the sites are denoted by $y_A$ and $y_B$ (for $S_A$ and $S_B$). We are interested in the change of the average separation between the binding sites in the bound state vs the unbound state, $\Delta y = \langle y_B - y_A \rangle_{\text{bound}} - \langle y_B - y_A \rangle_{\text{unbound}}$. The average contractile velocity (over many binding/unbinding events) is then $v = \Delta y/T$, where $T$ is the average time spent in one binding event and one unbinding event. If $\omega_{off}$ and $\omega_{on}$ are constants (as we shall assume hereafter) $T = \omega_{on}^{-1} + \omega_{off}^{-1}$. The averages are taken with respect to $\mathcal{P}(y_A, y_B; t)$, the probability to find the binding sites in positions $y_A$ and $y_B$ at time $t$. The positions of the polymer ends and the two binding sites can be described using a standard four-variable Fokker-Planck equation [20, 22] for the probability $\mathcal{P}(x_A, x_B; y_A, y_B; t)$, with potential $W(x_A, x_B; y_A, y_B) = U_r(x_B - x_A) + U_b(x_A - y_A) + U_b(x_B - y_B)$, mobilities $m_x$ and $m_y$ (for both polymer ends and for both binding sites, respectively), and unbinding rate $\omega_{off}$. The binding rate $\omega_{on}$ is taken to be constant, and the dynamics in the unbound state are assumed to be fast [23], leading to an initial, Boltzmann
distribution of the polymer end-to-end distance governed by $P_{eq}$. When detailed balance is satisfied, $\omega_{\text{off}} = \omega_{\text{on}} \exp[U_b(x_B - y_B)/(k_B T)]$ and the average distance between $S_A$ and $S_B$ in both the bound and unbound states is the same, i.e., $\Delta y = 0$ and no contraction ensues. However, as detailed balance is broken, a net contraction/expansion is possible. Indeed, if one takes $\Delta E/d \gg |dU_e(x_B - x_A)|/d(x_B - x_A)$, this microscopic model reduces to our minimal model, which shows contraction. In this case, after binding the polymer length changes instantaneously and its length distribution (at $t \to 0$) is given by $P_t$ of Eq. (2) (see [20]).

To further elucidate how the PMF asymmetry leads to contraction, we consider $m_x \gg m_y$, which allows us to treat $x_A$ and $x_B$ as fast variables and integrate them out (see details in [20]). This is, in fact, a physical limit corresponding to a polymer network substrate, whose dynamics are slower than those of a single polymer. We also assume $\Delta E \gg k_B T$, so it is unlikely for the polymer ends to hop to another binding site before they unbind, allowing us to consider relaxation only within the well of the initial binding site. The dynamics of the separation $y_B - y_A$ are then reduced to an effective 1-D Fokker-Planck equation for $P(y_B - y_A; t)$ [24], with an effective interaction between $S_A$ and $S_B$ [25]

$$W^*(y_B - y_A) = \int \frac{dx_A dx_B \chi(x_A, x_B, y_A, y_B)}{Z_Y(y_A, y_B)} \times W(x_A, x_B, y_A, y_B) e^{-W/(k_B T)},$$

where $\chi = \Theta(d/2 - |x_A - y_A|) \Theta(d/2 - |x_B - y_B|)$, $\Theta(x)$ is the Heaviside function, and $Z_Y(y_A, y_B) = \int dx_A dx_B \chi e^{-W/(k_B T)}$. The effective potential $W^*(x)$ is the result of the coupling between the symmetric binding potential and the asymmetric PMF. As shown in Fig. 3(b), $W^*(x)$ becomes asymmetric for finite $d$. The shape of the effective potential depends on $d$, becoming more asymmetric for small $d$. Interestingly, a particle moving in a periodic $W^*$ is mathematically equivalent to a motor binding on a polar filament [6], with the crucial distinction that the motor directional motion is dictated by the filament polarity, while the motion here is always contractile in character.

After obtaining the effective potential, we use the effective 1-D Fokker-Planck equation to find $\Delta y$ and the contractile velocity numerically. (For explicit derivation see [20].) Figure 3(c) shows the dependence of the contractile velocity on $d$. When $d \ll 1$, the velocity has quadratic dependence on $d$, in agreement with our minimal model above. However, since the strength of binding $\Delta E$ is finite, for large enough $d$, the binding potential becomes flat. The velocity is then decreased for $d$ exceeding a threshold that depends on $\Delta E$ and $m_y$. The non-monotonic $v$ implies that there is an optimal $d$.

We expect the spacing of binding sites $d$ to be no smaller than a few nm, the typical size of a globular protein or the spacing of monomers in a cytoskeletal filament. Taking $d \simeq 10$ nm and $\delta \ell \simeq 6$ nm, corresponding to an actin filament of length $1 \mu$m, the predicted contractility for large $\omega_{\text{off}}$ is nearly maximal, at a force estimated to be $\langle F \rangle \simeq 0.5pN$.

We have presented a minimal model to demonstrate how contraction can result from active (un)binding that violates detailed balance. This active process leads to a breaking of time-reversal symmetry, much as does the enzymatic cycle of molecular motors, e.g., fueled by the hydrolysis of ATP. Unlike a molecular motor, however, we show that contractility in our model does not depend on polarity or broken spatial symmetry of either filament or substrate. Rather, the mechanical asymmetry that is generic for any filamentous biopolymer is sufficient to rectify the active, cyclical (un)binding and generate contractile motion. Thus, this mechanism can lead to motor-like contractility even for apolar filaments, such as intermediate filaments, which has not been thought possible. In addition to cytoskeletal filaments, crosslinking proteins such as filamin may also provide the mechanical asymmetry needed for rectification and contractility. Interestingly, disordered/apolar actin bundles have been shown to exhibit contraction when crosslinked with filamin [26], although the active, non-equilibrium aspect of this system is unclear. Our model may provide an explanation for recent observations of...
non-myosin-dependent dynamics of the contractile ring during cell division or cellularization [12, 13]. It is possible that ATP-dependent crosslinking by myosin in disordered actin networks or other structures may generate contractility [27–33], without the need for a motor power stroke. It is even possible that septins, which are known to play a role in the contractile ring, may be responsible for force generation, even though they form apolar filaments [34, 35]. In any case, our model suggests a generic, steady-state mechanism for contraction even in apolar or fully disordered structures.

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[1] B. Alberts, A. D. Johnson, J. Lewis, D. Morgan, M. Raff, K. Roberts, and P. Walter, Molecular Biology of the Cell, 6th ed. (Garland Science, New York, 2017).
[2] D. A. Fletcher and R. D. Mullins, Nature 463, 485 (2010).
[3] C. P. Heisenberg and Y. Bellaïche, Cell 153, 948 (2013).
[4] J. A. Spudich, Nat. Rev. Mol. Cell Biol. 2, 387 (2001).
[5] L. E. Boltzmann, Wien. Ber. 66, 275 (1872).
[6] F. Jülicher, A. Ajdari, and J. Prost, Rev. Mod. Phys. 69, 1269 (1997).
[7] C. Battle, C. P. Broedersz, N. Fakhri, V. F. Geyer, J. Howard, C. F. Schmidt, and F. C. MacKintosh, Science 352, 604 (2016).
[8] C. Nardini, E. Fodor, E. Tjhung, F. van Wijland, J. Tailleur, and M. E. Cates, Phys. Rev. X 7, 021007 (2017).
[9] R. P. Feynman, The Feynman Lectures on Physics, Vol. 1 (Addison-Wesley, Massachusetts, USA, 1963) Chap. 46.
[10] M. O. Magnasco, Phys. Rev. Lett. 71, 1477 (1993).
[11] J. Prost, J. F. Chauwin, L. Peliti, and A. Ajdari, Phys. Rev. Lett. 72, 2652 (1994).
[12] C. Wloka, E. A. Vallen, L. Thé, X. Fang, Y. Oh, and E. Bi, J. Cell Biol. 200, 271 (2013).
[13] Z. Xue and A. M. Sokac, J. Cell Biol. 215, 335 (2016).
[14] F. C. MacKintosh, J. Käs, and P. A. Janmey, Phys. Rev. Lett. 75, 4425 (1995).
[15] T. Odijk, Macromolecules 28, 7016 (1995).
[16] J. Wilhelm and E. Frey, Phys. Rev. Lett. 77, 2581 (1996).
[17] C. Storm, J. J. Pastore, F. C. MacKintosh, T. C. Lubensky, and P. A. Janmey, Nature 435, 191 (2005).
[18] C. P. Broedersz and F. C. MacKintosh, Rev. Mod. Phys. 86, 995 (2014).
[19] J. F. Marko and E. D. Siggia, Macromolecules 27, 981 (1994).
[20] Supplementary material.
[21] I. Derenyi and T. Vicsek, Proc. Natl. Acad. Sci. 93, 6775 (1996).
[22] C. A. Brackley, J. Johnson, D. Michieletto, A. N. Morozov, M. Nicodemi, P. R. Cook, and D. Marenduzzo, Phys. Rev. Lett. 119, 1 (2017).
[23] Relaxing these assumptions will not change our results, but will make the formalism more intricate.
[24] To be precise, eliminating \( x_A \) and \( x_B \) results in a 2D Fokker-Planck equation for \( P(y_B - y_A, y_B + y_A; t) \), but it can be shown [20] that \( P(y_B - y_A, y_B + y_A; t) = P(y_B - y_A; t)P(y_B + y_A; t) \) and \( y_B + y_A \) has diffusive dynamics.
[25] M. O. Magnasco, Phys. Rev. Lett. 72, 2656 (1994).
[26] K. L. Weirich, S. Banerjee, K. Dasbiswas, T. A. Witten, S. Vaikuntanathan, and M. L. Gardel, Proc. Natl. Acad. Sci. 114, 2131 (2017).
[27] Y. Hatwalne, S. Ramaswamy, M. Rao, and R. A. Simha, Phys. Rev. Lett. 92, 118101 (2004).
[28] T. Shen and P. G. Wolynes, New J. Phys. 8, 273 (2006).
[29] S. Wang, T. Shen, and P. G. Wolynes, J. Chem. Phys. 134, 014510 (2011).
[30] M. S. e Silva, M. Depken, B. Stuhrmann, M. Korsten, F. C. MacKintosh, and G. H. Koenderink, Proc. Natl. Acad. Sci. 108, 9408 (2011).
[31] J. Alvarado, M. Sheinman, A. Sharma, F. C. Mackintosh, and G. H. Koenderink, Proc. Natl. Acad. Sci. 108, 114 (2013).
[32] E. Tjhung, D. Marenduzzo, and M. E. Cates, Proc. Natl. Acad. Sci. U.S.A. 31, 12381 (2013).
[33] T. Markovich, E. Tjhung, and M. E. Cates, Phys. Rev. Lett. 122, 088004 (2019).
[34] M. Mavrakis, Y. Azou-Gros, F. C. Tsai, J. Alvarado, A. Bertin, F. Iv, A. Kress, S. Brasselet, G. H. Koenderink, and T. Lecuit, Nat. Cell Biol. 16, 322 (2014).
[35] N. F. Valadares, H. d’ Muniz Pereira, A. P. Ulian Araujo, and R. C. Garratt, Biophys. Rev. 9, 481 (2017).
Supplementary Material
Motor-free contractility in active gels
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I. MINIMAL MODEL

A. Validation of the symmetric binding probability assumption

In the minimal model, we consider binding/unbinding of a segment of semiflexible polymer to/from a substrate. Let us denote the binding and unbinding rates as Ω_on(ℓ_b, ℓ_u) and Ω_off(ℓ_b, ℓ_u), where ℓ_b and ℓ_u are the polymer length in the bound and unbound state, respectively. For a system obeying detailed balance, the transition rates satisfy [1],

\[ \frac{\Omega_{on}(\ell_u, \ell_b)}{\Omega_{off}(\ell_b, \ell_u)} = e^{\beta [U_b(\ell_u) - U_e(\ell_b) - U_b(\ell_u)]}, \]

(S1)

with \( U_b \) being the binding energy and \( U_e \) the elastic energy. This relation results in a Boltzmann steady state distribution. In practice, \( U_b \) is large compared to both the thermal and elastic energy, \( |U_b| \gg k_BT, U_e(\ell) \). Hence, the binding process is mostly determined by \( U_b \), which can be regarded as a substrate property. Because we assume the substrate is isotropic (and therefore has also translational symmetry), \( \Omega_{on}(\ell_u, \ell_b) = \Omega_{on}(\ell_u - \ell_b) \). The crosslinker is not a motor, therefore the substrate should also have parity symmetry, allowing us to write \( \Omega_{on}(\ell_u, \ell_b) = \omega_{on} P_c(|\ell_b - \ell_u|) \), where \( P_c(|\ell_b - \ell_u|) \) is the probability distribution of the length change in the binding process, and \( \omega_{on} \) defines the average time spent in the unbound state.

We assume \( P_c \) can be characterized by the average binding site separation, \( d \). For simplicity we also take the dynamics in the unbinding state to be fast compared to the time-scales of binding/unbinding and the relaxation of the substrate, hence, the unbinding length probability is the equilibrium distribution, \( P_{eq}(\ell_u) \sim \exp [-U_e(\ell_u)/k_BT] \).

The probability for the polymer to bind with length \( \ell_b \) is then

\[ P_b(\ell_b) = \int P_{eq}(\ell_u) P_c(|\ell_b - \ell_u|) \, d\ell_u. \]

(S2)

When \( d \) is much larger than the width of the distribution \( P_{eq}(\ell_u) \) \( (d \gg \delta \ell) \) one may write \( P_{eq}(\ell_u) \simeq \delta(\ell_u - \ell_0) \), leading to a symmetric binding probability \( P_b(\ell_b) = P_c(|\ell_b - \ell_0|) \).

B. The width of the equilibrium distribution

In this subsection we calculate the width of the equilibrium distribution for both the two-spring and the semiflexible PMFs. The distribution width is denoted by \( \delta \ell \) and is defined as the square root of the distribution variance, \( \delta \ell^2 = \langle \delta \ell^2 \rangle = \langle \ell^2 \rangle - \langle \ell \rangle^2 \). The averages are taken with respect to the equilibrium distribution, \( P_{eq}(\ell) = \exp [-U_e(\ell)/k_BT]/Z \), with \( Z \) being the partition function, \( Z = \int \exp [-U_e(\ell)/k_BT] \, d\ell \). For the two-spring PMF (Eq. (3) in the main text), \( U_e \) is harmonic and \( \delta \ell \) reads,

\[ \delta \ell = \left[ \frac{(\pi - 2)K_1^2 + \pi K_1^3 K_2^{1/2} + 4K_1 K_2 + \pi K_1^{1/2} K_2^{3/2} + (\pi - 2)K_2^2}{\pi K_1 K_2 \left(K_1^{1/2} + K_2^{1/2}\right)^2} k_BT \right]^{1/2}. \]

(S3)

For the semiflexible PMF, we only consider the (realistic) case in which \( \mu \gg \tau_0 \), i.e., the polymer is nearly inextensible. In that case, we can take \( \delta \ell \) to be the one of the inextensible limit. This leads to \( \delta \ell = \sqrt{\frac{\mu}{\tau_0}} \ell_p/\ell_p \) [2].

C. Large \( d \) limit for the two-spring PMF

Let us calculate the contractile velocity (force) for a viscous (elastic) substrate in the limit of large \( d \) \( (i.e. \ d \gg \delta \ell) \), with the two-spring PMF (Eq. (3) in the main text). Our goal is to calculate \( \langle F_s \rangle_\ell \) of Eq. (1) in the main text. To
do so we need to find \( P_{on} \), which for constant on and off rates (as we consider in the main text) reads,
\[
P_{on}(\ell) = C_{on} \int d\ell_{b} P_{b}(\ell_{b}) \langle P(\ell, \ell_{b}; t) \rangle_{t}.
\]  
(S4)

Here \( C_{on} = \omega_{on}/(\omega_{on} + \omega_{off}) \) is the fraction of time spent in the bound state, and \( \langle P(\ell, \ell_{b}; t) \rangle_{t} = \omega_{off} \int dt P(\ell, \ell_{b}; t) \) is the time averaged length distribution of the polymer just before it unbinds. \( P(\ell, \ell_{b}; t) \) is the probability distribution of the polymer length \( \ell \), for a single binding event starting from \( \ell = \ell_{b} \) and time \( t = 0 \), with unbinding rate \( \omega_{off} \). Below we detail the calculation of \( P_{on} \) for the various cases.

1. Contractile velocity for a viscous substrate

For a viscous substrate, the polymer length in the bound state, \( \ell_{f} \), is a dynamic variable obeying a Langevin equation (Eq. (6) in the main text). Solving this equation gives the trajectory \( \ell_{f}(\ell_{b}; t) \):
\[
\ell_{f}(\ell_{b}; t) = \begin{cases} 
\ell_{0} + \frac{F}{K_{1}} + \left(\ell_{b} - \ell_{0} - \frac{F}{K_{1}}\right) e^{-K_{1}t/\gamma} & (\ell_{b} < \ell_{0} \quad \text{and} \quad t < t_{0}) \\
\ell_{0} + \frac{F}{K_{2}} \left(1 - e^{-K_{2}(t-t_{0})/\gamma}\right) & (\ell_{b} < \ell_{0} \quad \text{and} \quad t \geq t_{0}) \\
\ell_{0} + \frac{F}{K_{2}} \left(\ell_{b} - \ell_{0} - \frac{F}{K_{2}}\right) e^{-K_{2}t/\gamma} & (\ell_{b} \geq \ell_{0}),
\end{cases}
\]
(S5)

where \( t_{0} = -\frac{1}{K_{1}} \ln\left(\frac{\ell_{0} - \ell_{b} + F/K_{1}}{\ell_{0}}\right) \) is the time for which \( \ell_{f}(t_{0}) = 0 \). With this result we find explicitly the probability distribution of the polymer length \( \ell \) for a single binding event starting from \( \ell = \ell_{b} \) at \( t = 0 \) \cite{3}: \( P(\ell, \ell_{b}; t) = \delta(\ell - \ell_{f}) \exp(-\omega_{off} t) \). The contractile velocity under external force \( F \) for a viscous substrate with viscosity \( \gamma \) is defined as
\[
v = \frac{\langle [F_{s} - F] \rangle}{\gamma}.
\]  
(S6)

Using the probability distribution above with Eqs. (S4)-(S5) and Eq. (1) of the main text we obtain
\[
v = \frac{1}{\gamma} \left[ -F + \int d\ell P_{on}(\ell) \tau(\ell) \right]
\]
\[
= \left( K_{2} - K_{1} \right) \left[ 2F^{2} + dFK_{1} \right] \left( 1 + \frac{K_{1}d}{2F} \right) e^{-\gamma\omega_{off}/K_{1}} - 2F^{2}
\]
\[
+ \left( K_{1} - \gamma\omega_{off} \right) \left[ \frac{1}{4} d^{2} \omega_{off} (K_{2} - K_{1}) - dF(K_{1} + K_{2} + 2\gamma\omega_{off}) \right]
\]
\[
\times \frac{\omega_{on}\omega_{off}}{2d\gamma(\omega_{on} + \omega_{off})(K_{1} - \gamma\omega_{off}^{2})(K_{2} + \gamma\omega_{off})} - \frac{F\omega_{off}}{\gamma(\omega_{on} + \omega_{off})}.
\]  
(S7)

For vanishing external force, \( F = 0 \), the contractile velocity is calculated by taking limit of \( F \to 0 \) in Eq. (S7), yielding Eq. (7) in the main text.

2. Contractile force for an elastic substrate

For an elastic substrate with spring constant \( K_{s} \), the equation for the polymer length in the binding state, \( \ell_{f}(\ell_{b}) \), is calculated using \( \tau(\ell_{f}) = K_{s} (\ell_{f} - \ell_{b}) \), yielding,
\[
\ell_{f}(\ell_{b}) = \begin{cases} 
\ell_{0} + (\ell_{b} - \ell_{0}) - \frac{K_{s}}{K_{1} + K_{s}} & (\ell_{b} < \ell_{0}) \\
\ell_{0} + (\ell_{b} - \ell_{0}) - \frac{K_{s}}{K_{2} + K_{s}} & (\ell_{b} \geq \ell_{0}).
\end{cases}
\]  
(S8)

We then use the inverse relation \( \ell_{b}(\ell_{f}) \) and the fact that for an elastic substrate \( \langle P(\ell, \ell_{b}; t) \rangle_{t} = \delta(\ell - \ell_{f}) \) to find \( P_{on} \) of Eq. (S4) and to calculate the net contractile force:
\[
\langle F_{s} \rangle_{t} = \int d\ell P_{on}(\ell) \tau(\ell) = C_{on} \int d\ell_{b} P_{b}(\ell_{b}) \tau(\ell_{b}) \ell_{b} = \frac{C_{on}K_{s}^{2}(K_{2} - K_{1})}{(K_{1} + K_{s})(K_{2} + K_{s})} \frac{d}{8}.
\]  
(S9)
Figure 1. Contractile force as function of the typical binding-site spacing using (a) the two-spring PMF and (b) the semiflexible PMF. For the semiflexible potential, we use $\mu = 4.37 \times 10^{-8} N$, $\tau_0 = 0.68 pN$, $\ell_0 = 1 \mu m$, and $\delta \ell = 6.2 nm$, while for the two-spring PMF $K_2 = \mu / \ell_0$ and $K_1 = 0.35 \tau_0 / \delta \ell$ (both potentials have the same $\delta \ell$). The rescaled quantities are: $\tilde{d} = d / \delta \ell$, $\langle \tilde{F}_S \rangle \ell = \langle F_S \rangle \ell / \tau_0$ and $\tilde{K}_S = K_S \delta \ell / \tau_0$. The solid lines are the large-$d$ analytical solution of Eq. (S9). In both figures we assume $\omega_{on} \gg \omega_{off}$.

In Fig. (S1a) we plot this contractile force as function of $d$. The numerical results in the large-$d$-limit agree well with Eq. (S9). Since the force-extension relation is linear for both stretching and compression (for large $d$), the contractile force shows linear dependence on $d$. We also observe decreasing force for softer substrates, where the contractile force is reduced due to the deformation of the substrate. In the small $d$ regime we see that $\langle F_s \rangle \sim d^2$ which will be explained below in Section. F.

### D. Semiflexible PMF in the large-$d$-limit

The force-extension relation of an extensible semiflexible biopolymer with rest length $\ell_0$, persistence length $\ell_p$ and stretch modulus $\mu$ is written in Eq. (2) in the main text. The inverse relation $\tau(\ell)$, cannot generally be written explicitly, but as we show below, it can be approximated in the large-$d$-limit. In Eq. (2) we use the function $\epsilon(\phi) = 1 - 3 \pi \sqrt{\phi} \coth(\pi \sqrt{\phi})^{-1}$ to describe the force-extension relation of inextensible polymer [2]. This function has two asymptotic limits:

$$\epsilon(\phi) = \begin{cases} 1 & (\phi \to \infty) \\ -\infty & (\phi \to -1) \end{cases},$$

and the corresponding limits for $\tau(\ell)$ are:

$$\tau(\ell) \approx \begin{cases} \frac{\mu}{\ell_0}(\ell - \ell_0) & (\ell - \ell_0 > \delta \ell) \\ -\tau_0 & (\ell_0 - \ell \gg \delta \ell) \end{cases}. \tag{S11}$$

Equation (S11) shows that the polymer behaves like a spring with spring constant $\mu / \ell_0$ under large extension, while under compression it generates a constant force. It is then possible to approximate the contractile force by a spring that has the same average force. This leads to a spring constant of $2\tau_0 / d$. To conclude, in the large $d$ limit the semiflexible PMF is well approximated by a two-spring PMF with $K_2 = \mu / \ell_0$ and $K_1 \to 0$ (the rope limit). This is also verified in Fig. 2(a) of the main text.

### E. Details of the numerical simulation

In this subsection we detail the numerical procedure we use in order to calculate the contractile velocity (force) for a viscous (elastic) substrate for a general $d$. As we explain below, this includes accounting explicitly for fluctuations of both the polymer and the substrate. The aim in both subsections below is to find $P_{on}$ of Eq. (S4) which is then substituted in Eq. (1) of the main text to give $\langle F_s \rangle$, and the contractile velocity is obtained using Eq. (S6).
1. Contractile velocity for a viscous substrate

For a viscous substrate, thermal fluctuations should be considered in both $P_b$ and the Langevin equation (Eq. (5) in the main text). The length after binding, $\ell_b$, is obtained using Eq. (S2), where $P_c$ is chosen to be a squared distribution with width $d$ (similarly to Eq. (4) of the main text):

$$P_c(\ell_b - \ell_u) = \frac{1}{d}, \quad (|\ell_b - \ell_u| < \frac{d}{2})$$

(S12)

and $P_c = 0$ otherwise. The resulting $P_b$ is then

$$P_b(\ell_b) = \frac{1}{d} \int_{\ell_b-d/2}^{\ell_b+d/2} P_{eq}(\ell_u) d\ell_u.$$  

(S13)

The thermal noise in the Langevin equation modifies Eq. (5) of the main text:

$$\gamma \dot{\ell}_f = -\tau(\ell_f) + F + \eta(t),$$

(S14)

where $\eta(t)$ is a Gaussian white noise with zero mean and variance, $\langle \eta(t)\eta(t') \rangle = 2k_BT \gamma \delta(t-t')$. This Langevin equation is equivalent to the following Fokker-Planck equation [4]:

$$\frac{\partial}{\partial t} P_f(\ell_f, \ell_b; t) - \frac{1}{\gamma} \frac{\partial}{\partial \ell_f} \left[ P_f(U_e + F\ell_f) + k_BT \frac{\partial}{\partial \ell_f} P_f \right] = 0$$

(S15)

where $P_f(\ell_f, \ell_b; t)$ is the probability distribution of polymer length $\ell_f$ at time $t$ starting with length $\ell_b$ at $t=0$. The initial condition is thus $P_f(\ell_f, \ell_b; t) = \delta(\ell_f - \ell_b)$. We calculate $P_f(\ell_f; t)$ by numerically solving Eq. (S15). Note that in Eq. (S15) we do not consider the unbinding process. When the unbinding process is considered (with constant off rate, $\omega_{\text{off}}$) the length distribution becomes $P(\ell, \ell_b; t) = P_f(\ell, \ell_b; t) \exp(-\omega_{\text{off}} t)$. Finally we use this result to calculate $P_{on}$ of Eq. (S4).

2. Contractile force for an elastic substrate

For the elastic substrate thermal fluctuation are accounted in both $P_b$ and the state of the substrate (it is fluctuating about its rest position), where the polymer length after binding, $\ell_b$, is the same as in the viscous substrate case, Eq. (S13). The substrate position about its rest state is denoted by $s$ ($s = 0$ means the substrate does not generate force). The extension just after binding, $s_b$, is sampled from the equilibrium distribution of the spring, $P_s$, which is a Gaussian distribution with zero mean ($\langle s_b \rangle = 0$) and variance $\langle s_b^2 \rangle = K_BT/K_s$.

We continue by calculating the equilibrium distribution in the bound state, $P_f$. Since the polymer is bound to the substrate, its two ends do not move relative to the substrate, thus $\ell_f - \ell_b = s - s_b$. The equilibrium distribution of $\ell_f$ for a given $\ell_b$ and $s_b$ is:

$$P_f(\ell_f, \ell_b, s_b) = \frac{1}{Z(\ell_b, s_b)} \exp \left[ -\frac{[U_e(\ell_f) + K_s(\ell_f - \ell_b + s_b)^2/2]}{k_BT} \right],$$

(S16)

where $Z = \int d\ell \exp \left( -[U_e(\ell) + K_s(\ell - \ell_b + s_b)^2/2]/k_BT \right)$. The probability distribution of the polymer length is now found by choosing $s_b$ from its distribution, $P_s$:

$$P(\ell, \ell_b; t) = e^{-\omega_{\text{off}} t} \int P_f(\ell, \ell_b, s_b) P_s(s_b) \, ds_b.$$  

(S17)

Equation (S17) is numerically calculated and used to find $P_{on}$ (Eq. (S4)) for each $K_s$.

F. The small-$d$-limit

When $d \to 0$ the binding probability reduces to the equilibrium distribution, $P_{eq}$. For $d \ll \delta\ell$, the integration range in Eq. (S13) is within a small region around $\ell_u = \ell_b$, allowing us to expand $P_{eq}(\ell_u)$ around $\ell_b$:

$$P_b(\ell_b) \approx \int_{\ell_b-d/2}^{\ell_b+d/2} \left[ 1 + (\ell_u - \ell_b)P_{eq}'(\ell_b) + \frac{(\ell_u - \ell_b)^2}{2} P_{eq}''(\ell_b) \right] d\ell_u = P_{eq}(\ell_b) \left[ 1 + \frac{d^2}{24} \left( \frac{U_e''(\ell_b)}{(k_BT)^2} - \frac{U_e''(\ell_b)}{k_BT} \right) \right].$$

(S18)
where we have used \( P_{\text{eq}}(\ell_u) = \exp(-U_e(\ell_u)/k_BT)/Z \) and \( Z = \int \exp(-U_e/k_BT) d\ell_u \). As expected, Eq. (S18) shows that the equilibrium distribution is slightly perturbed by \( d \), where the difference scales with \( d^2 \). The resulting steady-state distribution, \( P_{\text{on}}(\ell) \) (Eq. (S4)), is also perturbed around the equilibrium distribution, and the deviation scales with \( d^2 \). Thus, we have \( \langle F_s \rangle_\ell \sim d^2 \), and both the contractile velocity for viscous substrates and the contractile force for elastic substrates show quadratic dependences on \( d \). To show this explicitly, let us consider a nearly rigid substrate, i.e., \( \gamma \omega_{\text{off}} \rightarrow \infty \) or \( K_s \rightarrow \infty \). In this case the polymer is not relaxing when in the bound state, and produces an average contractile force (on the substrate) of

\[
\langle F_s \rangle_\ell = \frac{d^2}{24} \int \! d\ell_b P_{\text{eq}}(\ell_b) U_e''(\ell_b). \tag{S19}
\]

This force is positive for any potential with a positive \( U_e''(\ell) \).

Note that the above result is obtained for constant on/off rates. In case that the on/off rates obey detailed balance (see Eq. (S1)) \( P_{\text{on}} \) would remain the equilibrium distribution even for finite \( d \) and \( \langle F_s \rangle_\ell \) would vanish.

II. MICROSCOPIC MODEL

A. 4D Fokker-Planck equation

The microscopic model considered in the main text describes the motion of the two polymer ends \((x_A, x_B)\) and the corresponding two binding sites on the substrate \((y_A, y_B)\) after a binding event. The probability distribution of the positions of these four coordinates, \( P(x_A, x_B, y_A, y_B; t) \), can be described using a standard four-variable Fokker-Planck equation [5]:

\[
\begin{align*}
\partial_t P(x_A, x_B, y_A, y_B; t) + \nabla \cdot J(x_A, x_B, y_A, y_B; t) &= -\omega_{\text{off}} (x_B - y_B) P, \\
\frac{\partial P(x_A, x_B, y_A, y_B; t = 0)}{\partial t} &= \frac{\chi(x_A, x_B, y_A, y_B)}{Z} \exp[-U_e(x_B - x_A) - U_b(x_A - y_A)],
\end{align*}
\]

where \( J_\alpha = -\mu_\alpha (k_BT \partial_\alpha P + P \partial_\alpha W) \) without the summation convention. We define \( \mu_x \) and \( \mu_y \) to be the mobilities of the ends and the binding sites, thus \( \mu_x = \mu_y \) for \( \alpha = x_A, x_B \) and \( \mu_x = \mu_y \) for \( \alpha = y_A, y_B \). Here \( \chi(x_A, x_B, y_A, y_B) = \Theta(d/2 - |x_A - y_A|) \Theta(d/2 - |x_B - y_B|) \) gives the potential well boundaries (\( \Theta(x) \) is the Heaviside function), \( W(x_A, x_B, y_A, y_B) = U_e(x_B - x_A) + U_b(x_B - y_B) + U_b(x_A - y_A) \) is the total energy in the binding state, and \( Z \) is the normalization factor. The initial condition is chosen to be the equilibrium distribution in the unbound state. We further choose the binding potential to be a periodic triangular potential with depth \( \Delta E \) and period \( d \), i.e., \( U_b(x) = \frac{2 \Delta E}{d} |x - nd| \) for \( d(2n - 1)/2 \leq x \leq d(2n + 1)/2 \).

In order to find the contractile velocity, one needs to calculate the average distance between two binding sites in the bound state,

\[
\langle y_B - y_A \rangle_{\text{bound}} = \omega_{\text{off}} \int_0^\infty \! dt \langle y_B - y_A \rangle P(x_A, x_B, y_A, y_B; t). \tag{S21}
\]

The average distance in the unbound state is \( \langle y_B - y_A \rangle_{\text{unbound}} = \ell_0 \). This can be understood as follows. The binding site \( S_B \) is sampled uniformly around \( B \), hence, \( \langle y_B - x_B \rangle_{\text{unbound}} = 0 \). Because the potential is symmetric we also have \( \langle y_A - x_A \rangle_{\text{unbound}} = 0 \), and since the polymer is relaxed in the unbound state with rest length \( \ell_0 \), \( \langle x_B - x_A \rangle_{\text{unbound}} = \ell_0 \). Then, \( \Delta y = \langle y_B - y_A \rangle_{\text{bound}} - \langle y_B - y_A \rangle_{\text{unbound}} \) and \( v = \Delta y/T \) are readily found (here \( T = \omega_{\text{on}}^{-1} + \omega_{\text{off}}^{-1} \) as explained in the main text).

B. Reducing to minimal model

In the limit where \( \Delta E/d \gg |dU_e(x_B - x_A)|d(x_B - x_A) \), the binding potential is very steep and it generates a large dragging force with amplitude \( 2\Delta E/d \) (unless the polymer end is in the center of the potential well). Thus, the polymer end \( B \) is dragged to the center of \( S_B \) in a short time denoted as \( \sigma \). For \( 0 < t < \sigma \), we can deterministically estimate the motion of \( B \) after it binds to the substrate:

\[
\begin{align*}
\frac{dx_B}{dt} &= \frac{2 \mu_x \Delta E}{d} \text{sign}(y_B - x_B), \\
\frac{dy_B}{dt} &= -\frac{2 \mu_y \Delta E}{d} \text{sign}(y_B - x_B). \tag{S22}
\end{align*}
\]
From Eq. (S22) we have \[ \frac{[x_B(t = \sigma) - x_B(t = 0)]}{\mu_x} = -\frac{[y_B(t = \sigma) - y_B(t = 0)]}{\mu_y}. \] Since \( x_B(t = \sigma) = y_B(t = \sigma) \), we can write,

\[
x_B(t = \sigma) - x_B(t = 0) = \frac{\mu_x}{\mu_x + \mu_y} \left[ y_B(t = 0) - x_B(t = 0) \right].
\] (S23)

Finally, because \( y_B(t = 0) - x_B(t = 0) \) has a uniform distribution of width \( d \), the polymer length distribution at \( t = \sigma \) is the same as \( P_b \) of Eq. (4) of the main text but with spacing \( d \to \mu_x d/(\mu_x + \mu_y) \).

### C. Variable Elimination: 4D Equation to 1D Equation

As explained in the main text, we treat \( x_A \) and \( x_B \) as fast variable because the polymer ends mobility is much larger than that of the substrate, \( \mu_x \gg \mu_y \). This allows us to write [6]

\[
P(x_A, x_B, y_A, y_B; t) = \frac{\exp[-W(x_A, x_B, y_A, y_B)/k_B T]}{Z_Y(y_A, y_B)} P_Y(y_A, y_B; t).
\] (S24)

where \( Z_Y = \int d x_A d x_B \chi e^{-W/k_B T} \). Because \( \omega_{\text{off}} \) is constant we can rewrite Eq. (20) in a simple form:

\[
\partial_t P_Y(y_A, y_B; t) + \nabla \cdot J^Y(y_A, y_B; t) = -\omega_{\text{off}} P_Y(y_A, y_B; t),
\] (S25)

\[
P_Y(y_A, y_B; t = 0) = \int d x_A d x_B P(x_A, x_B, y_A, y_B; t = 0),
\]

where \( J^Y_\alpha(y_A, y_B; t) = -\mu_\alpha [P_Y(y_A, y_B; t) W^*(y_A, y_B) + k_B T \partial_\alpha P_Y(y_A, y_B; t)] \) \((\alpha = y_A, y_B \) without the summation convention). This is a 2D Fokker Planck equation with an effective 2D potential

\[
W^*(y_A, y_B) = \int d x_A d x_B \frac{\chi(x_A, x_B, y_A, y_B) e^{-W/k_B T}}{Z_Y(y_A, y_B)} W(x_A, x_B, y_A, y_B).
\] (S26)

Since the system is symmetric under translations, \( W^*(y_A, y_B) \) can only be a function of \( y_B - y_A \). Then, we perform substitution of variables, \( u = y_B - y_A, \ r = y_B + y_A, \) and as \( W^* \) only depends on \( u \), these two variables are decoupled. We find that \( r \) follows simple diffusion dynamics, while \( u \) can be described by a 1D Fokker-Planck equation with distribution \( P_U \):

\[
\partial_t P_U(u; t) + \partial_u J_U(y_A, y_B; t) = -\omega_{\text{off}} P_U(u; t),
\] (S27)

\[
P_U(u; t = 0) = \int dy_A P_Y(y_A, y_B = y_A + u; t = 0),
\]

where \( J_U = -2\mu_y [P_U W^*(u) + k_B T \partial_u P_U] \). The average length in the bound state, Eq. (21), is also modified:

\[
\langle y_B - y_A \rangle_{\text{bound}} = \omega_{\text{off}} \int_0^\infty dt \ u P_U(u; t).
\] (S28)