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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 21 the study of cellular and organismal systems<sup>1-12</sup>. In addition, understanding the algorithmic 22 basis of social interactions in a causal and quantitative way offers an important foundation 23 for subsequently quantifying social deficits<sup>13-16</sup>. Here, we employ immersive Virtual Real-24 ity (VR)<sup>17</sup> to reverse-engineer the sensory-motor control of social response during schooling 25 in a vertebrate model: juvenile zebrafish (Danio rerio). In addition to providing a highly-26 controlled means to understand how zebrafish translate visual input to movement decisions, 27 networking our systems allows real fish to swim and interact together in the same virtual 28 world. Together, this allows us to directly test models of social interactions in situ. A key 29 feature of social response is shown to be single- and multi-target-oriented pursuit. This is 30 based on a quasi-2D egocentric representation of the positional information of conspecifics, 31 and is highly robust to incomplete sensory input. We demonstrate, including with a 'Tur-32 ing test' for pursuit behavior, that all key features of this behavior are accounted for by 33 individuals following a simple experimentally-derived proportional derivative control law, 34 which we term 'BioPD'. Since target pursuit is key to effective control of autonomous vehi-35 cles, we evaluate—as a proof of principle—the potential utility of this simple evolved control 36 law for human-engineered systems. In doing so, we find close-to-optimal performance in 37 autonomous vehicles (terrestrial, airborne, and watercraft) pursuit, while requiring limited 38 system-specific tuning or optimization. 39

Collective behavior arises from positive and/or negative local feedback loops, which enable 40 repeated local interactions to scale up into highly robust coordinated activities without the need 41 for regulation by global supervision or via a pre-established template<sup>1,2</sup>. Due to their ubiquity 42 and importance across scales of biological organization, the mechanisms that give rise to coordi-43 nated motion among cells<sup>3</sup> and organisms such as swarming insects<sup>4,5</sup>, schooling fish<sup>6–8</sup>, flocking 44 birds<sup>9,10</sup>, and humans in crowds<sup>11,12</sup>, have been of particular interest of multiple disciplines. In 45 addition to providing new insights into biology, an understanding of the evolved strategies ani-46 mals employ to coordinate collective behavior can offer new opportunities for the development of 47 engineered solutions<sup>18</sup>, such as for the coordination of autonomous vehicles<sup>19,20</sup>. 48

To date, however, it has been extremely difficult to infer the nature and causal structure of 49 biological interactions that give rise to collective behavior using conventional experimental ap-50 proaches<sup>13–15</sup>. Consequently, the sensory-motor feedback mechanisms that have evolved to regu-51 late collective behavior are often poorly understood<sup>21</sup>, with our inability to identify, or test among, 52 alternative hypotheses being a major bottleneck. Recent advances in immersive volumetric vir-53 tual reality (VR) technology<sup>17,22</sup> provide a new means to control, and thus interrogate, the causal 54 structure of social relationships among individuals. In addition, they allow the direct testing of 55 experimentally-derived hypothetical models of social interactions in situ, by allowing reciprocal 56 coupling between real organisms and virtual counterparts<sup>23</sup>. Thus, analogous to how the 'dynamic 57 patch clamp' method has revolutionized neuroscience, creating a realtime interface between liv-58 ing cells and experimentally-derived models<sup>24</sup>, virtual reality opens up a 'dynamic social clamp' 59 approach<sup>23</sup> to the study of animal behaviour. 60

Here, we employ this approach to investigate the sensory-motor control employed in regu-61 lating schooling behaviour in a model vertebrate, the juvenile zebrafish (Danio rerio)  $(1\pm0.1 \text{ cm})$ 62 in length, 24-26 days post fertilisation, Fig. 1). At this age zebrafish predominantly employ vi-63 sion to coordinate response to conspecifics when schooling (the lateral line being dominated by 64 self-generated motion due to viscous adhesion forming a boundary layer around such small fish<sup>25</sup>). 65 Since leading others is known to be driven by different internal processes, such as indifference to 66 others<sup>26</sup> and motion towards external 'goals'<sup>27</sup>, as a valuable starting point—and due to its general 67 importance—we focus here only on socially-mediated interactions. In addition to uncovering a key 68 algorithm employed in regulating schooling behavior (Fig. 1b-f, Supplementary Note 1, Supple-69 mentary Fig. 1, and Supplementary Table 1), we will demonstrate its application to motion control 70 in engineered systems (Fig. 1g). 71

Since our immersive virtual reality, for freely swimming animals, relies on correct volumetric 72 rendering from the perspective of a single individual (via the anamorphic illusion), it is not possible 73 to put more than one individual in each VR arena. We can, however, connect systems such that 74 individuals can see, and thus interact with, a realtime 'holographic' projection of the other (Fig. 1c 75 shows this principle for a pair of individuals), which we term "the Matrix". We find that, as in the 76 real world (Supplementary Figs. 2a-d, 3a-d, and 4a-c), individuals in "the Matrix" (Supplementary 77 Figs. 2e-h, 3e-h, and 4b-d) interact only when they occupy the same x - y plane, with even small 78 movements out of that plane (i.e., in the z dimension), either towards the surface, or to deeper 79 water, being associated with rapid decoupling of social interactions (Supplementary Fig. 5). The 80 structure, and strength, of the interactions within this plane (as quantified by decomposing motion 81

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 sensorymotor 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 frictiondominated 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 93 increasing approximately linearly as a function of the leader's speed (Fig. 2d-j), but with different 94 "times to collision" (with respect to the current position of the leader, if the leader were to suddenly 95 stop; Supplementary Fig. 8). The decomposed lateral  $(v_x)$  and forward  $(v_y)$  components of the 96 follower's speed, as a function of the spatial position of the follower relative to a leader positioned 97 at x=0, y=0, are shown in Fig. 2e, f, respectively. As shown in Fig. 2g, the average lateral speed 98 increases as a function of lateral distance (x-axis) up to a specific distance,  $r_x = 0.07$ m (determined 99 by finding the maximum lateral speeds following a bootstrapping procedure; see Supplementary 100 Note 2 for details), indicated by the dotted line, following which it starts to decrease. Lateral speed 101

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,  $r_y = 0.07$ 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<sup>28–31</sup>, we propose a parsimonious bio-inspired PD controller, 'BioPD':

1

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

where  $x_F$ ,  $y_F$  (and respectively,  $x_L$ ,  $y_L$ ) are the positions of the follower (leader) in a global coor-107 dinate system resolved in the x- and y- axes according to the leader (Fig. 2a).  $r_x$  and  $r_y$ , describe 108 the critical distances at which the strength of social interactions is largest (Supplementary Note 2). 109  $K_d$  and  $K_p$  are the derivative gain and proportional gain parameters, respectively, which are the 110 two main parameters in the model. We first determined the derivative parameter, based on the rela-111 tionship between the average forward swimming speed of real and virtual fish (see Supplementary 112 Note 2 for details), finding  $K_d$  =0.58 (Fig. 2i). The proportional parameter  $K_p$  is estimated based 113 on the stable distance lag under different average swimming speeds of the leader, which for our 114

<sup>115</sup> 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 122 over some period of time. Therefore, we further used our VR system to evaluate, directly, which 123 features of the speed of conspecifics are employed in regulating social response. Previously, it 124 has been suggested that the motion characteristics associated with burst-and-glide locomotion of 125 juvenile zebrafish may provide an important social cue<sup>32</sup>. However, we find no evidence that this 126 form of biological motion plays a role in schooling; zebrafish respond identically to continuous 127 motion as they do to biological (bursty) motion (abstracted in Fig. 3a, but see Supplementary Fig. 128 10 for a detailed comparison). 129

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  $\sim$ 5Hz 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 memory<sup>33</sup> 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, 140 we decoupled speed and position by manipulating the visibility of the virtual fish. As may be 141 expected of animals that need to deal with regular occlusions of others, such as by vegetation, or 142 in patches of high turbidity, they do not respond to the sudden disappearance, or appearance, of 143 a conspecific (Fig. 3c, d and Supplementary Figs. 12, 13). By adjusting both the duration of the 144 windows of time during which information is available (Supplementary Figs. 12, 13), as well as 145 whether the perceived speed in these windows is, or is not, congruent with the displacement (i.e., 146 the average speed) between these windows (Supplementary Fig. 13), we again find evidence that 147 the algorithm employed by zebrafish employs positional information as the input for speed control, 148 and not estimates of instantaneous speed (Fig. 3c, d and Supplementary Figs. 12, 13). 149

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; 159 we can also ask whether leaders react differently to real followers versus followers employing 160 BioPD. This can be thought of as a "Turing test" for the leader: is an agent employing BioPD 161 sufficiently convincing to allow natural bi-directional interactions? To do so, we now allow two 162 real fish, A and B, to interact in "the Matrix", but each time fish A becomes a leader (i.e., occupies 163 a frontal position), we can immediately replace the natural control of B with our BioPD control, 164 and vice versa (Fig. 4c, d). Thus we can compare what we predict fish will do to what they actually 165 do, for every pursuit event. We find that despite its simplicity, BioPD facilitates the maintenance 166 of qualitatively similar, and effective, reciprocal social relationships among hybrid simulated-real 167 individuals (Fig. 4g, h). 168

Having established the response to a single conspecific, we now ask whether BioPD can also predict the response of real fish to two conspecifics<sup>16</sup>. 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 181 selection for millennia—could, in principle, provide new, simpler and/or more robust solutions for 182 human-engineered problems<sup>18</sup>. The effective pursuit of mobile targets, along with the maintenance 183 of appropriate spacing with respect to a target (which can include interception, or pursuit while also 184 avoiding collisions, for example), is a central challenge in the effective control of autonomous ve-185 hicles, such as self-driving cars and guided aircraft and spacecraft. Man-made controllers, such 186 as the widely-employed model predictive controller (MPC)<sup>34</sup>, have been shown to be optimal for 187 certain tasks, but typically are highly complex, and need to be individually-optimized—a very 188 time-consuming process—for each specific application (since they depend on an accurate under-189 lying model of the dynamical systems in which they are to be embedded). Natural systems, by 190 contrast, are under the section to evolve highly robust and cheap strategies that approximate op-191 timal solutions under a wide range of conditions. Seldom, however, are such evolved solutions 192 evaluated in situ in real physical systems. 193

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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 195 3 for details) and BioPD in three very different robotic platforms; terrestrial vehicles, airborne 196 drones, and watercraft (Fig. 1h), the task being to follow a virtual leader on a predefined sine-197 shaped trajectory (Fig. 4m, Supplementary Video 2). Furthermore, unlike the MPC controller, 198 which required a complex and time-consuming optimisation procedure for each robotic system, we 199 employed BioPD with exactly the same parameters as estimated from zebrafish in all scenarios. 200 We found that without system-specific tuning, and despite its simplicity, BioPD exhibits highly 201 robust and effective performance, providing very close to optimal control energy<sup>35</sup> in the vehicle, 202 drone, and roboboat control tasks (Fig. 4n and Supplementary Figs. 17-19). This proof of principle 203 suggests that reverse-engineering evolved control laws may provide a complementary approach to 204 traditional methods, especially when designing controllers that must be efficient and robust, yet 205 require minimal sensing and computational requirements. 206

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#### 285 Methods

**Methodological overview** We developed and utilized a virtual reality platform to reverse engineer 286 the sensory-motor control algorithm for schooling behavior (Supplementary Fig. 1). To confirm its 287 effectiveness, we compared the speed control of a real fish to another real fish in a traditional plat-288 form with that to a virtual fish in our system. Subsequently, we conducted open-loop experiments 289 in the virtual environment with a single virtual fish, where we controlled the leader's swimming 290 properties, such as average speed, patterns, and visibility. By doing so, we developed a biolog-291 ically inspired proportional derivative control model for the following behavior and verified its 292 assumptions. Furthermore, we estimated the model through various means, including simulations, 293

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 296 26 days postfertilization raised in a room at 28 degrees on a 16-h light, 8-h dark cycle. The variation 297 in age was to allow us to always use fish of a similar body length ( $1\pm0.1$  cm). 498 zebrafish were 298 used (See Supplementary Table 1). Experiments were conducted in a fish virtual reality setup 299 procured from Loopbio GmbH (refer to ref. [17] for details). After a fish was introduced into 300 the arena (a bowl-shaped container with a diameter of 34 cm and a depth of 9 cm at the water 301 level), we allowed the fish to acclimate to the environment for 20 minutes. This was followed 302 by a 10-min control, during which the fish was presented with a single virtual conspecific (1 cm 303 in body length) swimming in a circle with a diameter of 16 cm. After this, the real fish was 304 exposed to the virtual fish, initialized with various swimming conditions (See Supplementary Note 305 1 for details). Each experiment lasted 90 minutes. We analyzed the data using custom Python 3.7 306 code. All experiments were conducted in accordance with the animal ethics permit approved by 307 Regierungspräsidium Freiburg, G-17/170. 308

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

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

**Robotic experiments** We tested both BioPD and an optimal controller on three different types of robots: the Crazyflie drone<sup>36</sup>, the SunFounders Robot PiCar-X, and a robot boat from MIT<sup>34</sup>. To 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 study<sup>34</sup>. 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.

#### **346** References for methods

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371 **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 374 diagram of the sensory-motor control of the social response to neighbors. We reverse engineer the 375 sensory-motor control (SMC) of following behavior to a model, which we term as 'BioPD' (see 376 explanation in the main text). **b**, A "traditional" experiment in which two real fish swim together in 377 one bowl-shaped arena. Note that trajectories are shown in 1:1 scale with respect to the dimensions 378 of the bowl, but the size of the fish is enlarged by a factor of 3x to ensure better visibility. c, "The 379 Matrix" system, where each arena contains a single individual, each of which can interact with a 380 realtime volumetric projection of the other. d, Open-loop experiments with one virtual fish as a 381 leader swimming back-forth at a recorded swimming speed (0.04 m/s in average). e, Experiments 382 with two virtual fish swimming side-by-side as two leaders to verify the sensory-motor control. f, 383 Experiments with two real fish interacting within "the Matrix" to verify the sensory-motor control 384 of the following behavior. A virtual fish becomes a follower controlled by the BioPD when the 385 real fish becomes a leader (e.g., the real fish swims in front). Otherwise, the virtual fish copies 386 the position and direction of the real fish in the other arena. g, Evaluating the performance of the 387 BioPD model by comparing it to a model predictive controller (MPC) in three robotic systems 388 (terrestrial, airborne, and watercraft). See Supplementary Videos 1 and 2 for a glimpse of the 389 experimental design. 390

Fig. 2. Reverse engineering sensory-motor control of fish to a bioinspired proportional-39 derivative controller, 'BioPD'. a, The local coordinate system is based on the position and direc-392 tion of the leader. The real fish's swimming speed is resolved into lateral speed  $v_x$  and forward 393 speed  $v_y$ . **b**, Schematic to show the experimental setup, where a real fish follows one virtual fish 394 which is swimming back-and-forth in a straight line. c, The virtual fish exhibits a realistic burst-395 and-glide swimming pattern for five different average swimming speeds  $\bar{v}_{VF}$  (0.04 to 0.08 m/s with 396 an interval of 0.01 m/s). d, The higher the average swimming speed of the leader, the greater is the 397 distance maintained by the follower to the leader. e-f, Lateral (e) and forward (f) speed control as a 398 function of the position of the follower in the local coordinate of the leader with different average 390 swimming speeds. g-h, Average lateral (g) and forward (h) speeds as a function of the follower's 400 position in the x (g) and y (h)-axis in the local coordinate of the leader. The shaded areas denote 401 the standard deviation after 100 bootstraps. i, The distribution of the derivative parameter  $K_d$  is 402 based on the maximum forward swimming speed at each average swimming speed of the leader. j, 403 The comparison between the experiments and simulations. 404

Fig. 3. Evaluating the perceptual information utilized in the regulation of social response to 405 a leader. a, Virtual fish swims with the same average but different instantaneous speeds: burst-406 and-glide as the control (i) or constant speed as the treatment (ii). b, Virtual fish swims with 407 different update frequencies at 100 Hz as the control (i) or at 5 Hz as the selected treatment (ii) 408 while keeping a fixed location between updates. c, Virtual fish swims with different visibilities 409 (always visible as the control (i), or periodically become invisible (time being visible and invisible 410 are both set to 0.2s) as the treatment (ii)) to decouple the presented position and speed information. 411 **d** is the same as **c**, except the virtual fish jumps to a location further away by increasing its speed 412 during the period of invisibility by a factor of 2 as compared to speed during being visible. Selected 413 swimming performances, including relative position (iii-iv), lateral speed (v-vi), and forward speed 414 (vii-viii), are presented (See Supplementary Figs. 10-13 for details). 415

Fig. 4. Evaluating the BioPD: simulations, experiments in "the Matrix" system and in two 416 virtual leader scenarios, and using robotics. a-b, Positions of real followers (a, RF) and sim-417 ulated followers controlled by the BioPD (**b**, VF) relative to a real leading fish (positioned at the 418 origin). c-d, Experimental verifications in "the Matrix" system. The virtual fish in the right arena 419 is an 'avatar' of the real fish from the left arena if the real fish in the right arena is not swimming in 420 front. Otherwise, the virtual fish (c, VF) in the right arena is controlled by the BioPD. The virtual 421 fish in the left arena is always controlled by the real fish from the right arena. In the left arena, the 422 real fish (**d**, RF) follows the virtual fish controlled by the real fish in the other arena. Virtual (**c**) 423 / real (**d**) follower's positions relative to the real (**c**) / virtual (**d**) leader's position in two arenas in 424 "the Matrix" system. e-h, Distributions of relative distance in the y- (e,g) and x- (f,g) axis of the 425 simulations (e, f) and experiments (g, h). Jensen Shannon Divergence, JSD=0.03, 0.0, 0.08, 0.0426 for (e-h) respectively. i, The setup for two virtual fish leaders swimming side-by-side at different 427 left-right distances and average swimming speeds. j, The definition of the coordinate system. Ori-428 gin is the center of the two virtual fish. Positive y points to the head direction of the virtual fish. 429 **k**, The model predicts the relative distance between the real fish and the virtual fish swimming at 430 different average swimming speeds. I, The model also predicts the bifurcations in the following 431 behavior of the real fish when they follow two virtual leaders. **m**, Three robots are controlled by 432 BioPD and model predictive controller (MPC) to follow a leader moving in a sinusoidal wave. n, 433 A comparison of the control energy of BioPD and MPC. 434



Figure 1: Fig1



Figure 2: Fig2



Figure 3: Fig3



Figure 4: Fig4

### **Supplementary Files**

This is a list of supplementary files associated with this preprint. Click to download.

- SIMovie1.mp4
- SIMovie2.mp4
- BioPDSI.pdf