

# Inferring the structure and dynamics of interactions in schooling fish

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Determining individual-level interactions that govern highly coordinated motion in animal groups or cellular aggregates has been a long-standing challenge, central to understanding the mechanisms and evolution of collective behavior. Numerous models have been proposed, many of which display realistic-looking dynamics, but nonetheless rely on untested assumptions about how individuals integrate information to guide movement. Here we infer behavioral rules directly from experimental data. We begin by analyzing trajectories of golden shiners (*Notemigonus crysoleucas*) swimming in two-fish and three-fish shoals to map the mean effective forces as a function of fish positions and velocities. Speeding and turning responses are dynamically modulated and clearly delineated. Speed regulation is a dominant component of how fish interact, and changes in speed are transmitted to those both behind and ahead. Alignment emerges from attraction and repulsion, and fish tend to copy directional changes made by those ahead. We find no evidence for explicit matching of body orientation. By comparing data from two-fish and three-fish shoals, we challenge the standard assumption, ubiquitous in physics-inspired models of collective behavior, that individual motion results from averaging responses to each neighbor considered separately; three-body interactions make a substantial contribution to fish dynamics. However, pairwise interactions qualitatively capture the correct spatial interaction structure in small groups, and this structure persists in larger groups of 10 and 30 fish. The interactions revealed here may help account for the rapid changes in speed and direction that enable real animal groups to stay cohesive and amplify important social information.

A fundamental problem in a wide range of biological disciplines is understanding how functional complexity at a macroscopic scale (such as the functioning of a biological tissue) results from the actions and interactions among the individual components (such as the cells forming the tissue). Animal groups such as bird flocks, fish schools, and insect swarms frequently exhibit complex and coordinated collective behaviors and present unrivaled opportunities to link the behavior of individuals with dynamic group-level properties. With the advent of tracking technologies such as computer vision and global positioning systems, group behavior can be reduced to a set of trajectories in space and time. Consequently, in principle, it is possible to deduce the individual interaction rules starting from the observed kinematics. However, calculating interindividual interactions from trajectories means solving a fundamental inverse problem that appears universally in many-body systems. In general, such problems are very hard to solve and, even if they can be solved, their solution is often not unique.

To avoid solving these inverse problems (and because detailed kinematic data were not available until recently), many attempts have been made to replicate the patterns observed in animal groups by so-called self-propelled particle models (1–11). These models use the basic ingredients believed to underlie collective motion such as schooling in fish (12–14): a short-range repulsion, a longer-range attraction, and/or an alignment among interacting agents. This is sufficient to generate patterns similar to those observed in animal groups [e.g., Couzin et al. (7)], and a number of observables such as nearest-neighbor distance, polarization, group speed, and turning rate have been successfully matched to experimental data (14–19).

Recent empirical studies (19–26) have collected large datasets of freely interacting individuals in order to infer the rules underlying their emergent collective motion. Ballerini et al. (22) and Cavagna et al. (26) have used the spatial structure of starling flocks to infer that starlings use topological rather than metric interactions and that information is transferred over large distances within flocks in a scale-free manner. High-temporal-resolution data from several species have been analyzed by employing model-based approaches. Lukeman et al. (25) fit data on the spatial configurations of surf scoters to a zonal model and identified best-fit parameter values as well as evidence for an additional frontal zone of interaction. Buhl et al. (21) used a statistical mechanical model to show how the transition in locusts from disorder to order depends on the density of individuals, and Bode et al. (24) used an individual-based model to provide evidence for asynchronous updating of positions and velocities in sticklebacks. In other species of fish, Grünbaum et al. (20) used a control theoretic framework to relate preferred nearest-neighbor positions to swimming speed, and Gautrais et al. (19) used a stochastic differential equation model based on correlations between consecutive turning angles to describe individual trajectories. Thus, models have also provided good fits to finer scale experimental and observational data.

Despite these successes, model-based approaches are inherently limited in that many sets of microscopic rules can produce the same macroscopic behaviors. Even if a model matches an experimental system across a set of observables, unless the underlying rules are also correct, there is no guarantee that it will give a reasonable representation of other observables or share the same response to perturbation. For example, when predators attack a fish school, information selectively becomes amplified to produce a rapid collective response (27–30). Models can produce qualitatively similar patterns to those seen during predation (31, 32), but they are likely to have difficulty generating the same dynamic response. This is because most models assume that individual movement decisions result from averaging pairwise interactions with neighbors. Averaging has the effect of damping out cues because each cue gets “diluted” when it is combined with the others in the average, making model groups difficult to perturb and hence failing to transmit pertinent information.

Here we introduce a force-based approach for inferring interaction rules directly from empirical data. Instead of assuming a specific model based on biological ansatzes and using data to fit its parameters or test its validity, we map the instantaneous acceleration (behavioral response) of a focal fish due to the influence of its neighbors. Following a classical mechanics framework, we define the effective social force (33, 34) as the total force  $F$  on a focal fish required to produce the observed acceleration  $a$  (using

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$F = ma$  and considering its mass to be 1). The effective force includes all physical forces in the system (hydrodynamics and self-propulsion), but their details can be ignored as their influences are accounted for in the total force responsible for the resulting acceleration. Indeed, the actual motion of individual fish may be ruled by a complex stochastic decision-making process based on interindividual interactions, environmental conditions, differences in body size (35), and even on hidden properties such as the internal state of each fish (36). However, such complex biological reactions can still be interpreted, on average, as individual fish accelerations in response to a given configuration of its neighbors' positions and velocities (37).

Our approach allows us to systematically study how social interactions depend on the motion of neighbors. In a shoal of many fish, it is difficult to infer these interactions without assumptions, because how individuals respond to one neighbor is confounded with how they combine their responses to multiple neighbors. To disentangle these two issues, we begin with a group of only two fish and compute the acceleration of one fish as a function of the position and velocity of its neighbor. Looking at shoals of three fish then allows us to calculate how the measured effective forces differ from what would be predicted if the fish simply averaged their would-be response to each of their neighbors. We find that the averaged quantities computed result in clear signatures describing the effective social response, and these persist in larger groups of 10 and 30 fish, revealing common mechanisms of coordination. Although the pairwise interactions capture the qualitative structure of the force, we find evidence for higher-order interactions that are not present in existing models of animal groups. In contrast to model-based approaches where hypothesized behavioral rules serve as inputs, this approach has the advantage that unexpected rules can be found.

## Results

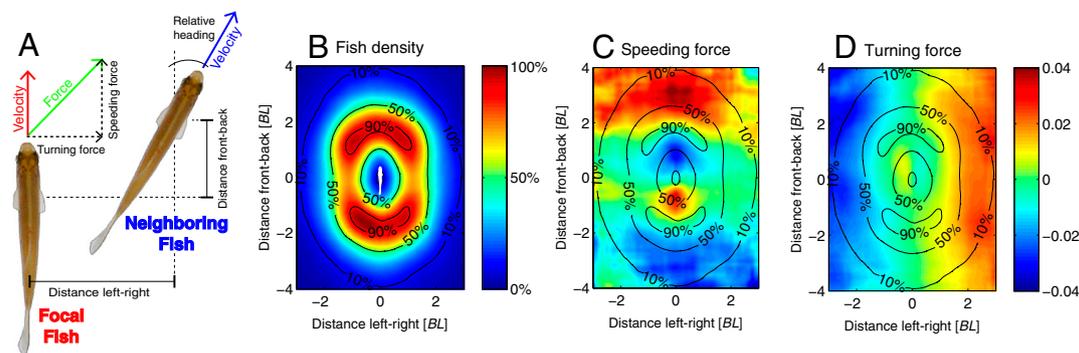
We begin by analyzing the free-swimming behavior of schools of just two fish. Pairs of golden shiners were placed in a large shallow tank and filmed from above at high spatial and temporal resolution. Shoals were approximately two-dimensional, which is appropriate as shiners often occupy shallow lakes in the wild (38, 39). In order to quantify fish behavior, we used custom tracking software to convert over 13 h of video data per group size for 2- and 3-fish shoals and over 6 h of video data per group size for 10- and 30-fish shoals into trajectories consisting of the center-of-mass positions of each fish at each point in time (see *SI Materials and Methods*).

**Analysis of Two-Fish Groups.** If we consider one fish the focal fish and place it at the center of our coordinate system heading north (Fig. 1A), the neighboring fish tends to be approximately 1.5–2 body lengths away and at a preferred angle of approximately  $-60$  to  $60^\circ$  with respect to the focal fish's heading (Fig. 1B). The neighboring fish is unlikely to be closer to the focal fish than approximately 1 body length or farther away than approximately 4 body lengths, and the fish school also tends to be elongated in its direction of motion (Fig. 1B).

From these trajectories, we can compute the force exerted on a fish by differentiating fish positions to get velocities, and differentiating fish velocities to get accelerations (force being proportional to acceleration). When we look at the force on a focal fish as a function only of the position of its neighbor (Fig. S1), repulsive and attractive zones become immediately apparent. When the neighboring fish is close to the focal fish, a repulsive force is exerted on the focal fish, pushing it away from its neighbor. When the neighboring fish is far away, an attractive force is exerted on the focal fish, pulling it toward its neighbor.

Fish control their motion by modulating their speeds and by turning. To reflect this, it is useful to decompose the force into two components (Fig. 1A), the component along a fish's direction of motion, which represents speeding up and slowing down (the "speeding force"), and the component perpendicular to its direction of motion, which represents turning (the "turning force"). By looking at a fish's speeding force as a function of its neighbor's position (Fig. 1C), we see that speed regulation is a crucial component of how fish interact. This interaction rule is neglected by many swarming models that assume constant speed (see refs. 2 and 24 for exceptions). When the neighboring fish is just behind the focal fish, the focal fish speeds up to avoid collision, and when the neighboring fish is just ahead of the focal fish, the focal fish slows down to avoid contact with its neighbor. From the full force field (Fig. S1), we see that the repulsive interaction is governed chiefly by speed modulation (when the neighboring fish is in the repulsive zone, most of the arrows are along the focal fish's direction of motion).

When the neighboring fish is farther away, speed modulation is also critical (Fig. 1C). When it is far ahead of the focal fish, the focal fish accelerates to catch up. When it is far behind, the focal fish slows down, presumably to let its neighbor catch up with it. Overall, the speeding force depends on how far the neighboring fish is to the front of or behind the focal fish (its distance along the focal fish's direction of motion, or its "front-back distance"), but is relatively insensitive to how far the neighbor is to its sides (its distance perpendicular to the focal fish's direction of motion,



**Fig. 1. Two-fish configurations.** (A) Diagram of dynamical variables. As the fish swim freely in the tank, their bodies form a natural Cartesian coordinate system. We place the focal fish at the origin, pointing north, and measure the relative position and heading of the neighboring fish. The effective force on the focal fish (i.e., its measured acceleration) is decomposed into its speeding and turning components. (B) Probability of finding the neighboring fish at a given position with respect to the focal fish using the framework in A. Each time the neighbor is at a particular position, one count is added to the corresponding bin (see *SI Materials and Methods*). Contours represent isolevels at 10, 50, and 90% of the "highest" (most visited) bin, which contains 37,481 events. (C and D) Speeding and turning components, respectively, of the mean measured effective force on the focal fish as a function of the neighboring fish's position. Note that regions of zero effective force correspond to high density regions in B. For all force maps, colors utilize the same scale. For the speeding forces, positive values indicate speeding up and negative values indicate slowing down. For the turning forces, positive values indicate a right turn and negative values indicate a left turn. Distances are expressed in units of body length [BL] and time in seconds [s]. Analysis was restricted to frames in which all fish were at least 2.5 body lengths away from the boundary and moving at a minimum speed of 0.5 [BL/s].

or its “left-right distance”), with the exception of the local avoidance regions. We have insufficient data to determine how the force decays outside of the mapped region (greater than four body lengths from the focal fish).

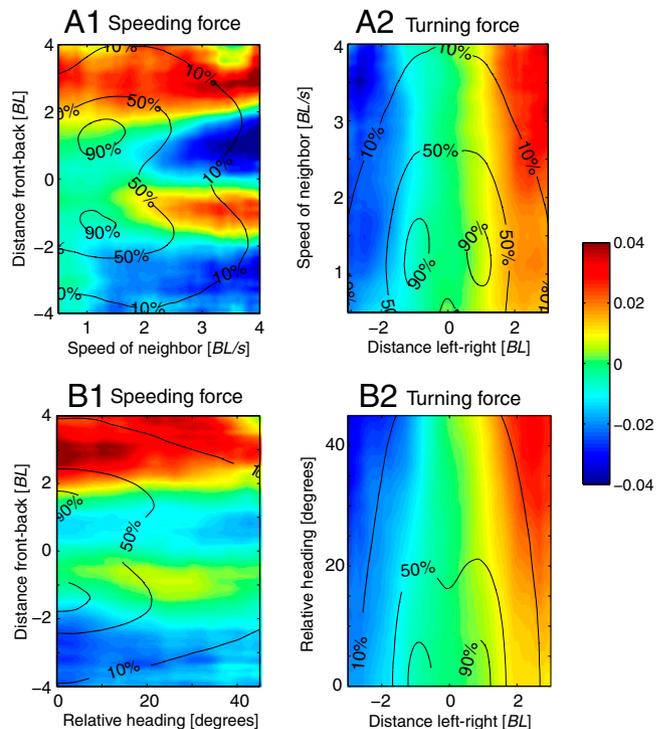
Turning is a second important component of fish interaction (Fig. 1D). When the neighboring fish is within a body length of the focal fish, there is a slight tendency to turn away from the neighbor, as shown by the small yellow and green-blue zones to the immediate left and right of the focal fish. However, when the neighboring fish is farther away from the focal fish, the turning forces are substantial. When the neighbor is far to the right of the focal fish, it turns right (positive values), toward it, and when the neighboring fish is far to the left of the focal fish, it turns left (negative values), toward it. In a complementary manner to the speeding force, the turning force depends almost exclusively on how far the neighboring fish is to the side of the focal fish, and not on its distance in front of or behind it. Note that the turning force shown here is an attractive rather than an alignment force because it depends on the position, not orientation, of the neighboring fish.

We can take advantage of our observations that the speeding force depends mostly on the neighbor’s position in front of or behind the focal fish and the turning force depends mostly on the neighbor’s position to the sides of the focal fish, and project these forces down to one dimension. To project the speeding force along the direction of motion of the focal fish, we take each position of the neighboring fish along the focal fish’s front-back axis and sum the force over all positions along its left-right axis (weighted by the number of observations), in effect neglecting how the speeding force depends on the summed-over dimension (quantified below). In an analogous manner, we project the turning force along the dimension perpendicular to the focal fish’s direction of travel, removing its dependence on the neighbor’s front-back distance and focusing on how it varies based on the position of the neighbor to the sides of the focal fish. When we do this (Fig. S2), we see that, within the interaction zone and outside the repulsion region, forces are spring-like, increasing approximately linearly with distance from the focal fish along the relevant directions.

Using these one-dimensional representations, we can now investigate how the speeding and turning forces depend on the position of the neighboring fish and other dynamical variables that are likely to be important determinants of schooling behavior (Fig. 2). We see that the speeding force (Fig. 2A1) and, to a lesser extent, the turning force (Fig. 2A2) increase with the speed of the neighboring fish. The forces on the focal fish also increase with the focal fish’s own speed (Fig. S3); however, because the speeds of the two fish are correlated, it is difficult to determine which factor or factors drive the change in behavior.

In many models, individuals match their directions of travel with their neighbors’ orientations (4, 7). We look for evidence of such an “alignment force” by mapping a fish’s acceleration as a function of its neighbor’s position and its relative heading. When fish are well aligned, the speeding force is greatest (Fig. 2B1). This is not surprising, as it only makes sense to accelerate to catch up with a neighbor who is traveling in the same direction as you are. The turning force, in contrast, becomes stronger as fish are increasingly out of alignment (Fig. 2B2). The direction of turning, however, is always toward the neighbor’s position rather than its heading (Fig. S4). That is, fish turn just as strongly toward a fish heading toward it as away from it. So, rather than an explicit alignment force, we find that alignment modulates the strength of attraction.

To ensure that we have not disregarded important information through our projections, we look at how the speeding force depends on the neighbor’s left-right distance from the focal fish and how the turning force depends on the neighbor’s front-back distance from the focal fish (Fig. S5). The forces are virtually zero everywhere, confirming that we have indeed preserved the dependence of the forces on the position of the neighboring fish. We also check that we have sufficient data to confidently estimate



**Fig. 2.** Mean measured effective forces as a function of the speed and heading of the neighboring fish. (A1 and A2) Speeding and turning forces as a function of the neighbor’s speed and its front-back or left-right distance, respectively. For a faster-moving neighbor, both measured forces are stronger, and the preferred distance to a neighbor in front becomes larger (the zero-force region in A1 is displaced forward in the front-back axis). (B1 and B2) Speeding and turning forces as a function of the relative heading of the two fish and the front-back or left-right distance, respectively. For the same spatial configuration, the focal fish displays a higher speeding acceleration when both fish are aligned and a higher turning acceleration when they are misaligned. Contours show the probability that fish are in particular configurations, as described in Fig. 1.

mean forces. We see that the variance of the force in our region of interest (Fig. S6) is never greater than approximately 25% of the mean force itself, and is often much smaller.

In reality, fish pay attention to other cues beyond their neighbors’ positions and velocities when making behavioral decisions. For example, we see that the forces felt by a focal fish are correlated with its neighbor’s acceleration (Fig. S7). These correlations are harder to interpret: Because the acceleration of the neighboring fish is also governed by the dynamical equations, decoupling its influence on the focal fish from reactions to other stimuli common to both individuals would require a different approach. It appears, however, that the force does have an acceleration dependence beyond the position and velocity dependencies that we have already seen, and after controlling for confounding effects, this could be quantified.

**Information Transfer.** To investigate whether there is spatial structure in the initiation and response to changes in behavior, we look at how the direction of the focal fish is correlated with the direction of its neighbor in time, depending on the relative positions of the two fish (Fig. S8A). We find that, on average, the fish are well aligned (orientation correlation is 0.8 at  $dt = 0$ ). When the neighboring fish is in front of the focal fish (red line), their correlation peaks significantly after zero (see *SI Materials and Methods*), at a delay time of approximately 1.2 s before decaying, whereas when the neighboring fish is behind the focal fish (blue line), their correlation simply decays in time. This implies that directional information flows from front to back but not from back to front. That is, fish turn in response to the turning of fish ahead of them but

not to fish behind them. Speed information, in contrast, flows bidirectionally (Fig. S8B; both red and blue lines peak at  $dt > 0$ ; peak times are not significantly different from each other), with fish accelerating and decelerating in response to their neighbors' speed changes regardless of whether they are ahead or behind.

**Analysis of Three-Fish Shoals.** Now that we have measured a fish's behavioral rules as a function of the position, speed, and orientation of its single neighbor, we want to know how a fish integrates information from multiple sources. In models, the most common assumption is that animals compute their would-be response to each of their neighbors separately and then average these pairwise responses (with added noise) to arrive at movement decisions (4, 7) (although see ref. 40 for an exception). The validity of this assumption is as yet untested, and although averaging is the simplest hypothesis for how animals might integrate information, it leads to the damping of responses that may be important for the animals. Indeed, real animal groups respond much more dynamically to perturbations (e.g., a predator attack) than model swarms based on averaging (27, 30). We address the question of how individuals combine social information from multiple sources by analyzing the behavior of fish in three-fish shoals and computing how the measured accelerations differ from what would be expected if the fish were averaging the corresponding pairwise forces measured in the two-fish shoals.

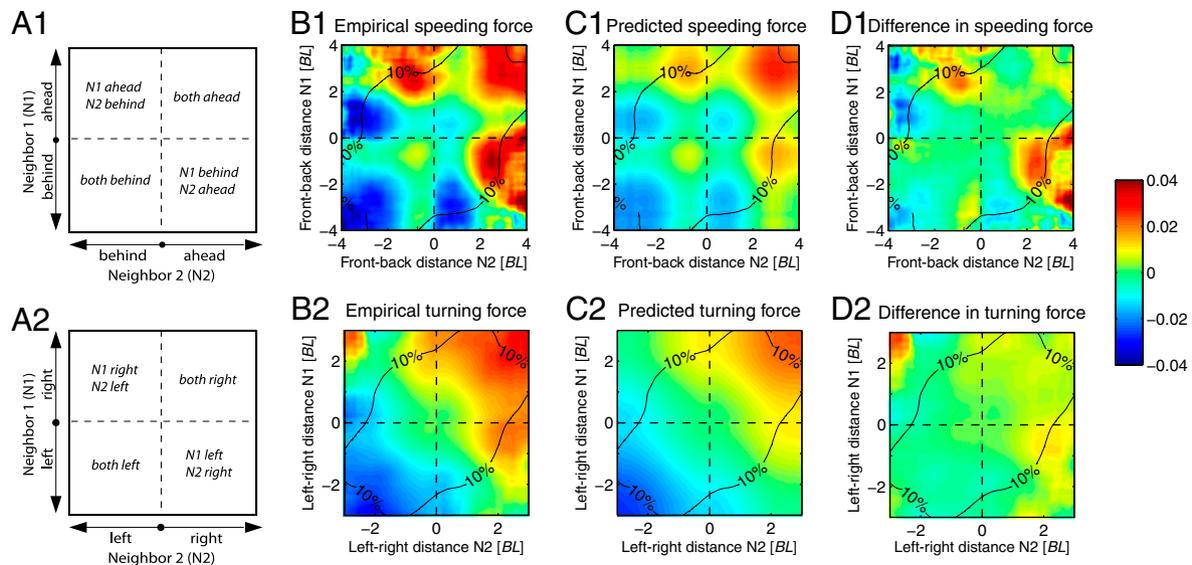
For shoals of three fish, we compute the speeding and turning forces felt by a focal fish as a function of the positions of its two neighbors (Fig. S9 and Fig. 3 A1 and A2). Because this yields a four-dimensional map (each neighbor contributes a 2D xy position relative to the focal fish), to visualize the data we project the position of each neighbor down to one dimension. For the speeding force, we project the positions of the neighbors along the direction of motion of the focal fish, because as we saw for the two-fish shoal, the speeding force depends chiefly on the distance of the neighbor

in front of or behind it. For the turning force, we project the positions of the two neighbors along the axis perpendicular to the direction of motion of the focal fish, because the turning force depends predominantly on a neighbor's distance to its left or right.

When both neighbors are far in front of, or far behind, the focal fish (approximately two to four body lengths), there is a strong tendency for it to speed up or slow down, respectively (Fig. 3B1). When one neighbor is far ahead and the other is close behind (approximately zero to two body lengths, so in its repulsive zone), the focal fish displays a large positive acceleration. Conversely, when one neighbor is far behind and the other is just ahead, the focal fish decelerates strongly. These trends are not unexpected based on our experience with the two-fish shoals: Because in each of these cases the fish has two independent reasons to change its speed in the way that it does, it displays a synergistic response. The variance in the speeding and turning forces for the three-fish shoals is also small (Fig. S10), so we can be confident in our estimates of the mean forces.

The turning forces that we observe for the three-fish shoals are also consistent with a combination of the turning forces we saw for the two-fish shoals (Fig. 3B2). When both neighbors are on the same side of the focal fish, the focal fish turns strongly toward the two neighbors. When the two neighbors are on opposite sides of the focal fish, the turning force cancels out and is close to zero.

Next we ask what we would expect these forces to look like if the fish in the three-fish shoal were simply averaging their individual responses to each of their neighbors. We compute this by averaging the force maps for the two-fish shoals shown in Fig. 1 C and D to obtain a four-dimensional representation of the force as a function of the position of two neighbors. As with the three-fish empirical data, we then project the position of each neighbor to one dimension, weighting by the measured density distribution for the three-fish shoal (Fig. 3 C1 and C2). Very similar results



**Fig. 3.** Nonpairwise interactions in three-fish shoals. (A) Diagram of dynamical variables describing the three-fish configurations. The relative positions of both neighboring fish are expressed in Cartesian coordinates with the focal fish at the origin. Velocities and effective forces are also expressed in the same way as in the two-fish system. For the speeding forces (Top), the positions of both neighbors are projected onto the axis along the focal fish's direction of motion, and for the turning forces (Bottom), the positions of both neighbors are projected onto the axis perpendicular to the focal fish's direction of motion. (B1 and B2) Measured speeding and turning forces exerted on the focal fish as a function of the front-back or left-right distances to both neighbors, respectively. Ten-percent contours as described in Fig. 1 are overlaid for reference. (C1 and C2) Predicted speeding and turning forces exerted on the focal fish under the hypothesis that fish average pairwise interactions. The maps show results from averaging the two-fish forces presented in Fig. 1. They are symmetric about the diagonal, because the identities of the two neighbors can be interchanged. Note that they display the same qualitative features as those measured for three-fish shoals (B1 and B2), but with significant residual three-body forces, (D1 and D2). (D1 and D2) Residual speeding and turning forces not accounted for by averaging pairwise responses to neighbors, obtained by subtracting panel C1 from B1 and C2 from B2. The residual forces show a substantial three-body effect producing stronger effective restitution forces (up to 100% stronger in the case of speeding and up to 25% stronger in the case of turning) when the focal fish is between both neighbors. The red patches in D1 occur when one neighbor is close behind and the other is farther ahead, showing a synergistic effect when the focal fish has two independent reasons to accelerate. Similarly, the blue patches occur when one neighbor is just ahead and the other is farther behind, showing a synergistic effect when the focal fish has two independent reasons to decelerate.



was chosen in order to capture the behavior at a time resolution that reflects the temporal correlations within our data (Fig. S8). Our force maps capture clear characteristics of fish dynamics, but we may slightly underestimate the forces at hand. A more accurate portrait could potentially be painted by taking decision times into account. A second limitation is that, when comparing two- and three-fish shoals, we concentrate on the position dependence of the force (due to computational limitations). The way fish integrate velocity and acceleration-dependent responses may also be important, and it would be interesting to explore this in future work.

The presence of significant three-body effects leads to the question of how interaction rules may change if more individuals are involved. Although suitable for small systems, our approach becomes impractical for three or more neighbors, as the amount of data needed as well as the computational cost grows exponentially with the number of fish. The data-driven spirit of our approach, however, could be extended to analyze groups of hundreds or even thousands of animals via force matching techniques, described in ref. 41. To reduce the interaction topology one could also make use of fine-grained information such as the visual field of each fish or discrete decision-making times that can be extracted from trajectory data.

It is unlikely that in reality animals literally measure and store dynamical variables such as the speed and heading associated with each of their neighbors. Given that vision is known to be an important sensory modality for schooling, fish may use proxies such as optical flow (detecting changes in intensity from moment

to moment) for quickly estimating these quantities (37). Potential candidates include the angular velocity of a neighbor's body on the retina of the focal fish or "loom," defined as the rate of change of the angle subtended by a neighbor's eye on the retina of the focal fish (47). Important future directions would be exploring how animals integrate information from widely disparate sources in real time (48) and how this nonlinear integration translates into higher-order computational capabilities that emerge at the level of the collective.

## Materials and Methods

Details of the experimental system, tracking, computation of velocity and acceleration, force maps, correlation function analysis, computation of three-fish residual interactions, and the force matching method can be found in *SI Materials and Methods*.

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