



OPEN Fish adapt and dynamically avoid an approaching robotic fish across repeated exposures

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Biomimetic robots are innovative tools for guiding animal behavior by triggering avoidance responses that steer movement away from the robot. Potential applications include livestock management and environmental conservation, such as directing fish away from pollution and oil spills. While predator-like replicas have traditionally been used to provoke avoidance, less is known about how conspecific-like robotic platforms may elicit threat-like responses depending on their approach behavior. To address this gap, we programmed a conspecific-like robot to repeatedly approach live fish in a free-swimming setup, with varying approach speeds in each trial. Our results show that repeated exposure increased the likelihood of avoidance responses, indicating changes in behavioral reaction over time. In some instances, fish displayed threat-associated responses, including freezing and evasive maneuvers characterized by extreme turns and accelerations relative to baseline swimming. The initiation of these evasive events depended on both robot–fish distance and relative speed, suggesting that avoidance responses in this context are not determined by distance alone. Additionally, avoidance speed increased dynamically with both robot speed and proximity. These findings provide quantitative insights into how approach dynamics shape avoidance behavior toward a conspecific-like robot, informing future models of fish interactions and the design of robotic systems aimed at guiding fish movement through controlled aversive cues.

Recent advancements in robotics have enabled the creation of biomimetic robots capable of interacting with live animals in a naturalistic manner^{1,2}. These robots mimic biological forms and behaviors, providing a gateway to the establishment of mixed animal-robot societies where robots and live animals mutually influence each other's behavior^{3–5}. Such systems offer significant advantages for studying animal behavior, as they allow for precise control of robots to test specific hypotheses about social interactions in real-world experiments with standardized, reproducible designs^{6–9}. Beyond research, these animal-robot systems have applications ranging from livestock management^{10,11} and environmental protection^{12,13}. For instance, robots could help steer fish away from ecological threats they may not naturally recognize, such as pollution¹⁴, by leveraging their avoidance behavior^{15,16}.

The field of animal-robot interaction has grown rapidly, particularly through the use of robotic fish to investigate behavioral responses across a wide range of species. Notably, robotic platforms have been employed to explore complex phenomena such as territorial displays in bettas¹⁷, courtship dynamics in guppies¹⁸, schooling and aggregation in golden shiners and zebrafish^{19,20}, and ecologically grounded decision-making in archerfish and neon tetras^{21,22}. These studies highlight species-specific behavioral repertoires and how robotic agents can selectively trigger or modulate them. For example, robotic guppies with species-typical coloration and motion patterns have been shown to elicit following and courtship behaviors²³, while predator-like replicas reliably provoke fear or avoidance responses^{24,25}. Moreover, recent work emphasizes methodological diversity—robots vary in morphology (e.g., rigid vs. flexible tails), interactivity (open-loop vs. closed-loop control), and presentation context (e.g., transparent barriers vs. free-swimming setups). This diversity has enabled researchers to isolate specific variables such as motion cues, approach trajectories, or visual features when probing animal responses. Together, these studies provide a rich methodological and conceptual foundation that situates the

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present work within a broader interdisciplinary framework that integrates ethology, robotics, and behavioral ecology.

Theoretical²⁶ and empirical^{27,28} studies have identified three primary interaction forces governing conspecific fish behavior: attraction, alignment, and avoidance. Previous research has focused primarily on how conspecific-like robots elicit attraction²⁹ and alignment³⁰. These robots mimic the appearance of a member of the same species. However, live animals do not always exhibit attraction toward their conspecifics. Depending on the behavioral context, they may instead display avoidance. In schooling, avoidance is commonly modeled as short-range repulsion for collision avoidance. In other social contexts, encounters between conspecifics with conflicting goals can become agonistic, ranging from mutual avoidance to fighting³¹. While avoidance behavior often incurs the cost of lost social benefits, it can be advantageous in certain contexts. For instance, guppies avoid infected conspecifics to mitigate the risk of disease transmission³². In the context of mating, male guppies may engage in chasing behavior, where one male flees and ceases courting a female after being rapidly approached by another male³³. These context-dependent forms of avoidance may involve different motivational mechanisms than the short-range repulsion term used in schooling models, but they nevertheless result in measurable movement away from another individual or stimulus. Understanding when avoidance occurs in response to conspecifics is crucial for a more comprehensive analysis of these social forces in animal behavior. This knowledge is also important for applications where robots aim to influence fish behavior by eliciting avoidance responses. Previous work has shown that fish reactions to robotic fish depend strongly on simple cues such as approach speed and relative size, and that the same robotic platform can elicit either attraction or avoidance depending on how these cues are presented³⁴. Thus, even a robot that resembles a conspecific may be perceived as threatening when it repeatedly approaches quickly and at close range. Using a conspecific-like design therefore allows us to examine how approach speed, proximity, and repeated exposure shape avoidance behavior in a controlled setting. Moreover, bio-inspired robotic fish are increasingly motivated by practical considerations of operating around live animals while minimizing disturbance and potential welfare impacts^{12,35}.

In this study, we present findings from an experiment in which live Trinidadian guppies (*Poecilia reticulata*) interacted with a mobile, conspecific-like robot in the same tank, without physical separation. The objective was to assess the guppies' behavioral responses to the approaching robot. Specifically, we sought to examine various factors that influence avoidance behavior, such as robot speed, proximity, and repeated exposure. Additionally, we aimed to investigate whether key anti-predator behaviors^{36–38}, such as freezing (where the fish remains motionless as a defense mechanism) and escape-like evasive maneuvers (a sharp turn followed by high acceleration to evade the robot), manifest during these interactions. Finally, we evaluated whether the observed responses align with predictions from established interaction force models between conspecifics. To explore this, the robot was programmed to approach a fish from an initial distance of 40 cm, continuing until it reached close proximity. Each fish underwent multiple consecutive trials for at least 10 minutes. In each trial, the robot's approach speed was set to a fixed value, ranging from 15 to 30 cm/s. These findings provide valuable insights for improving prediction models of fish behavior, which could potentially be used to guide fish away from threats by influencing their movement in response to robot approaches^{15,16}.

The growing body of research in animal-robot interactions has particularly emphasized the integration of robots with fish species^{18,39}. Much of this work has explored how biomimetic robots can be accepted by fish as conspecifics. For instance, recent findings suggest that biomimetic robots capable of adjusting their behavior in response to a guppy's actions can more effectively elicit following behavior and reduce avoidance reactions, further improving integration within fish groups²³. In contrast, studies on the avoidance behavior of fish are primarily conducted in the context of anxiety-related and anti-predator scenarios. In response to predation threat, guppies increase anti-predator behaviours including escape movements, freezing, predator inspections and thigmotaxis (i.e. area avoidance)⁴⁰. Escape responses typically involve rapid acceleration and a directional change in order to distance the fish from the threat³⁸. Success in avoiding predators depends on factors such as timing, reaction distance, locomotor performance, and escape direction. Studies have shown that prey do not escape at the furthest distance a threat is perceived, but at a distance determined by the relative costs and benefits of escaping, which is influenced by factors like predator approach speed⁴¹. Recent findings suggest that the avoidance-initiation distance is also influenced by repeated exposure to the threat⁴². Although the robot in our study mimics a conspecific, we hypothesize that its repeated approaches may lead the guppy to perceive it as a threat, thereby increasing the likelihood of avoidance behavior with successive trials.

Researchers have also employed interactive robots to simulate anxiety-related⁴³ and anti-predator^{24,25,44,45} scenarios to study the behavioral responses of fish. Most studies involved exposing live zebrafish to a 3D-printed predator-like replica of a red tiger. Spinello et al.²⁵ found that the robotic replica triggered fear-related responses, evidenced by geotaxis, although this effect diminished over time as the robot's interactivity increased. Surprisingly, the zebrafish's visual exposure to the replica did not result in a significant increase in the average distance from the robot. Ladu et al.²⁴ demonstrated a robotic replica of a predator induced significant fear responses in zebrafish, evidenced by increased thrashing behavior and spatial avoidance, compared to the control and computer-animated conditions. These studies consistently involve physical separation when investigating avoidance behavior. Removing such barriers could allow for a finer analysis of how relative distance and robot speed impact avoidance behavior, as well as the spatial aspects of the fish's responses.

To the best of our knowledge, few studies have examined avoidance behavior in live fish interacting with conspecific-like robots in free-swimming contexts. Kruusmaa et al.³⁴ found that collective avoidance responses in mackerel schools were influenced by both the size and speed of a robotic replica. However, their study only examined the probability of avoidance for two distinct speed levels, rather than analyzing fish speed in function of a continuous range of robot speeds. Examining a wider range of speeds is important, as speed regulation plays a critical role in avoidance behavior during interactions between conspecifics⁴⁶. This could help developers design robots that elicit specific fish speeds, which may be crucial for guiding fish with higher precision. Pino

et al.³⁵ focused on conceptual models to investigate stress, fear, and anxiety in zebrafish caused by bio-inspired robotic fish with varying components and designs. Their freely swimming robots enabled the analysis of fish speed relative to robot-fish distance, suggesting that a decrease in distance results in increased fish velocity, indicative of avoidance behavior. Nevertheless, their findings relied on descriptive results and did not account for individual differences through statistical analyses. Building on these studies, we hypothesize that both robot speed and proximity interact to influence fish avoidance speed, with their combined effects shaping the fish's response to the robot's approach.

Although these studies provide valuable insights, they do not address how fish actions, such as turns and accelerations, vary with the relative distance and speed of an approaching robotic conspecific. These actions are critical indicators of anti-predator behavior, such as escape maneuvers. Furthermore, analyzing how avoidance speed varies as a function of both robot speed and robot-fish distance could also help robot developers better understand which actions to program in order to elicit specific responses from fish. In the collective-motion literature, avoidance is most often formalized as a short-range repulsion term that depends primarily on distance, where fish move opposite to the average position of neighbors within a defined radius^{26–28}. More recent studies have incorporated decay functions that gradually decrease the strength of the avoidance force as the distance increases^{47,48}. While this captures collision avoidance in schooling, it remains unclear how well such formulations extend to threat-like avoidance responses elicited by directed robotic approaches. Here, we therefore use this framework as a baseline reference and quantify where additional factors such as approach speed and repeated exposure may become important.

We used the RoboFish system, originally introduced by Landgraf et al.²⁹, which enables an interactive guppy replica to engage with live guppies within the same tank. The 3D-printed replica is attached to a magnetic base below, aligned with a two-wheeled robot carrying a magnet on top that moves beneath the tank floor. This robot design has been shown to be accepted as a conspecific by guppies in multiple studies^{23,29,30,49,50}. We integrated high-definition video tracking with a closed-loop feedback system to steer the robot toward the fish in real time. Given that guppies naturally inhabit shallow waters, all analyses were conducted in two dimensions, focusing on horizontal movement within the tank. Fish behaviors were classified into avoidance, attraction, and slow motion to examine how repeated exposure to the robot's approach influences the onset of avoidance behavior. We also investigated the occurrence of anti-predator or stress behaviors, such as freezing and thigmotaxis, to assess whether the conspecific-like robot was perceived as a threat. Additionally, a fixed-effects model was used to examine how the robot's approach speed and relative distance influenced the fish's avoidance speed. Finally, we analyzed the execution of avoidance behavior, focusing on how relative speed and proximity to the robot influence the fish's decision-making process for avoidance. We also discuss whether these actions align with traditional models of avoidance behavior between fish.

Material and methods

Study organism and maintenance

For this study, we selected a fish species previously shown to exhibit a high level of acceptance of the robotic model as a conspecific²⁹. We used wild-type guppies (*Poecilia reticulata*), which have been bred in the laboratory for multiple generations. These guppies originally descended from individuals captured in the Arima River, Trinidad, in 2010. The test fish were sourced from large, randomly outbred single-species populations housed at the animal care facilities of the Faculty of Life Sciences, Humboldt University of Berlin. To prevent inbreeding, these stocks are regularly supplemented with wild-caught fish brought back from fieldwork conducted in Trinidad and Tobago. A natural light cycle of 12 hours of light and 12 hours of darkness was provided, with the water temperature consistently maintained at 26 °C. The fish were fed twice daily ad libitum with commercially available flake food (TetraMinTM). The experiments were conducted in the afternoon, three hours after the initial feeding. Afterwards, all fish were given a second feeding. In the experiments, only adult female guppies were used to avoid any potential influence of sex-specific and life stage-specific differences in behavior, and to ensure that the fish were large enough for the tracking device to accurately locate them. Adult fish were identified as those with a body length exceeding 15 mm and displaying external signs of maturity, such as a gravid spot.

Experimental apparatus

The RoboFish system (see Fig. 1), originally introduced by Landgraf et al.²⁹, enables an interactive fish replica to engage with live guppies within the same environment. The experimental setup consists of a glass tank measuring 120 cm × 120 cm, filled with 7 cm of aged tap water, which simulates the shallow conditions typically found in the guppies' natural habitats, such as rivers and streams. These low water levels are intended to encourage natural behavior in the fish. An experimental area of 100 cm × 100 cm is defined in the center of the tank by four plastic walls, while the surrounding space houses heating elements and a pump to maintain a consistent water temperature of 25 °C and to aerate the water. The tank is elevated 1.40 m above the ground, supported by an aluminum rack.

Beneath the tank floor, a two-wheeled differential drive robot operates on a transparent plastic surface, carrying an upward-facing neodymium magnet that aligns with a corresponding magnetic base inside the tank, to which a 3D-printed fish replica is attached. The replica's movement is directly controlled by the robot's motion. The robot is equipped with three red-light LEDs—two on the right side and one on the left—that are visible from below through the transparent pane, aiding in the estimation of the robot's current position and orientation. A Basler acA1300-200um camera (1280 px × 1024 px) is positioned on the floor to track the robot's location, while a second camera, the Basler acA2040-90uc (2040 px × 2040 px), is mounted 1.5 m above the tank to monitor both the live fish and the replica.

To minimize exposure to external disturbances, the entire system is enclosed within an opaque canvas. The tank is illuminated from above by artificial LED lights that mimic the daylight spectrum. The system operates



Figure 1. Figure from Maxeiner et al.²³ (CC BY 4.0), showcasing the RoboFish system. Left panel; a 3D-printed fish replica is attached to a magnetic base, which aligns with the robot. Hence the replica can be moved directly by the robot at constant height. Center panel; a wheeled differential-drive robot moves on a transparent platform below the test tank, carrying a neodymium magnet. Right panel; the tank is a quadratic (1 m × 1 m) with a triangular start box used as shelter for the live fish at the beginning of each experiment.

on a personal computer (i7-6800K, 64GB RAM, GTX1060) that runs custom software for robot control. This software tracks the robot via the bottom camera's feed and controls it through a WiFi connection. Additionally, a second program records video from the top camera, detects and tracks all agents within the tank, and transmits positional data to the robot control software. At each time step (25 Hz), the robot control software updates the positions and orientations of both the fish and the robot in an internal data structure. This frame rate is sufficient to quantify overall swimming speed modulation and avoidance dynamics, as done in other freely swimming robot–fish interaction studies^{23,35}. Behavior modules can access this data to calculate target positions for the robot based on the current or previously observed states. Once the active behavior determines a new target position, the robot moves toward it. If a significant turn is required, the robot first rotates before advancing forward. If only a slight adjustment is needed, the robot moves toward the target while subtly turning by adjusting the relative speeds of its two wheels.

A 3D-printed triangular retainer, with a side length of 19 cm, served as a shelter box to house the fish prior to the experiment. This shelter featured a cylindrical section with a 10 cm diameter, from which the fish could access the experimental area through a 3 cm × 2.5 cm door. Apart from the retainer, the environment was symmetrical and uniform in appearance.

Experimental procedure

In the experiment, we aim to assess the impact of the robotic fish's approach behavior on the avoidance responses of live fish. Each fish underwent a single initial habituation phase, following a protocol similar to that of Maxeiner et al.²³. For each trial, an adult female guppy was randomly selected from its holding tank and gently introduced into the shelter box. The front door of the shelter was then opened, and the robot remained stationary until the fish exited the shelter. If the test fish did not leave the shelter within two minutes, the shelter box was removed. Once the fish left the shelter, the robot commenced a circular milling movement in the center of the tank, with a circumference of 10 cm, for one minute. This milling behavior served as part of the acclimatization process.

Trials began immediately after the milling behavior was completed. The robot followed a consistent protocol for each trial. Initially, the robot remained stationary, waiting for the fish to be 40 cm distance away. If the fish did not reach this distance within 5 seconds, the robot relocated to maintain the desired separation. The 40 cm distance was chosen to maximize the space between the robot and the fish, given the constraints of the tank. Even when the fish was in the center, the robot could keep this separation while staying far enough from the tank walls. When the robot and the fish were sufficiently far apart, the robot began to approach the fish until one of two conditions was met. The first condition ensured that the distance between the robot and the fish was less than 2 cm, allowing the robot to approach closely to potentially trigger avoidance behavior. The second condition involved the follow metric, a measure introduced by Maxeiner et al.²³ to quantify the fish's avoidance response over a specified time window. It is defined as the time average of the dot product between the fish's velocity vector and the direction vector from the fish to the robot. Negative values indicate movement away from the robot, while larger values reflect faster movements. If the distance was less than 8 cm and the follow metric fell below -1 cm/s, the approach was halted, as it indicates that the fish is beginning to move away. Once either condition was satisfied, the trial concluded.

The robot was set to move directly towards the continuously updated tracked position of the fish. For each trial, the robot was set to approach the fish at a certain speed. We used ten speed configurations, ranging from 15 to 30 cm/s in 1.5 cm/s increments. The order of the speed configurations was independently randomized for each individual fish. Each subject experienced all ten speed configurations once before any were repeated. This randomization procedure was implemented so that no two consecutive trials of the same fish were exposed to the same robot speed, and the order differed across individual fish.

To prevent the robot from colliding with the tank walls, we implemented a wall avoidance feature. Since the robot may approach the fish at relatively high speeds in some trials, a significant buffer was necessary. Whenever the robot came within 10 cm of the walls, it relocated to the nearest suitable position that maintained an appropriate distance from the tank's edges. Each live fish underwent multiple trials over a continuous

period of at least 10 minutes before being returned to the holding tank (subject 0: 10m 42s; subject 1: 13m 7s; subject 2: 12m 25s; subject 3: 15m 22s; subject 4: 16m 22s). Individual trials lasted on average 9.96 ± 0.96 seconds, depending on how quickly one of the predefined stopping conditions was met. This method provided observations of the same fish to the robot approaching from various angles. Additionally, repeated measures allowed for the assessment of any changes in the fish's behavior over time as it adapted to the repeated scenario.

Data processing

A total of 276 trials were conducted with $n = 5$ subjects. Tracking data were manually and automatically checked for errors, processed to correct for missing frames, and converted to centimeters. For the missing frames, the positions were linearly interpolated. Given that our analysis involves the distribution of velocities, interpolation is not performed when there are 25 or more consecutive frames (i.e., one second or longer) without tracking data. Such frames were excluded from the analysis. Additionally, frames from the initialization phase (milling process) were also excluded. After processing, a total of 82,002 frames (approximately 54 minutes) of data were retained across all subjects. A detailed breakdown of the dataset at each step of the data processing pipeline can be found in Supplementary Table S1.

The tracking data provided two-dimensional positions $\vec{p} = (x, y)$ at a frame rate of 25 Hz for both the robot and the fish. These positions were smoothed using a running average with Gaussian weights over a time window of 5 frames. This time window effectively captures short, spurious changes in motion⁴⁹. From the smoothed positions, the instantaneous velocity vector \vec{q} with its norm as speed v , and acceleration vector \vec{u} with its norm as acceleration a , were computed for both the robot and the fish, while the distance d_{FR} between them was also calculated. The relative angle between the robot's position and the fish's heading direction was defined as $\theta_{RF} = \arctan(\vec{p}_{RF}) - \theta_F$ where $\vec{p}_{RF} = \vec{p}_R - \vec{p}_F$ is the relative position of the robot with respect to the fish, and $\theta_F = \arctan(\vec{q}_F)$ is fish's heading angle. Furthermore, the robot's approach speed was computed as $v_{app}^R = \vec{q}_R \cdot \hat{p}_{FR}$ and the fish's avoidance speed as $v_{avoid}^F = \vec{q}_F \cdot \hat{p}_{FR}$, with $\hat{p}_{FR} = \frac{\vec{p}_F - \vec{p}_R}{d}$ as the normalized relative position of the fish with respect to the robot. These two quantities, v_{app}^R and v_{avoid}^F , served as the primary variables in our analysis. Although it was possible to normalize the approach speed by the robot's speed and separately use the approach cosine, significant errors in the computed angle (and thus the cosine) were observed when the robot moved very slowly or remained almost stationary. These errors occurred because, at low speeds, even minor tracking inaccuracies disproportionately affected the angle calculation. By incorporating the robot's speed into the approach speed calculation, these inaccuracies were suppressed. The same principle applied to the fish's avoidance speed.

Trial selection

In a substantial portion of the trials, the fish remained in close proximity to the tank wall for the entire duration, which hindered the robot's ability to exhibit its intended behavior of continuously approaching the fish until an encounter occurred. In such instances, the robot executed wall-avoidance maneuvers and repeatedly attempted to approach the fish until one of the predefined halting conditions was met. These trials often contained no encounter or several encounter-like events, making it impossible to segment behavior consistently into pre-encounter, encounter, and post-encounter phases (see Data Analysis). To enable standardized phase-based analyses, we automatically selected trials in which the robot's relative approach speed, once reaching zero, remained non-positive for the remainder of the trial (see example in Fig. 2C). This criterion identifies trials in which a single, well-defined encounter occurred without sustained wall interference. This subset was later manually reviewed and confirmed, resulting in a final total of 88 trials out of the 276 original trials. This approach allows for a comprehensive evaluation, with the subset providing insights into fish behavior under more consistent robot performance.

Data analysis

The analyses in this study draw on two datasets: (i) the full dataset comprising 82,002 observations collected across all 276 trials, used for general behavioral analysis, and broad statistical modeling, and (ii) a subset of 88

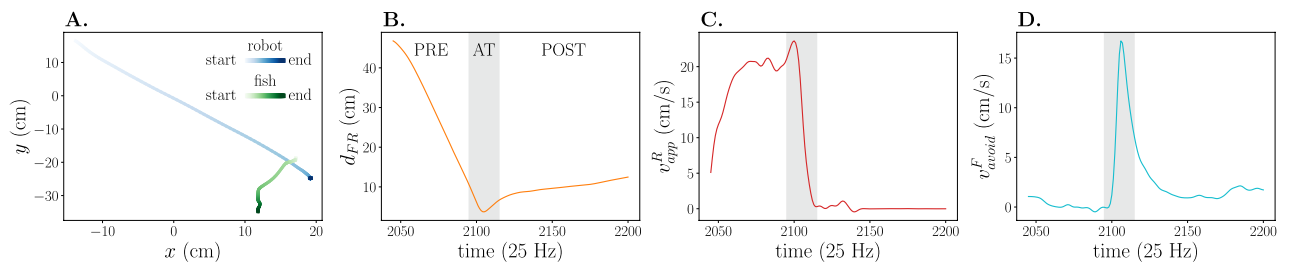


Figure 2. (A) The trajectories of both the robot (blue) and the fish (green) are shown in 2D space, with the progression over time indicated by a color gradient from light (start) to dark (end). Measurements over time include (B) the distance between the robot and the fish d_{FR} , (C) the robot's relative approach speed v_{app}^R , and (D) the fish's avoidance speed v_{avoid}^F . The different phases of the trial are labeled in (B), where the (at) encounter phase is highlighted by a gray overlay, also visible in (C) and (D). Time is recorded in frames at a frequency of 25 Hz.

manually selected trials, comprising 15,168 observations, used for in-depth phase-based behavioral analysis and extreme action classification.

Classification of fish behavior

We classified fish behavior to identify different responses to the robot, as well as to determine the occurrence of anti-predator behaviors. When the fish moved at speeds less than 2 cm/s, it was classified as slow motion, in accordance with prior research on Trinidadian guppies²³. A specific subbehavior of slow motion, referred to as freezing, has been identified as a characteristic stress or anti-predator response in fish, particularly in Trinidadian guppies^{51–53}. We initially applied the methodology described by Houslay et al.⁵¹, which defined freezing behavior of guppies as a continuous speed below 4 cm/s for at least 2.5 seconds. However, their threshold was developed for a fundamentally different context involving simulated bird strikes and the visual reveal of a predator in an adjoining tank. In our setup, where guppies interact with a robot within the same arena, this criterion produced a higher number of false positives during visual inspection. Because no previous study has quantified freezing in guppies interacting with a robot in the same tank, there is no directly transferable reference threshold. We therefore relied on two relevant empirical references: the 2 cm/s limit for slow movement established for guppies in the same experimental setup²³, and the definition used by Ladu et al.²⁴, who identified freezing as movement below 2 cm/s sustained for 2 seconds in zebrafish interacting with a robotic fish. Based on these sources, we defined freezing as movement below 2 cm/s maintained for at least 2 consecutive seconds. When the speed exceeded 2 cm/s, the behaviors were further classified based on avoidance speed (v_{avoid}^F): if $v_{avoid}^F > 0$, the behavior was identified as avoidance, whereas $v_{avoid}^F \leq 0$ indicated attraction behavior. The open field arena away from the tank walls, is assumed to be perceived as riskier by guppies⁵¹. Thigmotaxis has been defined as the tendency to stay close to physical boundaries, a behavior suggested to help avoid exposure to potential threats³⁶. A fish was considered to exhibit thigmotaxis when it was located within 10 cm of the nearest boundary ($d_{FW} < 10$). This threshold was determined based on the robot's programmed wall-avoidance behavior at this distance.

Statistical modeling of avoidance speed

We used a fixed-effects (FE) model to investigate how robot behavior affected the fish's avoidance speed v_{avoid}^F across the entire experiment (full dataset). The predictor variables included the distance d_{FR} between the robot and the fish, the robot's approach speed v_{app}^R , and the distance d_{FW} between the fish and the nearest tank wall. Taking response latency into account, we shifted the avoidance speed forward by $\Delta = 0.32s$ (8 frames), a value determined through preliminary analysis of the time gap between the initiation of an accelerative motion and the resulting speed increase. We replicated the model for shifts of 4, 12, and 16 frames, all of which yielded results consistent with the 8-frame shift (see Supplementary Table S2). To account for individual heterogeneity, an individual-specific fixed effect was included, with the fish's ID serving as a fixed effect. This approach allows the model to estimate a distinct intercept for each subject, which remains constant over time. In our study, this captured characteristics such as the fish's personality. For example, Houslay et al.⁵¹ found that Trinidadian guppies exhibited time-invariant behavioral differences (e.g., evasive behavior versus cautious exploration) when exposed to predator models. Their findings suggest that such behaviors in stressful situations are driven by stable personality traits rather than temporary states solely influenced by the environment. In addition to the main effects, we examined potential coupling between predictors by including an interaction term between robot-fish distance and robot approach speed ($d_{FR} \times v_{app}^R$). Predictors were mean-centered within experiments prior to constructing the interaction term to improve interpretability and reduce collinearity. The baseline model without the interaction term is reported in Supplementary Table S4, and the interaction model is presented in the main manuscript. The contribution of the interaction term was assessed via a robust Wald test comparing nested specifications (Supplementary Section S4). All models were estimated using the `plm` package in R. To provide inference robust to within-trial autocorrelation and heteroskedasticity, we computed cluster-robust (Arellano HC1) standard errors clustered at the individual (subject) level. We report coefficient estimates together with corresponding 95% confidence intervals. As a robustness check, we additionally estimated two-way FE specifications including time fixed effects, which yielded consistent results (see Supplementary Table S3, with applied Driscoll-Kraay correction).

Phase-based behavioral analysis

Phase-based behavioral analyses were conducted on the subset of 88 manually selected trials. Trials were divided into three phases based on d_{FR} : (i) pre-encounter, (ii) at encounter, and (iii) post-encounter. The encounter phase was defined as the period from 0.4 seconds before to 0.4 seconds after the moment of minimal distance. To investigate how fish adapt their behavior during a trial, we computed the marginal and transition probabilities of fish behaviors across the pre-encounter, encounter, and post-encounter phases. For this analysis, we focused on manually selected trials where the robot's behavior was consistent. In these trials, the robot reached a stable maximum approach speed (v_{app}^R) during the pre-encounter phase, encounters the fish, and then remained stationary ($v_{app}^R = 0$) in the post-encounter phase. Following the post-encounter phase, the robot moved to a new location to reset the scenario, but this phase was not included in the analysis, as the robot's influence on the fish was likely to vary during this time.

Classification of extreme fish actions

We classified fish turns and accelerations occurring within 40 cm of the robot by comparing them to a baseline dataset. This baseline (12,692 observations) comprised instances when the fish and robot were more than 40 cm apart, during which the robot was not programmed to actively approach, thereby minimizing interaction. This baseline data was used to define the reference distributions for each subject. For turns, baseline distributions

were modeled as normal distributions, parameterized by subject-specific means (μ_i) and standard deviations (σ_i), where i denotes the subject identifier. Extreme turns for each subject were then defined as those exceeding the threshold $\mu_i + 2\sigma_i$, calculated separately for each individual to account for variability in baseline behavior. In contrast, acceleration baseline data did not follow a normal distribution. Instead, we classified fish accelerations as extreme if they exceeded the 95th percentile of their respective baseline distributions. Both extreme action classifications were applied to the subset of 88 trials to provide insights under consistent robot performance.

Results

In this study, we investigate the interaction dynamics between a robot and a fish, focusing on spatial and behavioral responses during their encounter. Figure 2 presents the trajectories of both the robot and fish (Fig. 2A), along with the measured spatial and dynamic quantities (Fig. 2B–D) from a single trial. The trial is divided into three phases based on the fish-robot distance (d_{FR}): (i) pre-encounter, (ii) at encounter, and (iii) post-encounter. During the encounter phase (see grey area in Fig. 2B), the robot decelerates its approach speed (see Fig. 2C, where v_{app}^R decreases to zero) as it meets the halting conditions, while the fish accelerates its avoidance speed (v_{avoid}^F increases to a local maximum), demonstrating avoidance behavior as $v_{avoid}^F > 0$ (see Fig. 2D).

The robot's approach behavior induces avoidance in fish throughout the experiment

Figure 3A illustrates the percentage of time, averaged across all fish for the duration of their respective experiments, during which various behaviors were observed. These behaviors include attraction, slow motion, freezing, avoidance, and thigmotaxis. The first four are categorized as dynamic behaviors, while the last is considered a spatial behavior. Among the dynamic behaviors, the fish primarily engage in avoidance behavior, moving away from the robot. This is an expected response to the robot moving into the fish's space. The second most frequent behavior observed is slow motion, with a small percentage of this behavior identified as freezing. Attraction to the robot is also observed, but in much smaller quantities compared to avoidance. This pattern is consistent in most subjects, with the exception of one individual (Fig 3B, subject 4), which is the only one to show a substantial amount of freezing, resulting in a reduced percentage of avoidance compared to the others. The fish exhibit notable thigmotaxis, spending approximately half of the experiment near the tank walls. The inset of Fig. 3A illustrates, for each subject, the percentage of time the fish displays avoidance behavior as a function of the time spent exhibiting thigmotaxis. A strong linear correlation is observed (Pearson's $r = 0.93$, $p < 0.05$), as demonstrated by the linear fit applied to these data points. This correlation suggests that fish exhibiting more frequent avoidance behavior also spend more time near the walls. One possibility is that thigmotaxis serves

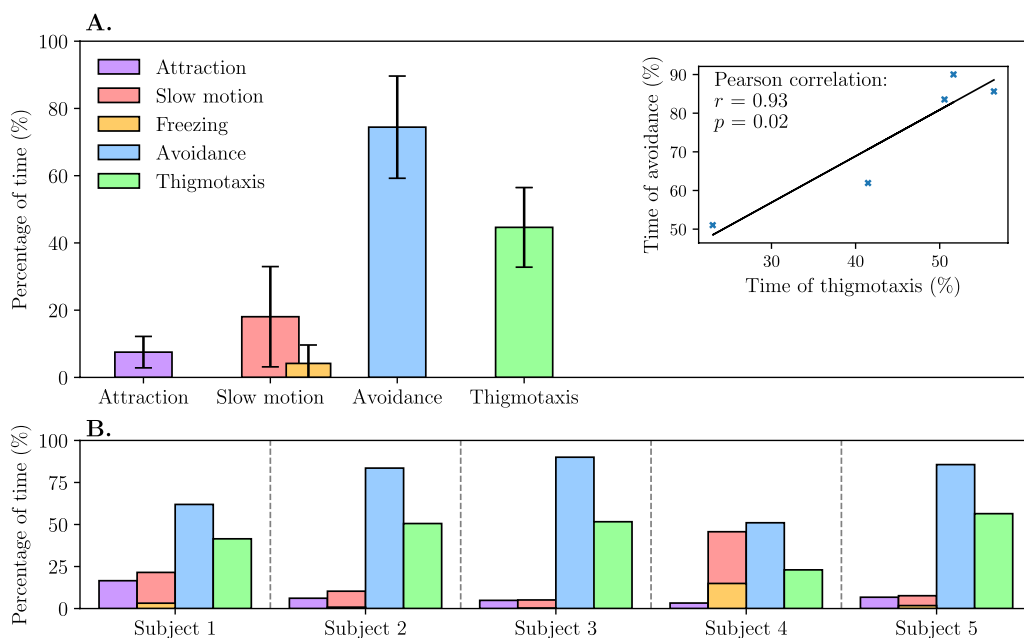


Figure 3. (A) The percentage of time the fish spent in various behaviors throughout the experiment: attraction (purple), slow motion (red), freezing (orange), avoidance (blue), and thigmotaxis (green). The bars represent the mean across all subjects, with error bars showing the standard deviation, based on $N = 82,002$ observations. The inset shows the correlation between the percentage of time spent in thigmotaxis and avoidance across subjects. The Pearson correlation coefficient is $r = 0.93$ with a significance of $p = 0.02$ and a 95% confidence interval of $[0.28, 1]$. The black line represents a linear fit, included as a visual aid to highlight the correlation trend. (B) The percentage of time each subject (1–5) spent in the different behaviors: attraction, slow motion, freezing, avoidance, and thigmotaxis. Each bar represents the proportion of time allocated to each behavior for the respective subject. Note that the freezing bar overlays the slow motion bar, and in some subjects, the minimal occurrence of freezing makes the bar less visible.

as a spatial strategy, with fish seeking the safety of the walls to avoid the robot's movements. Alternatively, thigmotaxis could be a natural consequence of the fish traveling farther as they attempt to avoid the robot, eventually reaching the walls where they remain because further movement to escape is no longer possible.

Repeated approaches by the robot increase avoidance behavior and reduce attraction behavior

As the fish were repeatedly exposed to trials, their tendency to avoid the robot increased, even before the robot fully approached during the pre-encounter phase. Figure 4A shows the cumulative proportion of fish exhibiting avoidance behavior during this phase, indicating that the elevated level of avoidance in this phase is attributed to repeated trial exposure. A generalized linear mixed model (GLMM) with a logit link function ($\chi^2(3) = 27.01$, $p < 0.001$) reveals that the likelihood of avoidance behavior significantly increases with each successive trial (Estimate = 0.206, $p < 0.001$). Detailed model outputs are provided in Supplementary Table S5. The model includes trial number and robot speed as fixed effects, and subject identity as a random effect. Robot speed did not significantly affect the likelihood of avoidance behavior in pre-encounter phase.

Figure 4B shows that, before the robot has encountered the fish (pre-encounter phase), most fish avoid the robot ($p = 0.73$), while the remainder are either moving towards the robot ($p = 0.16$) or moving at a slow pace ($p = 0.11$). Upon encounter, fish that were moving toward the robot transitioned to avoidance behavior in all instances. In most cases where the fish were moving slowly, they also switched to avoidance, with only a small fraction exhibiting freezing behavior ($p = 0.03$). After the robot becomes stationary in the post-encounter phase, the remaining slow or immobile fish also switch to avoidance. Only a minority (11%) of the fish that avoided the robot during the encounter remain stationary or nearly immobile in the post-encounter phase. Notably, none of the fish exhibit attraction behavior during or after encountering the robot, highlighting their aversive response following the robot's approach.

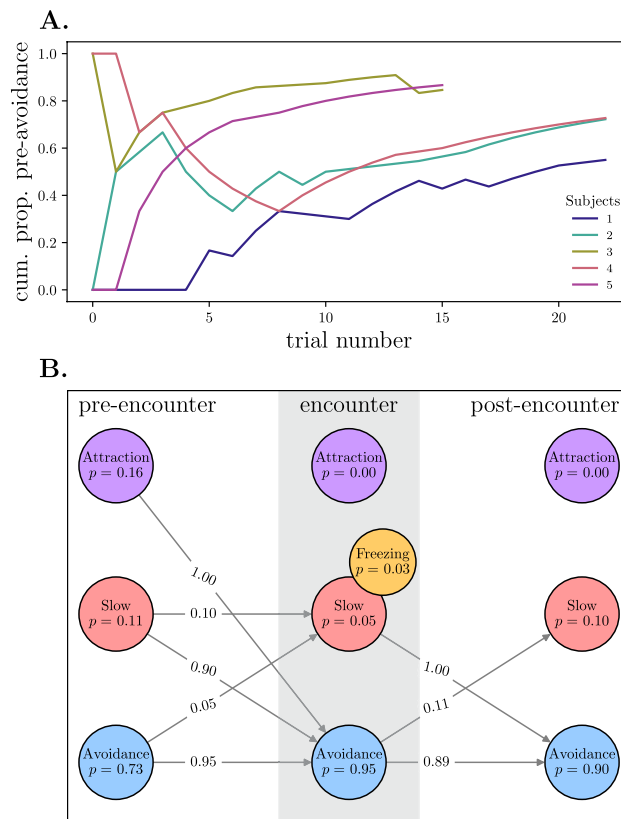


Figure 4. (A) The cumulative proportion of the fish displaying avoidance behavior before the robot's approach (i.e. pre-encounter phase), across trials for each subject. (B) Transition probability diagram of attraction (purple), slow motion (red), and avoidance (blue) behaviors during the pre-encounter, encounter, and post-encounter phases. The encounter phase is highlighted by a gray overlay. The arrows show the probability of transitioning from one behavior to another, and the associated marginal probabilities p indicate the probability of being in a specific behavior during each phase. Freezing (orange), shown as a sub-behavior of slow motion in the encounter phase, is also represented with its corresponding probability. Probabilities were computed based on $N = 88$ trials. Transitions with zero probability are not shown.

Fish moves away faster as the robot approaches faster and their relative distance decreases

We conducted a fixed-effects model to examine how the distance to the robot (d_{FR}), the robot's approach speed (v_{app}^R), and the distance to the nearest wall (d_{FW}) influence the fish's avoidance speed (v_{avoid}^F). The model is significant ($p < 0.001$), with coefficient estimates and their statistical significance shown in Table 1. Both the robot-fish distance and the robot's approach speed significantly affect the fish's avoidance speed ($p < 0.001$). Specifically, a negative coefficient for d_{FR} suggests that as the distance to the robot decreases, the fish's avoidance speed increases. Conversely, the positive coefficient for v_{app}^R indicates that the fish retreats faster when the robot approaches at higher speeds. In addition, we found evidence for a modest coupling effect between these predictors: the interaction term $d_{FR} \times v_{app}^R$ was statistically significant ($p < 0.05$), indicating that the influence of approach speed on avoidance responses depends on robot proximity. In particular, the effect of v_{app}^R is stronger when the robot is closer to the fish, consistent with a joint contribution of distance and approach dynamics. No significant effect of d_{FW} was found on v_{avoid}^F .

Figure 5A,B display the smoothed and unsmoothed heatmaps of v_{avoid}^F , averaged per bin, as a function of d_{FR} and v_{app}^R . These visualizations provide an intuitive representation of the dependency of v_{avoid}^F on both predictors and are in line with the fixed-effects model results. In particular, v_{avoid}^F tends to increase as the robot approaches faster (v_{app}^R increases) and as the robot–fish distance decreases (d_{FR} decreases). Notably, even when the robot is further away (10 to 40 cm), the fish continues to move away from the robot ($v_{avoid}^F > 0$) if it is approaching ($v_{app}^R > 0$). Conversely, when the robot is not approaching ($v_{app}^R < 0$), the fish remains still ($v_{avoid}^F \approx 0$), possibly indicating a sense of safety in this scenario.

Reactive turns and accelerations as key mechanisms of fish avoidance from the robot

Avoidance behavior in fish can be measured by their speed v^F and their directional movement relative to the robot, as indicated by the relative angle θ_{RF} . The actions of the fish, such as accelerations and turns, influence these measures. Within the broader context of avoidance behavior, we operationally classify escape-like evasive events as extreme turns and accelerations that exceed baseline behavior, representing more pronounced responses to the robot's approach. Figure 6A,C show that the frequency of these extreme actions increases as the distance to the robot decreases, consistent with the findings in Table 1. The fish perform extreme turns and accelerations, classified based on deviations from the baseline behavior, most frequently within the 5–10 cm range from the robot.

A GLMM analysis confirms that the likelihood of turning actions increases significantly as the distance between the fish and robot decreases and as the fish-robot speed ratio ($\frac{v^F}{v^R}$) decreases (see Supplementary Table S6). This suggests that fish are most likely to perform extreme turns when moving significantly slower than the robot. In contrast, the relative angle (θ_{RF}) does not have a statistically significant effect. One possible explanation is that the fish are likely to turn irrespective of where the robot is approaching from. This indicates that the primary purpose of the turn is to avoid immediate collision by moving out of the robot's path, rather than to align their movement directly opposite to the robot. Further supporting this explanation, the fish's turns do not appear to significantly affect their relative directional movement away from the robot. This is indicated by a separate FE analysis using the cosine of v_{avoid}^F (1 indicates direct retreat; -1 the opposite) as the response variable, which shows no significant difference before and after turns ($p > 0.1$). This interpretation is also reinforced by the sudden increase in the frequency of extreme turns at close proximity, compared to the more gradual rise in acceleration frequencies across distance bins (Fig. 6A,C). Additionally, pre-turn and post-turn speeds were measured as the maximum speed over a duration of 0.16 seconds, both before and after an extreme turn. An FE analysis reveals that post-turn speeds are significantly higher than pre-turn speeds (Estimate = 2.34, SE = 0.81, $t = 2.90$, $p < 0.01$), indicating that fish tend to accelerate following an extreme turn.

For the majority of trials, the fish do not perform extreme turns (Fig. 6A), suggesting that they often move at speeds comparable to or greater than the robot during its approach. The fish rely on accelerations, with the likelihood of these actions increasing as the robot approaches closer. Simultaneously, the fish make smaller

Response at $t + \Delta$ = fish avoidance speed v_{avoid}^F				
Predictor at t	Coeff.	CI (95%)	p-value	Test statistics
Robot-fish distance d_{FR}	-0.030	[-0.044, -0.017]	$p < 0.001$	$R^2 = 0.041$
Robot approach speed v_{app}^R	0.068	[0.040, 0.096]	$p < 0.001$	$Re = 0.199$
Robot interaction term $d_{FR} \times v_{app}^R$	-0.002	[-0.0038, -0.0004]	$p < 0.05$	$F_{(4,81953)} = 886.58$
Wall-fish distance d_{FW}	-0.019	[-0.064, 0.027]	$p > 0.05$	$p < 0.001$

Table 1. Fixed-effects regression results for fish avoidance speed (v_{avoid}^F) at time $t + \Delta$ with $\Delta = 8$ frames. Predictors measured at time t include robot-fish distance (d_{FR}), robot approach speed (v_{app}^R), their interaction ($d_{FR} \times v_{app}^R$) to assess coupling effects, and wall-fish distance (d_{FW}). The table reports estimates from a one-way individual-level fixed-effects model, where each fish is assigned its own time-invariant intercept. Coefficient estimates are reported together with 95% confidence intervals based on cluster-robust (Arellano HC1) standard errors clustered at the individual level. The model is estimated on $N = 82,002$ observations and is significant overall ($p < 0.001$). Repeatability ($Re = 0.199$) indicates that individual-level differences explain approximately 19.9% of the total variance.

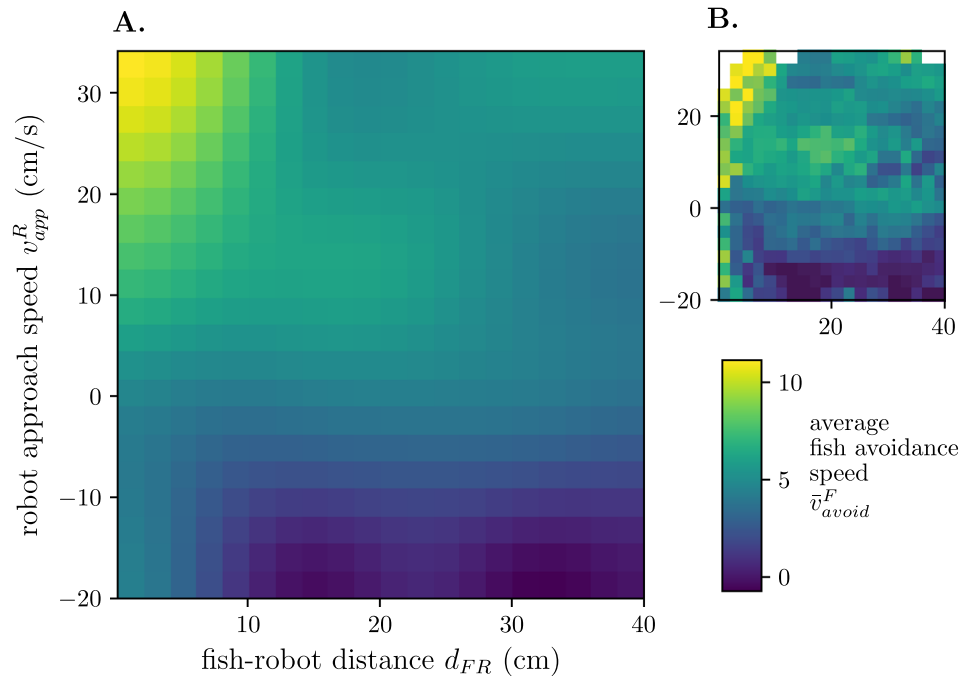


Figure 5. Smoothed (A) and unsmoothed (B) heatmaps showing the guppies' avoidance speed v_{avoid}^F at time $t + \Delta$, in function of the fish-robot distance (x-axis) and robot's approach speed (y-axis) at time t , with $\Delta = 8$. The heatmaps were each generated using $N = 69,265$ observations after applying range constraints to the x- and y-axes. Both axes are divided into 20 bins. To smooth the heatmap, missing data is first replaced with neighborhood averages, followed by Gaussian smoothing with $\sigma = 2$. The color scale indicates areas of high (yellow) and low (blue) speed. Missing data is represented in white in (B).

orientation adjustments to optimize their directional movement, gradually aligning their heading to move more directly opposite to the robot (i.e., $\theta_{RF} \rightarrow \pi$). Figure 6B illustrates a high-density clustering of θ_{RF} values between $\frac{10}{12}\pi$ and π during the post-encounter phase. This indicates that the fish predominantly end up moving in the opposite direction of the robot after the encounter, with a slight preference for veering to the right relative to the robot's trajectory (binomial test; $p < 0.01$). During the early pre-encounter phase, the distribution of θ_{RF} is more dispersed but remains concentrated between $\frac{1}{2}\pi$ and $\frac{3}{2}\pi$, indicating that the robot is generally positioned behind the fish to some extent. The fish also exhibit increased speeds following the encounter (Fig. 6D), driven by their accelerative responses. An FE model confirms that post-encounter speeds are significantly higher than those observed in the early pre-encounter phase (Estimate = 3.80, SE = 0.75, $t = 5.06$, $p < 0.001$).

Discussion

Our findings reveal several key insights into the avoidance behavior of guppies in response to a conspecific-like robot. We demonstrate that avoidance responses are influenced by robot speed and proximity with faster approach speeds and closer distances eliciting stronger avoidance behaviors. The fish became more avoidant of the robot due to repeated exposure to the approaches. Additionally, guppies displayed characteristic anti-predator responses, including freezing and escape-like evasive maneuvers, suggesting the robotic conspecific was perceived as a threat. Interestingly, avoidance behavior was dynamic, as the fish employed turns and accelerations that depended on relative speed and distance, diverging from traditional models which assume fixed responses based only on distance.

Between conspecifics, fish tend to move away from each other at close distances^{27,46}. We found that repeated approaches of the robot increased the likelihood of the fish moving away before close proximity (Fig. 4A), which also led to a reduced attraction to the robot. Notably, freezing was observed in only one of the five subjects. Conrad et al.⁵⁴ have discussed how individual personality traits, such as boldness or shyness, as well as body size⁵⁵, which is related to energy reserves and metabolic demands, can influence fish responses to perceived threats. Their concept of behavioral syndromes suggests that consistent behavioral patterns, including threat responses, are linked to individual variability among fish. This bidirectional relationship may explain why subject 4 showed a preference for freezing over avoidance as a defense strategy. Additionally, all instances where the fish initially froze upon encountering the robot eventually transitioned to movement after the encounter. Eilam⁵⁶ explains that the transition from freezing to movement, once the threat subsides, is a key component of dynamic defense strategies. This supports the notion that the robot's approach may be perceived as a threat, as freezing is recognized as an adaptive defense strategy.

Further analysis of the fish's behavioral patterns revealed a positive correlation between avoidance behavior and thigmotaxis. Given that this correlation is derived from only five individuals, it should be interpreted

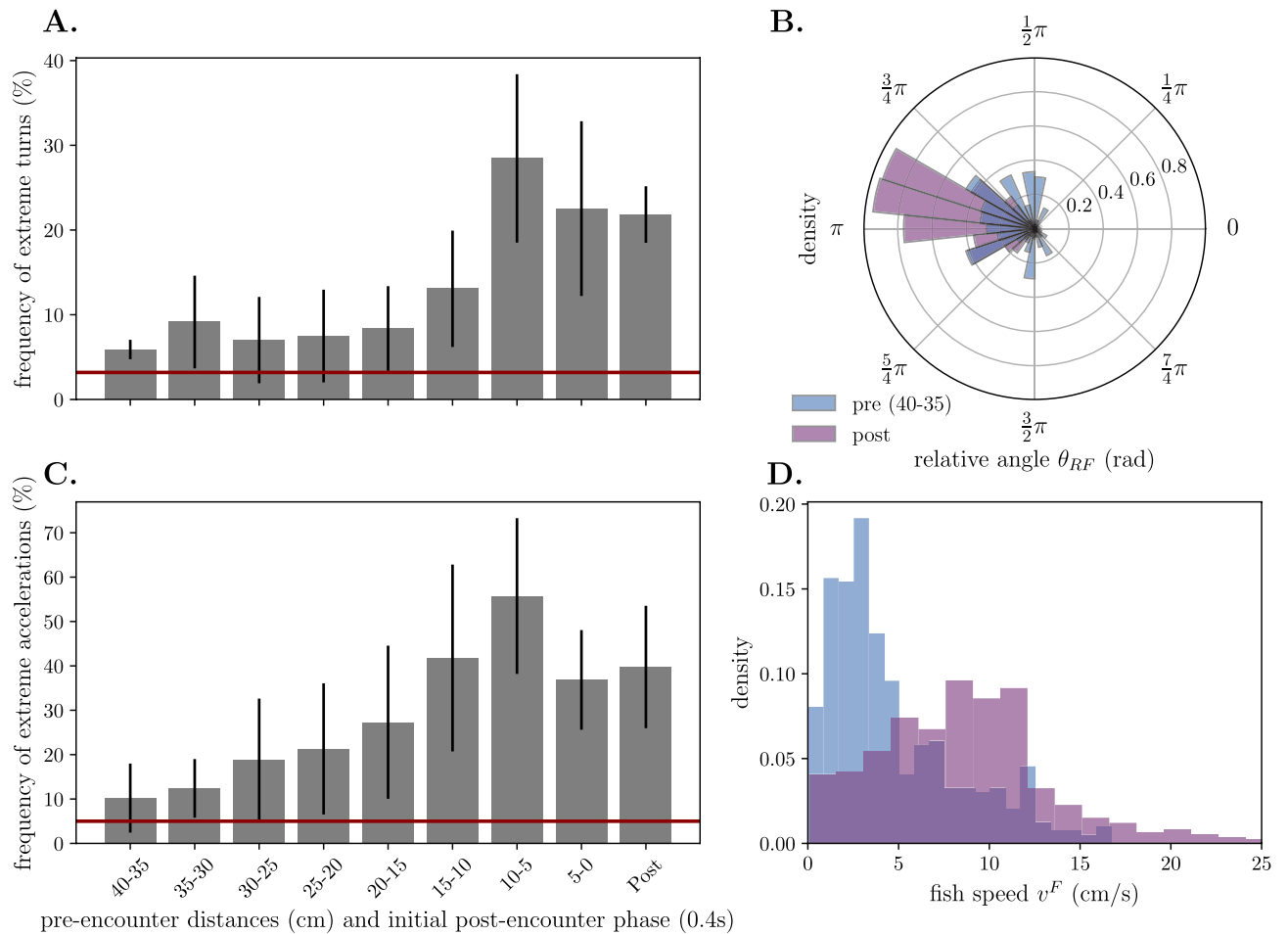


Figure 6. Frequencies of extreme turns (A) and accelerations (C) across fish-robot distances, calculated per distance bin during the pre-encounter phase and the first 0.4 seconds of the post-encounter phase. Extreme turns were defined as those exceeding the subject-specific threshold of $\mu_i + \sigma_i$, where μ_i and σ_i respectively represent the mean and standard deviation of the baseline turn distribution. Extreme accelerations were classified as those exceeding the 95th percentile of the baseline acceleration distribution for each subject. The bars represent the mean across all $N = 88$ trials and subjects, with error bars showing the standard deviation. Red horizontal lines indicate baseline frequencies for turns and accelerations, defined when the fish and robot are at least 40 cm apart. Density distributions of (B) the relative angle between the robot's position and fish's heading direction (θ_{RF}) and (D) the fish speed, sampled from the initial periods of the pre-encounter (blue) and post-encounter (purple) phases. When $\theta_{RF} = \pi$, the fish is moving directly away from the robot. The encounter with the robot increases both the fish's opposing movement and speed.

cautiously and not as evidence of a robust population-level relationship. Nonetheless, these findings are consistent with previous studies identifying thigmotaxis as a key indicator of avoidance behavior. Animals exhibiting thigmotactic behavior tend to avoid the center of an arena, staying or moving close to the walls. This evolutionarily conserved behavior is observed across various species, including fish⁵⁷⁻⁵⁹. Thigmotaxis is widely recognized as a measure of anxiety, as it is reduced by anxiolytic drugs and heightened by anxiogenic agents⁶⁰. Additionally, research has shown that guppies display thigmotactic behavior in response to stressors, such as threats^{36,61}.

The fish's avoidance speed was found to increase significantly with higher robot speed and decreased relative distance. These findings align with previous studies on fish-robot interactions in free-swimming contexts (without barriers), which suggest that higher robot speeds amplify avoidance responses³⁴, while reduced relative distance similarly intensifies these behaviors³⁵. The fish consistently evaded the robot across most of the approach speed and distance parameters; however, avoidance behavior was absent when the robot was moving away at high speeds (-10 to -20 cm/s) and was more than 10 cm from the fish. Furthermore, proximity to the tank walls did not significantly affect avoidance speed, suggesting that the fish's avoidance behavior in terms of speed was not influenced by the presence of the tank boundaries.

While most models treat the avoidance-initiation distance (the distance at which others can approach before the focal fish moves away) as a fixed radius or decay function, recent research suggests that individual factors, such as body size and prior exposure to threats, also influence this distance⁴². Our findings support this, as we

observed that repeated exposure to the approaching robot increased the likelihood of the fish exhibiting avoidance behavior earlier, during the pre-encounter phase. Furthermore, our results indicated that the avoidance-initiation distance is influenced by both the fish's speed and the speed of the approaching robot. When the fish moved slower than the robot (likely arising from within-subject dynamics; Supplementary Section S6), they were likely to execute an escape-like evasive response once the robot approached within approximately 10 cm. These events involved an extreme turn (characterized by sharp deviations from baseline turning behavior), which reoriented the fish's trajectory away from the robot's path, followed by high acceleration⁶². Such movement patterns are commonly associated with fast-start escape behavior, although our temporal resolution does not allow a precise biomechanical classification of these responses as C-start reflexes. We observed a bimodal distribution in the angles of these evasive trajectories (Supplementary Figure S1), a feature that has previously been linked to fast-start escape responses⁶³.

However, these high-intensity evasive events did not occur in all instances. In many cases, the fish were already moving away from the robot at significant speeds. Under such circumstances, they relied primarily on acceleration, initiating avoidance behaviors at distances even greater than 10 cm (Figs. 5 and 6C). After the robot's approach, fish tended to move almost directly opposite to its trajectory, which is qualitatively consistent with the directionality assumed in traditional repulsion-based collective motion models^{26–28}. Notably, a slight bias to the right was observed in their trajectories, consistent with findings reported by Domenici et al.⁶³. Additionally, our findings revealed substantial variability in fish speeds post-encounter, both between and within subjects (Supplementary Figure S2). This variability emphasizes that avoidance responses in threat-like robot encounters may involve dynamic speed modulation and escape decisions that extend beyond the constant or purely distance-dependent repulsion terms commonly used in schooling models. Together, these results highlight the need for extended modeling frameworks that account for approach dynamics, repeated exposure, and individual variability when describing avoidance elicited by directed robotic stimuli.

This study is not without limitations. While we collected a substantial dataset (82,002 observations) to investigate fish avoidance behavior, the sample size of subjects was relatively small (five fish). As a result, generalizing these behavioral patterns to the broader population should be approached with caution. Individual variability (e.g. personality traits) may influence behavioral responses and thus contribute to the variation observed across subjects. To partially compensate for this limitation, we modeled avoidance speed using a FE model, which leverages within-individual variation while controlling for all time-invariant differences between fish. This allowed us to isolate the effects of experimental factors from stable individual traits, although time-varying characteristics may still introduce unexplained variability. For other analyses that required a mixed-effects structure, the random intercept for subject served primarily as a device to account for the non-independence of repeated trials rather than to support population-level inference. With only five subjects, the corresponding variance component is estimated with limited precision, and we acknowledge that this uncertainty may affect the stability of the associated p-values. Additionally, because trajectories were recorded at 25 Hz, our acceleration-based measures capture evasive events at a coarse behavioral level but do not resolve the peak kinematics or latencies of fast-start escape reflexes. Accordingly, acceleration and turning metrics are interpreted as indicators of high-intensity evasive responses rather than precise biomechanical measurements of escape reflexes. Further research with a larger sample size is necessary to confirm the robustness of these patterns and to better characterize how individual differences shape avoidance behavior. Moreover, although we identified the conditions under which a robot can elicit varying degrees of avoidance in individual fish, future research should explore how these interactions unfold in a school of fish, where collective dynamics could offer new insights.

Our experiment provides evidence that a mobile conspecific-like robot can induce avoidance behavior on live fish. Our findings generally indicate that the fish perceived this robot as a threat to be avoided, and even displayed anti-predator behavior, such as freezing and escape-like evasive maneuvers⁶⁴. Conspecific-like robots have primarily been used in animal-robot interaction research to study attraction, following, or alignment within groups. In contrast, our results highlight that the same general class of biomimetic platform can also evoke avoidance responses, depending on the interaction context and movement characteristics. Our findings suggest that the robot's approach speed, proximity, and repeated exposure to the fish are key factors shaping the fish's avoidance response. An interesting direction for future work is to investigate whether biomimetic robotic fish could be equipped with adaptive control strategies that allow them to elicit different behavioral responses under different conditions. For example, triggering avoidance to steer fish away from a region or eliciting attraction when social integration is desired. Such extensions would require dedicated experiments that explicitly quantify attraction alongside avoidance. Understanding how fish-like robots influence a range of behaviors, including avoidance, is essential for advancing the development of mixed animal-robot societies^{3,5,8}. Such systems hold the potential not only for enhancing our knowledge of animal behavior^{65–67} but also for practical applications¹², such as guiding fish away from environmental hazards¹⁵ or promoting more harmonious coexistence between animals and robots⁶⁸.

Data availability

The video data from the experiments in this study have been deposited in the public Figshare repository and can be accessed via <https://doi.org/10.6084/m9.figshare.28669265> or via direct access at https://figshare.com/article/media/videos_zip/28669265.

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Author contributions

A.G., Y.K., T.L., P.S. and S.V.H. conceived the study. A.G. and S.V.H. designed and built experimental setups. D.M. and S.V.H. developed statistical analyses. S.V.H. conducted the experiments, analyzed data and wrote the main manuscript text. D.B., Y.K., T.L., D.M. and S.V.H. revised the manuscript. P.S. provided project administration.

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Declarations

Competing interests

The authors declare no competing interests.

Ethics note

All animal care and experimental protocols complied with local and federal laws and guidelines and were approved by the appropriate governing body in Berlin, Germany, the 'Landesamt für Gesundheit und Soziales' (LaGeSo G0117/16). Our study is in accordance with the ARRIVE guidelines. After experimental trials, fish remained in the husbandry.

Additional information

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