

Design patterns in the tuning of collective transitions

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Abstract

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. Making use of collective transitions that separate distinct aggregate-scale behaviors, connected to theories of phase transitions and bifurcations, is thought to be one way that these systems create functional behavior. We highlight here recent results in the functional consequences and uses of collective transitions, finding that (1) biological function often relies on active changes corresponding to motion relative to transition boundaries, 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 regulation that effectively move systems relative to these transitions, define recurring design patterns at a coarse-grained algorithmic level. Design patterns summarize strategies for navigating transitions that lead to specific functionality, such as stable coordination, constant or adjustable amplification of signals, bistable switching, and collective decisions. Reviewing 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 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 [2]; neurons jointly hold memories [3] and make decisions [4]. These are all examples of information processing, information storage, and control that is distributed over many components. Are there any recurring strategies, any general principles of collective intelligence, that are used by living systems use in order to create such functionality [5–10]?

While there seem to be analogies across different systems — for example, both neural populations and ant colonies use interactions among many components to produce collective decisions — 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 functional behavior in computational neuroscience, viewed collective behavior at 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 the problem at an algorithmic level of information flows, and we can think about the space of mechanisms that can implement a particular 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.

¹Marr and Poggio’s original formulation included a fourth level of “hardware,” which we merge here into “mechanism”.

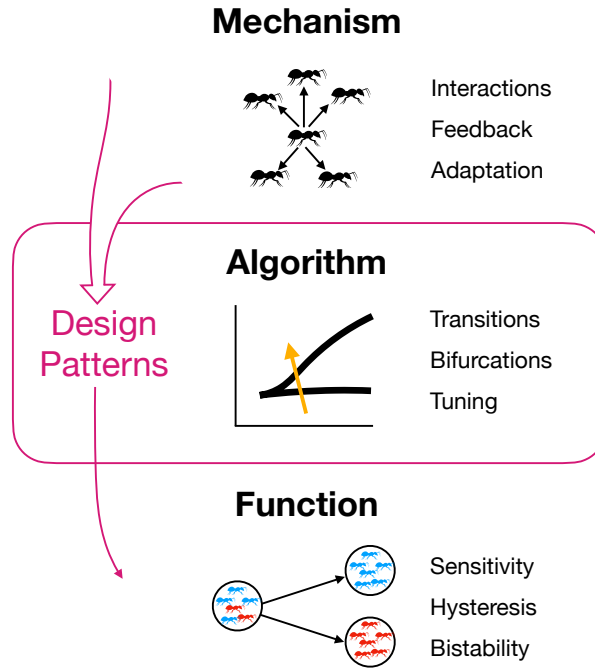


Figure 1: **Design patterns, defined at an algorithmic level, organize the space of possible mechanisms and predict their functional consequences.**

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 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 becomes powerful when system behavior can be approximated near a bifurcation manifold (the set of points at which a transition occurs; see Box 2), which 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 bifurcation manifolds is ultimately relevant, such that large

²This 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.

classes of mechanisms become equivalent at the algorithmic level. The codimension of a bifurcation manifold acts as a measure of the degree of regulation necessary to locate a given transition.

Historically, theories of the functionality of collective transitions 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 varying characteristic timescales; and functionality that depends on active changes to the effective positioning relative to transitions instead of remaining fixed (see Box 1).

How might we delineate the space of possible uses of collective transitions and how they can be realized in living systems? Here we review recent results that sample from this space. In doing so, we identify a number of algorithmic design patterns that characterize distinct ways in which transitions can lead to biological function. While we have books full of design patterns connecting structure to function in, for instance, electrical engineering [19], 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 [20]. We believe that similar patterns exist in collective behavior that require further coarse-graining across scales.

The basic picture is as follows: at the mechanistic level, positive feedback³ 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 biological variables are regulated 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.

³Here, 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 [21].

80 As a brief example, consider foraging in ants. In some ants, returning foragers increase the probability
81 of other ants to leave, leading to positive reinforcement. Depending on the strength of this positive
82 feedback, there are regimes in which adjustment can balance the responsiveness/robustness tradeoff,
83 and other regimes in which transitions cause sudden, discontinuous switches between foraging rates,
84 characterized by hysteresis and bistability [22].

85 Collective transitions are potentially functionally useful under a particular set of conditions: when (1)
86 some aspect of biological function is determined at a coarse-grained, group-level scale, (2) individual-
87 scale dynamics are fast enough compared to functional consequences that attractors of the dynamics are
88 important, (3) adaptation to external dynamics is slow enough compared to the dynamics that it is nat-
89 ural to describe regulation in terms of bifurcations, and (4) collective behavior is reproducible enough
90 that it can support a functional connection between environmental inputs and collective outputs.

Box 1: Important concepts for the use of collective transitions 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 a *codimension*, the number of independent control parameter directions that generally must be adjusted to locate a bifurcation.
4. Motion with respect to transition boundaries can often involve *trade-offs*, such as between speed and accuracy and between robustness and adaptability.

92 In this review, we survey collective transition design patterns across biology, emphasizing how transi-
93 tion geometries and modes of tuning are associated with distinct functional uses. Readers unfamiliar
94 with bifurcation theory and effective models can find a brief introduction in Box 2 and a more thorough
95 worked example in Appendix S2. At the end of our review, we consider challenges and open questions
96 for this framework, including the extent to which low-dimensional transition descriptions generalize
97 across systems and how such hypotheses can be tested empirically.

Box 2: **Bifurcation theory and effective models**

Here, we briefly introduce useful terminology from nonlinear dynamics [23] in the context of collective behavior. A more thorough introduction can be found in the Appendix S1.

Fixed points correspond to states that remain stationary over time. In collective behavior, we are typically interested in fixed points defined in terms of aggregate states of an entire group. For instance, in foraging ants, we may be interested in the aggregate rate of foraging summed across all ants, and a fixed point corresponds to an aggregate foraging rate that persists over time. Stable and unstable fixed points are characterized by whether small perturbations lead back to the fixed point or away from it, respectively. Changes in biological or environmental variables, which enter our framework as effective control parameters, can alter the location, number, and stability of fixed points. These qualitative changes are **bifurcations**.

Assuming otherwise smooth dynamics and one or two effective control variables, there are only a few distinct ways that it is possible for these qualitative changes to occur, which define bifurcation types. Here we focus on local bifurcations, which can be fully characterized by how fixed points change for parameter values near the bifurcation. Importantly, a system's dynamics near a local bifurcation are well-approximated by a generic normal form equation. Such a normal form can be used as a simplified **effective model** for the system, which depends only on the few effective control variables that define placement of the system dynamics with respect to the bifurcation point.

We start with bifurcations in which a single parameter is varied (Fig 2A). In a **forward-transcritical bifurcation**, one state (here one with zero activity) loses stability as another state (here one with growing activity) emerges continuously. **Backward-transcritical** and **saddle-node** bifurcations both create a stable and an unstable fixed point, producing a region in which low- and high-activity states can both be stable. Crossing the saddle-node can therefore cause an abrupt switch associated with hysteresis. In a (supercritical) **pitchfork bifurcation**, one state loses stability while two alternative stable states emerge.

More possibilities arise if two parameters are varied. The most important for our purposes is the **cusp bifurcation** (Fig 2B). At the cusp, two saddle-node bifurcations meet, and similar cusp-like

bifurcations arise from the meeting of transcritical and saddle-node bifurcations.

We refer to the set of control parameter values at which a bifurcation occurs as a **bifurcation manifold**, which has a **codimension** that is equal to the number of independent effective control directions that generally must be adjusted to locate it. Thus, if two variables can be controlled, a codimension-1 transition generally lies along a 1D curve in the 2D space of control variables (e.g., the black curves in Fig 2B), and a codimension-2 cusp occurs at a single point.

Importantly, even given a large number of control variables, effective tuning may occur along low-dimensional subspaces. Fig 2C illustrates how a two-parameter bifurcation structure arises as a slice through a larger space of mechanistic variables: tunable, coarse-grained effective parameters define a low-dimensional space in which the relevant collective dynamics can be controlled.

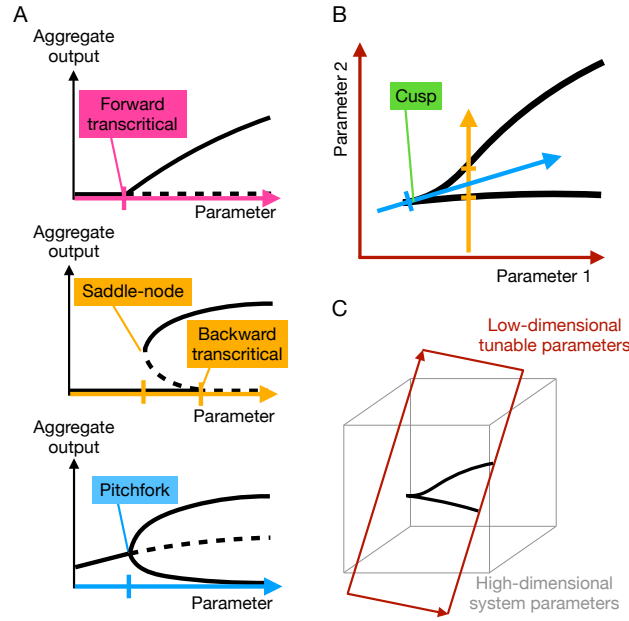


Figure 2: Bifurcations in increasing numbers of dimensions. (A) Bifurcations of codimension 1 require tuning a single parameter. Black curves represent fixed points (solid stable and dashed unstable) of the aggregate dynamics. (B) In a two-dimensional space, bifurcations of codimension 1 lie along curves (black) and those of codimension 2 occur at points (e.g., the cusp). (C) Tunable parameters make a low-dimensional slice through a potentially high-dimensional set of system properties.

100 Main Text

101 Our working hypothesis is that many living systems regulate their positioning relative to collective
102 transitions, and that the functional implications of this regulation are best understood at the level of
103 algorithmic design patterns. Here, we review examples of such tuning, organized roughly in order of
104 increasing complexity of active regulation (Fig 3). The examples we include are all connected to exper-
105 iments in some way—we want to emphasize that aspects of collective transitions are being measured
106 in real systems, not just toy models.

107 In the simplest type of tuning (Fig 3A and B), collective behavior is relatively fixed, with effective control
108 variables set over a slower evolutionary timescale, and potentially kept constant using active processes.
109 In other cases, collective behavior is actively changed based on environmental inputs. Changes to the
110 strength of interaction or coordination among components can up- or down-regulate social information
111 channels (Fig 3C), or tuning of a bias toward one or another aggregate state can lead to discontinuous
112 switching between coordinated states (Fig 3D). In more complicated examples of regulation, collective
113 behavior can vary both in the degree of coordination and in the specific aggregate states displayed by
114 the group. We may interpret these cases as collective decisions, in which environmental inputs are
115 integrated into a choice among two or more ordered states (Fig 3E), or as creating large numbers of
116 possibly useful ordered states (Fig 3F).

117 Note that some living systems may implement multiple types of computation [24], and it is likely
118 not possible to create a list of all possible useful design patterns (though it is possible to enumerate
119 all possible collective transitions under some constraints [25]). We organize our review in terms of
120 design patterns in an attempt to structure the space of distinct hypotheses for how transitions create
121 functionality in collectives.

122 “Stable coordination” design pattern

123 While our review focuses mostly on cases with active changes to collective dynamics, we begin with
124 cases of collective function via fixed positioning relative to a transition. The simplest cases create some

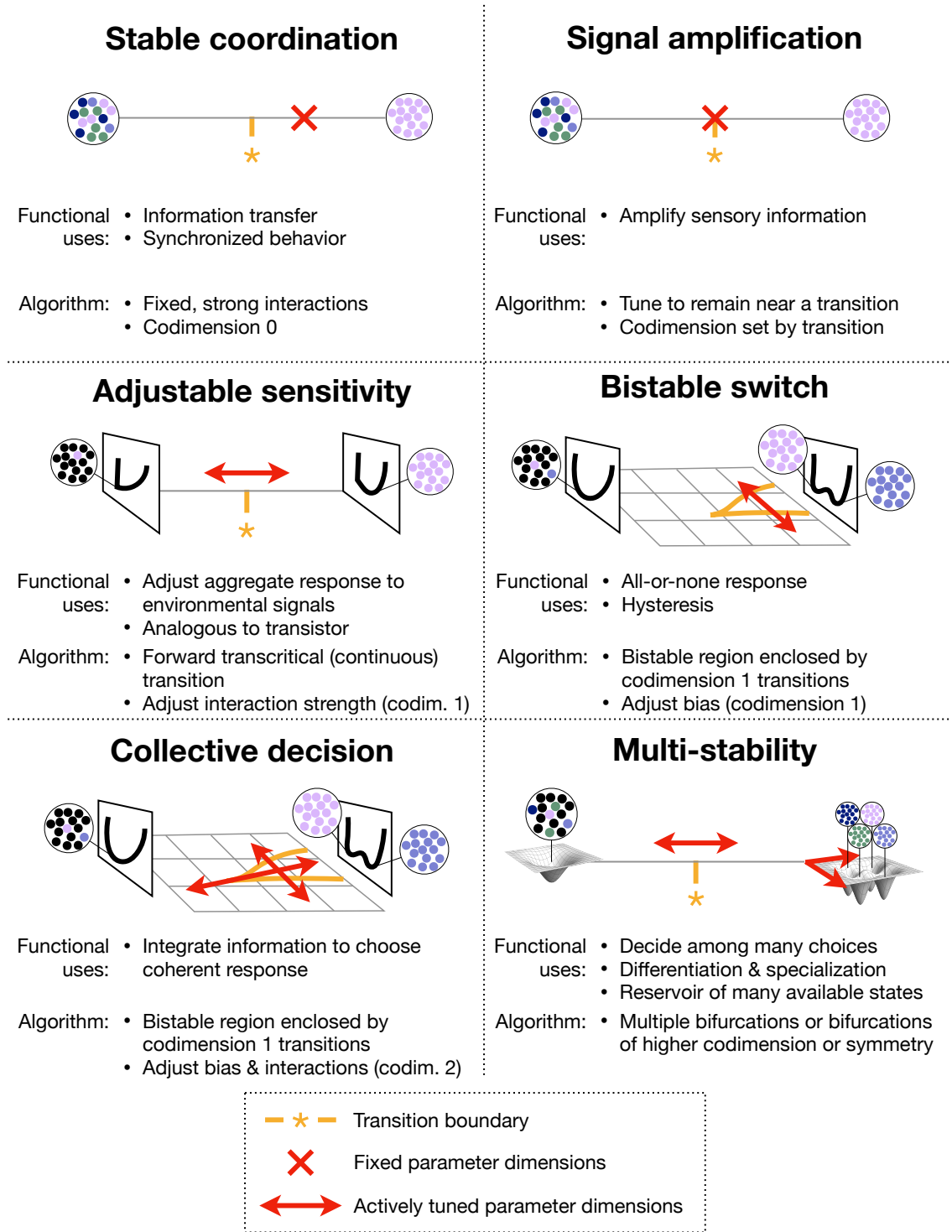


Figure 3: **Design patterns in collective transitions.** Different types of transitions (boundaries highlighted in gold) plus active adjustment of parameters (red arrows) produce design patterns with different functional abilities. We schematically represent a collective as dots with colors representing behavioral states, which can be coordinated (same colors) or uncoordinated (different colors) and active (bright) or inactive (dark). Bifurcations are defined in terms of changes in parameter space (horizontal gray axes), and the stability of collective states is represented schematically using potential landscapes along the vertical axis.

fixed stable coordinated aggregate state.

We see stable organization in many examples in biology. Some species of firefly strongly synchronize their flashes [26], and in large groups, locusts move together in strongly ordered waves [27]. 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 [28]. 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.⁴ Examples include the propagation of orientational waves in bird flocks [29] and continuous ring attractors in neuronal dynamics [30]. In these examples, components are stably coordinated, and some information is stored 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 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. The functionality arises from having an aggregate orientation that is marginally stable, which does not require being at a fixed distance from the transition between disorganized and coordinated behavior.

Because stable coordination does not require tuning to a specific transition point, we say that this design pattern has codimension 0 (see Box 1).

⁴This is known as a Goldstone mode in statistical physics.

150 “Signal amplification” design pattern

151 An oft-cited advantage of being near a continuous symmetry-breaking transition is that the aggregate
152 state becomes highly sensitive to small inputs. This optimal sensitivity advantage of transitions has
153 been explored extensively in the literature on phase transitions in biology; we briefly highlight it here
154 but also refer the interested reader to a number of existing reviews [12, 13, 31].

155 The sensitivity near continuous transitions means that the aggregate state can effectively become an
156 amplified representation of an environmental input at a much smaller scale. For instance, cochlear
157 hair cells are optimally sensitive to weak sounds by actively being tuned to sit near a Hopf bifurcation
158 to ordered oscillatory behavior [12]. Similarly, evidence has been found that the sensory organ in
159 snakes for detecting temperature effectively amplifies differences in temperature by remaining near
160 a saddle-node bifurcation [32]. In *Paratrechina longicornis* ants, there is experimental evidence that
161 suggests that susceptibility of the direction of motion to an external signal during collective transport
162 is maximized near a transition [33–35]. More speculatively, theories suggest that feedback among cells
163 in a tissue can lead to optimal sensing of slow changes to chemical concentrations when it is tuned
164 near a pitchfork bifurcation [36]. In cases like these, maintaining maximum sensitivity may require
165 tuning to remain near the transition, though the functionality does not require actively changing the
166 effective distance from the transition. As one example of such tuning, the Hopf bifurcation used by
167 the cochlea has codimension 1, requiring the regulatory tuning of variables controlling the dynamics
168 along a single dimension. This tuning is thought to happen through the active regulation of calcium
169 ion concentrations within hair cells [12].

170 “Adjustable sensitivity” design pattern

171 Contrasting with the conventional story about the optimality of criticality, recent literature has repeat-
172 edly found that living systems vary, in many cases over a relatively short timescale, in their locations
173 with respect to collective transitions [37–39]. We therefore include variation corresponding to move-
174 ment with respect to transitions in our categorization scheme.

A relatively simple way for collective behavior to adapt to changing conditions is by regulating the strength of social channels of information flow. This regulation corresponds to movement along a single effective control direction, varying the distance from a transition at which behavioral cascades change from staying localized to spreading through most of the group. In a sense, such a design pattern acts like an “informational transistor”: moving one effective control variable 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 has been well studied in epidemiology. The simplest such transition maps onto a forward transcritical bifurcation (Fig. 2A) [40, 41], with codimension 1, in which movement along an effective gain direction adjusts 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 [37], 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. More broadly, coordinated movement in animal groups, including flocking and schooling, may contribute to functions such as predator avoidance, although the functional value of particular collective states remains uncertain [42, 43]. Under higher predation risk, golden shiner fish are known to swim closer together and increase the collective sensitivity to startling [44]. The fish thereby vary their distance from a transition to large startle avalanches [37]. 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 [45]. In each case, the largest sensitivity happens near the transition at which the quiescent state becomes unstable, and movement along a single effective control direction sets the average cascade size.

In the schooling of fish, collective states include disordered swarming and ordered states such as schooling and milling [46]. 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 [39]. 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 [47].

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 [48]. 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 [49]. 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 [49]. 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 [49]. In this example again, movement along one effective collective control direction 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 [50, 51] based on attentional or vigilance states [38, 52, 53] and the sleep-wake cycle [54, 55]. In this sense, we can view the broadest scale dynamics of the brain as varying an effective control direction 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 [50, 56]. 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 [57]. We return to neuronal examples below, showing how the tuning of additional parameters near transitions relates to other functional abilities.

Harvester ant foraging: In harvester-ant foraging, returning foragers interact with workers waiting near the nest entrance, increasing the probability that those workers leave to forage; successful returns

therefore stimulate further departures and create positive feedback. Empirically, environmental conditions modify these interaction processes, with the effective feedback strength and colony sensitivity varying with environmental dryness [58–60]. It remains an open empirical question whether feedback in natural *P. barbatus* foraging is ever strong enough to produce a transition to 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 (Fig 2B). 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 effective bias toward 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 [61,62]. 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 [63,64]. 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 [65]. 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 [66]. Vespine wasps similarly exhibit recruitment cascades in which many workers attack a marked target or almost none respond [67]. 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 [68]. 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 2A) [69, 70].

Social insect foraging often involves feedback mechanisms that can in some cases lead to transitions to bistability. Stable pheromone trails in Pharaoh’s ants require a minimum number of ants to persist, displaying a transition from disordered to ordered foraging with bistability and hysteresis [71–73]. Across many models of social insect foraging, amplification of foraging activity can generate a discontinuous transition between low and high rates of foraging [22, 69, 70, 74]. We can speculate about functional consequences of such bistability. As bistable switches create hysteresis, recruitment can briefly persist even after returns begin to wane, appearing as an overshoot in outgoing effort. Such persistence may be adaptive if it reduces the risk of abandoning a profitable patch before it is fully harvested. The same mechanism could, in principle, confer robustness to danger. If foragers encountering predators retreat or fail to return, the social cue is damped, the effective control variable shifts less, and the system may remain on the low-activity branch, thereby avoiding a costly global activation in hazardous conditions.

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 in computational models requires tuning two effective control directions: bias between the two states and the strength of positive feedback [75]. 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” [75], and too much bistability being associated in the extreme case with 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 [76–78]. This suggests tuning of the strength of interactions to control the speed of decision dynamics [79]. In some cases, active regulation 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 [80]. Tuning across a transition from disorder to order is thought to be functional in allowing for changing 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 such exploration–exploitation control by modifying the strength of positive feedback

between pheromone deposition and trail following [81,82]. This could allow 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 [1,83,84]. Some ants lower the threshold for choosing a new nest site in more urgent situations, actively choosing to prefer speed over accuracy [77].

Neural decisions: The representation [85] and neural implementations [86, 87] of decisions in the brain have historically been tackled with variants of the drift diffusion model [88, 89]. 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, 90, 91]. This approach can naturally incorporate both deliberation and commitment by varying effective control variables with respect to a collective transition. For a binary decision, crossing a cusp bifurcation can combine a sensitive deliberation phase near the transition with commitment beyond the transition. Measured spiking data from perceptual decisions in monkeys show dynamics of neural decision information consistent with a dynamically varying distance from a phase transition, with sensitivity during the stimulus and coordination during the decision output [4]. Further theoretical work confirmed that the same mechanism can function in cases of quenched disorder (adding noise to coupling constants) [92] and in interaction networks with more complicated structure [79]. In computational models, two parameters must generally be tuned to reach the transition because the corresponding cusp bifurcation has codimension 2 [23]. These results suggest that, even for strong heterogeneity, functional decision-making requires tuning just two effective control variables [92].

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 [93]. 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.⁵

⁵In this model, the transition is somewhat more complicated, as there are up to three stable fixed points: one inactive state

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 [94]. 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 [25,95]. 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) [25]. 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 [96].

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 [97]. 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) [97].

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

and two active, symmetric decision states. With the bias fixed at zero, a single parameter controls the stability of the undecided state and therefore the timescales of integration of evidence.

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) [98]. 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 [99]. This binary splitting phenomenon has been measured in fruit flies, locusts, and larval zebrafish using immersive virtual reality environments [98]. The placement of system dynamics with respect to transitions 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 changes the sensory geometry, thereby moving the system across collective transitions. In models, varying other neural parameters alters 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, a rich set of possibilities 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 [100], 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 [75]. After a model neuronal network learns to produce dynamic patterns (by creating attractors, as in a Hopfield network), changing two effective model 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 [101]. There is some evidence that models in this regime are consistent with observed brain dynamics [102]. 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” [101].

Gene regulation: We finally note that a related transition into the so-called ‘spin-glass’ phase [103] 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 [104]. 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 [105].

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.⁶ 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. [107]), including joint responsiveness to environmental inputs [108]. 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 correlations, 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 are needed that actively modulate dynamics (varying external conditions or component states) and that look for features of specific transitions and motion relative to these transitions (sensitivity, bistability, hysteresis) in order to robustly identify design patterns.

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, 109]. 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

⁶Variation among individuals in response thresholds, including context-dependent modulation, can smooth collective input-output relationships and eliminate macroscopic bifurcations. In division-of-labor models, distributed thresholds allow colonies to adjust worker allocation gradually as task demands change, which demonstrates how selection may favor heterogeneity when continuous collective responses are advantageous [106].

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 [18]. Collective transitions are in an important sense more general, including more than just continuous phase transitions that display self-similarity. An obstacle in this endeavor is how to incorporate stochasticity (which is built in from the start in statistical physics) into bifurcation theory, a topic that has received attention in applied mathematics [110] but is not as well developed as singularity theory in deterministic systems.

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, it is straightforward to hypothesize aggregate-scale variables that are relevant to biological function: for instance, considering the adjustable sensitivity design pattern in foraging ants, a colony-level foraging rate is a simple sum over individual foraging rates. In other cases, such as collective decisions in cell fate and neuronal dynamics, the relevant aggregate states — cell types, behavioral states — are not always known, so it may be important to first search for previously unknown decision states. There are many potential dimensionality reduction techniques for finding relevant aggregate variables, including through estimation of the Fisher information [111], but the space of methods here is still in development (for an example of defining cell identity, see [112]).

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”) [113] 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 slop-

pininess 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 [114], and more generally, the codimension of a transition sets a lower bound on the number of stiff parameters [115].

What mechanisms do living systems use in tuning effective control variables? 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.⁷ 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. This will require experiments that can measure, and ideally control, relevant tunable variables. For example, in the adjustable sensitivity example of fish startle cascades, the experiment measured varying distances between fish (something the fish can presumably control) and connected this to the effective distance from a transition.

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 [117, 118]. 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 hypothesis could be tested in comparative studies that identify collective transitions that produce similar functional dynamics across species. We would predict that transitions with the lowest codimension necessary to produce a given dynamic would be most prevalent. This idea relates to the “edge of chaos” hypothesis [119]: 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

⁷Some parameters may be tuned “for free” through self-organized criticality, in which a conserved quantity and widely separated timescales drive the system toward a critical point without explicit tuning [116].

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 [120–123]. Heterogeneity can also round off sharp transitions, narrowing the circumstances under which hysteresis or bistability survives [122]. 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 transient over the timescale of decisions, and “solid brains,” made of neurons, in which interactions are relatively fixed [124]. 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 [125, 126]. 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 [127]. 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 [128]. When is control fundamentally distributed; when is it localized; can there be many loci of control [129]? These questions have been examined in computational models, and the experiments to test them are becoming feasible in neuronal and cell regulatory dynamics with advances in recording and manipulation of activity across large numbers of components.

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. We may speculate that earlier, less well-developed versions of collective behavior correspond to more generic design patterns like stable coordination, and highly regulated design patterns like collective decisions arise only later in evolution. Some have argued that, for similar reasons, collective transitions are useful in thinking about the origin of life [130, 131] and other major evolutionary transitions, at which previously autonomous entities become increasingly interdependent and form a new collective evolutionary individual [132–134]. The simplest such transitions perhaps involve only stable coordination, an early requirement for producing reproducible group-level phenotypes. Design patterns involving adjustable sensitivity, memory, switching, or collective decisions may require additional mechanisms that align lower-level interests and regulate effective control variables. The evolution of cooperation is known to involve reducing, regulating, or resolving conflict among a group’s components, often together with increasing division of labor and specialization [135–137]. These phenomena may be related to the regulation of collective transitions, an important avenue for future work. Suggestively, in fields such as ecology [138] and climate science [139], 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?

Conclusions

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

543 available for living systems to explore in producing functional collective behavior.

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550 **Glossary**

- 551 • “coarse-graining”: the act of simplifying the representation of a collective system, typically by
552 ignoring some details at the scale of individual components
- 553 • “component”: an individual constituent part of a group, defining the “micro” scale (e.g., one insect,
554 neuron, or gene)
- 555 • “aggregate state”: a coarse-grained description of the system’s dynamical state, usually incorpo-
556 rating an average over many components, defining the “macro” scale
- 557 • “collective transition”: a qualitative change in aggregate-scale behavior induced by changing one
558 or more control parameters
- 559 • “effective control variable”: a property, such as a strength of interaction between components or
560 an individual’s threshold to action, that can be varied in system components in order to regulate
561 the positioning of collective dynamics with respect to transitions
- 562 • “bifurcation”: a change in the number, stability, or nature of stationary points in a dynamical
563 system as a control variable is varied

- “bifurcation manifold”: the set of points in parameter space at which a bifurcation occurs
- “codimension”: characterizing a bifurcation, equal to the total dimension of parameter space minus the dimensionality of the bifurcation manifold, the codimension represents the number of control variable dimensions that must be tuned in order to generically locate a particular bifurcation
- “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 a control variable is changed, 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 effective control variables are positioned or moved relative to the corresponding bifurcation 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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920 **Supporting Information**

921 **S1 Appendix. Mathematical background for collective-transition design patterns.** A basic
922 overview of the mathematical concepts and terminology, including phase transitions, bifurcations, and
923 mean-field theory.

924 **S2 Appendix. Biological case study.** A more detailed example in social insect foraging demonstrating
925 how interactions among individuals can generate collective transitions.