Design patterns in the tuning of collective transitions

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Across many scales in biology, from genes to neurons to insects to vertebrates, groups coordinate and solve problems collectively. The strategies that create successful coordination remain in many cases mysterious. There has been lots of speculation that functional collective behavior often makes use of transitions that separate distinct aggregate-scale behaviors. We highlight here recent results in the functional consequences and uses of collective transitions, finding that (1) biological function often relies on active movement of dynamical parameters with respect to transition manifolds, and (2) transitions vary in the abilities they confer and the specificity of tuning that they require. This suggests a view that types of collective transitions, combined with types of parameter regulation near these transitions, define recurring design patterns at a coarse-grained algorithmic level. Design patterns include stable coordination, signal amplification, adjustable sensitivity, bistable switches, collective decisions, and more general multi-stability. This framework represents a convergence of ideas from statistical physics (coarse-graining and phase transitions), nonlinear dynamics (bifurcations), and the biology of collective behavior. Examining examples from neuroscience, gene regulation, and animal behavior, we highlight how this perspective brings specificity to the functional consequences of transitions, simplifies the modeling

of collectives, and clarifies the minimal regulation needed for successful, functional coordination in these systems.

Introduction

At many scales, groups of living things coordinate their actions in a way that provides benefits to the whole. Individual ants gather information and jointly move to an optimal location when their old nest is destroyed [1]; cells in an organism communicate and coordinate to create functional tissues and bodies [2]; neurons jointly hold memories [3] and make decisions [4].

These are examples of information processing, information storage, and control that is distributed over many components. What strategies do living systems use in order to create such functionality? Are there general principles of collective cognition or collective intelligence [5–10]?

While there seem to be analogies across different systems — neurons behave in some ways similar to ants — most often mathematical models are built and analyzed separately for each case. If we take these analogies seriously, it may be possible to rigorously define more general classes of coordination strategies that encompass diverse forms of collective behavior. Such an approach could give insight into the relative difficulty of different strategies and the abilities they confer, which would be useful both in understanding living systems and, more ambitiously, managing and regulating them ourselves.

Marr, in thinking about the implementation of functional behavior in computational neuroscience, gave us a useful way to pull apart the question of collective behavior into three levels (Fig 1) [11][1]. We can think about a problem that a group needs to solve at a functional level, we can think about the space of designs that would solve that problem at the algorithmic level of information flows, and for any given algorithm we can think about the space of mechanisms that can implement that algorithm. Here we focus on the middle "algorithmic" level, aiming to find a classification of collective behavior mechanisms that groups them in terms of the types of functionality that they can create.

[1]Marr and Poggio's original formulation included a fourth level of "hardware," which we merge here into "mechanism".

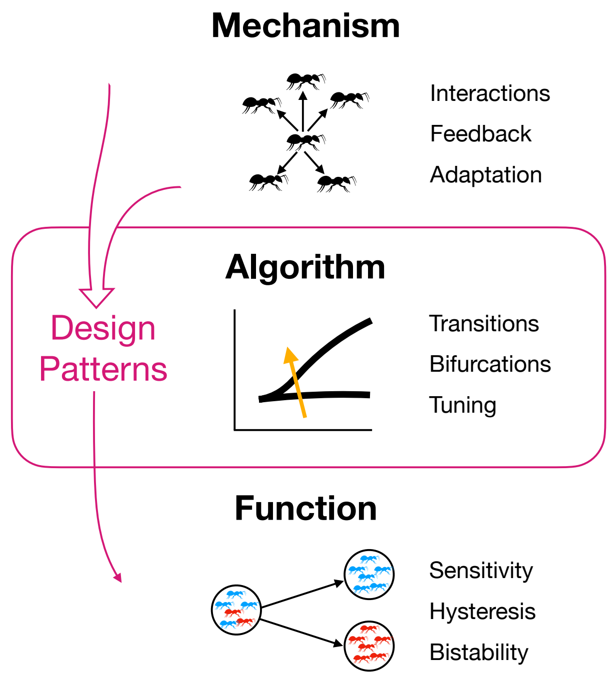

Figure 1: **Design patterns, defined at an algorithmic level, organize the space of possible mechanisms and predict their functional consequences.**

There is a long history in approaching emergent functionality of groups using the theory of collective transitions. Transitions can be carefully defined using the mathematics of nonlinear dynamics (bifurcation theory) and statistical physics (phase transitions). A large and detailed literature asks whether living systems are often near transitions [12, 13] and describes how transitions can create different aggregate states and allow for controlled changes among these states [14]. In Marr's conception, transitions live at an algorithmic level of analysis, providing a useful coarse-graining over the space of mechanisms.

The perspective of collective transitions is powerful in that positioning system behaviors in parameter space relative to transition manifolds gives an opportunity for immense dimensionality reduction and simplification.[2] This simplification is related to, but not limited to, universality near critical phase transitions in the narrower sense explored in statistical physics [18]. The basic idea is that, after mapping from mechanisms to transitions (top pink arrow in Fig 1), only movement relative to low-dimensional

[2] This is closely related to the ambitions of catastrophe theory [15], which largely fell out of favor many decades ago after being over-generalized [16, 17]. We feel that similar ideas are worth revisiting in an era of big data, when we can more carefully test the limits of generalization.

transition manifolds are ultimately relevant, such that large classes of mechanistic structures become equivalent at the algorithmic level.

Historically, theories of how collective transitions can be functionally useful focused mostly on continuous phase transitions, near which (1) aggregate-scale behavior becomes highly sensitive to individual-scale changes and (2) there exist many easily accessible aggregate states [12]. Increasingly, applications of transition concepts to biology are extending from this basic picture to discover the importance of other related phenomena: discontinuous transitions, dynamical effects such as hysteresis, memory, and timescales, and functionality that depends on moving parameters with respect to a transition instead of remaining fixed.

How might we delineate the space of possible uses of collective transitions and how they can be realized in living systems? Here we advance a perspective that begins to define this space. Specifically, we use this framing to identify a number of algorithmic design patterns, which we examine using examples from the recent literature.

The basic picture is as follows: at the mechanistic level, positive feedback[3] in collective systems produces amplification and the possibility of transitions to various ordered states. At an algorithmic level, design patterns in collective transitions are characterized by (1) the singularity that defines a transition (as in statistical physics and nonlinear dynamics) and (2) how parameters are tuned near the transition, across both short behavioral timescales and long evolutionary timescales. At the functional level, consequences result from occupying or moving through different regions of the corresponding phase diagram: sensitivity, multi-stability, timescales of information transfer and storage, individuality versus consensus, controllability, robustness, and specialization.

[3]Here, we define positive feedback effectively, noting that self-reinforcing processes do not need to be strictly excitatory, but can also occur through alternative pathways such as double-negative feedback [19].

Box: **Important concepts for understanding how collective transitions are used in living systems**

1. Biological function is often deeply influenced by *dynamical effects related to transitions*, including sensitivity, hysteresis, the timescales of transients, and symmetry breaking.

2. *Tuning with respect to transition points* is adaptively useful, with tuning dynamics over long evolutionary timescales and at short timescales of learning and active regulation.

3. The difficulty of tuning is naturally described in terms of the *codimension of transitions*.

4. Motion with respect to transition boundaries can often involve *trade-offs*, such as between speed and accuracy and between robustness and adaptability.

We believe that the collective transition perspective allows for more precise and explicit hypotheses about the algorithmic functions being implemented in living systems. While we have books full of design patterns connecting structure to function in, for instance, electrical engineering [20], this has proven more challenging in evolved systems. Some progress has been made by examining the functionality of network motifs, which connect small-scale structure to function [21]. We believe that similar patterns exist in collective behavior that require further coarse-graining across scales. We thus envision a parsimonious organization of the space of collective transitions, their difficulty of being tuned, and their functional benefits, usefully generalizing across the otherwise obfuscating details that muddle intuitive understanding of these complex systems.

The remainder of this review is organized as follows. We first introduce a case study from social insect foraging to illustrate how a specific biological mechanism can be mapped onto algorithmic design patterns with functional consequences. We next survey a range of collective transition design patterns across biology, emphasizing how different transition geometries and modes of tuning are associated with distinct functional uses. Finally, we consider challenges and open questions for this framework, including the extent to which low-dimensional transition descriptions generalize across systems and how such hypotheses can be tested empirically.

Case study: Social insect foraging

Social insect foraging provides an intuitive example of how interactions among individuals can generate collective transitions and how the tuning of those transitions can create ecologically useful dynamics. In the ant *Pogonomyrmex barbatus*, a known mechanism leads to positive feedback in foraging activity, and the colony must balance the benefits of exploiting food resources against the costs of sending workers into a dangerous environment. This makes the system useful for illustrating how a mechanistic rule can be mapped onto an algorithmic design pattern and then onto biological function.

Mechanism

The red harvester ant *Pogonomyrmex barbatus* is a seed-harvesting desert ant of the southwestern United States. Colonies forage for spatially scattered seeds that can be retrieved by individual workers, so unlike trail-recruiting ants, they do not need to direct nestmates to a particular food location. What matters is not where food is, but the rate at which successful foragers return to the nest [23–26].

The decision rule operates in the entrance chamber (Fig 2A). Returning foragers pass through this chamber and briefly interact with ants waiting to go out. These antennal and chemical interactions make waiting ants more likely to leave the nest. The probability of departure can be represented by an approximately sigmoidal input–output rule [22, 27–31] (Fig 2B). At the colony level, this creates a positive feedback loop: more successful returns stimulate more departures, which can ultimately generate still more returns.

This amplifying architecture differs sharply from systems in which regulation is based primarily on implicit negative feedback. Positive-feedback systems are often "default off": activity does not begin unless reinforcing events occur. By contrast, negative-feedback systems are "default on": activity continues unless something interrupts or suppresses it [24–26]. Harvester ant foraging fits the first picture. The colony does not fully activate unless returning foragers provide sufficient evidence that conditions are worth the cost. At the same time, the system is not purely runaway amplification: slower processes can damp the response. If return flow remains low for several minutes, ants waiting near the entrance

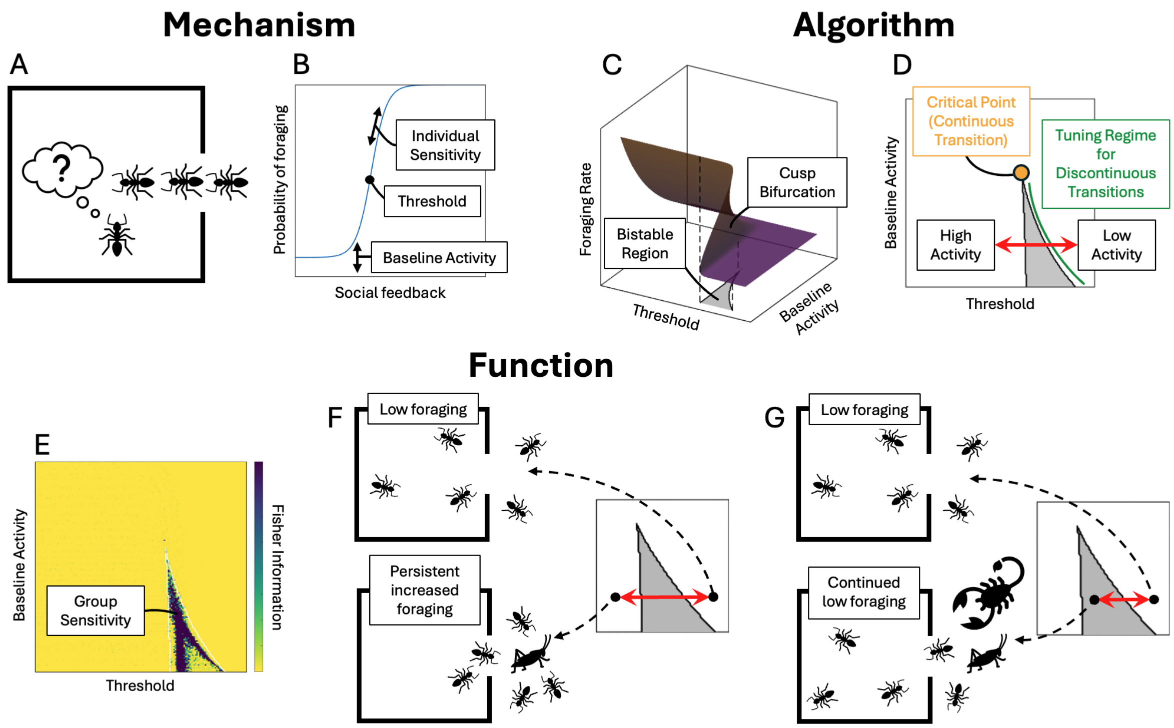

Figure 2: **A case study: social insect foraging with tunable feedback. Mechanism** (A) Returning foragers provide brief social contacts to ants waiting near the entrance, and these interactions inform a focal ant's decision to forage. (B) A decision curve links social feedback (interaction rate from returning foragers) to the probability that an available forager exits the nest. Parameters control the baseline foraging activity of individuals, the threshold to social spreading, and the sensitivity of individuals to social feedback. **Algorithm** (C) A cusp bifurcation characterizes changes to the fixed points of foraging dynamics as two control parameters are varied. (D) A bistable region (gray) separates two monostable regions in which collective foraging rates are always high or low. Saddle-node bifurcations occur at the edge of the bistable region (black curves), and the cusp or critical point happens where the two saddle-node boundaries meet (orange dot). A hypothesized tuning region (green) lies on the low-activity side of the bistable boundary, where environmentally driven parameter shifts can trigger discontinuous transitions into the high foraging state. **Function** (E) Sensitivity, measured by the Fisher information, is largest near the edges of the bistable region, where small parameter changes can induce large changes in the collective output [22]. (F and G) Strong bistability can create all-or-nothing responses that depend on the availability of resources and whether a predator is present. In the no-predator case (F), small baseline foraging transitions into coordinated and persistent recruitment to a food item (e.g., a cricket) and then returns to low activity after the resource is exhausted. In the predator case (G), the same resource is paired with a predator (e.g., a scorpion), eliciting retreat and limited recruitment. The parameter trajectory terminates within the bistable interior, failing to reach the high-activity branch.

move deeper into the nest, reducing the pool of workers available for rapid activation [31,32]. Thus the core leaving rule is positively reinforcing, but it is embedded in a broader regulatory mechanism that can also withdraw availability.

Algorithm

To analyze the foraging dynamics at the algorithmic level, we coarse-grain the activity into a single colony-level rate of foraging. In a mean-field analysis, the surface of possible fixed points as a function of parameters can fold over itself, creating transitions in the form of dynamical bifurcations. In the case considered here, the relevant geometry is a cusp [22]: two saddle-node bifurcations bound a bistable region and meet at a cusp bifurcation (Fig 2C). The cusp is the critical point of the corresponding phase diagram,[4] and the edges of the bistable region act as phase boundaries separating low-activity and high-activity monostable regimes from the region in which both attractors coexist. Within this picture, the same colony can display qualitatively different transitions depending on how parameters are varied. Some trajectories through parameter space produce gradual, continuous changes in activity, whereas others cross a fold and generate abrupt, discontinuous switching with hysteresis.

This algorithmic description is useful because it abstracts away from mechanistic particulars. The same bifurcation structure occurs across many potential mechanisms. This hints at a limited form of universality: the functionality may be fully characterized by the bifurcation geometry without referring to details of any one ant model. Across broader families of positive-feedback and threshold-like models, modifying the form of memory, heterogeneity, or response functions can produce different bifurcation structures, including epidemic-threshold-like onset, critical-mass dynamics, and cusp-like bistability [33, 34].

At this coarse-grained, lower dimensional level, questions about tuning also become simpler to reason about. Tuning toward a particular transition point involves a predictable number of dimensions

[4] More precisely: In mean-field, the critical point as encountered in the all-to-all coupled Ising model maps onto a cusp bifurcation [22]. The saddle-node bifurcations correspond to the discontinuous transition that occurs at lower temperatures in the Ising model. The description in terms of bifurcation theory has the advantage that it does not require taking the thermodynamic limit in which the number of individuals is taken to infinity.

in parameter space depending on the transition type. If selection favors a discontinuous, "default-off" switch, then colonies need not sit exactly at a single critical point. A possibility posed here is that a single baseline parameter is tuned to the low-activity side of a phase boundary, close enough that environmentally induced shifts can push the colony across it when appropriate [25, 26, 35, 36]. This parameter can then be dynamically altered across the bistable region (red arrows in Fig 2D). This is a useful generalization of the idea of critical tuning. Instead of requiring the colony to remain fixed at one special point, it requires the colony to occupy a region of parameter space from which functionally distinct collective outcomes can be reached quickly. In this way, the algorithm provides the map between mechanism and function. The form of interactions creates a low-dimensional bifurcation structure, and position within that structure determines what kinds of collective functionalities are available.

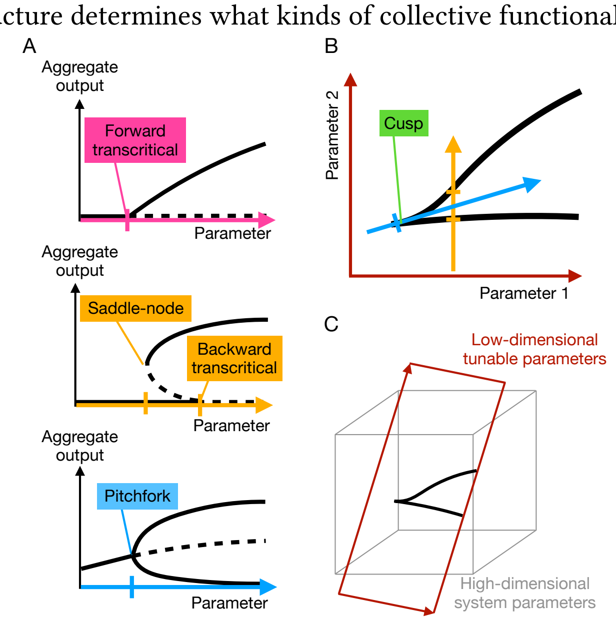

Figure 3: **Tuning across transitions in increasing numbers of dimensions.** Bifurcations structure parameter space, with the codimension setting the number of parameters that must be tuned to locate a particular transition. (A) Bifurcations of codimension 1 require the tuning of a single parameter. Black curves represent fixed points of the aggregate-scale dynamics, with solid curves stable and dashed curves unstable. (B) In a two-dimensional space, bifurcations of codimension 1 lie along curves (black curve) and those of codimension 2, like the cusp, occur at points. (C) Tunable parameters make a low-dimensional slice through a potentially high-dimensional set of system properties.

We refer to the number of system parameters needed to be tuned in order to poise a system at a given transition as the "codimension" of the transition (see Fig 3).[5] In the ant foraging example, the codi-

[5]Note that multiple notions of codimension are used in the literature when describing bifurcations. Here we are interested in the number of parameter dimensions that must be constrained to remain on the relevant singular manifold on which

mension of the discontinuous transitions at the edge of the bistable region is 1: while parameters can drift in some directions without qualitative changes to the collective behavior, moving along the dimension perpendicular to the transition manifold leads to large-scale changes. We describe parameter tuning using the concept of codimension because it generalizes well. First, we can easily describe transitions that require more tuning—for instance, the continuous transition in this model (the yellow cusp point in Fig 2D) has codimension 2. Second, in most cases we can imagine many more parameters that could affect collective behavior than the two that we highlight in this simple example. Through such a higher-dimensional parameter space, a smaller set of tunable parameters makes a low-dimensional slice (Fig 3C). The codimension, equal to the total number of parameters minus the dimensionality of the manifold on which a given transition happens, represents the number of parameters we expect to need to tune for such a slice to intersect a given transition manifold.

Function

At the functional level, the existence of a collective transition creates a system that is highly sensitive when sensitivity is useful, yet still capable of withholding commitment. Sensitivity is greatest near the phase boundaries, where Fisher information is maximized [37] (Fig 2E). This means that small changes in control parameters (for example, in how strongly returning ants stimulate nestmates, or in the effective threshold needed to trigger departure) can lead to large changes in the colony's aggregate foraging rate. Near such boundaries, the colony is poised so that small differences in local evidence can be amplified into large differences in collective outcome. While it is not known exactly where in such a phase diagram real harvester ants sit, we can speculate about the functional consequences for colonies that regulate collective behavior by passing through such transitions.

Harvester ants forage in arid environments, where workers pay a substantial cost simply by being outside the nest. Colonies effectively spend water to obtain food and water in these hot, dry conditions [24–27,38]. Unnecessary activity is costly: workers outside the nest risk desiccation risk and predators, so the colony should not fully mobilize unless conditions justify it [25, 26, 35, 38].

a particular bifurcation occurs.

A colony can shift from a low-activity monostable regime into a high-activity monostable regime by tuning individual thresholds such that fewer incoming ants are needed to trigger other ants to leave, crossing the bistable region (Fig 2F). Response-threshold theory offers a useful language for interpreting how such effective thresholds might change. In those models, experience or task performance can alter response thresholds over time, through processes such as reinforcement [39, 40].

At the same time, the signal can be damped (Fig 2G). Unfavorable dry air, a decline in food return, or exposure to a danger can reduce return flow or reduce responsiveness after ants experience the outside environment, thereby shrinking the excursion through parameter space and preventing the colony from fully committing to the high-foraging branch [28, 31, 32, 38, 41]. In that context, the value of the switch is not merely that it can turn on rapidly, but that it can also fail to engage or can be interrupted before the colony overcommits to a dangerous situation.

Synthesis: Design patterns

Taken together, this case study demonstrates two potential design patterns that make use of a collective transition. The starting point is a positively reinforcing mechanism that can amplify small differences in return flow into much larger differences in colony-level activity.

The tuning of this amplification may itself be functionally useful. This is what we call the "adjustable sensitivity" design pattern. Functionally, adjustable sensitivity allows a collective to modulate how strongly local information is amplified into a group-level response. This can be beneficial when the relevance of social information varies across environments: greater sensitivity can promote rapid responses to weak but important cues, whereas lower sensitivity can reduce costly responses to noise or false alarms. Adjustable sensitivity therefore provides a way to balance the responsiveness/robustness tradeoff.

If amplification is large enough, this will produce bistability, with a discontinuous transition between alternative activity regimes. Discontinuous transitions of this kind can be ecologically advantageous because they implement a fast, state-like shift between low- and high-activity regimes without relying on a centralized controller (Fig 2F). We call this the "bistable switch" design pattern. This can allow for exploitation of resources that may be transient due to competition or environmental loss. As the resource is depleted, return flow declines, interaction rates drop, and the control parameter relaxes back toward baseline, returning the colony to the low-activity state. Because bistable switches create hysteresis, recruitment can briefly persist even after returns begin to wane, appearing as an overshoot in outgoing effort. Such persistence may itself be adaptive if it reduces the risk of abandoning a profitable patch before it is fully harvested. The same mechanism can confer robustness to danger. If foragers encountering predators retreat or fail to return, the social cue is damped, the control parameter shifts less, and the system may remain on the low-activity branch, thereby avoiding a costly global activation in hazardous conditions.

In this example, tuning near and above a cusp bifurcation creates access to tunable sensitivity and bistability, but the broader lesson is more general. The functionality does not depend on the mechanistic details by which the bifurcation is implemented. Rather, it depends on the existence of a collective transition with the right dynamical geometry. It is in this sense that we refer to design patterns. Framed this way, the present example motivates a broader search for other design patterns generated by tuning parameters near collective transitions, which we explore in the next section.

Importantly, even when the underlying control-parameter space is high-dimensional, effective tuning may occur along low-dimensional subspaces. In our schematic figure (Fig 3), we illustrate how a two-parameter bifurcation structure can be viewed as a slice through a larger-dimensional space of mechanistic parameters: a small set of tunable, coarse-grained "effective" parameters defines a low-dimensional space in which the global dynamics can be controlled. Within this reduced space, different trajectories can traverse the same bifurcation structure in qualitatively different ways, producing either discontinuous switching (for example, by crossing a saddle-node boundary into a distant attractor) or continuous onset (for example, by moving through a forward transcritical transition), depending on how the effective parameters are regulated. While the aggregate-level bifurcation geometry can often be inferred from such low-dimensional descriptions, the individual-scale dynamical mechanisms that generate particular transition types (continuous versus discontinuous) and particular mean-field bifurcations (transcritical versus cusp) are only worked out in some classes of models, such as social spreading-type models [33, 34, 42], and remain an active area of research.

Collective transition design patterns across biology

Our working hypothesis is that many living systems regulate their positioning relative to collective transitions, and that the functional implications of this regulation are best understood at the level of algorithmic design patterns. In this section, we highlight examples of such tuning, organized roughly in order of increasing complexity of active regulation (Fig 4). For each design pattern—consisting of a collective transition combined with tuning relative to the transition—we highlight multiple examples across living systems, emphasizing the functional uses of the collective dynamics. The examples we include vary in closeness to experimental data, but all are connected to experiments in some way—we want to emphasize that aspects of collective transitions are being measured in real systems, not just toy models.

In the simplest type of tuning (Fig 4A and B), the parameters governing collective behavior are relatively fixed, with values set over a slower evolutionary timescale, and potentially kept fixed using active processes. In other cases, active tuning changes parameters based on environmental inputs. Changes to the strength of interaction or coordination among components can actively up- or down-regulate social information channels (Fig 4C), or tuning of a bias toward one or another aggregate state can lead to discontinuous switching between coordinated states (Fig 4D). In more complicated examples of regulation, collective behavior can vary both in the degree of coordination and in the specific aggregate states displayed by the group. We may interpret these cases as collective decisions, in which environmental inputs are integrated into a choice among two or more ordered states (Fig 4E), or as merely creating large numbers of possibly useful ordered states (Fig 4F).

These design patterns serve as distinct hypotheses for how tuning relative to transitions may be used functionally in collectives. We note, however, that we are not trying to classify biological systems into rigid categories. As we learn more, we may find that some living systems are implementing more complicated computations than we thought, or may even be simultaneously implementing multiple

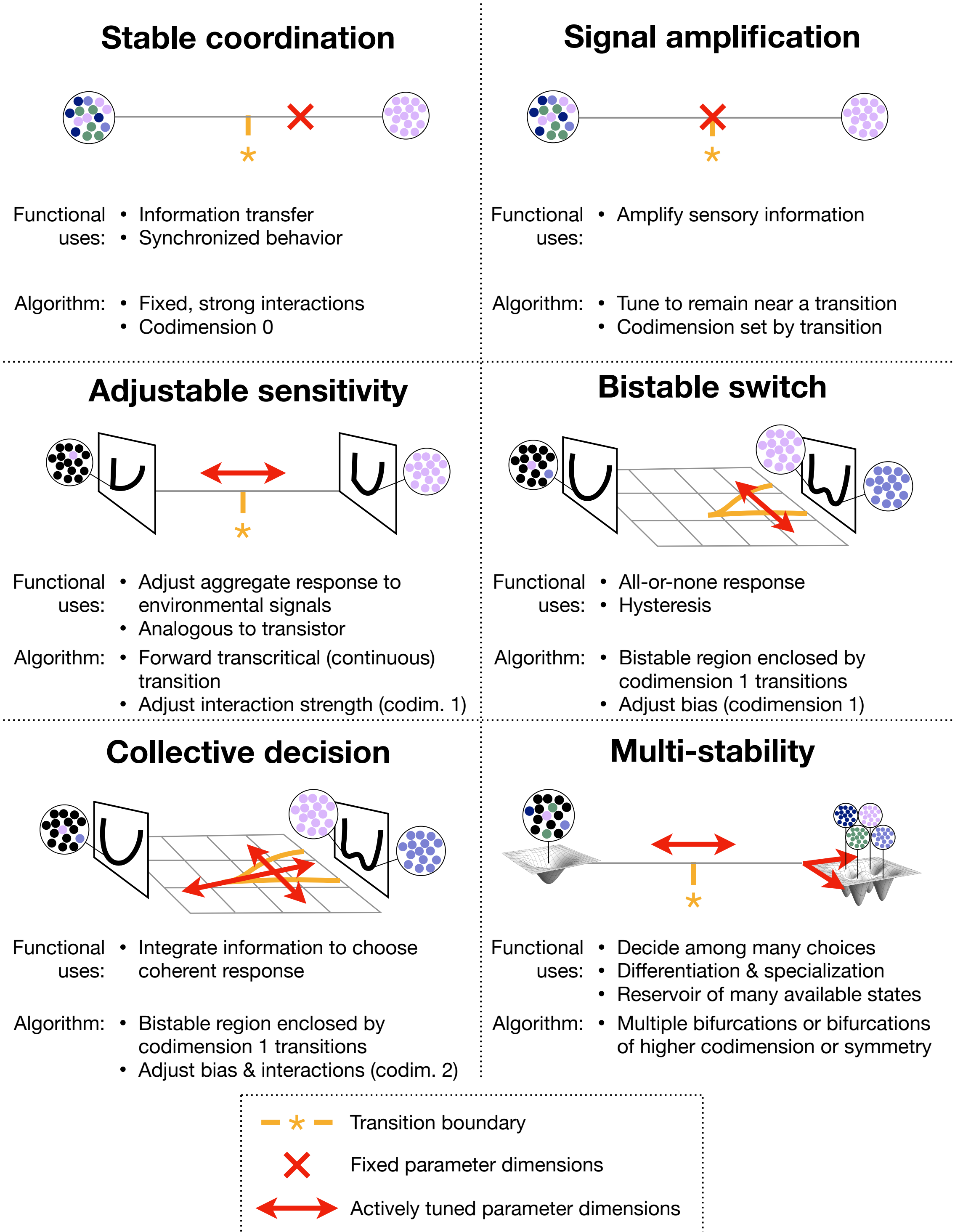

Figure 4: **Design patterns in collective transitions.** Different types of transitions plus active adjustment of parameters produce design patterns with different functional abilities.

types of computations [43]. Note, too, that this is not a comprehensive listing of all possible useful design patterns — indeed, this is probably impossible. Yet efforts are underway to categorize at least all possible collective transitions under some constraints: Siggia and coworkers have made progress in this endeavor by enumerating all local and global bifurcations among three fixed points [44].

"Stable coordination" design pattern

While our analysis of collective algorithms focuses mostly on cases in which parameters are actively varied, we begin with cases of collective function via fixed positioning relative to a transition. The simplest cases create some fixed stable coordinated aggregate state.

We see stable organization in many examples in biology. Some species of firefly strongly synchronize their flashes [45], and in large groups, locusts move together in strongly ordered waves [46]. Though there are certainly effects on the fitness of organisms in these groups, the details are still debated. The function of coordination is more clear in cardiac cells, which synchronize their activity to create a stable productive heartbeat: the lack of strong coupling creates fatal arrhythmia [47]. In these cases, to retain the ordered collective behavior does not require precise tuning, merely that interactions are strong enough to maintain stabilizing feedback.

Another strategy for collective coordination that does not require precise tuning of interactions arises in strongly ordered group dynamics that break a continuous symmetry.[6] Examples include the propagation of orientational waves in bird flocks [48] and continuous ring attractors in neuronal dynamics [49]. In these examples, components are stably coordinated, and there is some information being stored or transmitted in continuous symmetries. This functionality requires that interactions are sufficiently strong so that the system is deeply in the ordered phase with respect to a collective ordering transition, and it also requires that the relevant continuous symmetry is respected in the absence of other inputs (that is, there should be no bias toward any specific ordered state). Functionally, this can be useful in that the aggregate state serves as an easily modified collective memory of a continuous variable, such as a direction in space. For instance, birds in a flock may benefit from a coordinated aggregate direction

[6]This is known as a Goldstone mode in statistical physics.

that stays fixed in the absence of input but can also quickly change in the presence of a predator that is observed by a subset of birds. Similarly, ring attractors are used in brains as a stable memory of orientation that can be easily updated during turns.

Because stable coordination does not require tuning to a specific transition point, we say that this design pattern has codimension 0.[7]

"Signal amplification" design pattern

An oft-cited advantage of being near a continuous symmetry-breaking transition is that the aggregate state becomes highly sensitive to small inputs [13]. This means that the aggregate state can effectively become an amplified representation of an environmental input at a much smaller scale. For instance, cochlear hair cells are optimally sensitive to weak sounds by actively being tuned to sit near a Hopf bifurcation to ordered oscillatory behavior [12]. Similarly, evidence has been found that the sensory organ in snakes for detecting temperature effectively amplifies differences in temperature by remaining near a saddle-node bifurcation [50]. More speculatively, theories suggest that feedback among cells in a tissue can lead to optimal sensing of slow changes to chemical concentrations when it is tuned near a pitchfork bifurcation [51]. In cases like these, maintaining maximum sensitivity may require tuning to remain near the transition, but the functionality does not require actively changing parameters.

The number of parameters needing to be tuned in order to remain at the transition is equal to the codimension of the corresponding transition. For example, the Hopf bifurcation used by the cochlea has codimension 1, requiring the tuning of parameters along a single dimension, which is thought to happen through the active regulation of calcium ion concentrations within hair cells [12].

[7]This is a slight abuse of our definition of codimension above in the sense that we are not near a transition in this case. Instead, we are using a more generic notion of codimension that specifies the number of parameter dimensions needed to be finely tuned in order to retain a relevant biological function.

"Adjustable sensitivity" design pattern

Contrasting with the conventional story about the optimality of criticality, recent literature has repeatedly found that living systems vary, in many cases over a relatively short timescale, in their locations with respect to collective transitions. We therefore include the variation of parameters in our categorization of collective transition design patterns.

A relatively simple way for collective behavior to adapt to changing conditions is by regulating the strength of social channels of information flow. This varying of a single parameter regulates the distance from a transition at which behavioral cascades change from staying localized to spreading through most of the group.

We highlight here four examples in which the effective strength of interactions varies over time (or is hypothesized to vary over time), moving the system with respect to a transition boundary. This variation changes the responsiveness of an aggregate state to individual-scale perturbations. In a sense, such a design pattern acts like an "informational transistor": varying one parameter alters how strongly information in another variable is amplified.

This design pattern may involve one of many transition types, with the simplest involving a percolation transition, which as been well studied in epidemiology. The simplest such transition maps onto a transcritical bifurcation [52, 53], with codimension 1, varying a gain parameter to adjust the sensitivity.

Alarm spread and schooling in fish: The spreading of alarm signals in animal groups is likely optimized by balancing the costs of false positives against false negatives [54], altering the degree to which individuals' alarmed behavior is amplified to a colony-level response. In fish schools, the spreading of startle behavior is thought to aid fish in being alerted to predators in the environment. Under higher predation risk, golden shiner fish are known to swim closer together and increase the collective sensitivity to startling [55]. The fish thereby vary their distance from a transition to large startle avalanches [54]. A similar story comes from wild coral reef fish, where the best fit of startling cascades is consistent with fish modifying their response thresholds dynamically based on recent input rates.

This can be interpreted as the dynamic control of gain that may be able to suppress the spread of misinformative false alarms [56]. In each case, the largest sensitivity happens near the transition at which the quiescent state becomes unstable, and the variation of a single parameter sets the average cascade size.

In the schooling of fish, collective states include disordered swarming and ordered states such as schooling and milling [57]. There is evidence in one species of fish that schools vary in their proximity to an optimally sensitive point near a collective transition, becoming more sensitive when in small groups and when there is an external stressor [58]. Functionally, we can speculate that social information about predation risk becomes more valued to individuals in more uncertain environments. This then has collective effects in that cascades of socially initiated behavior become larger in riskier environments. The functional effects of this adjustable sensitivity of collective behavior are complicated in that there can be a tension between individual and group fitness [59].

Macaque conflict: In societies of macaque monkeys, the spreading of conflict behavior has functional implications in that large fights are disproportionately costly to individuals, and fight outbreaks are regulated by specialized "policer" roles [60]. In a branching process model inferred from data tracking a colony of 48 individuals, the colony was below a collective transition to much larger fights [61]. The distance from that transition can be characterized in terms of the number of individuals who would need to be simultaneously aggressive to bring the group to a collective instability: 3 to 5 individuals [61]. Some individuals have an outsized ability to change the group's distance from the transition, which they may use to regulate the tradeoff between adaptability and robustness of social hierarchies [61]. In this example again, varying one collective parameter can tune the average size of fight cascades.

Neuronal systems: In systems of neurons, recent work has focused on the fact that brains are not typically "at" a critical transition, but adjust to be closer or further from criticality [62, 63] based on attentional or vigilance states [64–66] and the sleep-wake cycle [67, 68]. In this sense, we can view the broadest scale dynamics of the brain as varying a single parameter that changes the propensity of information to flow. In neuroscience, it is commonly assumed that active homeostatic processes control the balance of excitation and inhibition to keep the system away from quiescent or synchronized activity states [62, 69]. It remains unknown how much active regulation is required. It is known that the distance from a transition can be modified by, for instance, the addition of drugs [70]. We return to neuronal examples below, showing how the tuning of additional parameters near transitions relates to other functional abilities.

Harvester ant foraging: In the case study above, harvester ant foraging dynamics depend on the strength of feedback. There is evidence that this feedback strength varies as a function of the dryness of the environment [27, 30, 71], modifying how sensitive the colony is to an increase in available food sources. It is unclear whether feedback is strong enough to create a transition that includes bistability, as explored in the next design pattern.

"Bistable switch" design pattern

When collective dynamics produce two distinct ordered states, dynamics can be mapped onto cusp or cusp-like transitions, which result in the creation of bistable regimes that lie between codimension 1 transitions such as saddle-node or transcritical bifurcations. Varying degrees of gain (interaction strength) and of bias toward the two collective states create both order-disorder transitions (controlled by the strength of information flow between individual components) and order-order transitions (controlled by bias toward a particular ordered state). We start with examples of a bistable switch, in which strong fixed interactions put the system into a bistable regime and the parameter controlling bias into one of the two ordered states is varied.

All-or-nothing responses can be thought of as order-order binary switches in which the two stable states differ primarily in activity level: low engagement versus a high-engagement, mobilized state. The key functional signature is that intermediate engagement is not merely suboptimal, but actively disadvantageous. For example, in **cooperative transport in social insects**, a sufficient number of workers must simultaneously commit in order to move an object coherently. Intermediate organization can be actively wasteful: partially aligned teams deadlock or stall, burning time and effort while leaving the item exposed to competitors and predators [72,73]. Accordingly, selection can favor mechanisms that drive rapid convergence to a coherent transport regime (and maintain consensus even while navigating complex terrain), rather than continuously tracking stimulus strength through prolonged, weakly coordinated pulling [74,75]. Bivouac formation likewise becomes protective and functional only after sufficient structure is assembled; a partially formed bivouac would immobilize workers while still leaving queen and brood exposed [76]. In these cases, the adaptive value is not simply a steep response, but the avoidance of "half measures" that incur costs without delivering returns.

Comparable all-or-nothing dynamics occur in **defensive systems across eusocial taxa**, where intermediate responses can be especially costly. In honey bees, alarm pheromone released by guards recruits nestmates to sting vertebrate predators; deterrence rises steeply with the number of stings, so a small response can both fail to repel the threat and incur high mortality, whereas a large, coordinated attack can quickly drive predators away [77]. Vespine wasps similarly exhibit recruitment cascades in which many workers attack a marked target or almost none respond [78]. In termites, vibrational alarm signals can trigger colony-wide freezing or retreat; rapid, near-binary coordination can evacuate exposed tunnels, whereas a weak or localized response would leave workers and brood vulnerable while still diverting effort from foraging [79]. Though these examples of bistability have not yet been approached using the mathematics of collective transitions, we suspect that they arise from similar dynamics that could be usefully described in a bifurcation framework. In particular, the existence of all-or-nothing bistability in behavioral cascades can often be traced to backward transcritical bifurcations (Fig 3A) [80, 81].

As highlighted in our case study above, **social insect foraging** often involves feedback that can lead to a transition to bistability [22]. Stable pheromone trails in Pharaoh's ants require a minimum number of ants to persist, displaying a sudden transition from disordered to ordered foraging [82–84], creating bistability and hysteresis. And across many social insect foraging models, amplification of foraging activity can create a similar discontinuous transition between low and high rates of foraging [22, 80, 81, 85].

Neural dynamics: While neural transitions may also implement collective decisions that integrate specific information (next section), there may be other functional advantages for all-or-nothing switches. Some initial evidence of this comes from studies of overall brain dynamics, which has also emphasized that locating a transition to bistability via positive feedback requires tuning two parameters that effectively control bias across the two states and the strength of positive feedback [86]. In *in vivo* data from electrical activity in the human neocortex, bistability in oscillatory behavior was observed across multiple frequencies, and was shown to occur in a computational model along a codimension-1 band of parameter space that had dynamics indicative of a transition. Further, there seems to be functional relevance of this transition state, with "moderate bistability ... positively correlated with executive functioning" [86], and too much bistability leading in the extreme case to epileptic seizure.

"Collective decision" design pattern

When dynamics are such that the symmetry between two or more aggregate states is broken by a relevant environmental input, we call this collective decision making. Such a collective decision design pattern arises from an order–disorder transition. From social insect colonies choosing a new nest site to primate brains making a perceptual discrimination, avoiding coming to a hasty conclusion based on little evidence requires restricting the amplification of information or increasing thresholds for action [87–89]. This suggests tuning of the strength of interactions to control the speed of decision dynamics [90]. In some cases, active tuning of parameters is thought to happen across different phases of a decision process: a phase in which the system is susceptible to inputs, followed by a consensus phase in which the chosen decision is amplified and other alternatives are removed from consideration [4].

Social insect decisions: Social insects are well-known for making collective decisions by amplifying information known to individuals in order to guide the coordinated behavior of an entire colony [91]. Tuning across a transition from disorder to order can be functional insofar as it regulates when the group explores versus when it exploits—shifting between a disordered regime that supports broad, parallel sampling of alternatives and an ordered regime that concentrates effort into coordinated commitment. For example, trail-based recruitment can implement this exploration–exploitation control by coupling a disordered search phase to an ordered commitment phase. Positive feedback between pheromone deposition and trail following can amplify small initial biases and produce symmetry breaking in how foragers are allocated among alternatives [92, 93], allowing colonies to transition from distributed sampling of options to stable exploitation of a single route even when overall foraging effort is similar. Quorum-threshold systems are closely related. Once support for a site or option exceeds a critical level, the collective switches into a committed recruitment or action mode, converting graded evidence accumulation into discrete commitment [1,94,95]. Some ants lower the threshold for choosing a new nest site in more urgent situations, actively choosing to prefer speed over accuracy [88].

Neural decisions: The representation [96] and neural implementations [97, 98] of decisions in the brain have historically been tackled with variants of the drift diffusion model [99, 100]. A mostly separate strand of the research literature has focused on decisions represented as attractors. This alternative approach uses feedback to create stable equilibria representing the possible decisions [4, 101, 102]. This approach can naturally incorporate both deliberation and commitment by varying parameters with respect to a collective transition. For a binary decision, crossing a cusp bifurcation along the symmetry-breaking path in parameter space can combine a deliberation phase near the transition with commitment beyond the transition. Functional decision-making may require a change from high sensitivity during a stimulus to high coordination during the decision output [4]. Measured spiking data from perceptual decisions in monkeys show dynamics of neural decision information consistent with a dynamically varying distance from a phase transition [4]. Further theoretical work confirmed that the same mechanism can function in cases of quenched disorder (adding noise to coupling constants) [103] and in interaction networks with more complicated structure [90]. Two parameters must generally be tuned to reach the transition because the corresponding cusp bifurcation has codimension 2 [104]. These results suggest that, even for strong heterogeneity, functional decision-making requires tuning just two global parameters [103].

Recent work has combined the drift-diffusion picture with the attractor picture by assuming an integrator that builds a decision variable by integrating the summed activity of interacting neurons [105]. Depending on the relative strength of excitatory interactions and global inhibition, the dynamics enters different phases with different decision properties, allowing for tuning between fast rough decisions and slow accurate ones. This has been connected to experimental evidence that inhibition, as measured by levels of inhibitory neurotransmitter (GABA), increases during more difficult decision tasks.[8]

[8] In this model, symmetry between the two decision states is assumed *a priori*, and the transition type is somewhat more complicated: up to three stable fixed points consisting of one inactive state and two active decision states (with mirror symmetry between the decision states). The upshot is that, with the bias fixed at zero, a single parameter (the inhibi-

Gene regulation: In gene regulatory networks, it is known that positive feedback can create bistability and the degree of bistability can be adjusted by tuning the strength of this feedback. Creating bistability where there was none before has been demonstrated experimentally by increasing the strength of a positive feedback loop in regulatory gene expression dynamics [106]. The emergent states of gene regulation can then look like a collective decision in which an initial "undecided" gene expression state falls into one of two types. These transitions into discrete aggregate states are thought to be how specialized cell types are created [44, 107]. The binary decision becomes a base case for thinking about more complicated cases with multiple cell types.

In the process of development, we expect multiple dynamic transitions that destabilize pluripotent aggregate states and create stable attractors corresponding to differentiated cell types. There are multiple forms that such transitions can take, and progress has been made in enumerating the possibilities by focusing first on collective decisions that start with one stable attractor and end with two (with the assumption that more complicated transitions with larger codimension will be less commonly employed) [44]. Though still describing collective decisions, these can include bifurcations beyond the cusp-like variety that we have highlighted here. Experimental gene expression data has been shown to be consistent with the predictions of models that minimally reproduce particular bifurcations by constructing an effective potential [108].

This picture of differentiation extends, too, to super-organisms, with individuals transitioning among different states with specialized gene expression and behavior. Such a transition to bistability in gene expression related to behavior was recently found in honey bees [109]. Young honey bees perform in-hive tasks and later transition to foraging. This behavioral transition is thought to be connected to a feedback loop in gene interactions within bees that can also be influenced by external signals. Gene expression measured across ensembles of age-matched bees reveals the appearance and growth of bistability consistent with movement past a continuous transition (pitchfork bifurcation) [109].

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tion) controls the stability of the undecided state, which therefore controls the timescales of integration of evidence, and therefore the speed and accuracy can be tuned by varying the distance from the transition. Though the original work did not explicitly identify the transitions in terms of bifurcations, it appears that changing inhibition at fixed temperature corresponds to a subcritical or supercritical pitchfork bifurcation, depending on the temperature. And we surmise that the supercritical case would unfold into a cusp bifurcation when allowing for nonzero bias. The subcritical case allows three stable states: an "intermittent" state involving switching between an uncommitted state and two "ballistic motion" states corresponding to the two possible decisions.

Ant collective transport: A study of *Paratrechina longicornis* ants showed that, when the ants carry large objects back to their nest, ants acting to lift the load mostly continue to carry it in the same direction it is already moving, while the collective direction of travel is transiently affected by ants that newly attach to the load [110]. There is an optimal amount of social amplification at which the group direction remains most sensitive to information from new ants picking up the load. For small objects, the path of the object toward the nest is more tortuous but the ants are better able to navigate around barriers, while for large objects, paths become straighter but the object can get stuck if there are obstacles blocking the way. Variation in amplification is connected to the size of the object, which sets the number of ants contributing to lifting the object and thereby controls the effective strength of amplification and where the group sits with respect to the collective transition between diffusive and directed motion [111].

Animals moving toward multiple alternatives: Imagine an animal viewing multiple equally desirable targets. Intuitively, we can predict that the animal will move toward the middle of the group of targets when far away, but will switch to move toward just one of them when the perceived angle between targets becomes large. This behavior can be explained by collective neural activity that forms a ring attractor (which can be created, for example, using neurons that are physically arranged in a ring topology, with locally excitatory and globally inhibitory interactions) [112]. As the animal moves toward the targets, there is a transition between a "compromise" aggregate state, centered at the mean perceived angle of targets, and "decision" aggregate states, each centered on an individual target. With multiple targets at different angles, and in the absence of other symmetries, this model predicts multiple pitchfork transitions that each involve a binary decision: splitting the remaining possible targets into two groups and heading toward the mean of one of the groups [113]. This binary splitting phenomenon has been measured in fruit flies, locusts, and larval zebrafish using immersive virtual reality environments [112]. The relation to tuning of parameters in this case is somewhat more complicated. Note that the decision dynamics rely on a symmetry breaking from among the continuous states defined by the ring attractor. This requires tuning to produce an emergent continuous symmetry, such that there is no bias toward any particular orientation. Also note that, in this example, physical motion in space tunes parameters across collective transitions. Other neural parameters alter where in physical space these transitions occur, effectively tuning the certainty an animal needs to have before committing to a single target instead of hedging its bets with multiple options.

"Multi-stability" design pattern

Dynamics that create the possibility of large numbers of ordered states can create a variety of functionally important transitions as parameters are tuned. The existence of many metastable states leads to a rich set of possibilities, with potentially many transitions and more complicated transitions, an avenue that we leave open-ended here.

Neuronal metastable states: It is a natural and popular hypothesis that the functioning of brains is related to their ability to create many different collective states, among which they can switch relatively easily. Dynamics that produce large numbers of metastable states are then clearly a good place to start in thinking about neuronal function. This idea has been explored for a long time in models connected to real data [114], with the simplest conclusion being that models near a critical phase transition produce many metastable states.

Recent work has focused on how the interplay between positive local feedback and global negative feedback creates tunable regimes near a critical point: both continuous and discontinuous transitions organized around bistable regimes [86]. After a model neuronal network learns to produce dynamic patterns (by creating attractors, as in a Hopfield network), changing two parameters (the strengths of global inhibition and learned excitatory interactions) moves the system toward or away from a bistable area with hysteresis or a continuous area that shows large fluctuations and persistent changing between learned patterns [115]. There is some evidence that models in this regime are consistent with observed brain dynamics [116].

The exact structure of transitions (the points at which individual metastable attractors gain or lose their stability as a function of global parameters) is less of a focus here, instead looking for global parameters at which, for instance, the typical timescale for staying near an attractor diverges. Presumably, focusing instead on particular attractors (memories) could also reveal parameter directions that produce discontinuous transitions between different memories (akin to the bistable switch design pattern) or continuous transitions that could create individual collective decisions.

In terms of function, it is easy to believe that both regimes would be useful. As the authors point out, "hysteresis is necessary, for example, for sensory and memory persistence, while operation close to criticality advantageously optimizes dynamical range, information capacity, and flexibility" [115].

Gene regulation: We finally note that a related transition into the so-called 'spin-glass' phase [117] can produce many metastable states in heterogeneous dynamical networks. This has been hypothesized to be related to how gene regulatory networks can create functional behavioral states and perhaps evolve to learn new ones. There is growing evidence that biological regulatory networks have dynamics tuned near such a transition [118]. This is similar to the story with neuronal networks: this hypothesis does not produce precise functional details about how individual metastable aggregate states are useful, but is suggestive that having multiple aggregate states available may be useful for learning and evolution of new stable functionality [119].

Challenges and open questions

The use of low-dimensional theories of tuning near transitions is promising as a foundation for describing and predicting the dynamics of collective computations throughout living systems. There are, however, many remaining obstacles to be resolved and open questions to be explored.

Are low-dimensional transitions in fact ubiquitous in collective computation in living systems? There are other ways for systems to have adaptive collective behavior that do not involve sharp transitions. For instance, ant foraging rates can still change with external inputs without the positive feedback that leads to a sharp transition, just not as dramatically [22]. This makes the use of collective transitions in biology a hypothesis that needs testing and not just a reinterpretation of data and models. We may similarly ask whether some computational functions, such as decisions or transistor-like adjustment of sensitivity that we highlight here, are in some sense optimally or most easily implemented using collective transitions, as compared to other potential mechanisms.[9] This question is related to the more specific question of whether scale-free or heavy-tailed distributions can be blamed on a more restrictive notion of a "critical point": a continuous phase transition displaying self-similarity. A number of alternative explanations have been found—heavy-tailed distributions that instead can be traced to mechanisms other than critical transitions (e.g. [120]), including joint responsiveness to environmental inputs [121]. Similar objections can be raised to the assumption that a given collective behavior can be traced to transitions in a more general sense. Sudden changes to dynamics may, for instance, arise from independent responses to changing inputs instead of from collectively amplified responses. This highlights the importance of pinning down causal connections among components as opposed to merely correlation, which is often difficult in complex systems. While there is arguably a consensus that collective transitions of one type or another happen often in biological systems, it is still not well-established which specific types of transitions occur most often and how they are related to specific functionality. Experiments that produce not just observational data but also actively perturb dynamics will be necessary to tease out these distinctions.

Is there a precise sense in which collective transitions fall into classes that can be considered universal? This dream of universality via normal forms in bifurcation theory has been around for quite some time [15, 122]. In this view, identifying collective transitions using bifurcation theory retains some but not all of the properties of universality classes in statistical physics. Normal forms of bifurcations give rise to simplified, low-dimensional model formulations that ignore dynamics along unimportant dimensions — analogous to how universality classes in statistical physics motivate the use of simplified models that share the same scaling exponents but ignore microscopic fluctuations along irrelevant dimensions. Collective transitions are in an important sense more general, including more than just continuous transitions with self-similarity (and phenomena like long-range correlations and heavy-tailed fluctuation distributions). An important obstacle in this endeavor is how to incorporate stochasticity

[9] Large enough variation among individuals in response thresholds, or context-dependent modulation of thresholds, can smooth collective input–output relationships and even eliminate macroscopic bifurcations. In division of labor, for example, distributed response thresholds can yield graded, flexible allocation of workers across tasks, allowing colonies to adjust smoothly to changing demands rather than switching discretely between alternative collective states. This perspective is central to response-threshold models of task allocation and their empirical motivation, and highlights how selection can favor heterogeneity in thresholds when a more continuous mapping from demand to workforce is advantageous [39].

into bifurcation theory.

What dimensionality reduction techniques are best for defining aggregate-scale order parameters related to transitions? An important requirement for defining collective transitions that is not present in traditional bifurcation theory is defining relevant aggregate-scale variables. In statistical physics, such variables are called order parameters. In some cases, relevant aggregate-scale variables are straightforward: for instance, a colony-level foraging rate is a simple sum over individual foraging rates. In other cases, such as transitions in cell fate and neuronal dynamics, the relevant aggregate states — cell types, behavioral states — are not always known *a priori*. There are many potential dimensionality reduction techniques for finding relevant aggregate variables, including through estimation of the Fisher information [37], but the space of methods here is still very much in development.

What is the relationship between the codimension of collective transitions and the phenomenon of parameter sloppiness? One can think of the tuning of collective behavior in terms of the space of parameters that produces some desired output, or some desired input/output function. Intuitively, we may expect that a low-dimensional constraint on the aggregate output of a high-dimensional system is likely to be well-approximated by tuning only a small number of parameter directions. Recent results in parameter degeneracy in functional outputs ("sloppy models") [123] are also confronting the question of how much tuning is required for functional output. At least under some assumptions, the codimension of the required transition is equal to the number of "stiff" parameter dimensions that are well-constrained by data and are most consequential to aggregate behavior. A few studies have explicitly related sloppiness to transitions: at a continuous phase transition, the number of stiff parameters is equal to the number of relevant parameter directions in the renormalization group transformation [124], and more generally, the codimension of a transition sets a lower bound on the number of stiff parameters [125].

What mechanisms do living systems use in tuning relevant parameters? On different timescales, we use different names for tuning: evolution at the slowest scales, learning and memory formation at medium scales, and adaptation or regulation at the fastest scales. We know mechanisms at each scale that could produce this tuning—genomic changes, synaptic plasticity, homeostatic dynamics, neurotransmitters, transcription factors, cognitive dynamics, social regulation—but in many cases, we do not know for sure which of these are in play.[10] There may also be other physical or environmental symmetries that make it easier to tune toward a symmetry-breaking instability: for instance, rotational symmetry in bird flocking or ant collective transport.

Is there a more general connection between the difficulty of "finding" collective transitions and their computational abilities? There is a long history of viewing algorithmic structure in biological systems as arising from random network ensembles that are put under selection pressure based on their functional outputs [127, 128]. In this case, the codimension would set part of the difficulty of making use of a particular design pattern (assuming an ensemble corresponding to a relatively uniform prior over parameters). This relates to the "edge of chaos" hypothesis [129]: In this context, the hypothesis would imply that evolution favors restricting parameters near such an edge because useful transitions are more prevalent there.

How does heterogeneity affect the phenomenology of collective transitions? Heterogeneity—stable differences among individuals in thresholds, responsiveness, or interaction rates—can qualitatively reshape phase transitions in collective systems. In disordered models from statistical physics, such "quenched disorder" can produce Griffiths phases, extended parameter regions with slow relaxation, broad variability, and power-law-like dynamics, even though the system is not precisely tuned to a critical point [130–133]. Heterogeneity can also round off sharp transitions, narrowing the circumstances under which hysteresis or bistability survives [132]. This arises in heterogeneous ant foraging models, where large heterogeneity blurs transitions but still broadens trial-to-trial variability in final foraging levels [22]. Different types of heterogeneity — variability in response thresholds, interaction rates, persistence times, sensory noise, spatial fidelity, or energetic constraints — could preserve, shift, or destroy transitions in distinct ways.

How does network structure determine the types of transition and localization? Clearly, the structure of connectivity within a group plays a crucial role in defining collective dynamics. Research has begun to explore the distinction between "liquid brains," such as insect colonies, in which interactions are

[10] In addition, some parameters may effectively be tuned "for free". This connects to the concept of "self-organized criticality," a mechanism for approaching a critical point without tuning, requiring only a conserved quantity in combination with a large separation of timescales [126].

transient over the timescale of decisions, and "solid brains," made of neurons, in which interactions are relatively fixed [134]. Basic arguments in statistical physics tell us that, in the "liquid" case, well-mixed systems have dense connectivity and can be treated as effectively high-dimensional, with a phase diagram well-approximated by mean-field theory [135, 136]. In the "solid" case, fixed interactions can lead to more complicated dependence on network structure. The effects of network structure have been studied extensively in the literature on phase transitions [137]. Less is known about how network structure relates to the precision with which interactions must be regulated to create functional dynamics.

In navigating collective transitions, at what scale are parameters being controlled? This question lies at the intersection of questions about tuning mechanisms and network structure. Roughly speaking, we may expect that spectral properties of network structure will predict whether tuning near transitions can be optimally controlled by a few key components or requires larger-scale changes [138]. When is control fundamentally distributed; when is it localized; can there be many loci of control [139]?

Are there typical stages to the evolution of adaptive collective behavior? The "magic" that leads to the effective coordination of living systems, as we have argued, necessitates some degree of careful tuning. Without feedback and tuning, collective behavior may not be a good match to the environment, even when the individuals making up the collective are themselves well-adapted. This suggests an evolutionary process over which the advantageous regulation may be learned (and some have argued that, for similar reasons, collective transitions are useful in thinking about the origin of life [140, 141]). Suggestively, in fields such as ecology [142] and climate science [143], collective transitions are seen mainly as a risk to be avoided. Is this because the collectives involved are at a less-well-developed stage of evolution, in which collective behavior has become relatively predictable and consequential but is not yet well-regulated?

The Future

The advantage of viewing collective behavior through such a coarse-grained lens, one that only tracks the stability of aggregate-scale attractors and transitions among these, is the immense dimensionality reduction compared to building models at the level of individual components and interactions. At the same time, we believe this way of characterizing functional strategies—in terms of collective transitions and tuning around these transitions—opens a new perspective for considering the space of possibilities available for living systems to explore in producing functional collective behavior.

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Glossary

- "coarse-graining": the act of simplifying the representation of a collective system, typically by ignoring some details at the scale of individual components
- "component": an individual constituent part of a group, defining the "micro" scale (e.g., one insect, neuron, or gene)
- "aggregate state": a coarse-grained description of the system's dynamical state, usually incorporating an average over many components, defining the "macro" scale

- “collective transition”: a qualitative change in aggregate-scale behavior induced by changing one or more control parameters

- “codimension”: characterizing a bifurcation, equal to the total dimension of parameter space minus the dimensionality of the manifold on which the bifurcation occurs, the codimension represents the number of parameter dimensions that must be tuned in order to generically locate a system on a particular bifurcation manifold

- “bifurcation”: a change in the number, stability, or nature of stationary points in a dynamical system as a control parameter is varied

- “criticality”: the regime near a continuous phase transition in which fluctuations become large and long-ranged, correlation times increase, and collective responses to perturbations are typically maximized

- “phase transition”: a discontinuity in the value or a derivative of an order parameter as an external parameter is varied, defined exactly only in the limit of an infinite number of components

- “universality”: the idea that different microscopic mechanisms can produce the same collective behavior, so that key macroscopic properties are effectively independent of many microscopic details

- “collective transition design pattern”: a recurring functional use of collective dynamics, characterized at an algorithmic level by (i) a type of collective transition and (ii) how control parameters are positioned or moved relative to the corresponding transition manifold to achieve a goal (e.g., sensing, switching, memory, decision)

- “amplification”: the strengthening of a collective response through interactions among components, such that small individual-level perturbations or biases can produce large changes at the aggregate scale

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