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Understanding collective behavior through neurobiology

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Abstract

A variety of organisms exhibit collective movement, including schooling fish and flocking birds, where coordinated behavior emerges from the interactions between group members. Despite the prevalence of collective movement in nature, little is known about the neural mechanisms producing each individual's behavior within the group. Here we discuss how a neurobiological approach can enrich our understanding of collective behavior by determining the mechanisms by which individuals interact. We provide examples of sensory systems for social communication during collective movement, highlight recent discoveries about neural systems for detecting the position and actions of social partners, and discuss opportunities for future research. Understanding the neurobiology of collective behavior can provide insight into how nervous systems function in a dynamic social world.

Introduction

Many species navigate in groups, including flocks of birds and schools of fish that cohesively move as large collectives [1,2]. Collective movement benefits the individuals in the group [1–5], each of whom can obtain information from their social partners. This "many eyes effect" [6] allows groups to coordinate their actions and achieve behaviors not accessible to individuals alone [1,2,7–9].

The flocking of birds and the schooling of fish [1,2] are two well-studied classes of collective movement that emerge from interactions among individuals. Mobile animals in these collectives adhere to a set of well-defined interaction rules: individuals are attracted towards distant neighbors to promote cohesion, repelled by close neighbors to avoid collision, and align their posture and orientation with neighbors to enable movement coordination [10]. When individuals follow these rules, group behavior emerges with regularly-spaced animals moving in coherent directions. Despite substantial progress

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[a] Equal contribution.

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in describing and modeling how individual interactions produce group-level collective movement [1,2,10–13], much less is known about how each individual implements these rules [11]. Ethologists have been quantifying collective animal behaviors for decades [1,2], but the complexity of these behaviors presents challenges for understanding the mechanisms of underlying interactions. Recent developments in technology for tracking and quantifying the interactive movements of individual organisms within groups are providing new opportunities to quantitatively study collective behavior (see Box 1), by revealing more about how individual interactions and decisions-making processes produce the emergent properties of the group.

We believe that studying the neurobiological basis of each individual's social interactions within groups will provide additional advances in the study of animal collectives. To view collective movement through the lens of Marr's three levels of analysis [14], to move as a cohesive group (the computational level), individuals must follow specific interaction rules (the algorithmic level). To address the third level – implementation – we must determine how individuals perceive the actions of their social partners, integrate this information with prior knowledge and context, and produce the required actions to follow their group and provide reciprocal sensory input to their neighbors. We believe this question can be addressed with neurobiological investigations of the coupled sensory, cognitive, and motor processes of individuals within collectives. These efforts will be aided by the embrace of diverse model organisms that naturally engage in collective movement [15], and leveraging existing knowledge about the behavioral interactions of these animals and the sensory systems used for communication between animals [1,2,11,12].

Here we discuss the sensory basis of collective movement in a variety of species and highlight recent advances in understanding neural systems for sensory detection of conspecific behavior in animal collectives. Studying the cells, circuits, and networks underlying the individual choices and interactions within a social network can inform us about how the properties of collective behavior arise from individual brains, inter-animal communication, and/or their interactions.

Sensory systems underlying collective movement

In order to study the neural basis of collective action, it is essential to first identify the sensory systems each animal uses to acquire information about the position and actions of their social partners. We review a few prominent examples of collective movement, and emphasize the range of sensory features used to detect the actions of conspecifics (Figure 1).

Many animal collectives interact using vision, including shoals and schools of fish, where large numbers of animals act cohesively in aquatic environments with limited visual obstruction [16]. In the wild, schools form primarily in daylight, and fish are incapable of schooling if blinded [17]. In lab environments, individual fish will swim towards conspecifics across a clear divider [18] and will show preference for larger groups [19]. Furthermore, zebrafish will shoal with a visual stimulus possessing conspecific-like size and movements, including a simple bottom-projected dot [20] and a realistic perspective-matched zebrafish model [21]. Taken together, fish show strong behavioral attraction solely towards socially-relevant visual stimuli, demonstrating the importance of visual stimuli in driving aquatic collective behaviors [20,22].

Birds also form large groups where individuals coordinate their speed and orientation based on vision [23]. Theories of collective behavior have derived from the quantification of videos and model simulations of bird flocks in the wild [1,2]. For example, in some social hierarchies, influential individuals in the flock tend to occupy specific positions in the moving group, suggesting the existence of biased visual inputs for individuals based on positions and/or rank [24].

In addition to vision, many animals can sense their neighbors with mechanosensation, either through direct physical contact or detection of air or water displacement. Direct touch has been reported to underlie the collective grouping of *Drosophila melanogaster*, where leg bristles mediate mechanosensory transduction of socially-relevant information to enable more effective odor avoidance behavior in groups [25]. In contrast to this direct contact, the lateral line system of fish detects water flow over the body through displacement of hair cells. The lateral line can detect both self-motion and the actions of nearby animals [26,27], and is thought to complement or modify visually-driven schooling [26] when information is available from both sensory modalities [28].

In most cases, it is likely that animals use multisensory information to guide their collective movements. This is clear in the case of locust aggregations, in which individuals can form marching bands that have the potential for mass agricultural disruption [29]. Several sensory modalities contribute to the transition from the disordered aggregation of solitary locusts to aligned and coordinated group movements, including chemosensation [30], mechanosensation [31], and vision [32]. Another example is bats, where groups interact and communicate with social partners in roosts, and perform long distance navigation and foraging upon emergence from dark caves [33]. While their ability to precisely locate nearby objects with echolocation has been extensively studied [34], recent research has also found they can integrate auditory and visual inputs depending on the availability and resolution of sensory information that fluctuates with the environment [35].

Studying these and other systems can provide insight into how individual animals use socially-relevant information during collective behavior, and how each animal arbitrates between social and non-social information while making movement decisions. These decisions may depend on the influence of other internal and external factors, including metabolic needs and risk of predation.

Knowledge of the sensory modalities underlying each animal's interactions in the group can provide insight into the neural systems mediating their behaviors, which produce collective movement. Studying the neural basis of conspecific sensory detection across species that use different sensory systems may reveal either common core computations performed on these inputs in central circuits, or a bespoke neural solution unique to each animal's specific sensory world.

Neural signatures of conspecific action detection

Each individual in a collective is continuously moving in response to the sensation of their neighbors' actions, but the structure and dynamics of the neural systems that achieve this feat have yet to be discovered [11,36].

Some previously-studied aspects of sensory perception and motor control are likely to be involved in group behavior, including the perception of conspecific identity [37,38] or motion [39,40] in early sensory neurons, and the control of body posture and movement by descending motor circuits [41–43]. The organization of central neural networks linking sensation and action to produce collective behaviors are unknown (Figure 2), but recent studies have made progress in analyzing the neural basis of some features of group behavior, particularly the detection of social partners and their actions.

The movement patterns of conspecifics provide instructive visual input to animals moving in a collective [2,3,16,21]. Recent work has demonstrated that juvenile zebrafish exhibit collective shoaling behavior with a simple visual mimic – a zebrafish-sized dark dot that moves at the same speed and kinetics (intermittent bout-like motion) as an age-matched zebrafish [20]. Whole-brain quantification of immediate-early gene expression after social interactions to both a real conspecific and the social-moving dot assay [44,45] has revealed activation of multiple brain regions across the conserved vertebrate social behavior network [46,47].

To specifically identify neurons sensitive to biological motion, Kappel et al. presented the zebrafish-sized dot mimic to head-fixed juvenile zebrafish while performing multi-region two-photon calcium imaging [45]. They identified a neural circuit linking the optic tectum to a downstream dorsal thalamic population specifically responsive to the biologically-realistic movement parameters of dots. Ablation of either brain region reduced social attraction [45], but did not influence short-range avoidance in freely-moving fish. This suggests that these two components of collective behavior are implemented by separate neural systems: social aggregation behavior is regulated by a tecto-thalamic pathway responsive to biological motion, and short-range avoidance may be implemented by neural pathways common to innate visual avoidance behaviors [48,49]. Furthermore, recent work has demonstrated that group aggregation and postural alignment develop at different timepoints in schooling fish [50], suggesting that these aspects of collective behavior may also be implemented via separable processes.

In animals with visually-mediated collective behaviors, such as the fish or the bird, implementation of avoidance, aggregation, and alignment can potentially be implemented by neural circuits in the optic tectum and interconnected midbrain and brainstem regions [51]. Across vertebrate species, the optic tectum/superior colliculus maintains a retinotopic map of space, encodes aspects of the size and speed of moving objects, selects salient objects through competitive midbrain circuits, and directs orienting responses in the brainstem [51–54]. These mechanisms can be used to produce orienting and steering movements in response to the positions and actions of conspecifics.

It remains to be seen how these visuomotor circuits interact with the telencephalon in the context of collective movement, and how such interactions have changed along with the increasing complexity of the forebrain in vertebrate evolution [55]. In adult zebrafish, ablation of the ventral telencephalon results in impaired social interaction [56]; however, the function of these neurons are unknown, as neural activity imaging in the most ventral portions of adult zebrafish are challenging [57]. Large-scale functional imaging in juvenile zebrafish allows for optical access to telencephalic populations in animals capable of social attraction and shoaling [44,45,58,59], but larval zebrafish - where true whole-brain cellular-level calcium imaging is possible [60] - typically show social avoidance instead of attraction and collective movement [20,22] (but see Refs. [61–64] for examples of social attraction and coordination in larvae). An exciting alternative model system to study collective behavior is glassfish in the genus *Danionella*, which show visually-based schooling behavior, and remain small and near-transparent as adults to enable brain-wide functional imaging [65,66,50,67]. For instance, a recent study has found that neural populations in the optic tectum and telencephalon of adult *Danionella cerebrum* are driven by schooling-related biological motion stimuli [50].

Animals moving in collectives are commonly arranged in specific spatial patterns, but their relative moment-to-moment positions fluctuate, with potentially relevant information for social partners [11,36]. The relative positioning of animals in groups can provide important information to group members about rank, leadership, and sensory availability. One model system where this has been studied is in bats, where groups use vocal communication and echolocation [68] to emit and receive acoustic signals that contain information about the sender's location, identity, and their behavioral context [69]. Recent studies in navigating mammals have revealed that the hippocampal formation of rats and bats contain "social place cells" selective to the spatial location of conspecifics [70,71], similar to the well-characterized self-location system in the mammalian hippocampus [72]. Other classes of hippocampal neural activity patterns, such as encoding of elapsed time, have also been found for social partners in the hippocampus [73]. Within larger groups of animals, neurons in bat frontal cortex have been reported to encode the identity of a vocalizing bat within a group [74], and hippocampal neurons have been shown to respond to the collective spatial movements of their social partners [75]. These results present an emerging picture of how the hippocampus and other cortical regions in the bat brain encode multiple features of social partners and their actions. It remains to be discovered how bats use these representations to guide the emergent collective navigation and foraging behaviors of their large groups [69].

While progress is being made in the discovery of the perceptual systems for conspecific action detection, many questions remain: How are representations of conspecific action quickly and continuously transformed into appropriate motor outputs? How are such representations integrated with past experience, internal state [76], and other features of the environment? How does the vertebrate social behavior network [46,47] interact with these sensory-motor circuits for rapid detection and action? Do animals attend to individuals in their group, or the global group motion? Can animals switch between such strategies based on context? Is there a role for inter-brain synchrony in collective movement [77]? Furthermore, while we have focused on collective movements where individuals in the group play common roles, there are many types of complex collective behaviors that emerge from active sensing and hierarchical or distributed social organizations (see Box 2); these behaviors may be driven by distinct classes of neural mechanisms and communication regimes.

The questions posed above can be addressed by applying large-scale neural activity recordings and manipulation to the brains of single or multiple individuals in naturally interacting groups, and integrating experimental findings with models of collective movement. This type of approach can be implemented in freely-moving animals such as birds and bats that are large enough to carry wireless neural recording devices. Alternatively, if head-tethered animals can engage in sufficiently realistic virtual reality environments [21,57,78], experimenters can apply high-resolution functional imaging, electrophysiology, and optogenetics. In each case, neuronal recordings can be augmented by the use of methods for monitoring hormones and neuromodulators related to social motivation and valence [76].

Conclusions and outlook

Here we have argued that the study of collective behavior will benefit from understanding the mechanisms behind each individual's actions, requiring the methods and approaches of neurobiology. By investigating the cellular and circuit basis of how individuals rapidly sense their social partners in order to behave in accordance with their group, we will gain insight into how the remarkable capacities of animal collectives emerge from the neurobiology of its members and their communication. We have highlighted examples of sensory systems underlying collective movement that follow simple spatial interactions, considered how these systems are used during group behaviors, and discussed pioneering early studies of the neurobiology of collective sensing and action.

While neurobiology can advance our understanding of collective behavior, studying collective behavior can also advance fundamental neurobiology research. Many neurobiologists are interested in moving from the structured but limited paradigms of laboratory tasks to more natural behaviors, in an effort to study brains under the conditions in which they evolved [15,79]. However, the techniques, analysis tools, and worldview of the systems neuroscientist do not easily accommodate the complexity and variability of many naturally occurring behaviors. We believe that collective movement offers a compromise between the task structure of experimental psychology and neurophysiology with the uninstructed natural behaviors favored by ethologists; animals behave freely in the absence of experimenter reinforcement, but follow a clear set of rules defined by the spatial and temporal organization of their social partners, who also follow these same rules [1,2,12–14]. Studying the neural basis of these interactions can therefore allow for a quantitative description of how nervous systems implement behavioral algorithms to achieve collective movement. This area of study can be especially fruitful in the case of bird flocks and fish schools, which may offer particularly suitable model systems to investigate their neurobiology, building upon prior knowledge about the anatomical and functional organization of bird and fish brains [52,53,80,81]. We believe the neurobiology of collective behavior will advance in the coming years and will mutually benefit both fields of study.

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Data availability

No data was used for the research described in the article.

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Box 1.

Technologies for tracking collective animal behavior

The study of collective behavior has benefitted from the rapid growth of tools for measuring and quantifying the behavior of animals, with advances in both software and hardware.

Software for image-based tracking

Animal behavior is commonly measured using video recordings, producing a computational challenge of how to parse and analyze the relevant information from these videos. After early successes using machine vision for behavioral studies of small animal groups [82], the field has been revolutionized by advances in deep learning for markerless animal tracking and pose estimation, in both individuals [83,84] and groups [85,86]. Several versions of these tracking algorithms incorporate interfaces for closed-loop behavior tracking and posture-triggered experimental intervention [86,87]. Most recently, these methods have been extended to track individuals and groups in 3D [88,89]. These methods continue to advance rapidly, for use with conventional cameras as well as customized hardware for animal recording, such as the use of aerial drones in the wild [90,91] or high-density multimodal recording in large laboratory conditions [92].

Hardware for animal-tethered tracking

Not all animals can execute collective behavior in environments captured on camera, and therefore different methods have been developed for tracking groups of animals moving over larger distances. This includes a class of small tracking devices that are attached to an animal, allowing for high resolution positional tracking and integration of data from on-board sensors: accelerometers, magnetometers, microphones, and sensors of pressure and temperature. These sensors have been applied to pigeon flocks [24], sheep [93], baboon groups [94] and wild dogs [95]. Miniaturized trackers can be combined with methods for wireless neural recording in the lab, allowing for integration of group behavior with neural activity recording in groups of animals [74,75]. Continuous development of GPS systems and improved battery technology will allow for even smaller, lighter, and less-disruptive devices well-poised for longitudinal tracking of animals of all sizes.

Box 2.

Diverse forms of complex collective behavior

While cohesive group movement is an important class of collective behavior, there are many other collective behaviors that are manifest in stationary animals or involve more complex information transfer. For example, while visual, tactile, and chemosensory communication may be sensed continuously as animals move in groups, active sensing mechanisms such as vocalization [96], echolocation, or electric communication [97] require the purposeful engagement of sensory systems for information gathering and exchange (Figure 1).

In the case of vision, this includes flash synchronization in fireflies [98] and the waggle dances of honey bees to communicate about the location of food [99]. Animals also use acoustic and chemical signaling to communicate and coordinate collective actions. For instance, auditory communication can initiate the formation of groups to maintain cohesion [100] and reunite distant members [101]. Animals can use chemical or auditory information to recognize specific conspecifics of the same social group, including primates [102] and eusocial insects such as ants [103]. These signals can be produced in a context-dependent manner to coordinate collaborative efforts. For example, animals can emit calls to initiate a consensus group departure from the current location [104], and to coordinate collaborative efforts such as sentinel responsibility [105], group hunting, or defense against predation [106]. Furthermore, several pheromones in ants are used flexibly to recruit group members to navigate dynamic environments [107] in the context of collective foraging [108], alarm behavior [109], and nest leaving [110].

Studying collective movement such as schooling and flocking are likely to yield insights into the underlying neural mechanisms of social interactions, owing to the tractable interaction rules of individuals in these groups. While the examples discussed above may be more challenging to study, it will be interesting to investigate the neurobiology of these complex collective behaviors as the field progresses.

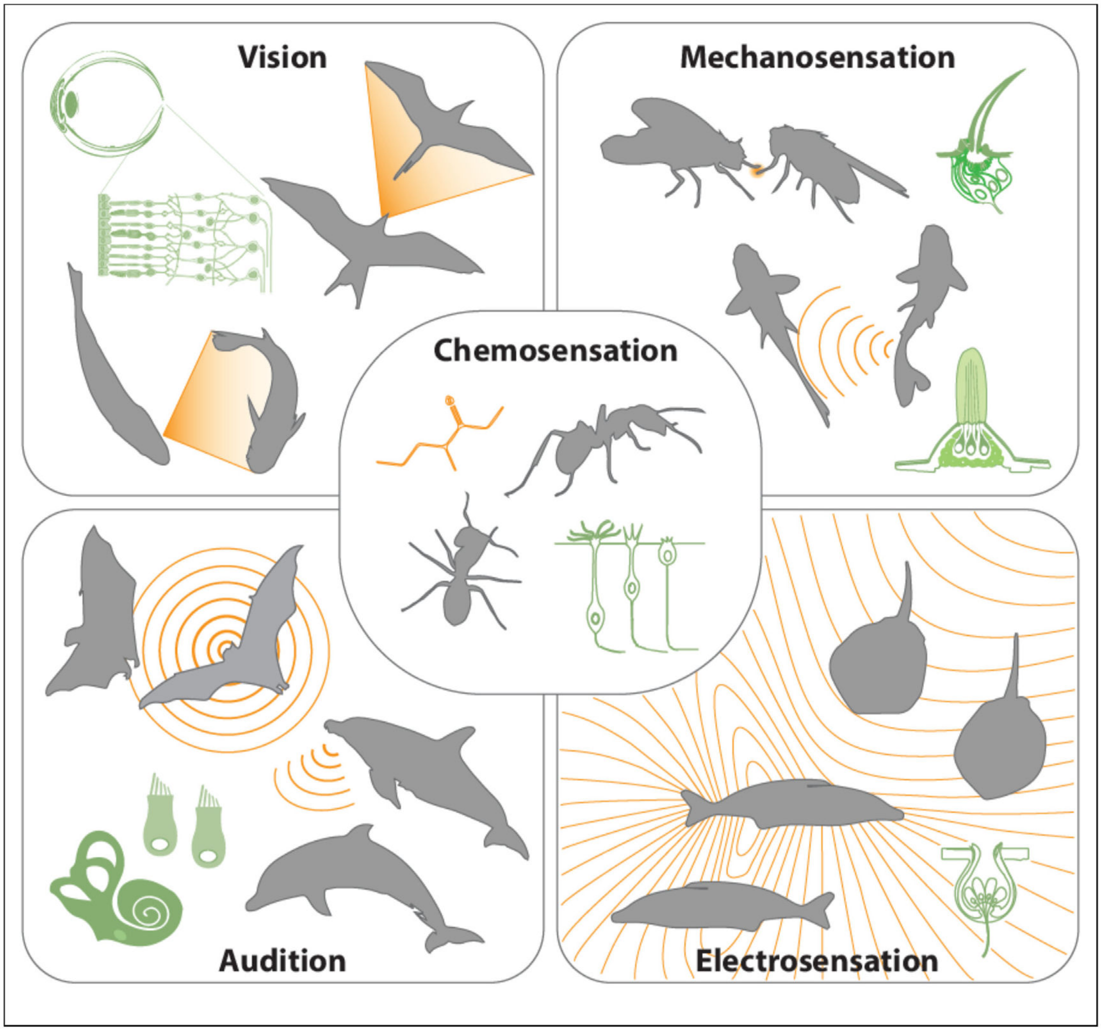

Figure 1. Diversity of sensory systems underlying collective behavior.

Displayed are examples of the diverse set of sensory systems underlying collective behavior in various species, where individuals sense the position and actions of others to produce cooperative movement. Schematics of sensations and primary sensory organs are depicted in orange and green, respectively. Vision: eye and retinal ganglion cells in the retina of schooling fish and flocking birds. Mechanosensation: hair cells in *Drosophila* leg bristles and in neuromasts of fish lateral line. Chemosensation: olfactory receptor neurons in ants. Audition: hair cells in the cochlea of bats and dolphins. Electrosensation: electroreceptors in the ampullary and tuberous organs of the electric fish and skates.

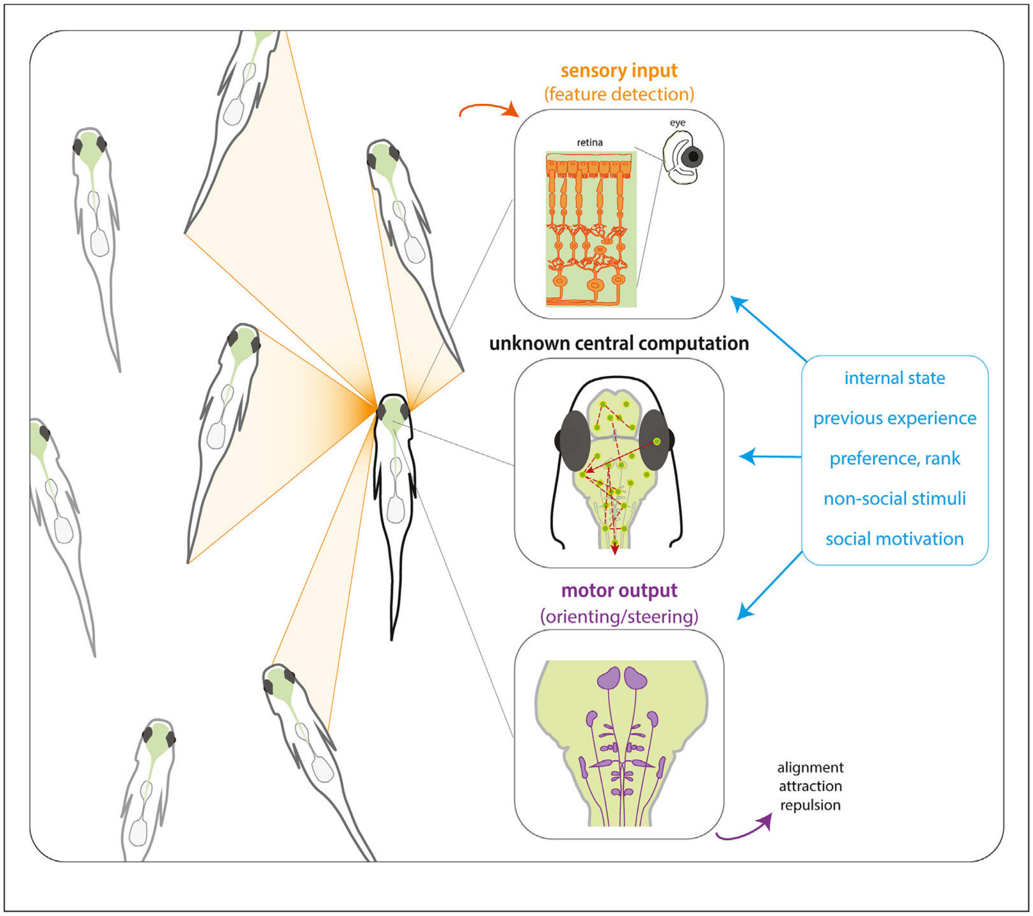

Figure 2. Neural circuits in individuals that support emergent collective behavior.

Displayed is a schematic of our current neurobiological understanding of how an individual animal perceives its social partners in its environment. On the left is a school of fish coordinating their movements with one another. Although all members of the school are actively observing the others, we focus on one focal fish to illustrate this process - with its visual fields depicted in orange. On the right is a broad schematic of the hypothesized sensory-motor transformation that occurs within the fish brain during collective movement, including the unknown central computations that link sensory detection to motor translation. At the top is the primary visual system of the fish (orange) – the retinal neural layers that transduce visual information. In the center are hypothesized neural circuits, whose structure and dynamics are unknown. On the bottom is the premotor system of the fish (purple), with a focus on brainstem spinal projection neurons that control movement - in this case the alignment, repulsion, and/or attraction to the other fish. Multiple stages of this network are likely influenced by a number of other factors, including but not limited to each of the items denoted in blue on the right.