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Persistent worms are better at navigating in complex media

Locomotion of Active Polymerlike Worms in Porous Media
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Recommended with a Commentary by Emanuele Locatelli, Department of Physics and Astronomy, University of Padova and INFN, Padova Division

Motile organisms often live in complex environments, characterized by the presence of spatial confinement, disorder and heterogeneity. From the perspective of these organisms, the ability to explore their surroundings is strictly tied to their survival, to escape a predator or to maintain a favourable balance between energy consumption and available resources. However, from the physicist's perspective, their challenges bring about other fundamental questions: how is this strategy tied to their locomotion pattern? and how do their shape and structure enter into the equation?

In their work, Sinaasappel, Fazelzadeh *et al.* looked at the locomotion of living worms in a model porous environment, investigating the difference between ordered and disordered arrays of pores. Worms are macroscopic organisms (of length $L_c \approx 10 - 30$mm), often found in complex environments, such as soil and mud[1]. They move primarily by contracting their segments: this allows them to swim or to propel by crawling onto a surface. They often display fascinating properties, such as the ability to adapt to changes (in temperature, chemical, physical composition, etc.) in their surroundings[2].

From a physicist's perspective, worms are out-of-equilibrium active systems, characterized by their elongated nature. This potentially allows them to significantly change their shape, organising their body to better fit the environment. However, as for all filaments, this critically depends on their rigidity, that is, the resistance of a their body to bending: filaments of different rigidity attain different typical conformations. Worms are definitely flexible, as they are usually characterized by a persistence length l_p* between 10 and 30% of their length ($0.1 < l_p/L_c < 0.26$). The work of Sinaasappel, Fazelzadeh et al. brings together the active and filamentous nature of the worm in a minimal framework, yielding an impressive comparison between model and experiments and insight into the physics of the

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*This is better understood as an *effective* persistence, as will be discussed later.

locomotion of active filaments.

The authors experimentally realized a minimal, controllable version of a porous medium using ordered or disordered arrangements of plastic pillars and compared the long-time mobility of the worms, which quantifies their ability to navigate in the medium, in the two cases. In the ordered case, the worms' mobility decreases with increasing pillar density (that is, in a more complex medium); conversely, it increases in the disordered case. Further, worm activity can be varied through the temperature of the environment[2, 3]: with varying activity, surprisingly, worms with lower activity (at $T = 5°$ C) exhibit an enhanced long-term mobility than those with higher activity (at $T = 30°$C); in free space, the trend would be the opposite.

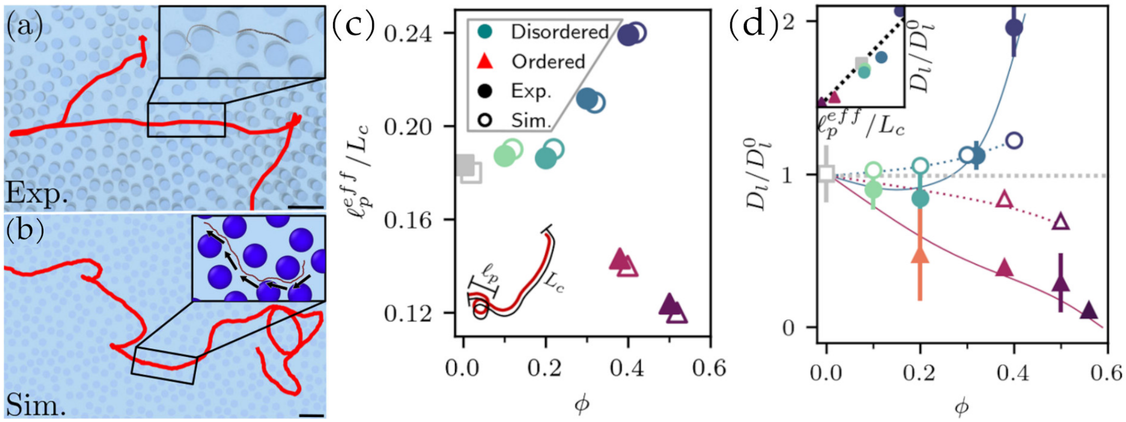

Figure 1: (a), (b): Trajectories of the center of mass of a worm (a) and simulations (b) in randomly distributed 2D pillar array with surface fraction $\phi = 0.4$. Insets: zooming in highlights distinct worm conformations. (c) Effective persistence length l_p^{eff}/L_c as a function of ϕ in experiments and simulations. (d) Normalized long- time diffusion coefficient $D_l/D_{0,l}$ as a function of ϕ. Inset shows the linear relationship between D_l and l_p^{eff}/L_c. Reproduced with permission from the recommended paper.

To rationalise these findings, experiments are compared with a bead-spring model of tangentially active polymers: tangential self-propulsion, characterised by a force f^a per monomer, is a minimal representation of the segmental contractions that propel real worms. The polymer model is Gaussian and two-dimensional, to mimic the crawling motion on the surface, and is completed with the introduction of a bending stiffness κ, which models the inherent rigidity of the worm body.

A crucial point concerns the match of experiments and model. The authors estimate of the two parameters f^a and κ by matching conformations and dynamics across the two systems. Extracting the coordinates of the worm's body from video recordings, one can measure the effective persistence length l_p^{eff} and use it to set the bending κ in simulations. It is worth noting that this is not the "standard" persistence length, which is tied to the filament mechanics; tangential forces also tend to align neighbouring beads and, as such, tuning the bending rigidity is not trivial. Estimating the active force is also difficult, without dedicated experiments: however, because both the long time diffusion coefficient $D_{a,0}$ and the relaxation time of the end-to-end vector $\tau_{e,0}$ in free space scale linearly with f^a, rescaling the time through $\tau_{e,0}$ eliminates the explicit dependence on the active force. This is a very important observation, that makes the precise value of f^a less critical and, globally, facilitates the modelisation of these systems.

The comparison between model and experiment allows the authors to pinpoint the importance of the filament rigidity in these complex environments. While stiff self-propelled filaments can only move through porous media with a motion that resembles reptation[4], a flexible active polymer can bundle up inside pores, leading to a hopping-trapping scenario. As already said, worms are definitely floppy. In the presence of disorder, they can reptate along curvilinear tubes formed by randomly positioned pillars, intermittently trapping before switching paths, as in Fig. 1(a),(b); this also yields an increase of l_p^{eff}, shown in Fig. 1(c). In contrast, a "tube" can not be formed in an ordered pillar arrangement: worms will tend to fit the cavities, due their flexible nature, lingering in pores and occasionally hopping between them.

The results can be further rationalized using the theory of active polymers: theory suggests looking at the orientational time scale τ_e and the persistence length because, for active polymers, $D_l \propto \tau_e \langle R_e^2 \rangle$, with D_l the long time diffusion coefficient and R_e the end-to-end distance[5]. While τ_e depends weakly on the obstacle surface fraction, l_p^{eff} increases in the presence of disorder: since for flexible filaments $\langle R_e^2 \rangle = 2 l_p L_c$, one gets $D_l \propto l_p$, which explains the observed trends (see Fig. 1(d)).

Changing the activity via environmental temperature adds a final layer of complexity. Temperature changes not only the activity (that is, the value of f^a) but also the rigidity of the filament: lowering T increases spreading in disordered media by increasing persistence length. The previous argument stands, as worms more than compensate for the loss of activity with increased stiffness, from $l_p^{eff}/L_c = 0.12$ to $l_p^{eff}/L_c = 0.6$. However, worms are definitely complex organisms and the authors highlight the limits of this modeling at high temperature, where the model fails to capture the dynamics of the worm, suggesting the need for further development.

To summarize, the work highlights the fact that, in living worms, there is a subtle interplay between the locomotion and the mechanical properties of the filament. Given the increasing interest in the physics of active filaments at all scales, I personally think this work will stand as a reference for future investigations.

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