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Reverse engineering the control law for schooling in zebrafish using virtual reality

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Revealing the evolved mechanisms that give rise to collective behavior is a central objective in the study of cellular and organismal systems^{1–12}. In addition, understanding the algorithmic basis of social interactions in a causal and quantitative way offers an important foundation for subsequently quantifying social deficits^{13–16}. Here, we employ immersive Virtual Reality (VR)¹⁷ to reverse-engineer the sensory-motor control of social response during schooling in a vertebrate model: juvenile zebrafish (*Danio rerio*). In addition to providing a highly-controlled means to understand how zebrafish translate visual input to movement decisions, networking our systems allows real fish to swim and interact together in the same virtual world. Together, this allows us to directly test models of social interactions in situ. A key feature of social response is shown to be single- and multi-target-oriented pursuit. This is based on a quasi-2D egocentric representation of the positional information of conspecifics, and is highly robust to incomplete sensory input. We demonstrate, including with a ‘Turing test’ for pursuit behavior, that all key features of this behavior are accounted for by individuals following a simple experimentally-derived proportional derivative control law, which we term ‘BioPD’. Since target pursuit is key to effective control of autonomous vehicles, we evaluate—as a proof of principle—the potential utility of this simple evolved control law for human-engineered systems. In doing so, we find close-to-optimal performance in autonomous vehicles (terrestrial, airborne, and watercraft) pursuit, while requiring limited system-specific tuning or optimization.

Collective behavior arises from positive and/or negative local feedback loops, which enable repeated local interactions to scale up into highly robust coordinated activities without the need for regulation by global supervision or via a pre-established template^{1,2}. Due to their ubiquity and importance across scales of biological organization, the mechanisms that give rise to coordinated motion among cells³ and organisms such as swarming insects^{4,5}, schooling fish^{6–8}, flocking birds^{9,10}, and humans in crowds^{11,12}, have been of particular interest of multiple disciplines. In addition to providing new insights into biology, an understanding of the evolved strategies animals employ to coordinate collective behavior can offer new opportunities for the development of engineered solutions¹⁸, such as for the coordination of autonomous vehicles^{19,20}.

To date, however, it has been extremely difficult to infer the nature and causal structure of biological interactions that give rise to collective behavior using conventional experimental approaches^{13–15}. Consequently, the sensory-motor feedback mechanisms that have evolved to regulate collective behavior are often poorly understood²¹, with our inability to identify, or test among, alternative hypotheses being a major bottleneck. Recent advances in immersive volumetric virtual reality (VR) technology^{17,22} provide a new means to control, and thus interrogate, the causal structure of social relationships among individuals. In addition, they allow the direct testing of experimentally-derived hypothetical models of social interactions *in situ*, by allowing reciprocal coupling between real organisms and virtual counterparts²³. Thus, analogous to how the ‘dynamic patch clamp’ method has revolutionized neuroscience, creating a realtime interface between living cells and experimentally-derived models²⁴, virtual reality opens up a ‘dynamic social clamp’ approach²³ to the study of animal behaviour.

Here, we employ this approach to investigate the sensory-motor control employed in regulating schooling behaviour in a model vertebrate, the juvenile zebrafish (*Danio rerio*) (1 ± 0.1 cm in length, 24-26 days post fertilisation, Fig. 1). At this age zebrafish predominantly employ vision to coordinate response to conspecifics when schooling (the lateral line being dominated by self-generated motion due to viscous adhesion forming a boundary layer around such small fish²⁵). Since leading others is known to be driven by different internal processes, such as indifference to others²⁶ and motion towards external ‘goals’²⁷, as a valuable starting point—and due to its general importance—we focus here only on socially-mediated interactions. In addition to uncovering a key algorithm employed in regulating schooling behavior (Fig. 1b-f, Supplementary Note 1, Supplementary Fig. 1, and Supplementary Table 1), we will demonstrate its application to motion control in engineered systems (Fig. 1g).

Since our immersive virtual reality, for freely swimming animals, relies on correct volumetric rendering from the perspective of a single individual (via the anamorphic illusion), it is not possible to put more than one individual in each VR arena. We can, however, connect systems such that individuals can see, and thus interact with, a realtime ‘holographic’ projection of the other (Fig. 1c shows this principle for a pair of individuals), which we term “the Matrix”. We find that, as in the real world (Supplementary Figs. 2a-d, 3a-d, and 4a-c), individuals in “the Matrix” (Supplementary Figs. 2e-h, 3e-h, and 4b-d) interact only when they occupy the same $x - y$ plane, with even small movements out of that plane (i.e., in the z dimension), either towards the surface, or to deeper water, being associated with rapid decoupling of social interactions (Supplementary Fig. 5). The structure, and strength, of the interactions within this plane (as quantified by decomposing motion

to lateral speed v_x , which is perpendicular to the leader's head direction, and forward speed v_y , which is along the leader's head direction (Fig. 2a)), is found to be near-identical when they interact within the physical world (Supplementary Fig. 4a-c) as when they interact in the same 'holographic' world (Supplementary Fig. 4b, d and Supplementary Fig. 6, Kolmogorov–Smirnov test, $p=0.26$ for v_x , $p=0.9$ for v_y). This suggests our VR system is ideal for dissecting sensory-motor feedback control.

To do so, we first employ open-loop experiments since these enable us to control the causal flow of information from a leading (virtual) fish to a follower (Fig. 2b), allowing us to establish how both spatial factors, and average swim speed (evaluated over its natural range, while also taking into account its 'bursty' nature resulting from rapid tail undulations followed by a friction-dominated glide, Fig. 2c; see Supplementary Fig. 7 for details), impact social response.

Fish tend to follow/pursue the virtual leader at a relatively stable distance, with this distance increasing approximately linearly as a function of the leader's speed (Fig. 2d-j), but with different "times to collision" (with respect to the current position of the leader, if the leader were to suddenly stop; Supplementary Fig. 8). The decomposed lateral (v_x) and forward (v_y) components of the follower's speed, as a function of the spatial position of the follower relative to a leader positioned at $x=0$, $y=0$, are shown in Fig. 2e, f, respectively. As shown in Fig. 2g, the average lateral speed increases as a function of lateral distance (x -axis) up to a specific distance, $r_x = 0.07\text{m}$ (determined by finding the maximum lateral speeds following a bootstrapping procedure; see Supplementary Note 2 for details), indicated by the dotted line, following which it starts to decrease. Lateral speed

is minimally impacted by swim speed (as seen by the similarity of panels in Fig. 2e and the average plots in Fig. 2g). The magnitude of the forward speed component as a function of the front-back distance, shown in Fig. 2h, also increases up to a similar distance, $r_y = 0.07\text{m}$ (see Supplementary Note 2 for details), but, unlike lateral speed, it increases in absolute magnitude as a function of average swim speed of the leader.

According to the above properties (speed control being proportional to the distance lag and to the average swimming speed of the leader, plus a lateral point of speed reduction at a specific distance), and following reverse engineering methods in biological studies^{28–31}, we propose a parsimonious bio-inspired PD controller, ‘BioPD’:

$$\left\{ \begin{array}{l} x_e = x_F - x_L \\ v_x = -(K_p x_e + K_d \dot{x}_e) e^{-\frac{x_e^2}{2r_x^2}} \\ y_e = y_F - y_L \\ v_y = -(K_p y_e + K_d \dot{y}_e) e^{-\frac{y_e^2}{2r_y^2}} \end{array} \right. \quad (1)$$

where x_F, y_F (and respectively, x_L, y_L) are the positions of the follower (leader) in a global coordinate system resolved in the x - and y - axes according to the leader (Fig. 2a). r_x and r_y , describe the critical distances at which the strength of social interactions is largest (Supplementary Note 2). K_d and K_p are the derivative gain and proportional gain parameters, respectively, which are the two main parameters in the model. We first determined the derivative parameter, based on the relationship between the average forward swimming speed of real and virtual fish (see Supplementary Note 2 for details), finding $K_d = 0.58$ (Fig. 2i). The proportional parameter K_p is estimated based on the stable distance lag under different average swimming speeds of the leader, which for our

zebrafish is found to be a constant with value $K_p=2.3$ (Fig. 2j).

Despite its simplicity, we find that the BioPD model can account for all of the main features observed in our experiments, including the stable swim speed of the follower, which is matched to that of the leader (Supplementary Fig. 9a, b), a similar spatial probability density with respect to the leader and similar lateral and forward swimming speeds as a function of x_e and y_e (Supplementary Fig. 9c-f). This indicates that fish exhibit a simple PD controller when regulating schooling, and that they employ the same parameters regardless of the average swim speed of the leader.

Speed input in a PD controller can be either perceived instantaneous speed or average speed over some period of time. Therefore, we further used our VR system to evaluate, directly, which features of the speed of conspecifics are employed in regulating social response. Previously, it has been suggested that the motion characteristics associated with burst-and-glide locomotion of juvenile zebrafish may provide an important social cue³². However, we find no evidence that this form of biological motion plays a role in schooling; zebrafish respond identically to continuous motion as they do to biological (bursty) motion (abstracted in Fig. 3a, but see Supplementary Fig. 10 for a detailed comparison).

This suggests that fine-scale instantaneous speed is not employed in the regulation of schooling. To evaluate this further, we investigated how the temporal resolution of visual input influences social response. By systematically changing the temporal update frequency, such that the virtual fish is always visible, but that its position is only updated at a certain rate (e.g., if the frequency is 10 Hz, the position of the virtual fish will be updated 10 times per second, the frames between

which it does not change position, Supplementary Fig. 11), we find that only if the update rate falls below $\sim 5\text{Hz}$ is social response impacted (Fig. 3b). This indicates that zebrafish integrate information over approximately 0.2s, a timescale close to the typical period of their burst-and-glide gait (Supplementary Fig. 7), which may imply the use of spatial working memory³³ and is captured in the model by averaging speed with a similar time window.

To establish how robust the schooling response is in the face of incomplete information, we decoupled speed and position by manipulating the visibility of the virtual fish. As may be expected of animals that need to deal with regular occlusions of others, such as by vegetation, or in patches of high turbidity, they do not respond to the sudden disappearance, or appearance, of a conspecific (Fig. 3c, d and Supplementary Figs. 12, 13). By adjusting both the duration of the windows of time during which information is available (Supplementary Figs. 12, 13), as well as whether the perceived speed in these windows is, or is not, congruent with the displacement (i.e., the average speed) between these windows (Supplementary Fig. 13), we again find evidence that the algorithm employed by zebrafish employs positional information as the input for speed control, and not estimates of instantaneous speed (Fig. 3c, d and Supplementary Figs. 12, 13).

With the core assumptions of BioPD validated, we now ask whether it can account for further dynamical features of natural schooling. In order to establish this control law above, we employed virtual conspecifics that move in a constant direction and at a constant average swim speed. In reality, however, fish dynamically modulate both properties. By presenting exactly the same trajectories, obtained from real fish leaders, both to real fish and to agents employing BioPD (Fig. 4a,

b), we can compare directly the response of real followers with agents employing BioPD. We find that BioPD provides robust and effective response to the dynamic changes in speed and direction exhibited in the natural system, and results in highly-comparable pursuit behavior to that exhibited by real fish (Fig. 4e, f).

Our VR systems allow us to take an even further step in establishing sensory-motor control; we can also ask whether leaders react differently to real followers versus followers employing BioPD. This can be thought of as a “Turing test” for the leader: is an agent employing BioPD sufficiently convincing to allow natural bi-directional interactions? To do so, we now allow two real fish, A and B, to interact in “the Matrix”, but each time fish A becomes a leader (i.e., occupies a frontal position), we can immediately replace the natural control of B with our BioPD control, and vice versa (Fig. 4c, d). Thus we can compare what we predict fish will do to what they actually do, for every pursuit event. We find that despite its simplicity, BioPD facilitates the maintenance of qualitatively similar, and effective, reciprocal social relationships among hybrid simulated-real individuals (Fig. 4g, h).

Having established the response to a single conspecific, we now ask whether BioPD can also predict the response of real fish to two conspecifics¹⁶. To do so, we consider its response to two leaders swimming side-by-side at a range of inter-individual lateral distances and swim speeds (Fig. 4i, j). We simply applied the BioPD controller for an agent receiving sensory input from the two leaders, but taking into account the linear perspective in the fish eye (see Supplementary Note 2 for details). We find that BioPD accounts, quantitatively, for a key experimental finding; that real

fish will both change their distance lag (Fig. 4k) and will suddenly switch from adopting a position in-between the ‘targets’ (here, the leaders) to deciding among them (i.e., swimming predominantly with one of the virtual fish) as a function of increasing the lateral distance, l , between the virtual leaders (Fig. 4l and Supplementary Fig. 14). Furthermore, it also accounts for the observed increase in the critical distance (l_c) at which this transition occurs as a function of increasing swim speed (Fig. 4l and Supplementary Figs. 15, 16).

Reverse engineering natural control laws—which have been subject to evolution by natural selection for millennia—could, in principle, provide new, simpler and/or more robust solutions for human-engineered problems¹⁸. The effective pursuit of mobile targets, along with the maintenance of appropriate spacing with respect to a target (which can include interception, or pursuit while also avoiding collisions, for example), is a central challenge in the effective control of autonomous vehicles, such as self-driving cars and guided aircraft and spacecraft. Man-made controllers, such as the widely-employed model predictive controller (MPC)³⁴, have been shown to be optimal for certain tasks, but typically are highly complex, and need to be individually-optimized—a very time-consuming process—for each specific application (since they depend on an accurate underlying model of the dynamical systems in which they are to be embedded). Natural systems, by contrast, are under the selection pressure to evolve highly robust and cheap strategies that approximate optimal solutions under a wide range of conditions. Seldom, however, are such evolved solutions evaluated *in situ* in real physical systems.

To gain insight into such potential application domains, we implemented, and compared

the pursuit performance of a state-of-the-art optimal MPC controller (see Supplementary Note 3 for details) and BioPD in three very different robotic platforms; terrestrial vehicles, airborne drones, and watercraft (Fig. 1h), the task being to follow a virtual leader on a predefined sine-shaped trajectory (Fig. 4m, Supplementary Video 2). Furthermore, unlike the MPC controller, which required a complex and time-consuming optimisation procedure for each robotic system, we employed BioPD with exactly the same parameters as estimated from zebrafish in all scenarios. We found that without system-specific tuning, and despite its simplicity, BioPD exhibits highly robust and effective performance, providing very close to optimal control energy³⁵ in the vehicle, drone, and roboboat control tasks (Fig. 4n and Supplementary Figs. 17-19). This proof of principle suggests that reverse-engineering evolved control laws may provide a complementary approach to traditional methods, especially when designing controllers that must be efficient and robust, yet require minimal sensing and computational requirements.

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Methods

Methodological overview We developed and utilized a virtual reality platform to reverse engineer the sensory-motor control algorithm for schooling behavior (Supplementary Fig. 1). To confirm its effectiveness, we compared the speed control of a real fish to another real fish in a traditional platform with that to a virtual fish in our system. Subsequently, we conducted open-loop experiments in the virtual environment with a single virtual fish, where we controlled the leader’s swimming properties, such as average speed, patterns, and visibility. By doing so, we developed a biologically inspired proportional derivative control model for the following behavior and verified its assumptions. Furthermore, we estimated the model through various means, including simulations,

experiments in the virtual reality system, experiments with two virtual leaders, and tests with three types of robots (terrestrial, airborne, and watercraft).

Virtual reality experiments We conducted experiments with zebrafish (*Danio rerio*) of age 24 to 26 days postfertilization raised in a room at 28 degrees on a 16-h light, 8-h dark cycle. The variation in age was to allow us to always use fish of a similar body length (1 ± 0.1 cm). 498 zebrafish were used (See Supplementary Table 1). Experiments were conducted in a fish virtual reality setup procured from Loopbio GmbH (refer to ref. [17] for details). After a fish was introduced into the arena (a bowl-shaped container with a diameter of 34 cm and a depth of 9 cm at the water level), we allowed the fish to acclimate to the environment for 20 minutes. This was followed by a 10-min control, during which the fish was presented with a single virtual conspecific (1 cm in body length) swimming in a circle with a diameter of 16 cm. After this, the real fish was exposed to the virtual fish, initialized with various swimming conditions (See Supplementary Note 1 for details). Each experiment lasted 90 minutes. We analyzed the data using custom Python 3.7 code. All experiments were conducted in accordance with the animal ethics permit approved by Regierungspräsidium Freiburg, G-17/170.

Simulations We utilized the BioPD algorithm to simulate the behavior of following a virtual leader in the VR experiment, as well as a real leader in a pair of fish performing leader-follower behavior extracted from real fish data. For following the virtual leader, we set the follower's initial position to a range of -0.05 to 0.05 m on the x -axis and -0.05 to 0 m on the y -axis. We introduced variability by adding white noise to the follower's speed control, with a standard variance of 0.016 for the x -axis and 0.45 times the average speed of the follower for the y -axis. The maximum

315 swimming speed was limited to 0.1 m/s. In contrast, for following a real fish leader, we initialized
316 the geometry position and swimming probabilities of the follower to match the starting point of
317 leader-follower behavior in the pair of real fish swimming in the same arena. The only difference
318 in this model from the previous one is that the leader is extracted from real fish leader data, which
319 dynamically changes both average swimming speeds and directions. No noise was added in the
320 second simulation.

321 **Parameter estimation for the model** The BioPD model has four primary parameters (r_x , r_y , K_p ,
322 K_d), which we determined by measuring real fish data collected in the virtual reality experiments.
323 In the following behavior, when the distance between the leader and follower is larger than the
324 threshold distance r_x (r_y), the follower reduces its speed to follow the leader. Therefore, we mod-
325 eled the turning point of speed as a first-order Gaussian derivative function, with the threshold
326 distance corresponding to the peak of the function. We determined the threshold distance by boot-
327 strapping (see Supplementary Note 2 for details). Since the follower must be within the distance
328 threshold to catch up with the leader, we simplified the model to a traditional PD controller. By
329 analyzing the PD controller, we found that the average swimming speed of the leader and follower
330 is determined by a first-order linear function, where the slope is determined by K_d only, and the
331 intercept is determined by both K_p and K_d . We obtained these two parameters through a similar
332 bootstrap analysis, and detailed derivations are given in the Supplementary Note.

333 **Robotic experiments** We tested both BioPD and an optimal controller on three different types of
334 robots: the Crazyflie drone³⁶, the SunFounders Robot PiCar-X, and a robot boat from MIT³⁴. To
335 create a virtual leader for the robots to follow, we programmed it to move in a sinusoidal curve.

We applied BioPD with the same mathematical model and parameters, which were scaled by the body size of the robots. Additionally, we considered a model predictive controller (MPC) based on our previous study³⁴. Parameters are optimized for each type of robot. Further details can be found in the Supplementary Note 3.

Data availability All data supporting this study’s findings have been privately uploaded on figshare (<https://figshare.com/s/bc3fda7db65dd958bf5e>) and will be made public after publication.

Code availability All the data analyses were performed using custom scripts written in Python (Python Software Foundation, 2018). All codes supporting this study’s findings have been privately uploaded on figshare (<https://figshare.com/s/bc3fda7db65dd958bf5e>) and will be made public after publication.

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Author Contributions L.L., M.N., and I.D.C. conceived the idea and designed the project; L.L. conducted the experiments and collected data, L.L. and G.A. conducted experiments and collected the 3D tracking and matrix data. L.L. and M.N. analyzed data with contributions from I.D.C.; L.L. and W.W. conducted experiments on robots and collected data with contributions from O.D. and D.R.; L.L., M.N., and I.D.C. wrote the initial draft and all authors contributed to the revision of the text.

Competing Interests The authors declare that they have no competing financial interests.

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Fig. 1. Schematic of the study of sensory-motor control of schooling behavior. **a**, The flow diagram of the sensory-motor control of the social response to neighbors. We reverse engineer the sensory-motor control (SMC) of following behavior to a model, which we term as ‘BioPD’ (see explanation in the main text). **b**, A “traditional” experiment in which two real fish swim together in one bowl-shaped arena. Note that trajectories are shown in 1:1 scale with respect to the dimensions of the bowl, but the size of the fish is enlarged by a factor of 3x to ensure better visibility. **c**, “The Matrix” system, where each arena contains a single individual, each of which can interact with a realtime volumetric projection of the other. **d**, Open-loop experiments with one virtual fish as a leader swimming back-forth at a recorded swimming speed (0.04 m/s in average). **e**, Experiments with two virtual fish swimming side-by-side as two leaders to verify the sensory-motor control. **f**, Experiments with two real fish interacting within “the Matrix” to verify the sensory-motor control of the following behavior. A virtual fish becomes a follower controlled by the BioPD when the real fish becomes a leader (e.g., the real fish swims in front). Otherwise, the virtual fish copies the position and direction of the real fish in the other arena. **g**, Evaluating the performance of the BioPD model by comparing it to a model predictive controller (MPC) in three robotic systems (terrestrial, airborne, and watercraft). See Supplementary Videos 1 and 2 for a glimpse of the experimental design.

Fig. 2. Reverse engineering sensory-motor control of fish to a bioinspired proportional-derivative controller, ‘BioPD’. **a**, The local coordinate system is based on the position and direction of the leader. The real fish’s swimming speed is resolved into lateral speed v_x and forward speed v_y . **b**, Schematic to show the experimental setup, where a real fish follows one virtual fish which is swimming back-and-forth in a straight line. **c**, The virtual fish exhibits a realistic burst-and-glide swimming pattern for five different average swimming speeds $\bar{v}_{VF}$ (0.04 to 0.08 m/s with an interval of 0.01 m/s). **d**, The higher the average swimming speed of the leader, the greater is the distance maintained by the follower to the leader. **e-f**, Lateral (**e**) and forward (**f**) speed control as a function of the position of the follower in the local coordinate of the leader with different average swimming speeds. **g-h**, Average lateral (**g**) and forward (**h**) speeds as a function of the follower’s position in the x (**g**) and y (**h**)-axis in the local coordinate of the leader. The shaded areas denote the standard deviation after 100 bootstraps. **i**, The distribution of the derivative parameter K_d is based on the maximum forward swimming speed at each average swimming speed of the leader. **j**, The comparison between the experiments and simulations.

Fig. 3. Evaluating the perceptual information utilized in the regulation of social response to

a leader. **a**, Virtual fish swims with the same average but different instantaneous speeds: burst-and-glide as the control (i) or constant speed as the treatment (ii). **b**, Virtual fish swims with different update frequencies at 100 Hz as the control (i) or at 5 Hz as the selected treatment (ii) while keeping a fixed location between updates. **c**, Virtual fish swims with different visibilities (always visible as the control (i), or periodically become invisible (time being visible and invisible are both set to 0.2s) as the treatment (ii)) to decouple the presented position and speed information. **d** is the same as **c**, except the virtual fish jumps to a location further away by increasing its speed during the period of invisibility by a factor of 2 as compared to speed during being visible. Selected swimming performances, including relative position (iii-iv), lateral speed (v-vi), and forward speed (vii-viii), are presented (See Supplementary Figs. 10-13 for details).

Fig. 4. Evaluating the BioPD: simulations, experiments in “the Matrix” system and in two virtual leader scenarios, and using robotics. a-b, Positions of real followers (**a**, RF) and simulated followers controlled by the BioPD (**b**, VF) relative to a real leading fish (positioned at the origin). **c-d**, Experimental verifications in “the Matrix” system. The virtual fish in the right arena is an ‘avatar’ of the real fish from the left arena if the real fish in the right arena is not swimming in front. Otherwise, the virtual fish (**c**, VF) in the right arena is controlled by the BioPD. The virtual fish in the left arena is always controlled by the real fish from the right arena. In the left arena, the real fish (**d**, RF) follows the virtual fish controlled by the real fish in the other arena. Virtual (**c**) / real (**d**) follower’s positions relative to the real (**c**) / virtual (**d**) leader’s position in two arenas in “the Matrix” system. **e-h**, Distributions of relative distance in the y - (**e,g**) and x - (**f,g**) axis of the simulations (**e**, **f**) and experiments (**g**, **h**). Jensen Shannon Divergence, JSD= 0.03, 0.0, 0.08, 0.0 for (**e-h**) respectively. **i**, The setup for two virtual fish leaders swimming side-by-side at different left-right distances and average swimming speeds. **j**, The definition of the coordinate system. Origin is the center of the two virtual fish. Positive y points to the head direction of the virtual fish. **k**, The model predicts the relative distance between the real fish and the virtual fish swimming at different average swimming speeds. **l**, The model also predicts the bifurcations in the following behavior of the real fish when they follow two virtual leaders. **m**, Three robots are controlled by BioPD and model predictive controller (MPC) to follow a leader moving in a sinusoidal wave. **n**, A comparison of the control energy of BioPD and MPC.

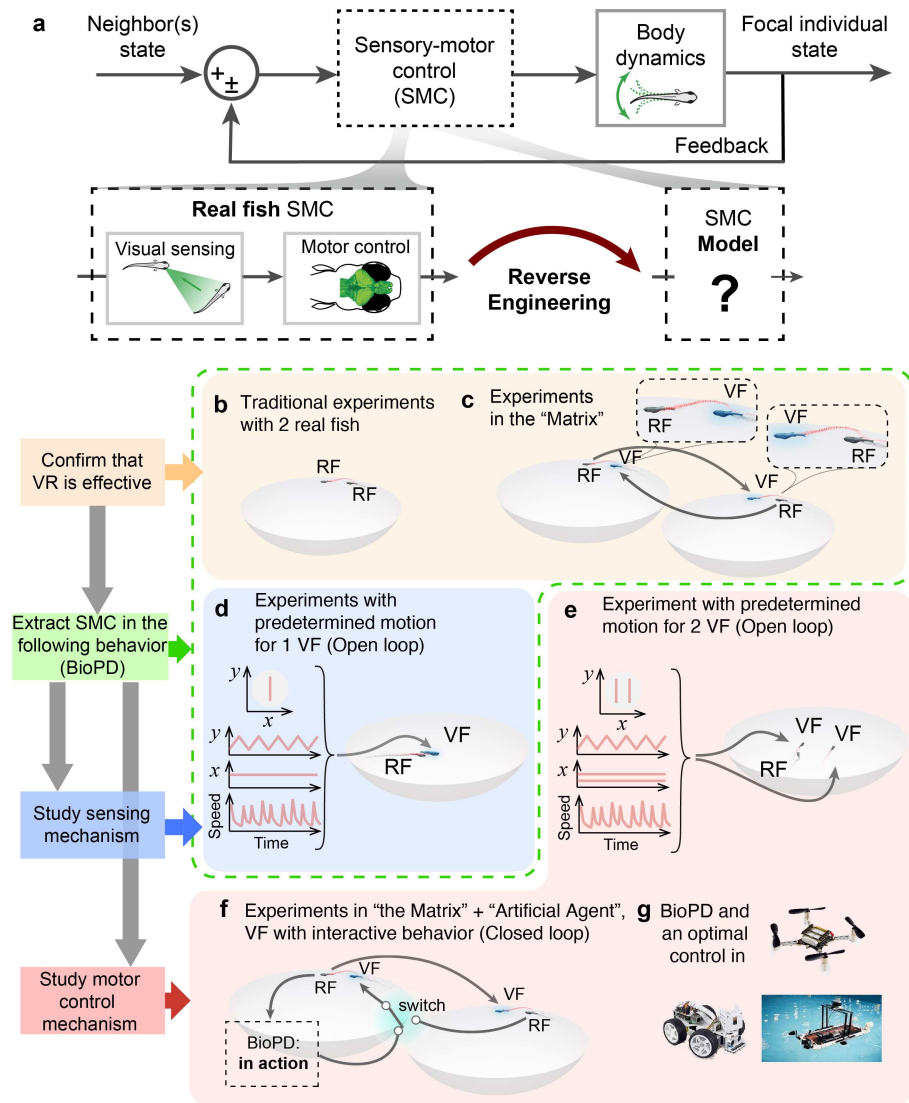


Figure 1: Fig1

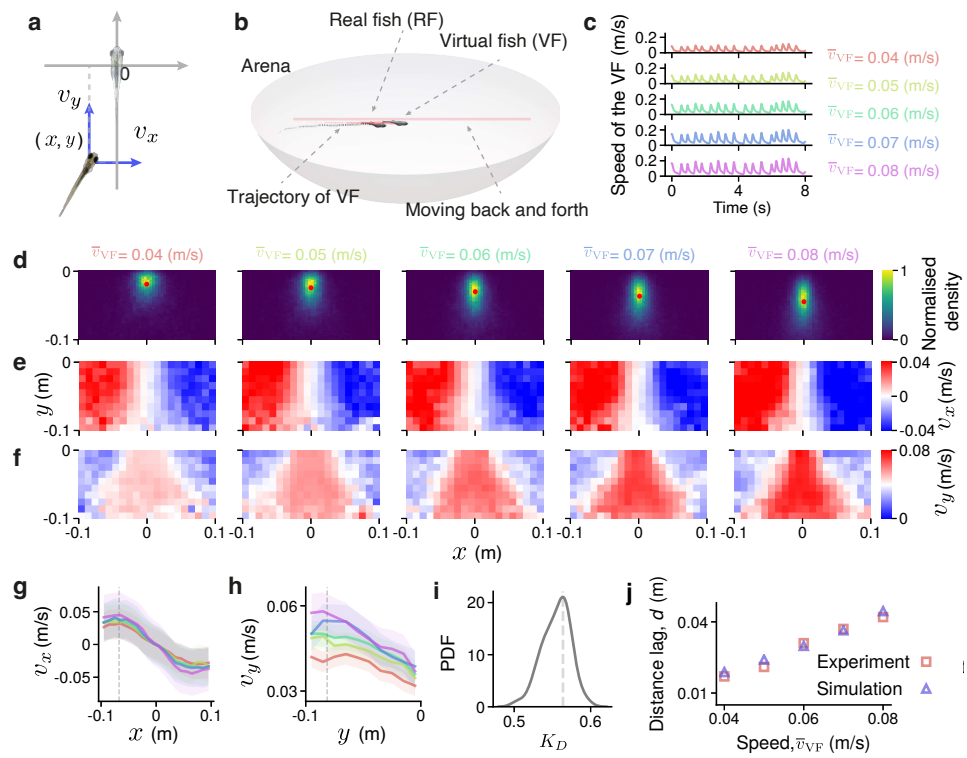


Figure 2: Fig2

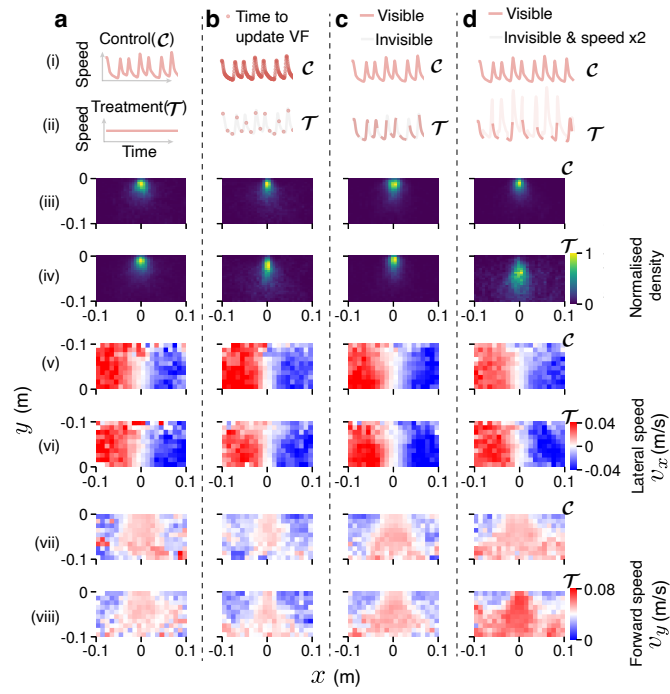


Figure 3: Fig3

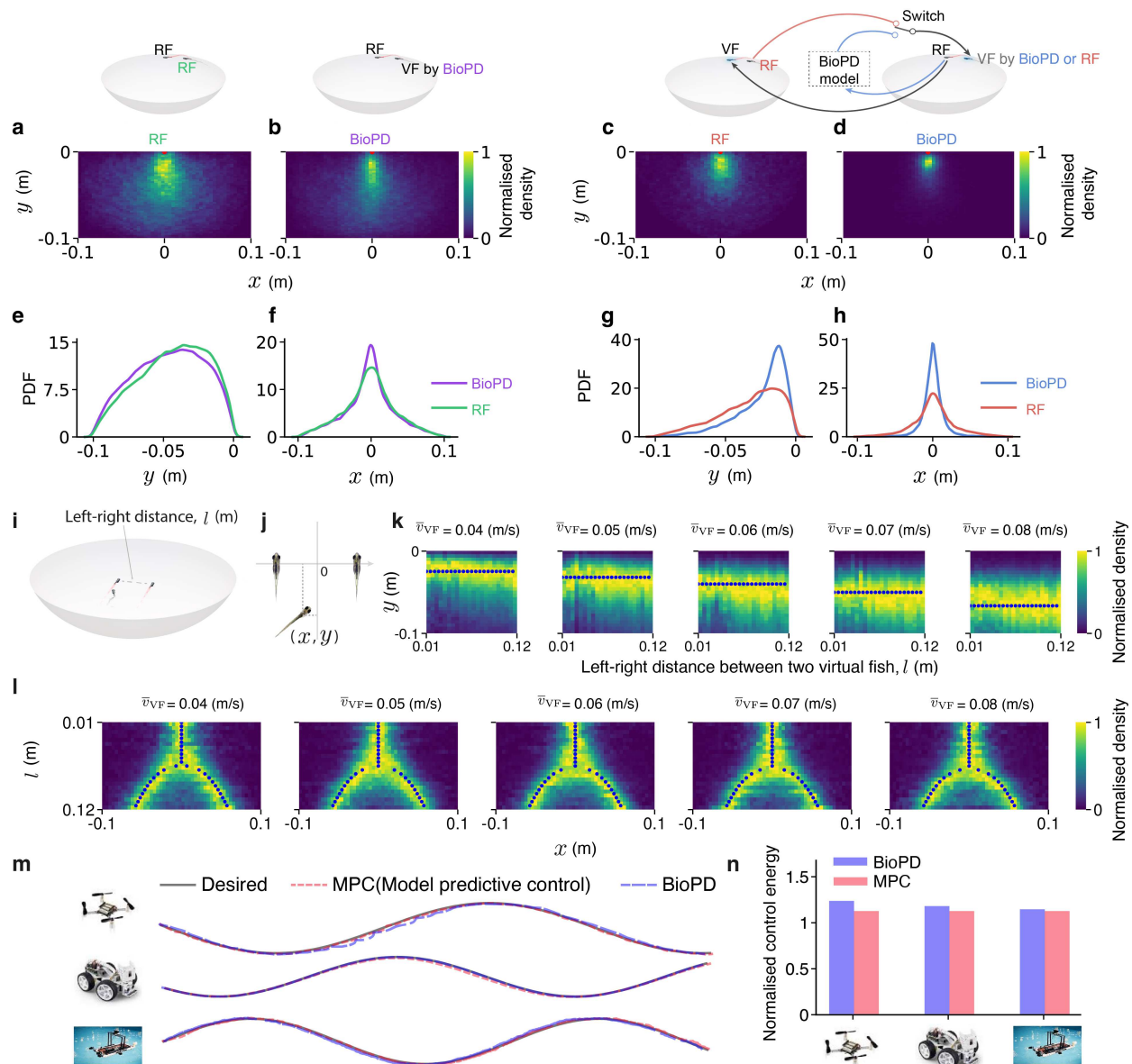


Figure 4: Fig4

Supplementary Files

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