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Decentralized neural dynamics and sensory constraints shape brittle star locomotion

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Brittle stars move with remarkable whole-body coordination despite lacking a central brain. With five identical arms radiating from a central disc, they predominantly adopt a bilaterally symmetrical *rowing* gait: one arm leads, two neighbouring arms row in synchrony and the remaining arms trail. This raises a puzzle: how does a brainless nervous system generate coherent whole-body gaits, and why does it favour rowing? To address this, this work introduces an *in silico* framework combining (i) a three-dimensional model of brittle star morphology in a physics simulator, (ii) an artificial neural network (ANN) architecture that mirrors the decentralized arm-level ganglia, which interconnect through the nerve ring and (iii) reinforcement learning (RL) to optimize controllers for locomotion. Analysis of optimized controllers shows that ganglia behave as distributed oscillators whose coupling via the nerve ring yields synchronization, analogous to that of central pattern generators (CPGs). Gait analysis reveals that rowing emerges as the strategy most compatible with the arms' dual role as effectors and sensors. Taken together, these results provide a mechanistic view of how decentralized neural dynamics and sensory constraints shape brittle star locomotion. The presented framework offers an open-ended test bed for hypotheses inaccessible *in vivo*, and more broadly, for exploring decentralized control in embodied agents. We provide a link to our project web page and interactive results dashboard: <https://airo.ugent.be/projects/brittle-star>.

1. Introduction

Brittle stars (Ophiuroidea) are echinoderms with typically five arms that radiate from a circular body. Each arm is composed of serial ossicles ('arm vertebrae') actuated by intrinsic muscles [1]. Unlike sea stars (Asteroidea), which rely on tube feet, brittle stars achieve locomotion through coordinated arm strokes that give rise to two principal gaits. In the predominant *rowing* gait, one arm leads and points forward, its two neighbours row in synchrony to generate thrust and the remaining two arms trail passively (figure 1A). In *reverse rowing*, which is less commonly observed, a trailing central arm points backward while the four others row in unison [2,3]. Despite their radial body plan, brittle stars thus express *bilaterally symmetrical* gaits. They are among the fastest-moving echinoderms and reorient their movement direction rapidly by switching arm roles rather than rotating the disc [2]. This ability to flexibly reassign roles simultaneously confers remarkable damage robustness, allowing effective locomotion to persist even after the loss of one or more arms [4].

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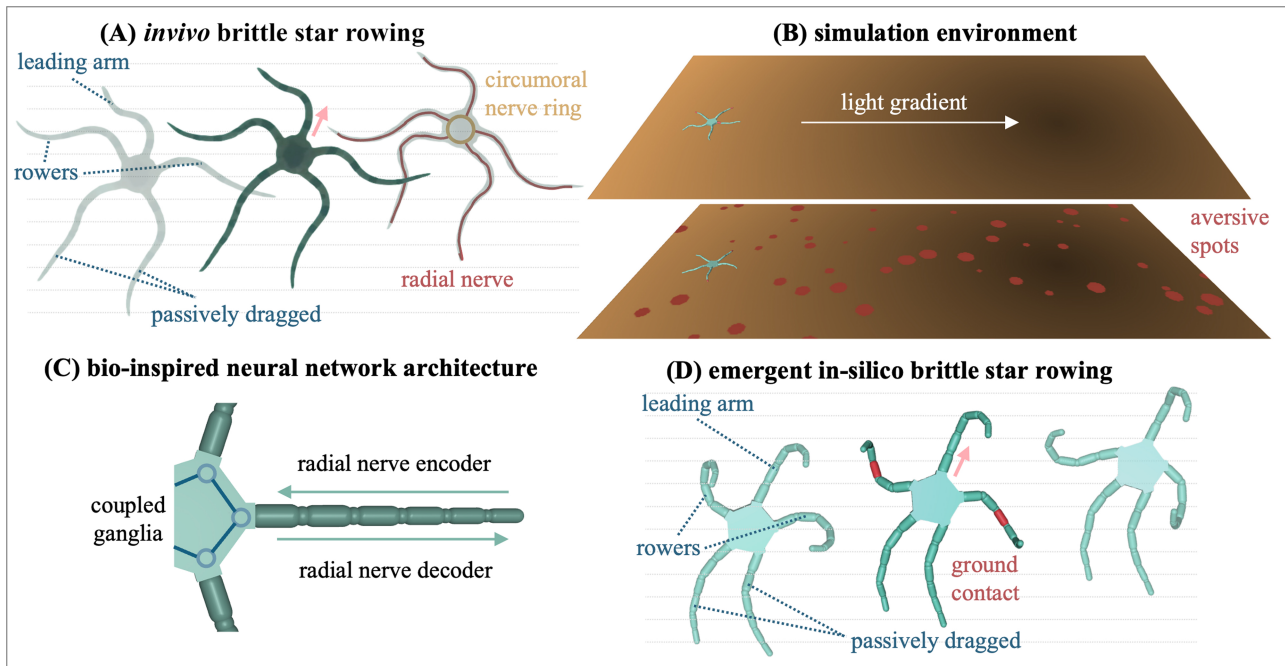


Figure 1. Overview of brittle star locomotion and modelling framework. (A) Biological organization: snapshots of *in vivo* brittle star rowing (*Ophiopsis superba*), with movement direction and arm roles annotated: a leading arm aligned with movement direction, two synchronous rowers and passively dragged arms. Each arm is innervated by a radial nerve and basal ganglion connected through the circumoral nerve ring. (B) Simulation environment: a parametrized morphology with distributed sensing and actuation is embedded in an aquarium-like arena featuring a light-escape task and optional aversive spots to evade. (C) Bio-inspired decentralized controller: each arm is governed by an identical recurrent neural network, coupled through neighbour-to-neighbour communication around the nerve ring. The network is optimized with reinforcement learning (RL) to reduce light intake, minimize energy use and avoid aversive spots when present. (D) Emergent rowing gait: optimization yields bio-realistic kinematics with natural role division.

Remarkably, this complex coordination arises without a central brain [5]. Instead, brittle stars possess a circumoral nerve ring that interconnects regional ganglia (i.e. neuronal clusters) at the bases of the arms, from which radial nerve cords innervate each limb (figure 1A) [6,7]. Information flow along the ring is bidirectional [8] and direct connections are confined to neighbouring ganglia [9].

This organization raises a fundamental open question: how can a nervous system without a central brain generate coherent, whole-body gaits? Experimental studies have shown that local ganglia are indispensable for intra-arm coordination, as arms deprived of their basal ganglion fail to generate rhythmic motion [6,10]. Moreover, the connections between these ganglia are essential for inter-arm coordination, as locomotor synchrony weakens when the nerve ring is disrupted [8]. Together, these findings point to a distributed control architecture [2], yet the neural principles by which decentralized ganglia generate rhythmic motion and synchronize into a global periodicity remain unresolved. In other animals, rhythmic locomotion often emerges from central pattern generators (CPGs)—neural circuits that produce sustained oscillations even in the absence of rhythmic input [11–14]. While no direct evidence for CPGs has been shown in brittle stars, their coordinated, brainless locomotion suggests an analogous principle: local ganglia may function as distributed oscillatory units whose coupling through the nerve ring yields coherent, whole-body gaits.

Beyond the question of how coordination arises, an equally unresolved question is why it converges on rowing as the predominant gait. A possible explanation lies in the fact that the same arms used for propulsion also function as the primary sensory organs. The brittle star's main sensory modalities are distributed throughout the arms: proprioceptors in the hyponeural system report posture and loading, while mechanoreceptors, photoreceptors and chemosensory cells detect touch, light and dissolved chemical cues [7,15,16]. The need to simultaneously move and sense with the same appendages constrains viable locomotor strategies: arms must maintain a reliable perception of the surroundings while generating movement. In rowing, the leading arm plays a distinctive role by orienting forward and seemingly probing the environment, effectively guiding locomotion while the adjacent arms generate thrust. Notably, these rowing arms also reach forward before the power stroke, suggesting that they may contribute to environmental sensing in addition to propulsion. Rowing may therefore represent a stable compromise between sensory engagement and locomotor efficiency, possibly at the cost of raw energetic efficiency. This interpretation resonates with embodied cognition theory [17,18], which emphasizes that behaviour arises from the continuous interplay between the body's sensorimotor system and its environment. In other words, the body shapes the behaviour.

Addressing either of these questions *in vivo* is inherently challenging. The circumoral nerve ring is protected by ossicles, limiting experimental access to the neural dynamics needed to reveal how distributed oscillatory activity arises and synchronizes. Moreover, gait selection cannot be tested under controlled and repeatable sensory conditions. This makes it unfeasible to directly compare locomotion in environments that provide reliable sensory information with those that require more active probing and

cautious exploration. Taken together, these constraints prevent a clear *in vivo* disentanglement of both the neural mechanisms underlying gait emergence and the role of *sensory dependency*¹ in gait selection. Following recent work that leverages robotic and computational models to study animal behaviour [19–22], we therefore turn to *in silico* physics-based models as a tractable means to bridge these gaps.

Previous mathematical and robotic models of brittle star locomotion have already provided important insights into how coordinated movement can arise in a radially symmetric, brainless system. These studies (i) demonstrated how decentralized coordination rules, modulated by ground reaction forces, can reproduce characteristic gaits [4,10], (ii) explained role assignment among arms [23–25] and (iii) accounted for the remarkable resilience of locomotion under arm loss or neural lesions [4,24]. However, across these approaches, coordination rules, gait kinematics and movement-direction decision mechanisms are specified *a priori*. As a result, ganglion activity is not modelled as an adaptive dynamical process shaped by sensory–motor interaction, but is instead fixed by hand-crafted rules or abstract analogical models. Moreover, although sensory signals have been used to influence coordination within these frameworks, gait kinematics cannot be freely shaped in response to systematically varied sensory conditions. While these models are well suited to reproducing observed behaviours, they are therefore neither appropriate for testing our hypotheses concerning the internal dynamics of ganglion activity nor for explaining how gaits are shaped by sensory dependency.

To address this gap, we developed an integrative *in silico* framework (figure 1) combining (i) a parametrized three-dimensional model of the brittle star morphology in a physics simulator, (ii) a decentralized artificial neural network (ANN) architecture that couples sensing and actuation in a manner faithful to nerve-ring and radial-nerve connectivity and (iii) reinforcement learning (RL) to optimize controllers for locomotion in an ecologically relevant context. In essence, this framework provides a computational test bed in which controllers can be optimized under systematically varied environmental conditions. The optimized controller networks can then be analysed to uncover the neural dynamics underlying the emergent gaits, while the gaits themselves reveal how environmental conditions shape locomotion. Crucially, no gait-specific constraints or reward terms are introduced during optimization, ensuring that the resulting neural dynamics and gaits emerge naturally from the interaction between the biologically grounded morphology, controller and environment. This constitutes a methodological departure from earlier approaches, which were explicitly designed coordination rules to reproduce observed kinematics.

To test the hypothesis that the dual role of arms as effectors and sensors biases locomotion towards rowing, controllers are optimized under two scenarios differing in sensory demands (figure 1B). In the first, the controller escapes a radial light gradient while minimizing energy expenditure, mimicking the animal's natural tendency to move towards darker regions [6,26]. The second extends this task with randomly placed aversive spots that must be detected and avoided, placing greater emphasis on each arm's role as a sensory appendage. Comparing the gaits that emerge across these two conditions directly reveals how sensory dependency constrains viable locomotor strategies.

Using this framework, we show that bio-realistic rowing gaits can emerge spontaneously, without imposing gait-specific rules. Analysis of the underlying neural dynamics reveals that ganglia develop self-sustaining local oscillations, and that global coordination arises through synchronization across the nerve ring. This supports the view that brittle star locomotion is underpinned by decentralized oscillator networks, operating similarly to the CPGs observed in other animals. Moreover, the comparison between gaits optimized under the two distinct environmental conditions shows that when sensory demands are heightened, the resulting gaits become more structured, stable and more often resemble the characteristics of natural rowing. This substantiates the hypothesis that rowing is the strategy most compatible with the arms' dual role as effectors and sensors. Together, our findings shed light on how decentralized neural dynamics and sensory constraints shape brittle star locomotion. Beyond the present findings, the framework serves as an open-ended test bed for hypotheses inaccessible *in vivo* and, more broadly, for exploring decentralized control in embodied agents.

2. Methods

2.1. *In silico* brittle star model and environment

We implemented the model in the Multi-Joint dynamics with Contact (MuJoCo) physics simulator [27], which efficiently models articulated, contact-rich systems and is increasingly used in biomechanics [22,28–30]. This makes it particularly suitable for brittle stars, whose locomotion emerges from repeated arm–substrate interactions mediated by flexible, multi-joint appendages.

2.1.1. Morphology

We model the brittle star as a central disc from which five articulated arms extend as chains of serial segments (figure 1D). The disc has a pentagonal shape, while the arm segments are represented as capsules that taper progressively from proximal to distal. Each segment possesses two primary degrees of freedom—one in-plane and one out-of-plane—allowing lateral and vertical bending consistent with observed brittle star kinematics. The model is fully parametrized (disc size, number of arms, number and sizes of segments and joint properties), but for the experiments presented here, we fix the morphology to five arms with six segments each. This configuration yields a total of 60 controllable degrees of freedom. Densities of structural elements are set based on biological

¹We define *sensory dependency* as the reliance on acquiring and processing sensory input in order to generate appropriate behaviour.

Table 1. Key morphological and controller parameters. Morphological values are reported per arm, with totals across all five arms in parentheses. ANN dimensions refer to the hidden size of each module; full architectural details are provided in the supplementary material.

parameter	value
morphology: values per arm (total)	
num. segments	6 (30)
num. actuated degrees of freedom	12 (60)
num. sensors	9 (270)
ANN dimensions	
segment sensory embedder	64×32
radial nerve encoder	128
ganglion neighbour state embedder	128
ganglion	256
radial nerve decoder	128
total ANN parameter count	626 354

measurements, resulting in arms that are more dense than the central disc, consistent with reports that arm skeletons are heavier than the body core [31]. Each joint is actuated by a torque motor whose strength scales with the radius of the corresponding segment, approximating the assumption that larger segments support stronger muscles.

The model integrates a suite of proprioceptive and exteroceptive sensors. Proprioception includes joint positions, joint velocities and actuator torques, providing information about posture and effort. Exteroception includes contact forces with the substrate, light-intensity input from the arena light gradient and aversive-spot contacts when present. All sensory observations are provided at the level of individual segments, thereby mimicking the distributed sensing of real brittle stars. This segment-level design ensures that no global sensory state is imposed; instead, it emerges from the aggregation of locally available information. A summary of key morphological parameters is listed in table 1.

Several abstractions ensure computational tractability while preserving the essential mechanical properties needed for realistic locomotion. We do not model individual ossicles, plates or spines, but instead represent the arm as a continuous tapered chain of capsules. The number of skeletal elements is reduced relative to the situation in real brittle stars, and arm flexibility is configured in an ad hoc but biologically representative manner. Self-collision between arms is disabled to simplify contact dynamics, and muscles are represented by torque actuators rather than explicit contractile elements.

Arm length is shorter than *in vivo*: in our model, the ratio of arm length to disc diameter is approximately 1.7, whereas in *Ophirolepis superba*—the species typically used as a reference in locomotion studies—arms are reported to be 2–4 times the disc diameter. Nevertheless, behavioural studies by Kano *et al.* [4] showed that trimmed arms behave similarly to intact ones during locomotion, indicating that the reduced relative arm length used here remains biologically representative. Increasing arm length would extend the spatial range over which each arm samples the environment, effectively enlarging the perceptual field available to the model. This perceptual field, however, remains determined by how the arms move. The fundamental coupling between sensing and propulsion therefore persists irrespective of absolute arm length. Consequently, although longer arms with greater sensory range may shift the threshold at which environmental differences translate into distinct gaits, they are unlikely to qualitatively alter our conclusions. The fundamental gait patterns that emerge with the current set-up would probably persist, though specific kinematics, such as arm curvature and stroke shape, may differ, consistent with kinematic variation observed across species with different arm lengths [3].

2.1.2. Bio-inspired environment and light-escape task

The brittle star is placed in a simplified aquarium environment consisting of a flat ground plane. To approximate the effect of water, we employ MuJoCo's inertial fluid model, which applies drag forces proportional to body velocity relative to the medium, along with an added-mass term accounting for displaced fluid inertia. While this approximation neglects complex flow interactions, it captures the dominant resistive forces relevant at the scale of brittle star movement.

To drive this behaviour, a radial light gradient is projected on to the arena floor, which converges towards a dark region positioned opposite to the animal's initial location (figure 1B). The controller's task is to move towards this dark region, mimicking the natural light-avoidance response observed in brittle stars. Crucially, the gradient is not provided as a global signal: the model must infer the direction of decreasing illumination solely from the distributed light-intake values sensed by its arm segments.

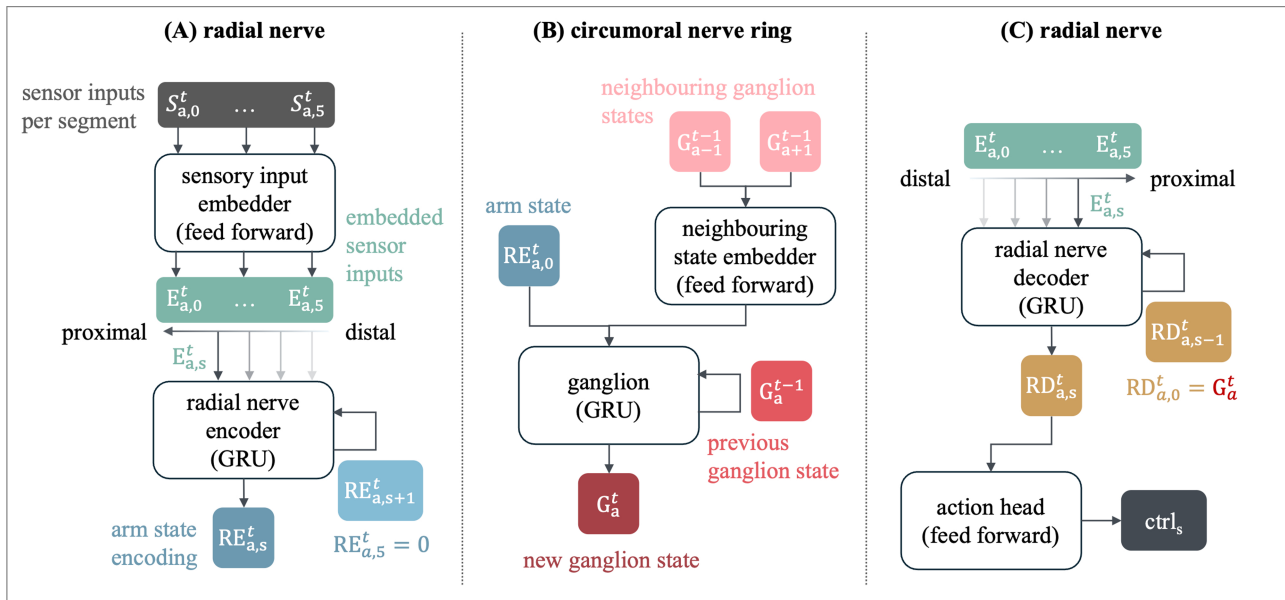


Figure 2. Schematic overview of the bio-inspired neural architecture. Each arm is controlled by an identical recurrent neural network that mirrors the organization of the brittle star nervous system. Indices denote time (t), arm (a) and segment (s). (A) Sensory inputs from all arm segments are embedded and sequentially integrated by a radial nerve encoder gated recurrent unit (GRU) scanning from tip to base, producing a compact arm-state representation. (B) The arm's ganglion (GRU) combines the arm-state encoding, its own state and the embedded states of the two neighbouring ganglia to compute an updated ganglion state. This interaction reflects the inter-arm coupling through the circumoral nerve ring. (C) The updated ganglion state initializes a radial nerve decoder that sequentially scans from base to tip to generate control commands for each arm segment's actuators.

To manipulate sensory challenge, a configurable number of aversive spots are projected on to the arena (figure 1B). These spots are randomly repositioned and resized at each environment instantiation, with the constraint that none overlap the animal's starting location. The brittle star perceives an aversive spot only when one of its arm segments overlaps with it, at which point the corresponding aversive-spot sensor activates. This set-up requires the controller to integrate multiple sensory streams—light avoidance and aversive avoidance—to achieve successful locomotion.

Here again, several abstractions ensure computational efficiency. The ground plane is modelled as a rigid frictional surface without obstacles, avoiding costly collision checks. Sand-like mechanics are not included, and advanced fluid phenomena such as turbulence, vortices and currents are omitted, leaving only the inertial drag approximation. These design choices accelerate simulation while preserving the essential environmental constraints needed to study sensory-driven locomotion.

2.1.3. Bio-inspired decentralized artificial neural network controller

We design a decentralized ANN controller that mirrors the organization of the brittle star nervous system. Each arm is governed by an identical copy of the same network, ensuring parameter sharing across arms while preserving decentralization. Communication between arms occurs exclusively through their connections in the circumoral nerve ring, which constrains information flow to biologically realistic pathways. Figure 2 provides a schematic overview of the architecture and inference flow. Within a single control cycle, the inference process that maps sensory inputs to motor commands proceeds in three sequential stages: (i) segment-level sensory signals are embedded and spatially integrated along the arm by the radial nerve encoder, (ii) temporal integration and inter-arm communication occur at the ganglion level through the nerve ring and (iii) motor commands are generated by the radial nerve decoder. Below, we go over each stage in more detail.

At the beginning of a control cycle, sensory signals from all arm segments are independently transformed into compact feature representations ('embeddings') that summarize the local sensory state. This transformation is performed by a small multilayer perceptron (MLP). An MLP is a simple feed-forward neural network that maps inputs to outputs through successive layers of nonlinear processing. In essence, the MLP acts as a local processing unit, distilling raw sensory signals into concise numerical descriptors that are easier to integrate downstream. These embedded segment representations are then processed by a *radial nerve encoder*, implemented as a gated recurrent unit (GRU). Whereas the MLP captures instantaneous, local relationships, the GRU is an extended neural circuit that can store and update information across a sequence of inputs. Here, it scans spatially along the arm—from the distal tip towards the base—integrating information from each segment in sequence. This makes it analogous to a biological pathway that progressively combines sensory signals along the arm. The result is a compact representation of the arm's overall state at its base.

This arm-level state is then passed to the *circumoral ganglion*, modelled as a second GRU. Unlike the GRU in the radial nerve—which integrates sensory information spatially along an arm—this recurrent unit operates over time. At each time step, each ganglion receives its own arm's state along with the embedded internal states of its two neighbouring ganglia. This mimics the

bidirectional information flow around the nerve ring. The GRU's internal state functions as a form of short-term memory: a continuously updated signal that compresses the recent history of inputs into a low-dimensional representation. Through this recurrent process, each ganglion gradually aggregates information from its own arm and its neighbours across time. This enables the system to build a temporally integrated, whole-body representation that supports coordinated motion. Importantly, these internal ganglion states can be recorded and analysed over time, providing direct access to the network's underlying neural dynamics and offering insights into how coordinated gaits emerge.

Finally, the updated ganglion state initializes the *radial nerve decoder*, a third GRU that propagates information back down the arm. At each segment, this spatial decoder combines its internal state with the local sensory embedding to generate torque commands for the actuators. Together, these modules create a bidirectional hierarchy—from segment-level sensing to arm-level integration to whole-body coordination—that mirrors the flow of information in the brittle star's nervous system. Table 1 lists the chosen layer dimensions for each module. Further architectural details, including activation functions and layer initialization schemes, are provided in the supplementary material.

Several architectural choices explicitly reflect biological observations. Cobb & Stubbs [9] report that axons in the circumoral nerve ring do not extend beyond adjacent radial nerves, implying that ganglia exchange information only with immediate neighbours. Moreover, coordinated locomotion persists even after the ring is cut once [8], suggesting that these connections must be bidirectional. We therefore restrict message passing to adjacent, bidirectional communication. In principle, multiple message-passing iterations could be performed within the nerve ring during one control cycle. However, neurophysiological measurements indicate nerve conduction velocities of approximately 38–139 cm s⁻¹ [32]. Given a nerve ring length of 3–6 cm, a signal requires approximately 20–160 ms to complete a full loop. Since our control frequency is 50 Hz (20 ms per step), we limit the architecture to one neighbour-to-neighbour transmission per time step. Thereby, the rate of information propagation in the model matches the time scale of observed conduction delays in real brittle stars. This, however, neither implies a full neurophysiological calibration of neural conduction velocities nor necessarily reflects a quantitatively realistic ratio between local sensory processing and inter-ganglion communication. In our implementation, both processes occur within the same control step, resulting in an effective one-to-one mapping between arm-level sensory integration and inter-ganglion exchange. This simplification abstracts away potential temporal asymmetries in biological processing but enforces a conservative upper bound on information propagation. In this sense, biological plausibility is enforced at the structural level: the model constrains information flow to match the neural topology and time scales observed *in vivo*, thereby avoiding unrealistically fast global inter-arm synchronization while maintaining the decentralized layout.

Through this architecture, each arm both senses and acts locally, while global coordination can arise from recurrent, distributed message passing along the circumoral nerve ring. This decentralized design provides a biologically grounded substrate for testing how whole-body locomotion patterns, such as rowing, can emerge from local sensing and neural interactions. Conceptually, the architecture is also capable of implementing CPG-like dynamics: as a recurrent network with local feedback, it can in principle converge to oscillatory attractors. Crucially, such dynamics are not hard-coded, and their emergence depends on the optimization process and the demands of the task. This openness ensures that we do not bias the controller towards our hypothesized mechanism of CPG-like dynamics. Instead, coordination is allowed to emerge freely from the interaction of morphology, sensory constraints and decentralized neural dynamics.

2.2. Reinforcement learning

RL is used here as a general-purpose framework for optimizing control policies in our physics-based simulation environment (figure 3 provides an intuitive overview). In this setting, the controller iteratively interacts with its environment by sensing, acting and receiving scalar feedback that evaluates locomotion performance. This feedback is then used to progressively adjust the parameters of the ANN control policy. This allows effective strategies to be identified through repeated interaction rather than explicit supervision. RL is particularly well-suited to our problem, where locomotion must emerge from decentralized sensing and actuation without predefined movement patterns or hand-crafted coordination rules.

Importantly, RL is not employed as a model of biological learning in brittle stars, but as an open-ended optimization method to explore control strategies that arise under specified sensory and environmental constraints. In this respect, RL fulfills a role comparable to other black-box optimization approaches, such as evolutionary algorithms, which could be equally applied without changing the biological interpretation of the results. Specifically, we employed a recurrent implementation of proximal policy optimization algorithm (further methodological details are in the supplementary material) [33].

2.2.1. Reward design

In our set-up, the reward function combines three components as a weighted sum: (i) reduction of light intake measured at the disc, (ii) an energy expenditure penalty and (iii) a penalty when the disc enters an aversive spot. Reward term weights were empirically tuned based on the preliminary experiments in which we tested to what extent the energy penalty and aversive-spot penalty weights could be increased while still permitting movement to arise. Specifics regarding the reward term and weight calculations are available in the supplementary material.

Although sensing occurs at the arm-segment level, both the light-reduction term and the aversive-spot penalty are defined at the level of the central disc. This design choice serves two purposes. First, it encourages the decentralized neural architecture

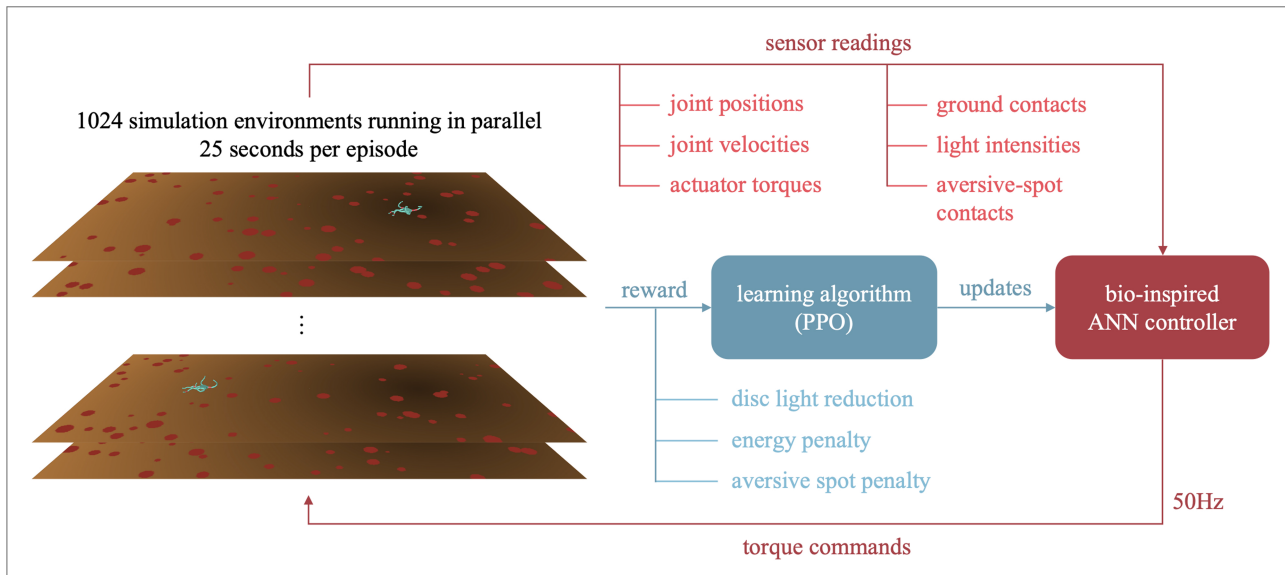


Figure 3. Overview of the RL set-up and the underlying environment-controller interactions. A total of 1024 simulation environments run in parallel, each containing a brittle star controlled by the same bio-inspired ANN. At every control step (50 Hz), the policy receives sensor readings from all environments and output torque commands to their actuators. Moreover, at every control step, a composite reward is computed based on disc light reduction (encouraging movement away from light), an energy penalty (discouraging excessive energy expenditure) and an aversive-spot penalty (discouraging contact with noxious zones). The learning algorithm (proximal policy optimization) updates the shared policy parameters using this reward, progressively improving performance. Each simulation episode lasts 25 s, after which the environments are reset—randomizing the brittle star’s initial orientation and, in scenario B, the position and size of the aversive spots. Scenario A follows the same set-up but omits aversive spots from the environment, sensor inputs and reward function.

to produce coordinated whole-body movement. Because reward is assigned based on the disc’s state rather than individual arm segments, optimization pressure shifts from ‘my arm segment should improve its local condition’ to ‘we collectively should improve the global state of the body.’ In the case of aversive spots, this means preventing the disc from entering noxious zones; in the case of light avoidance, it means coordinating propulsion to move the disc towards darker regions. In both cases, the objective promotes inter-arm coordination rather than purely local reactions. Second, applying the aversive penalty only at the disc level allows arms to sense their environment freely without becoming overly cautious.

Importantly, this reward design specifies *what* the controller should achieve—efficient light avoidance and evasion of noxious zones—but not *how* it should achieve it, thereby allowing locomotor strategies to emerge autonomously through repeated interaction with the environment. By contrast, adding reward terms that directly encode stability or bilateral symmetry could have biased the outcome towards specific gaits, such as rowing. Because our objective is to investigate how environmental and sensory constraints shape locomotion, we deliberately kept the solution space open and avoided any such prescriptive terms.

3. Results

We conducted 20 independent training runs under two environmental conditions: (A) minimal sensory dependency, in which the model experienced only a light gradient, and (B) heightened sensory dependency, in which additional aversive spots had to be avoided while escaping the light. In what follows, we first validate that our framework can produce bio-realistic rowing gaits without imposing gait-specific reward terms. We then quantify how varying sensory demands influence the resulting locomotor patterns and, finally, analyse the underlying neural dynamics that give rise to coordinated movement.

3.1. Emergence of bio-realistic rowing

As expected given the high-dimensional search space, the large number of degrees of freedom in the morphology (60 in total) and the absence of gait-specific reward shaping, the optimization landscape supports diverse locomotor solutions across individual training runs. Therefore, we first investigate whether rowing—the dominant natural gait of brittle stars—can emerge from our set-up. In the following analyses, we highlight a representative controller trained under condition B (with aversive spots), which developed stable rowing behaviour. Because it is impractical to present the full breadth of results within the paper, all trained controllers, together with their videos and analysis plots, are made accessible through an interactive online dashboard [34]. The representative rowing controller analysed below can be found under scenario B: run_0.

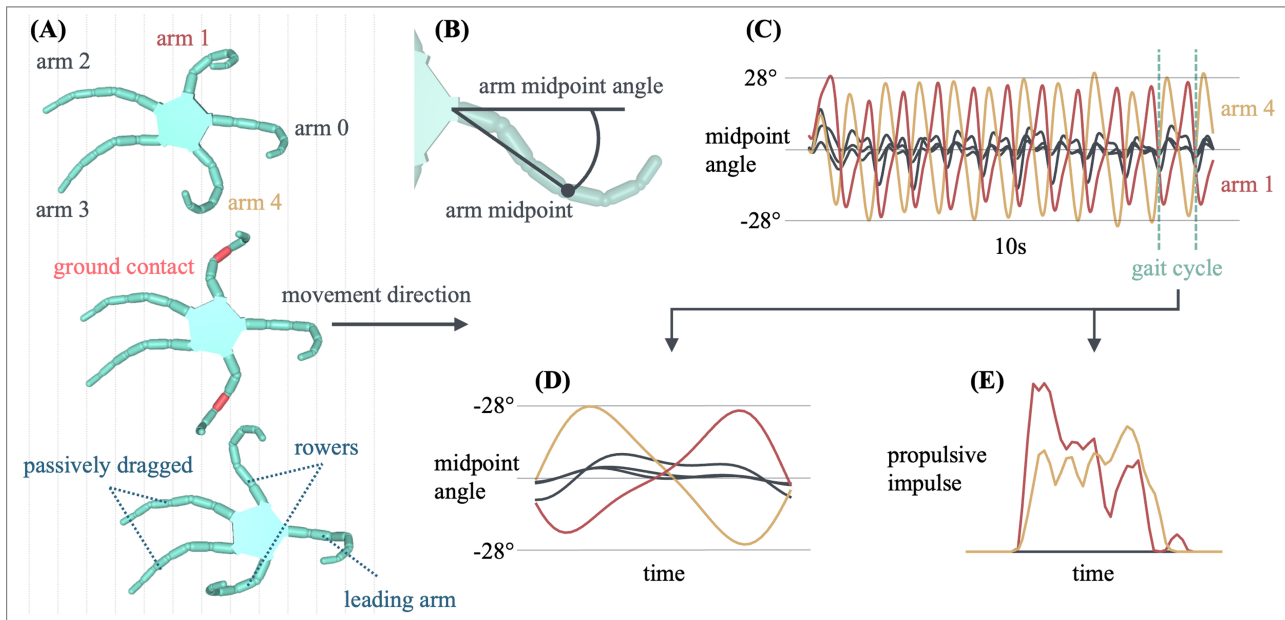


Figure 4. Emergence of bio-realistic rowing. (A) Simulation snapshots of a single gait cycle showing the characteristic role division: one arm functions as a forward-oriented leader, two adjacent arms act as synchronized rowers and the two hind arms trail passively. Red highlights indicate ground-contact segments, demonstrating that propulsion is generated primarily by mid-arm regions rather than distal tips (note that different segments contact the ground at other phases of the cycle). (B) Annotation of an arm's midpoint and the corresponding midpoint angle, defined as the deviation of the arm from its straight, radially extended configuration. (C) Time series of arm midpoint angles reveal stable, periodic oscillations consistent with a locomotor limit cycle. (D) Close-up of a single gait cycle showing that the two rowing arms move in coordinated synchrony: although they appear in anti-phase in their local reference frames owing to the opposite orientation of the arms, they move in unison in the global frame. The other arms remain close to their mean postures, exhibiting little motion. (E) Propulsive impulse traces, quantifying ground reaction forces of each arm projected on to the movement direction, confirm that the thrust is produced exclusively by the rowers and in a temporally coordinated manner. Together, these results show that the framework is capable of yielding bio-realistic rowing gaits with natural leader–rower–passive role division, inter-arm synchronization and mid-arm propulsion, closely matching empirical observations in real brittle stars.

3.1.1. Gait kinematics

To first illustrate which gait the controller intrinsically encodes, we evaluated it in an environment without aversive spots, to avoid stochasticity and simply observe its preferred mode of locomotion when following the light gradient. Figure 4 depicts the emergent rowing gait. Simulation snapshots of a single gait cycle reveal the characteristic pattern [2,23]: one arm assumes the role of *leader*, orienting in the movement direction, while its two neighbours act as synchronized *rowers* and the two hind arms are passively dragged (figure 4A). Ground-contact analysis (red-highlighted segments) shows that propulsion is generated primarily by the mid-arm segments rather than the distal tips, consistent with empirical observations in real brittle stars [6]. Time series of arm midpoint angles confirm stable, periodic oscillations, consistent with a locomotor limit cycle (figure 4B–C). A limit cycle is a closed trajectory in the system's state space that the dynamics naturally converge to, meaning the motion repeats in a stable, self-sustained rhythm. In biological terms, it corresponds to the regular cyclic patterns that underlie walking, swimming or rowing, which persist even when the system is slightly perturbed. The presence of such a limit cycle is important because it demonstrates that the gait is not a transient artefact of training but a self-sustained, dynamically stable rhythm—a defining feature of biological locomotion that enables robustness against perturbations. A close-up view of a single gait cycle further highlights that the two rowing arms oscillate in coordinated synchrony (figure 4D). When expressed in their own local reference frames, the midpoint angles appear in anti-phase, since the rowers are oriented on opposite sides of the disc. However, in the global frame of movement they move forward and backward simultaneously, such that both rowers symmetrically reach forward and pull backward at the same time. The remaining arms display only limited deviations around their mean postures, indicating passive trailing. Correspondingly, the propulsive impulse traces, which measure the ground reaction force generated by each arm projected on to the global movement direction (details in the supplementary material), show that only the rowers contribute thrust, and that they do so in a temporally coordinated manner (figure 4E).

3.1.2. Direction change through role reassignment

Beyond steady forward locomotion, the exemplar controller also displayed bio-realistic turning behaviour (figure 5). When evaluated in its original training environment with randomly placed aversive spots, the controller successfully rowed towards the darker region while avoiding noxious zones. Upon encountering the first spot on its straight path, only a minor correction was required, and the original leading arm was maintained. However, a subsequent pair of aversive spots necessitated a major change

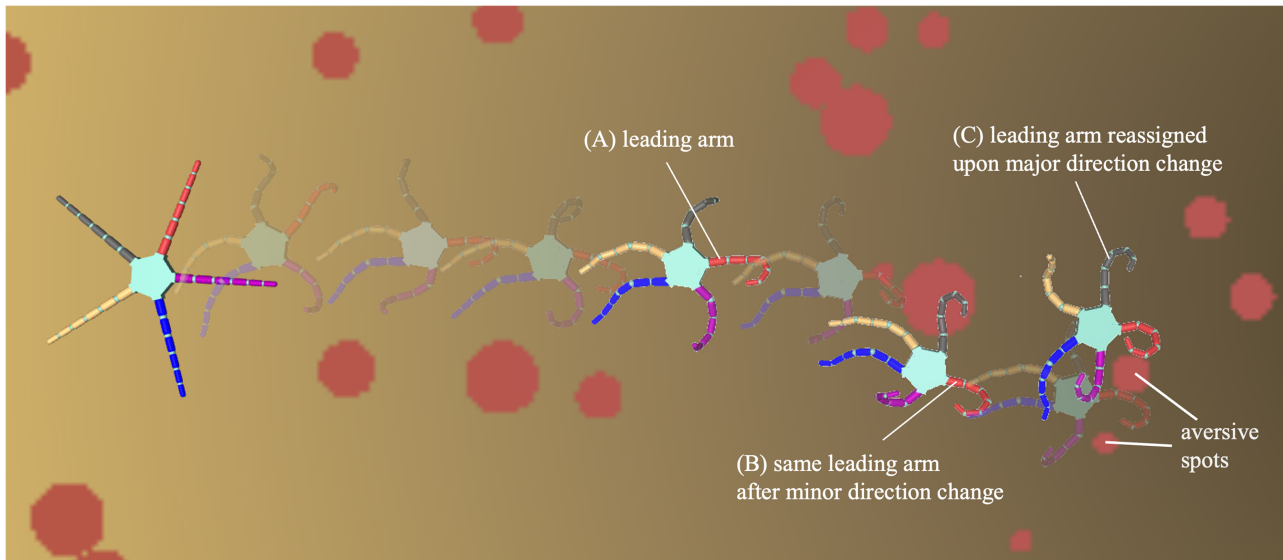


Figure 5. Emergence of bio-realistic turning through role reassignment. Evaluation of the exemplar controller in an arena with aversive spots shows how it redirects locomotion while moving towards the darker region. To facilitate visual tracking of arm roles through the motion, each arm is assigned a distinct colour. (A) The brittle star begins with a defined leading arm and coordinated rowing pair. (B) Upon encountering a single aversive spot, only a minor correction is needed and the same leading arm is maintained. (C) A subsequent pair of spots requires a major change in direction. Instead of rotating the body disc, the controller reassigns arm roles: the old leader becomes one of the synchronized rowers, while a new leader is recruited. This emergent strategy mirrors *in vivo* observations that brittle stars turn by redefining limb identities rather than reorienting the entire body. A video of this behaviour is available on the online dashboard under scenario B: run_0 [34].

in direction. Rather than rotating the body disc, the controller reoriented by reassigning arm roles: a new arm became the leader, its two neighbours acted as synchronized rowers and the former leader switched to a trailing role. This emergent strategy mirrors *in vivo* observations that brittle stars redefine their forward axis by switching limb identities rather than turning the body [2].

Importantly, the avoidance behaviour in the model arises from a continuous trade-off between light reduction, energy expenditure and aversive-spot penalties. Unlike *in vivo* studies that examine responses to isolated stimuli [23,35], the controller operates under a persistent directional objective: it must continue progressing towards darker regions while avoiding noxious zones. Consequently, redirection does not necessarily occur directly opposite the stimulus, as often observed *in vivo*. In many cases, the controller instead performs local corrections—either by temporarily recruiting an adjacent arm as leader or by subtly skewing left-right propulsive forces—to maintain overall progress. In more challenging configurations with multiple aversive spots aligned along the path, the controller may appear momentarily constrained, reflecting the competing objectives encoded in the reward function. Thus, the simulated avoidance resembles navigation around non-permissive regions rather than a dedicated escape reflex, and should be interpreted within the context of this multi-objective optimization. Videos demonstrating this behaviour are accessible through the online dashboard.

Together, these results demonstrate that our framework is capable of producing *bio-realistic rowing gaits in an emergent manner*, i.e. without embedding gait-specific rules through reward shaping. The simulated gait reproduces the defining hallmarks of natural rowing, including a leader–rower–passive role division, inter-arm synchronization, propulsion generated primarily by the mid-arm segments of the rowers and movement direction changes through dynamic role reassignments. These features match with prior behavioural studies [2,6,23]. Beyond rowing, the optimization also produced a diversity of alternative locomotor strategies, such as reverse rowing gaits and asymmetric gaits in which left and right arms alternated as rowers, which can be explored in the online dashboard.² Nevertheless, the critical point is that rowing lies within this space of possible outcomes.

3.2. Sensory dependency shapes behaviour

Having established that our framework can generate realistic rowing gaits, we next investigate how increased sensory dependency influences the locomotor strategies that emerge. To this end, we compare the 20 optimized controllers from scenario A (light gradient only) with the 20 from scenario B (light gradient with additional aversive spots). Importantly, all controllers were evaluated in a light-gradient arena without aversive spots, even if they were trained under condition B. This avoids stochasticity from random spot placement and allows us to focus the comparison purely on the converged gait strategy embodied by each controller.

We first qualitatively compared the gaits that emerged in each scenario. Clearly identifiable forward rowing gaits were observed in seven controllers trained under scenario B (visible on the dashboard under runs 0–3, 7, 12 and 16), whereas only a single instance occurred in scenario A (run 11). By contrast, reverse rowing patterns were more prevalent in scenario A, appearing in six controllers (runs 0, 3, 4, 8, 12 and 18), but were not observed in scenario B. Overall, rowing behaviour was, therefore, common

²Exemplar reverse rowing and asymmetric gaits can be found under scenario A: run_8 and scenario A: run_5, respectively.

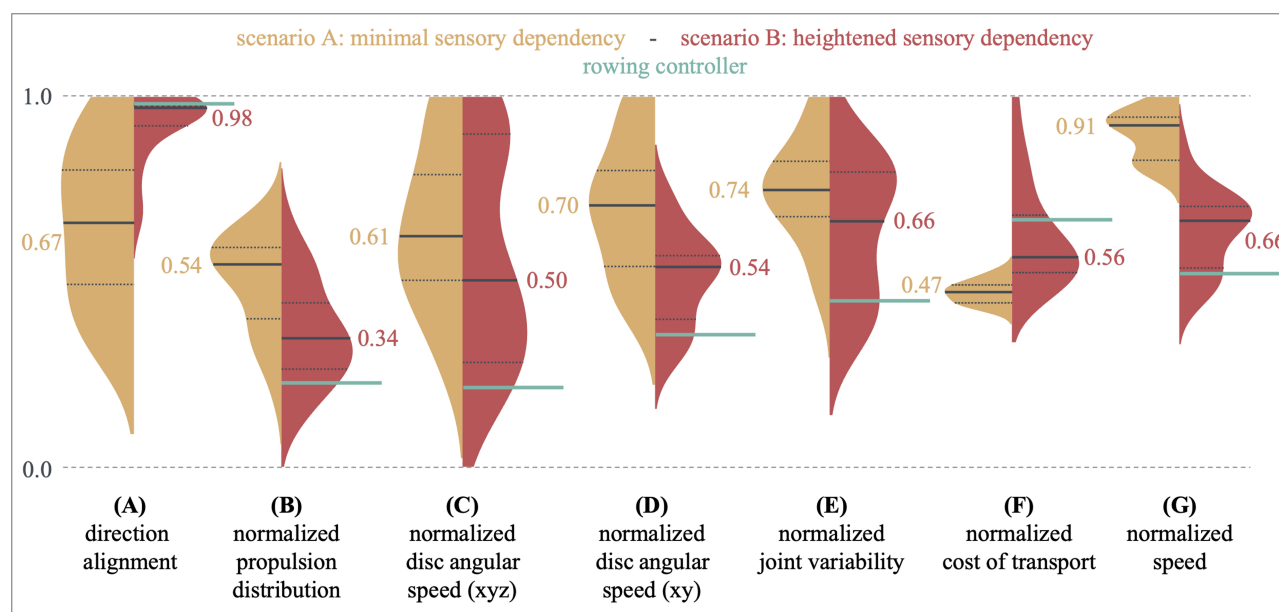


Figure 6. Violin plots of gait metrics for controllers trained under minimal (scenario A: light gradient only) and heightened sensory dependency (scenario B: light gradient with aversive spots). Horizontal bars indicate median values and dashed lines mark the first and third quartiles. Within each metric, both scenario violins share a common density scale, so that differences in width directly reflect differences in density across scenarios. The exemplar rowing controller analysed in §3.1 is annotated with a green bar for reference. (A) Direction alignment: cosine similarity between an arm's midpoint vector and the global movement direction, reflecting leader recruitment. (B) Propulsion distribution: evenness of propulsive force generation, ranging from zero when a single arm produces all propulsion to one when propulsion is perfectly distributed across all arms. (C) Disc angular speed: rotational instability of the disc, measured as the average norm of disc angular velocity. (D) Joint variability: mean standard deviation of all joint angles over time. (E) Cost of transport: actuator torque expenditure per unit displacement. (F) Speed: average disc velocity norm. Metrics were calculated from a single representative gait cycle per controller and—except for direction alignment—normalized to the maximum across all controllers. These show that increasing sensory dependency shifts distributions towards the characteristics of biologically realistic rowing, thereby meaningfully constraining the locomotor solution space. Notably, the annotated exemplar rowing controller consistently follows this shift in each distribution, reinforcing the observed trend.

under heightened sensory dependency (scenario B) but rare in the light-gradient-only condition (scenario A), indicating a clear shift in the dominant locomotor strategy across the two populations. This qualitative difference suggests that increased sensory dependency does not merely modulate gait parameters, but biases the system towards specific locomotor regimes. In particular, heightened sensory dependency appears to favour forward rowing over reverse rowing, providing a potential explanation for why brittle stars predominantly employ forward rowing.

This population-level shift is further substantiated by the quantitative comparisons presented in figure 6. With the exception of direction alignment, all reported metrics were normalized to the maximum value observed across all controllers. This normalization emphasizes relative shifts in distributions rather than absolute magnitudes, which is appropriate given that our goal is to compare how heightened sensory dependency alters gait characteristics rather than to establish absolute values. As manual inspection confirmed that all controllers converge to a stable cyclic gait, all metrics were calculated from a single representative gait cycle (see the supplementary material for details on cycle detection).

First, controllers trained in scenario B more consistently established a clearly defined leading arm, as indicated by higher maximal direction alignment scores (significance $p < 0.001$ based on a two-sided Mann–Whitney U test; effect size $r = 0.71$ as a rank-biserial correlation;³ figure 6A). Arm direction alignment quantifies the cosine similarity between each arm's midpoint vector (as annotated in figure 4B) and the global movement direction, taking the maximum value across arms. It therefore reflects how closely the best-aligned arm points in the movement direction. Furthermore, propulsion was dominated by fewer arms in scenario B, as shown by lower values of the propulsion distribution metric ($p < 0.002$; $r = 0.57$; figure 6B). This metric measures how evenly propulsive forces are generated across the arms, ranging from zero when a single arm produces all thrust to one when propulsion is equally distributed. Together, these results indicate that heightened sensory demands promote a reliable recruitment of one arm as a probing leader and sharpen the division of labour among arms. In other words, increased sensory challenge stimulates the natural role assignment of leader, rowers and passive arms that characterizes brittle star rowing [2].

Second, metrics related to gait stability showed a more complex pattern under heightened sensory dependency. While the median of the rotational instability measure, which is quantified as the average norm of disc angular velocity, was lower in scenario B than in scenario A, the reduction did not reach statistical significance ($p = 0.15$; $r = 0.27$; figure 6C). However, the shape of the distribution provides additional insight: under the heightened sensory dependency of scenario B, the measure exhibits bimodality. This indicates that at least a subset of the controllers converged towards a more stable regime with reduced disc rotations. By contrast, the distribution of scenario A is unimodal and centred at higher instability values. The bimodality in scenario B arises

³Effect sizes are reported as rank-biserial correlations, where $|r| \geq 0.1$, $|r| \geq 0.3$ and $|r| \geq 0.5$ indicate small, medium and large effects, respectively [36].

from the interplay between two coordination regimes. High disc angular speeds result from anti-phase stroking, in which left and right rowers alternate rather than stroke in unison. This is a local optimum that both scenarios converge to with similar frequency. Low disc angular speeds correspond to symmetric, in-phase coordination, which is more energy-efficient and produces more directionally stable movement. In scenario B, the additional pressure of aversive-spot avoidance favours this symmetric regime, driving a subset of controllers towards markedly lower disc instability. In addition, the intermediate values present in scenario A, which reflect partially out-of-phase coordination, are largely eliminated, producing the observed bimodal split.

A similar distributional pattern is observed for the joint variability measure ($p = 0.10$; $r = 0.305$; figure 6D), computed as the average standard deviation of all segment joint angles over time. This captures how consistently the arms maintain their postures. Here too, scenario B produces a subset of controllers with notably lower variability, while scenario A maintains a unimodal distribution centred at higher values. The emergence of a more stable subset of gaits in scenario B suggests that increased sensory dependency, although not sufficient to enforce uniform stability, still drives part of the optimization landscape towards more stable coordination regimes. Because the arms serve as the primary sensory structures, maintaining stability is critical: excessive fluctuations would add noise to sensory signals, making it harder to reliably detect light gradients or locate noxious stimuli. In this sense, the observed tendency towards greater stability under heightened sensory dependency can be interpreted as an adaptive strategy to improve the reliability of sensory input, ensuring that environmental cues are not obscured by self-induced motion.

Finally, locomotion under heightened sensory dependency incurred a higher cost of transport ($p < 0.001$; $r = 0.925$; figure 6E) while producing a slower forward speed ($p < 0.001$; $r = 0.965$; figure 6F). The cost of transport was calculated as the sum of all actuator torques over disc displacement, providing a measure of energy expenditure per unit distance travelled. This reflects that, under heightened sensory dependency, controllers were stimulated to redirect part of the locomotor effort from straightforward forward propulsion towards active probing and sensing of the substrate. Such a strategy prioritizes sensory reliability and careful motion over raw energetic efficiency. We note, however, that the magnitude of the observed trade-off is not intended as a quantitative prediction for *in vivo* brittle stars, where additional biomechanical and ecological adaptations are likely to mitigate the energetic cost of stable locomotion. Rather, our focus is on the qualitative trend that heightened sensory demands shift control strategies away from pure propulsion towards more cautious, information-gathering movement.

Taken together, these findings demonstrate that increased sensory dependency constrains the locomotor solution space in a meaningful way. Rather than producing a wider diversity of gaits, heightened sensory challenge pushes the system towards the characteristics that resemble natural rowing. Notably, the exemplar rowing controller analysed in §3.1 consistently lies at the extreme of each distribution in figure 6, in the same direction towards which heightened sensory dependency shifts the set of controllers as a whole. This supports our central hypothesis that rowing emerges because it represents a locomotor strategy compatible with the dual role of arms as both effectors and sensors. In this view, embodied sensory constraints actively shape the coordination patterns, resonating with embodied cognition theory [17]. These results show that gait emergence is not solely a product of mechanical efficiency, but of the interplay between sensing and actuation. From this perspective, rowing can be interpreted as an attractor shaped by embodied sensory constraints: a robust compromise between propulsion, stability and reliable perception. Our model, therefore, suggests that brittle stars converge on rowing not simply because it is efficient, but because it represents the most viable trade-off in a high-dimensional space of movement and sensing. This has two key implications: (i) it provides a functional explanation for why rowing is observed so ubiquitously *in vivo*, and (ii) it highlights that modelling naturalistic gait emergence requires explicit consideration of sensory demands, not just mechanical constraints.

3.3. Ganglia behave as distributed oscillatory units

A unique advantage of our *in silico* framework is that it provides direct access to the internal dynamics of the decentralized controller, an aspect that remains experimentally inaccessible in living brittle stars. Analysing these internal dynamics is particularly valuable because it offers insight into how coordinated gaits are generated: rather than inferring control principles only from observed motion, we can directly study the patterns of ganglion activity that underlie locomotion. To visualize these dynamics, we projected the activity patterns of the five ganglia of the exemplar rower described in §3.1 into a two-dimensional space using UMATO [37]. The activity of each ganglion corresponds to its internal state, denoted as G_a in figure 2. UMATO is particularly well-suited here as a dimensionality reduction technique, as it preserves both local structure (neighbouring states remain proximal in the embedding) and global structure (the relative arrangement of manifolds is retained). As shown in figure 7A, the activity of each ganglion traces out a closed, recurring loop during a 10 s evaluation. Importantly, trajectories from different arms remain distinct and do not converge to a single region, confirming that the controller operates in a truly decentralized manner rather than collapsing on to a shared global state.

The recurrent loops indicate the presence of oscillatory attractors consistent with limit cycle dynamics. A limit cycle is a closed trajectory in state space towards which the system converges, representing a self-sustained oscillation that is stable against small perturbations. This suggests that the periodicity of the gait is encoded intrinsically in the ganglion activity, rather than being imposed externally or arising purely from mechanical resonance. To test this interpretation, we disconnected the controller from the simulator and supplied it with constant, unchanging sensory input for 5 s, then visualized the final 1 s of ganglion activity (figure 7B). Even under this constant drive, ganglion trajectories traced closed orbits, demonstrating that oscillatory activity is self-sustaining and does not depend on rhythmic sensory cues. Importantly, the presence of intrinsic neural oscillations does not imply that rhythmic arm movements are continuously expressed at the mechanical level. Consistent with this distinction, our *in silico* brittle star did not exhibit locomotor behaviour when the controller was driven by constant, time-invariant sensory inputs, despite the persistence of oscillatory ganglion dynamics. Behavioural studies have shown that brittle star arms fail to

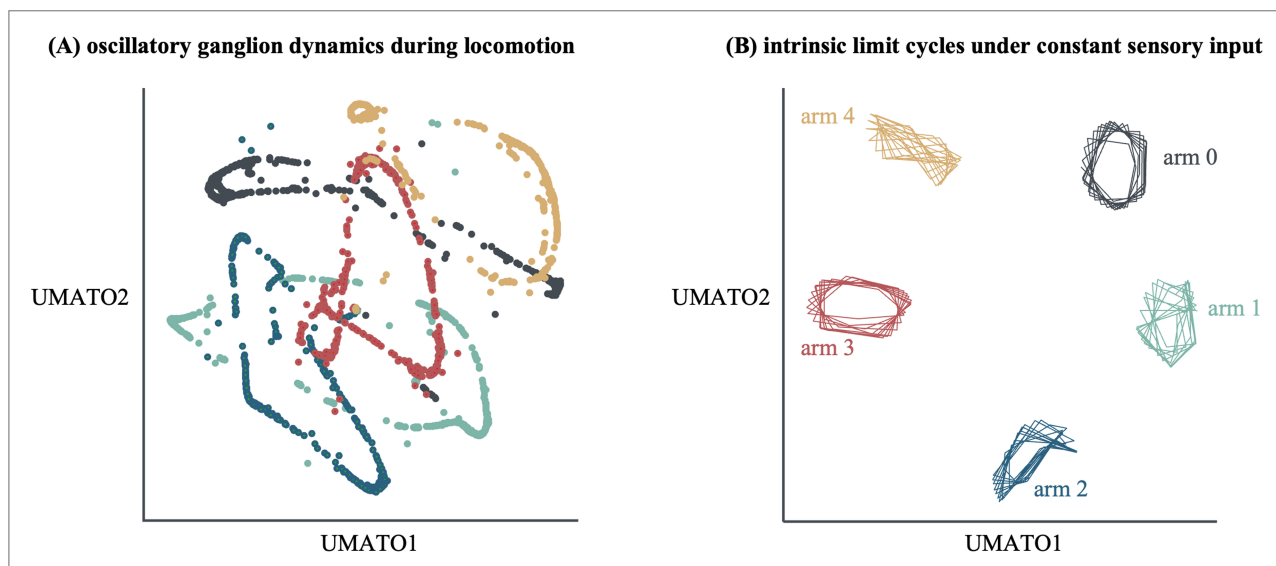


Figure 7. (A) Two-dimensional UMATO embedding of the activity patterns of the five ganglia during a 10 s simulation of the exemplar rower discussed in §3.1. Each ganglion's trajectory forms a closed loop, consistent with self-sustained oscillatory attractors. Notably, ganglion trajectories remain distinct and do not converge to a single state, confirming decentralized operation. (B) Two-dimensional UMATO embedding of the final 1 s of ganglion states after 5 s of constant sensory input. Even under constant input, trajectories trace closed orbits, demonstrating that the oscillations are intrinsic to the network rather than imposed externally or by mechanical resonance.

generate coordinated periodic motion when lifted off the substrate, highlighting the critical role of physical interaction with the environment in producing locomotion [4]. This observation is consistent with a view in which decentralized neural oscillators act as latent pattern generators whose motor expression is gated and shaped by sensory feedback and mechanical loading, rather than autonomously driving rhythmic motion at all times. Similar principles are well established in studies of CPGs in other animals, where intrinsic neural rhythms require appropriate sensory or mechanical triggers to be transformed into overt locomotor behaviour [11]. In our framework, ganglia thus function as local oscillatory units, while the modulation and translation of these oscillations into coordinated rowing motions depend on sensory–motor coupling with the environment.

These results align with empirical *in vivo* findings. Matsuzaka *et al.* [6] and Kano *et al.* [10] showed that an arm deprived of its basal ganglion fails to coordinate joint activity, underscoring the ganglion's role as a local organizer of rhythmic motion. Clark *et al.* [8] reported that arms no longer interconnected through the circumoral nerve ring lose the ability to coordinate. Our simulations reconcile these views: ganglia naturally develop local oscillatory attractors, which then synchronize through circumoral connections to generate coherent, whole-body gaits. Conceptually, these results demonstrate how a 'brainless' nervous system can implement coordinated pattern generation. In many animals, rhythmic locomotion is driven by CPGs: neural circuits that produce sustained oscillations even in the absence of rhythmic input [11]. Although CPGs have been demonstrated in many invertebrates (e.g. mollusks, crustaceans and leeches) [38], no direct evidence for CPG-like circuits in brittle stars has yet been published. Our results suggest a functionally analogous principle: each ganglion functions as an independent rhythmic oscillator whose activity is intrinsically sustained, while the expression of these oscillations into coordinated locomotion is initiated and shaped by sensory input and synchronized through coupling by the circumoral nerve ring. Rather than relying on a central pacemaker, brittle stars thus achieve robust locomotion through the collective dynamics of sensory-modulated and decentralized oscillatory units. This provides a mechanistic explanation for how coordinated periodicity arises from a network of decentralized ganglia.

4. Conclusion and outlook

In this work, we developed the first model of brittle star locomotion that enables neural dynamics and gait kinematics to emerge freely under environmental constraints, rather than being prescribed *a priori*. This is achieved by integrating morphology, sensing and a bio-inspired decentralized ANN controller within a general-purpose physics simulator. Using this integrative *in silico* framework, we addressed two unresolved questions: (i) how decentralized ganglia generate rhythmic activity and synchronize it across the circumoral nerve ring to produce coherent, whole-body coordination, and (ii) why such coordination converges on rowing as the predominant locomotor gait. Our results provide computational answers to both.

First, we demonstrated that bio-realistic rowing gaits can emerge spontaneously in our framework, i.e. without embedding gait-specific rules in the optimization scheme. Subsequent neural analysis revealed that each arm's ganglion develops a self-sustained oscillatory attractor and that synchronization across the ring produces coherent whole-body gaits. This supports the view that brittle star locomotion is underpinned by decentralized oscillator networks that operate similarly to CPGs found in other animals. Importantly, this is a functional analogy rather than a claim of anatomical or mechanistic equivalence; determining whether brittle stars possess these dedicated CPG-circuits will require targeted neurophysiological studies.

Second, we showed that increased sensory dependency constrains the locomotor solution space, biasing the system towards more structured and bio-realistic gaits. In particular, gaits trained under higher sensory challenge better resembled the characteristics of natural rowing. These findings support the hypothesis that the dual role of arms as both effectors and sensors imposes intrinsic constraints that favour rowing as a robust compromise between movement and reliable perception. We emphasize, however, that we interpret sensory dependency as a contributing selective pressure towards rowing, rather than a complete explanation of the natural gait. Consistent with this, optimization did not reliably converge to a single, stereotyped rowing solution across runs, suggesting that additional pressures probably further shape *in vivo* rowing. To further improve both the realism of and the reliability with which highly bio-realistic gaits are obtained, additional selective pressures and modelling ingredients may, therefore, be required. Introducing elements such as uneven terrain, particulate surfaces or scattered obstacles would create richer physical interactions and further increase the system's sensory dependency. We hypothesize that such conditions would amplify the trend observed here—driving the controllers to rely more heavily on sensory feedback and thereby converge more consistently towards biologically realistic gaits.

4.1. Implications for robotics

Beyond its biological contributions, this work also carries implications for robotics. The controller demonstrates how robust coordination can emerge from local recurrence and restricted communication, a principle relevant for modular and reconfigurable robots. Moreover, our results emphasize that appropriate environmental demands during training are essential for eliciting stable and meaningful behaviours. This reflects the design philosophy articulated by Pfeifer *et al.* [18], emphasizing that adaptive behaviour arises not solely from top-down control but also from the continuous interplay between the body's sensorimotor system and its physical environment.

In addition, the framework further supports the development of brittle star-inspired robots that translate these principles into physical form [4]. Such a robot could inherit the animal's distinctive advantages: the ability to navigate complex, unstructured terrains, robustness to limb loss or mechanical failure [4] and even the potential to repurpose its limbs for grasping or manipulation [1]. Exploring these properties first in a simulation environment, where both morphology and control can be systematically varied, provides a principled guidance for future physical realizations. The presented framework thus not only illuminates how brittle stars move but also helps to pave the way towards embodied machines that leverage similar modular, decentralized and adaptive principles.

4.2. Future directions

Looking ahead, our *in silico* test bed enables a novel range of controlled experiments that are currently unfeasible *in vivo*.

First, it can probe the neural consequences of arm loss. This is a biologically relevant perturbation given the brittle star's natural ability to autotomize and regenerate arms. Such simulations could extend the results of Kano *et al.* [4] and reveal what role the ganglion of a lost arm continues to play within the decentralized network.

Second, although our focus here lies on rowing, the optimization has also produced reverse rowing gaits. This opens the possibility to further investigate the neural and sensory mechanisms that govern the selection between the brittle star's two principal locomotor strategies [2].

Third, the test bed can be used to explore morphological variations. While most brittle stars have five arms, some species possess six or seven [23,39]. By systematically varying the number of arms in simulation, the test bed can probe why pentaradial symmetry is the dominant configuration, and how additional arms affect coordination, stability and robustness. In addition, brittle star species differ in arm stiffness and compliance, which are known to affect gait characteristics. Varying joint stiffness within the model would allow systematic investigation of how these mechanical properties shape locomotor patterns and coordination regimes [3].

Finally, the test bed permits manipulations that transcend natural constraints. Circumoral connectivity can be altered to probe the limits of decentralization, from the biologically realistic case of strictly neighbour-to-neighbour communication to full interconnection between all arms. Similarly, the balance between local and inter-arm processing can be varied: in the current implementation, arm-level sensory integration and inter-ganglion communication occur on the same time scale, but systematically adjusting this ratio would reveal how the relative speed of local versus global processing affects gait emergence and stability. The framework also enables direct comparison between decentralized and hypothetical centralized architectures—a question of biological relevance, since a central brain would need to integrate vast sensory inputs and coordinate many degrees of freedom simultaneously across a radial body plan. In contrast, the decentralized architecture naturally partitions this complexity, allowing coordination to emerge from local interactions. Such comparisons would clarify whether distributed control offers adaptive advantages in robustness, scalability and fault tolerance, with implications for both biology and robotics.

These avenues underscore the broad potential of the framework as an open-ended computational test bed for brittle star biology and, more broadly, for exploring decentralized control in embodied agents.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. A snapshot of the source code and data underlying the experiments are available online [40].

Supplementary material is available online [41].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. D.M.: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing—original draft, writing—review and editing; D.A.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—review and editing; F.W.: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

- Tomholt L, Friesen LJ, Berdichevsky D, Fernandes MC, Pierre C, Wood RJ, Weaver JC. 2020 The structural origins of brittle star arm kinematics: an integrated tomographic, additive manufacturing, and parametric modeling-based approach. *J. Struct. Biol.* **211**, 107481. (doi:10.1016/j.jsb.2020.107481)
- Astley HC. 2012 Getting around when you're round: quantitative analysis of the locomotion of the blunt-spined brittle star, *Ophiocoma echinata*. *J. Exp. Biol.* **215**, 1923–1929. (doi:10.1242/jeb.068460)
- Goharimanesh M, Stöhr S, Ghassemzadeh F, Mirshamsi O, Adriaens D. 2023 A methodological exploration to study 2D arm kinematics in Ophiuroidea (Echinodermata). *Front. Zool.* **20**, 15. (doi:10.1186/s12983-023-00495-y)
- Kano T, Sato E, Ono T, Aonuma H, Matsuzaka Y, Ishiguro A. 2017 A brittle star-like robot capable of immediately adapting to unexpected physical damage. *R. Soc. Open Sci.* **4**, 171200. (doi:10.1098/rsos.171200)
- Cobb JLS, Stubbs TR. 1981 The giant neurone system in ophiuroids. I. The general morphology of the radial nerve cords and circumoral nerve ring. *Cell Tissue Res.* **219**, 197–207. (doi:10.1007/bf00210028)
- Matsuzaka Y, Sato E, Kano T, Aonuma H, Ishiguro A. 2017 Non-centralized and functionally localized nervous system of ophiuroids: evidence from topical anesthetic experiments. *Biol. Open* **6**, 425–438. (doi:10.1242/bio.019836)
- Zueva O, Khoury M, Heinzeller T, Mashanova D, Mashanov V. 2018 The complex simplicity of the brittle star nervous system. *Front. Zool.* **15**, 1. (doi:10.1186/s12983-017-0247-4)
- Clark EG, Kanauchi D, Kano T, Aonuma H, Briggs DEG, Ishiguro A. 2019 The function of the ophiuroid nerve ring: how a decentralized nervous system controls coordinated locomotion. *J. Exp. Biol.* **222**, jeb192104. (doi:10.1242/jeb.192104)
- Cobb JLS, Stubbs TR. 1982 The giant neurone system in ophiuroids. III. The detailed connections of the circumoral nerve ring. *Cell Tissue Res.* **226**, 675–687. (doi:10.1007/bf00214794)
- Kano T, Kanauchi D, Ono T, Aonuma H, Ishiguro A. 2019 Flexible coordination of flexible limbs: decentralized control scheme for inter- and intra-limb coordination in brittle stars' locomotion. *Front. Neurobot.* **13**, 104. (doi:10.3389/fnbot.2019.00104)
- Ijspeert AJ. 2008 Central pattern generators for locomotion control in animals and robots: a review. *Neural Netw.* **21**, 642–653. (doi:10.1016/j.neunet.2008.03.014)
- Leung B, Gorb S, Manoonpong P. 2024 Nature's all-in-one: multitasking robots inspired by dung beetles. *Adv. Sci.* **11**, 2408080. (doi:10.1002/advs.202408080)
- Pan M, Liu M, Lei J, Wang Y, Linghu C, Bowen C, Hsia KJ. 2025 Bioinspired mechanisms and actuation of soft robotic crawlers. *Adv. Sci.* **12**, 2416764. (doi:10.1002/advs.202416764)
- Zhou Q, Xu J, Fang H. 2023 A CPG-based versatile control framework for metamer earthworm-like robotic locomotion. *Adv. Sci.* **10**, 2206336. (doi:10.1002/advs.202206336)
- Lawrence JM. 1987 *A functional biology of echinoderms*. Baltimore, MD: Johns Hopkins University Press.
- Moore A, Cobb JLS. 1985 Neurophysiological studies on photic responses in *Ophiura ophiura*. *Comp. Biochem. Physiol. A* **80**, 11–16. (doi:10.1016/0300-9629(85)90669-3)
- Pfeifer R, Bongard J. 2007 *How the body shapes the way we think: a new view of intelligence*. Cambridge, MA: MIT Press.
- Pfeifer R, Lungarella M, Iida F. 2007 Self-organization, embodiment, and biologically inspired robotics. *Science* **318**, 1088–1093. (doi:10.1126/science.1145803)
- Sellers WI, Margetts L, Coria RA, Manning PL. 2013 March of the titans: the locomotor capabilities of sauropod dinosaurs. *PLoS One* **8**, e78733. (doi:10.1371/journal.pone.0078733)
- Ijspeert AJ. 2014 Biorobotics: using robots to emulate and investigate agile locomotion. *Science* **346**, 196–203. (doi:10.1126/science.1254486)
- Marzougui D, Das R, Mazzolai B, Adriaens D, Wyffels F. 2025 Exploring the evolutionary adaptations of the unique seahorse tail's muscle architecture through *in silico* modelling and robotic prototyping. *J. R. Soc. Interface* **22**, 20240876. (doi:10.1098/rsif.2024.0876)
- Vaxenburg R *et al.* 2025 Whole-body physics simulation of fruit fly locomotion. *Nature* **643**, 1312–1320. (doi:10.1038/s41586-025-09029-4)
- Wakita D, Kagaya K, Aonuma H. 2020 A general model of locomotion of brittle stars with a variable number of arms. *J. R. Soc. Interface* **17**, 20190374. (doi:10.1098/rsif.2019.0374)
- Kano T, Kanauchi D, Aonuma H, Clark EG, Ishiguro A. 2019 Decentralized control mechanism for determination of moving direction in brittle stars with penta-radially symmetric body. *Front. Neurobot.* **13**, 66. (doi:10.3389/fnbot.2019.00066)
- Watanabe W, Kano T, Suzuki S, Ishiguro A. 2011 A decentralized control scheme for orchestrating versatile arm movements in ophiuroid omnidirectional locomotion. *J. R. Soc. Interface* **9**, 102–109. (doi:10.1098/rsif.2011.0317)
- Cowles RP. 1910 Stimuli produced by light and by contact with solid walls as factors in the behavior of ophiuroids. *J. Exp. Zool.* **9**, 387–416. (doi:10.1002/jez.1400090209)
- Todorov E, Erez T, Tassa Y. 2012 MuJoCo: a physics engine for model-based control. In *2012 IEEE/RSJ Int. Conf. Intell. Robot. Syst.*, Vilamoura-Algarve, Portugal, pp. 5026–5033. Piscataway, NJ: IEEE.
- Aldarondo D *et al.* 2024 A virtual rodent predicts the structure of neural activity across behaviours. *Nature* **632**, 594–602. (doi:10.1038/s41586-024-07633-4)
- Wang H, Caggiano V, Durandau G, Sartori M, Kumar V. 2022 MyoSim: fast and physiologically realistic MuJoCo models for musculoskeletal and exoskeletal studies. In *2022 Int. Conf. Robot. Autom. (ICRA)*, Philadelphia, PA, pp. 8104–8111. Piscataway, NJ: IEEE.
- Barbera VL, Bohez S, Hasenclever L, Tassa Y, Hutchinson JR. 2025. Motion tracking with muscles: predictive control of a parametric musculoskeletal canine model. (doi:10.48550/arXiv.2506.23768)
- Patterson ZJ, Astley HC, Majidi C. 2025 Soft robotic brittle star shows the influence of mass distribution on underwater walking. *Bioinspir. Biomim.* **20**, 036003. (doi:10.1088/1748-3190/adbcb)
- Tuft PJ, Gilly WFM. 1984 Ionic basis of action potential propagation along two classes of 'Giant' axons in the ophiuroid, *Ophiopertis papillosa*. *J. Exp. Biol.* **113**, 337–349. (doi:10.1242/jeb.113.1.337)

33. Schulman J, Wolski F, Dhariwal P, Radford A, Klimov O. 2017. Proximal policy optimization algorithms. (doi:10.48550/arXiv.1707.06347)
34. Marzougui D. 2025 Project web page and interactive dashboard. Available at <https://airo.ugent.be/projects/brittle-star>.
35. Yee A, Burkhardt J, Gilly WF. 1987 Mobilization of a coordinated escape response by giant axons in the ophiuroid, *Ophiopteris papillosa*. *J. Exp. Biol.* **128**, 287–305. (doi:10.1242/jeb.128.1.287)
36. Cohen J. 2009 *Statistical power analysis for the behavioral sciences*, 2edn. New York, NY: Psychology Press.
37. Jeon H, Ko H-K, Lee S, Jo J, Seo J. 2022 Uniform manifold approximation with two-phase optimization. In *2022 IEEE Visualization and Visual Anal. (VIS)*, Oklahoma City, OK, pp. 80–84. Los Alamitos, CA: IEEE.
38. Selverston AI. 2010 Invertebrate central pattern generator circuits. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 2329–2345. (doi:10.1098/rstb.2009.0270)
39. Wakita D, Hayase Y, Aonuma H. 2019 Different synchrony in rhythmic movement caused by morphological difference between five- and six-armed brittle stars. *Sci. Rep.* **9**, 8298. (doi:10.1038/s41598-019-44808-w)
40. Marzougui D. 2025 Snapshot of the source code and data underlying the experiments. Available at <https://zenodo.org/records/17367619>.
41. Marzougui D, Adriaens D, wyffels F. 2026 Supplementary material from: Decentralised neural dynamics and sensory constraints shape brittle star locomotion. FigShare. (doi:10.6084/m9.figshare.c.8456935)