A Mechanistic Model for Collective Motion from Sensorimotor Regularities

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Abstract. Collective behavior in animals has long been modeled through self-propelled particle models, which reproduce striking group-level phenomena through abstract interaction forces. Yet these models are fundamentally descriptive: they leave open the question of how collective behavior is actually produced. Recent empirical work makes this gap concrete: locusts do not align with neighbors, sensory and cognitive mechanisms mediate interaction instead. A mechanistic model must therefore operate at the sensorimotor level, grounded in what individual organisms can actually perceive, estimate, and physically execute. We present such a model based on a modeling framework from robotics, extended here to collective motion. Each agent perceives neighbors through bearing and apparent-size cues within a limited field of view, maintains uncertain internal state estimates, and selects actions through gradient descent on a desired social distance—without any prescribed interaction forces. This simple model produces diverse collective behaviors including polarized motion, milling, ring formations, and subgroup fragmentation. A global sensitivity analysis shows that behavioral transitions are governed by sensorimotor parameters corresponding to measurable biological quantities: field of view geometry, sensory noise, turning agility, and memory. Collective behavior can therefore be understood as the emergent outcome of interacting sensorimotor regularities, and differences across species as the emergent outcome of differences in embodiment and environment.

Keywords: collective motion · sensorimotor regularities · mechanistic model · emergent behavior · uncertainty · embodiment · field of view · flocking · active sensing

1 Introduction

Collective behavior is one of the most striking phenomena in the natural world. Flocks of birds [2, 5], schools of fish [9, 16], and swarms of insects [1, 4] produce coherent group-level patterns from purely local interactions, without centralized control or global information. The mystery is not just that groups coordinate, but that they do so with so little: each individual sees only a handful of neighbors,

yet the group behaves as if guided by something more. It is this question—how so much order arises from so little—that has driven a rich tradition of computational modeling in biology, physics, and robotics [23, 25].

Self-propelled particle models [6,24] have been the dominant modeling framework for collective behavior. Agents align with neighbors within a fixed radius, subject to noise, and the result is polarization, milling, cohesion, and phase transitions [7]—establishing collective behavior as a field of rigorous quantitative inquiry with broad influence [10]. These models are compelling precisely because of their simplicity, but that simplicity comes at a cost. Their parameters—interaction radii, alignment strengths, noise levels—are fit to observed patterns and carry no necessary correspondence to biological quantities. They characterize what collective behavior looks like rather than how it is produced. Particle models also assume agents have direct access to neighbors' positions and headings, quantities that may simply not be available under realistic sensory constraints [22]. Recent empirical work makes this concrete: Sayin et al. [18] showed that locusts do not align with neighbors at all; sensory and cognitive mechanisms mediate interaction instead. This calls for a different level of modeling: one grounded in what organisms can actually perceive and physically execute, with parameters corresponding to measurable biological quantities, so that predictions transfer to new species without refitting.

We present such a mechanistic model for collective behavior based on *Active InterCONnect* (AICON) [11, 12], a framework from robotics that generates behavior by composing sensorimotor regularities without directly encoding behavior itself. This makes it a natural substrate for a mechanistic model of collective behavior. The components that determine how an agent perceives, estimates, and acts are precisely the quantities that vary across species and environments. AICON has been applied to biological information processing [14], including collective opinion dynamics [13]. Here we extend it to collective motion. Each agent perceives neighbors through bearing and apparent-size cues within a limited field of view, maintains uncertain internal state estimates, and selects actions through gradient descent on a desired social distance—without any prescribed interaction forces. Unlike models grounded in instantaneous visual responses [3, 15], abstract Bayesian objectives [8], or specific neural implementations [17], AICON maintains persistent uncertain representations and operates at the sensorimotor level without prescribing how perception translates into social response.

The model recovers the behavioral diversity that particle models reproduce—polarized motion, milling, ring formations, and subgroup fragmentation—but from sensorimotor parameters alone: field of view geometry, sensory noise, and turning agility. These are not fitted constants but measurable biological quantities. The same parameters that govern coordination also govern its breakdown, and varying them generates predictions about how collective behavior should differ across species with different sensory systems, motor capabilities, and environments. Differences in collective behavior across species may reflect differences in sensorimotor properties rather than differences in interaction rules.

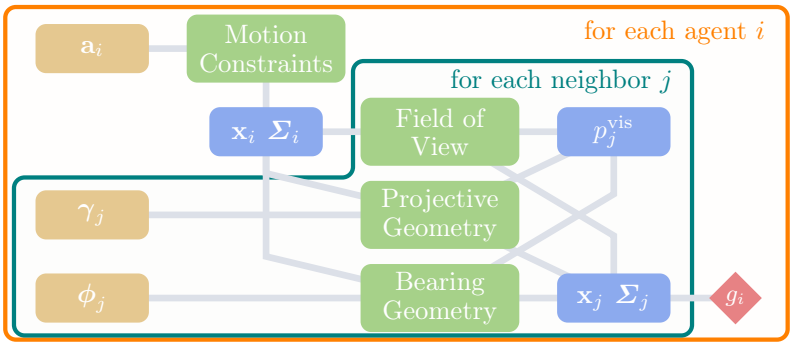

Fig. 1. Collective behavior emerges from the composition of local sensorimotor regularities, with no interaction forces prescribed at the collective level. Each agent i maintains recursive estimators for its own pose $(\mathbf{x}_i, \boldsymbol{\Sigma}_i)$ and, for each neighbor j, for position $(\mathbf{x}_j, \boldsymbol{\Sigma}_j)$ and visibility p_j^{vis}. Active interconnections couple these states: *Bearing Geometry* and *Projective Geometry* update neighbor position from observations ϕ_j and γ_j, modulated by visibility and own pose; *Field of View* computes visibility from own and neighbor states; *Motion Constraints* propagate pose from actions $\mathbf{a}_i$. The goal g_i, minimizing expected deviation from a desired social distance d_0, drives action selection through gradient descent along three emergent paths: position adjustment toward d_0, active sensing to reduce estimation uncertainty, and reorientation to maintain neighbors within the field of view—none of which are explicitly encoded.

2 A Sensorimotor Model of Collective Motion

AICON generates behavior through the dynamic composition of sensorimotor regularities, without directly encoding behavior itself. It provides two structural elements: *recursive estimators* that maintain probabilistic beliefs about task-relevant quantities over time, and *active interconnections* that encode regularities in the relationships between those quantities as differentiable functional dependencies. By composing these elements, AICON builds a network through which gradients can be propagated from goals back to actions. Behavior emerges from following these gradients, not from a predefined set of rules or a policy, but from the structure of the sensorimotor regularities themselves and the current state of the world.

We instantiate this architecture for collective motion as shown in Figure 1. Each agent maintains estimators for its own pose and, for each neighbor, for position and visibility. Neighbors are perceived through two angular cues: bearing ϕ, the direction to the neighbor relative to the agent's heading, and apparent size γ, the angular size of the neighbor as seen by the agent. Together these encode directional and distance-related information without requiring explicit depth sensing, grounding interaction in what the agent can actually observe. Perception is constrained by a limited field of view ψ: the visibility state p^{vis} is computed from ego and neighbor position estimates and modulates how strongly observations update the neighbor belief. When a neighbor leaves the field of view, its estimator

continues propagating the last belief forward, accumulating uncertainty. The flow of social information is therefore explicitly state- and uncertainty-dependent—a structural consequence of composing these regularities, not a prescribed rule.

Goal-directed behavior arises from a single differentiable cost function: each agent i minimizes the expected deviation from a desired social distance d_0 across all estimated neighbors $\mathcal{V}_i$,

$$g_i = \sum_{j \in \mathcal{V}_i} \mathbb{E}\Big[\big|\, \|\mathbf{x}_j\| - d_0 \big|\Big], \tag{1}$$

where the expectation over the belief implicitly couples the cost to estimation uncertainty over the neighbor's relative position $\mathbf{x}_j$. This is the only objective, yet when pursued with simple gradient descent through the model it gives rise to three distinct gradient paths without any of them being explicitly programmed. The first adjusts position to reduce deviation from d_0. The second flows through uncertainty: since uncertainty enters the expected cost, there is a gradient to reduce it—producing active sensing and triangulating motions without this being encoded anywhere. The third flows further still: because the uncertainty is modulated by p^{vis}, there is a gradient to reorient toward neighbors near the field of view boundary. This gradient ensures visibility and thus group cohesion even under narrow fields of view, without implicit encoding. Of these gradients for different neighbors each agent selects the steepest at each time step [12], while angular velocity is bounded by $\omega_{\max}$, enforcing a physical turning constraint that, as we will show, has a dominant influence on emergent collective structure.

No interaction forces are prescribed at the collective level. Coordination emerges entirely from agents following local gradients through their own sensorimotor regularities, interacting through shared space and mutual perception, yielding a simple mechanistic model that, as we show, produces a diverse range of collective behaviors governed by sensorimotor parameters.

3 Experimental Setup

We simulate groups of $N = 250$ agents in a two-dimensional continuous environment. Each agent is modeled as a circular body of unit radius with unicycle kinematics, controlled by linear velocity v and angular velocity ω, with $|\omega| \leq \omega_{\max}$. All simulations use a fixed timestep of $\Delta t = 0.1$ and are initialized from identical spatial configurations with a fixed random seed to ensure reproducibility. The desired social distance is fixed at $d_0 = 50$ throughout. We vary sensing, estimation, and motor parameters as summarized in Table 1, running each configuration both with memory (neighbor estimates propagated during invisibility) and without (estimates discarded and re-initialized on re-entry).

Metrics and Quantitative Analysis We evaluate emergent collective behavior using five complementary metrics that together capture the behavioral diversity the model aims to produce. *Polarization* P [24] measures directional alignment as the magnitude of the mean unit velocity vector across all agents, averaged over time; values near 1 indicate coherent directed motion, while values

Parameter	Description	Values
ψ	Field of view	$\left\{\frac{\pi}{2}, \pi, \frac{3\pi}{2}, 2\pi\right\}$
$\omega_{\max}$	Maximum angular velocity	{0.1, 0.3, 0.6, 0.9}
σ_ϕ	Assumed bearing noise std.	{0.001, 0.01, 1, 10, 100}
σ_γ	Assumed apparent size noise std.	{0.001, 0.01, 1, 10, 100}
Q	Assumed process noise for other agents	{0.01, 0.1, 1, 10}

Table 1. Varied parameters and their ranges.

near 0 indicate dispersed or rotational motion. *Relative Circular Area* (RCA) [15] quantifies spatial compactness by measuring how closely the convex hull of agent positions resembles a circle; high RCA indicates compact circular formations, low RCA elongated or fragmented ones. *Maximum mean displacement D* captures global translation as the maximum displacement of the group center of mass over the simulation. *Center Distance C* measures spatial cohesion as the time-averaged minimum distance from any agent to the group center of mass. *Directional fragmentation* is quantified by applying DBSCAN [19] to agent headings in circular space, yielding the average number of heading clusters K and clustered fraction F, capturing whether the population persistently splits into subgroups moving in distinct directions. To quantify parameter influence we compute Sobol first-order (S_1) and total-order (S_T) sensitivity indices [21]; the gap between them indicates the degree to which a parameter acts through interactions rather than in isolation.

4 Behavioral Diversity from Sensorimotor Parameters

4.1 Emergent Collective Behaviors

Starting from identical initial conditions, variation of sensorimotor parameters alone produces qualitatively distinct collective behaviors without any change to the underlying interaction architecture—exactly what a mechanistic model grounded in sensorimotor regularities should produce. *Stable rings* emerge at low uncertainty, where agents maintain reliable neighbor estimates and accurate distance control; high turning agility keeps agents on circular orbits at d_0 (Figure 2, **p**), while lower agility produces the same pattern with larger, smoother orbits (Figure 2, **a**). *Milling* emerges under increased uncertainty, where degraded distance estimation prevents stable orbit maintenance; moderate uncertainty produces loose irregular rings (Figure 2, **m**) while high uncertainty collapses agents into dense rotating clusters (Figure 2, **j**).

Fragmentation into groups moving along a line occurs under narrow field of view with high noise and no memory: without predictive belief propagation, agents preferentially follow whoever is directly ahead, producing elongated drifting groups (Figure 3, **d**). *Fragmentation into parallel streams* occurs under similar conditions but lower noise: reliable estimates allow lateral spacing mainte-

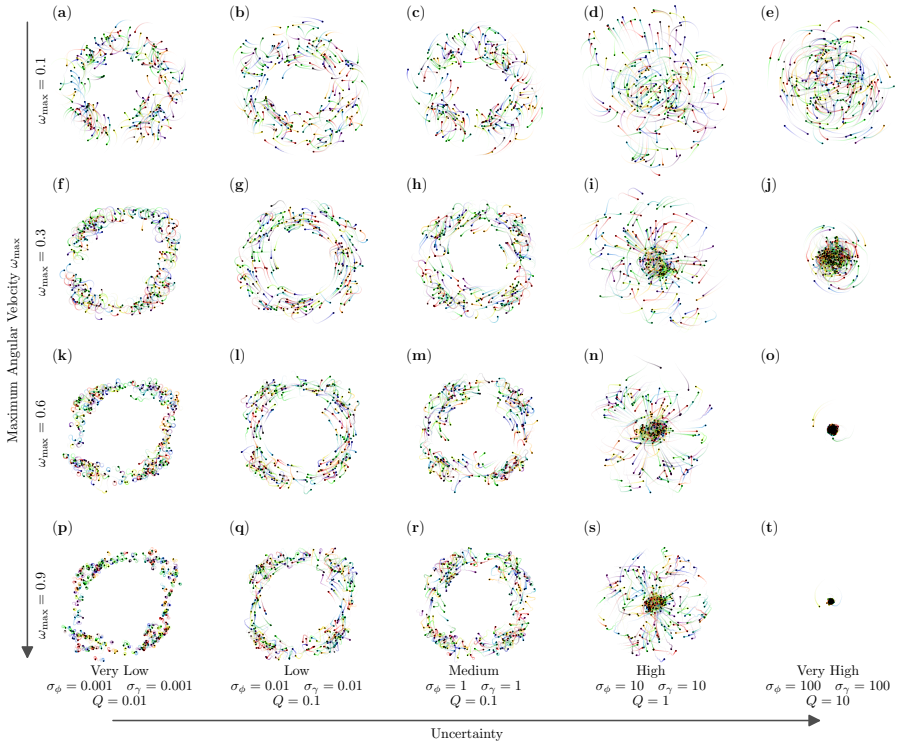

Fig. 2. Turning agility and sensory uncertainty jointly determine collective structure, with high uncertainty collapsing all formations into dense clusters regardless of motor capability. At low-to-medium uncertainty (cols. 1–3), increasing ω_{max} produces a graded transition from large smooth rings to tighter compact orbits. This breaks down at higher uncertainty (cols. 4–5): estimation error overwhelms the gradient signal sustaining rotational motion, collapsing all configurations into dense milling clusters whose tightness increases with ω_{max}.

nance, but absent memory causes the group to split into side-by-side streams (Figure 3, **b**). The same model, the same cost function, the same architecture—only the sensorimotor parameters change, and each regime emerges without prescribing rules for it.

4.2 Sensorimotor Parameters Govern Behavioral Transitions

We now examine how three biologically interpretable parameter groups shape the behavioral regimes described above.

Motor constraints ω_{max} governs formation geometry when estimation is reliable but becomes less relevant at high uncertainty. Low angular velocity produces smooth large-radius rings; higher values produce tighter orbits (Figure 2). Beyond a threshold uncertainty, ω_{max} instead determines only the tightness of

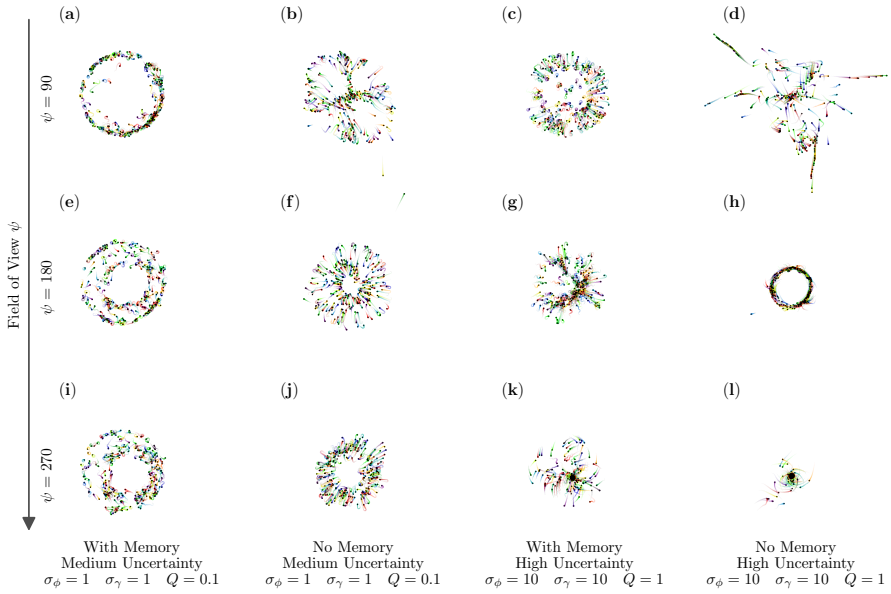

Fig. 3. Memory is critical for cohesion under narrow fields of view, while its absence can produce qualitatively different but stable structures under wider fields. At $\psi = 90$, memory yields a ring (**a**, **c**) while its absence causes complete fragmentation (**b**, **d**). As field of view widens, cohesion is preserved even without memory, though structures differ—compare the loose ring in (**e**) with the tight milling ring in (**h**).

the resulting milling cluster (Figure 2, last two rows). This parameter has no counterpart in classical particle models, where heading changes are instantaneous and unconstrained. Crucially, it is not a fitted constant but a measurable property of the organism—the kind of biologically grounded parameter a mechanistic model should be governed by.

Perceptual uncertainty Bearing and apparent size noise degrade collective structure through qualitatively different mechanisms. High bearing noise disrupts directional localization, driving a transition toward disordered aggregation (Figure 4, **a**–**b**). High apparent size noise instead degrades distance estimation while leaving directional coordination intact, producing inward-spiraling formations as agents triangulate to recover distance information (Figure 4, **e**–**f**). Where process noise is low, agents partially compensate through temporal integration and active sensing. That bearing and apparent size noise produce distinct behavioral signatures reflects the distinct roles of these two sensory channels—a distinction invisible to models that treat noise as a scalar perturbation.

Memory Memory determines whether gradient continuity is preserved across periods of visual occlusion, and its effect is qualitative rather than graded. Under narrow fields of view, removing memory causes complete fragmentation despite identical parameters and initial conditions (Figure 3, first row). Under

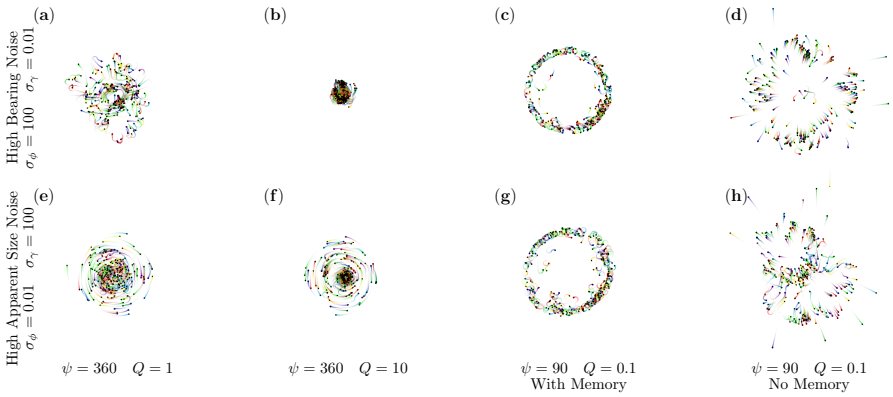

Fig. 4. Bearing and apparent size noise degrade collective structure differently, reflecting distinct emergent compensation strategies. High bearing noise (top row) disrupts directional estimation, producing disordered clusters (**a**–**b**), though low process noise enables recovery through temporal integration and active triangulation (**a**, **c**). High apparent size noise (bottom row) leaves directional information intact but degrades distance estimation, producing inward-spiraling rings via distance-reducing triangulation (**e**–**f**). Without memory, both regimes lose coherence and fragment into aligned subgroups (**d**, **h**). Bearing and apparent size noise are thus not interchangeable—a distinction no scalar noise model could capture.

wider fields, memory loss shifts the attractor toward qualitatively different stable formations (Figure 3, **b**). Whether an organism retains estimates of occluded neighbors is a property of its cognitive architecture—and here it determines qualitatively different collective regimes, not just quantitative variation.

4.3 Global Sensitivity of Collective Behavior

The qualitative patterns above are confirmed and quantified by a global variance-based sensitivity analysis (Figure 5). Field of view ψ and process noise Q are the strongest direct drivers across nearly all metrics and both memory conditions, consistent with ψ's role as the primary gating factor for neighbor visibility and gradient continuity, and with Q's role in shaping spatial cohesion through overall estimation uncertainty. Sensory noise parameters σ_ϕ and σ_γ show similarly modest first-order contributions but elevated total-order indices, indicating they act primarily through interactions. The angular velocity limit $\omega_{\max}$ contributes consistently but modestly in isolation, in line with its role as a shaping rather than gating parameter. Memory substantially flattens the sensitivity landscape: first- and total-order indices become more evenly distributed, indicating that predictive belief propagation reduces the system's dependence on any single sensorimotor quantity and distributes sensitivity more evenly across the full parameter space. Taken together, these results confirm that behavioral transitions are governed by sensorimotor quantities—field of view, noise, turning agility,

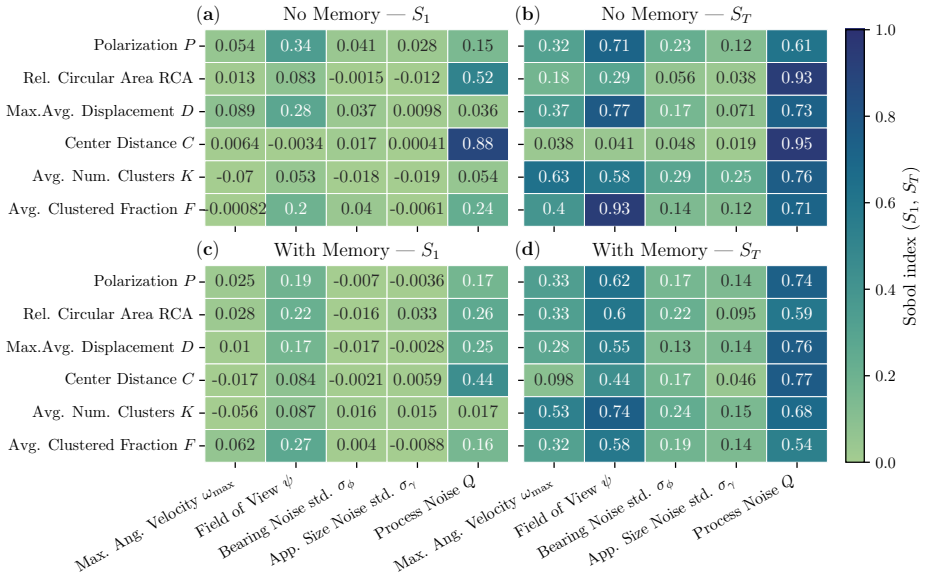

Fig. 5. Field of view and overall uncertainty are the dominant direct drivers of collective behavior, while memory redistributes sensitivity away from individual parameters. Only ψ and Q show substantial first-order contributions (S_1); σ_ϕ, σ_γ, and $\omega_{\max}$ instead act primarily through interactions (low S_1, elevated S_T). With memory (**c**–**d**), sensitivity is more evenly distributed, suggesting predictive belief propagation absorbs variance that would otherwise concentrate on ψ and Q.

memory—rather than abstract tuning parameters, and that their influence operates through the coupled structure of perception, estimation, and action rather than in isolation.

5 Discussion

This work presents collective behavior as the emergent outcome of interacting sensorimotor loops, grounded in what individual agents can actually perceive, estimate, and physically execute. A diverse range of behaviors arises from variation of sensorimotor parameters alone. Behavioral transitions and coordination breakdowns alike are governed by parameters with direct biological interpretations, connecting cross-species variation and failure modes within a single explanatory framework.

Comparison to Particle Models The core limitation of classical particle models is not that they are wrong about collective phenomena—*they are not*—but that they are descriptive rather than mechanistic. Their parameters are free constants with no necessary correspondence to biological quantities, meaning they cannot transfer predictions to new species or environments without refitting, and cannot explain why coordination breaks down under specific sensory

or motor conditions. As Sayin et al. [18] recently demonstrated, the mechanistic assumptions underlying these models are not empirically supported even for a paradigmatic species: locusts do not align with neighbors, sensory mechanisms mediate interaction instead. Our results demonstrate a constructive alternative: behavioral diversity is a prediction of the sensorimotor architecture, and the parameters governing transitions correspond to quantities measurable independently of collective behavior experiments.

Comparison to Perceptual Models Several recent models move beyond particle models by incorporating perceptual mechanisms. Vision-based response models [3,15] ground sensory input in visual geometry, but their response parameters remain phenomenological and the models are stateless and memoryless—there is no estimation, no uncertainty, and no mechanism for behavior to depend on prior observations. Active inference models [8] ground coordination in Bayesian belief updating, a genuine advance, but the generative model uses abstract sector-wise representations and hyperparameters with no biological referent; motor constraints are absent and field of view is approximated rather than geometrically grounded. Ring attractor models [17] connect collective behavior to neural architecture, but the empirical evidence for ring attractor dynamics applies specifically to heading direction encoding in *Drosophila* [20]; whether social bearing to neighbors is encoded through the same architecture remains open for virtually all collective behavior species. Our model differs from all three: it operates at the sensorimotor level with parameters corresponding to measurable biological quantities, maintains persistent uncertain internal representations, and couples perception to action through sensorimotor geometry rather than abstract rules or neural commitments. The active sensing behavior that emerges—agents triangulating to reduce bearing uncertainty and reorienting to maintain neighbors within the field of view—cannot arise from memoryless response laws or abstract belief updating, and the Sobol analysis demonstrates that behavioral transitions are governed by a sensitivity landscape defined by biological quantities rather than fitted constants.

Limitations The cross-species prediction claim remains a hypothesis: parameter regimes corresponding to plausible biological values produce qualitatively distinct collective behaviors, but these predictions have not yet been validated against empirical data from specific organisms. In the current instantiation, neighbor interactions are also not geometrically localized: all estimated neighbors contribute to the cost regardless of occlusion or spatial configuration, which likely constrains observable structures toward ring-like formations. Empirical work suggests that visual neighborhoods based on ray-casting better account for individual responses than metric or topological alternatives [16], motivating geometrically localized interaction as a natural next extension alongside neighbor velocity estimation, validation against species-specific behavioral data, and structured environmental perturbations such as attraction points or external flow fields. The present model also treats all agents as identical; incorporating individual variation in sensorimotor parameters would bring it closer to biological reality and may reveal additional collective phenomena.

6 Conclusion

We have shown that a diverse range of collective behaviors—polarized motion, milling, line formation, and subgroup formation—emerges from the composition of individual sensorimotor regularities, without prescribing interaction forces or fitting descriptive parameters to observed group patterns. Behavioral transitions are governed by parameters corresponding to measurable biological quantities—turning agility, field of view geometry, sensory noise, and memory—the same parameters that determine both successful coordination and its breakdown. This demonstrates that collective behavior is not a phenomenon requiring special interaction mechanisms, but a consequence of embodied agents pursuing simple goals under sensorimotor constraints, and that differences across species can productively be understood as differences in embodiment and environment.

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