

Adult zebrafish favor vision over flow sensing in increasingly complex hydrodynamic environments

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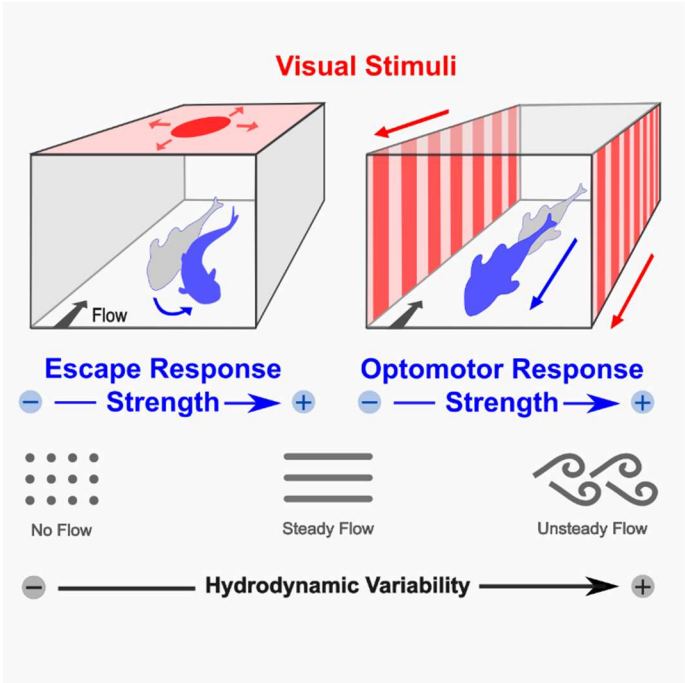
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Table of contents

Graphical Abstract	2
Introductory Summary	2
Results	3
Discussion	9
Methods	12
Resource availability	16
Acknowledgements	17
Supplemental figures and table.....	18
References	23



27 **GRAPHICAL ABSTRACT**



28

29 **INTRODUCTORY SUMMARY**

30 Vertebrate life originated in water, where attenuated light and hydrodynamic currents challenge the
31 sensorimotor abilities of animals differently than in terrestrial environments.¹⁻³ The mechanosensory
32 lateral line system, which evolved alongside vision from deep genetic blueprints inherited from
33 invertebrate ancestors,^{4,5} allows fish to sense changes in water velocity and pressure.^{6,7} Vision and
34 the lateral line have been shown to work inextricably in tandem to detect predators, prey, and
35 conspecifics.⁸⁻¹⁰ Despite the growing interest in elucidating the sensory integration underlying
36 ecological behaviors,^{11,12} our understanding of how mechanosensation and vision interact in fish
37 remains limited. Here, we challenge the lateral line system of adult zebrafish (*Danio rerio*) with
38 hydrodynamic conditions ranging from more predictable (i.e. still water)^{13,14} to less predictable (i.e.
39 turbulent flow)^{15,16} and quantify their behavioral responses to controlled visual perturbations using an
40 augmented reality flow-tank assay. We find that fish exhibit compensatory optomotor responses to
41 maintain position under turbulent, but not uniform, flow conditions during station-holding behavior.
42 Furthermore, escape responses to looming visual stimuli are heightened when fish swim against
43 water flow compared to still water, whether individually or in a group. Our results demonstrate an
44 elevated role of vision in fish as hydrodynamic complexity increases. We propose that fish sensory
45 strategies are not fixed but are dynamically tuned to the predictability of external water flow, favoring
46 lateral line input under more predictable environments and visual cues under less predictable
47 environments.

RESULTS

To understand how fish use vision under varying hydrodynamic conditions, we study the station-holding behavior of adult zebrafish swimming against steady (uniform) or unsteady (turbulent) water currents and quantify their responses to wide-field visual perturbations (Figure-1; see *Method Details*). For each treatment, we observe responses from 4 individuals and repeat 4 trials, for a total of 16 unique independent trials. At stimulus onset ($t = 0$ s), vertical visual gratings projected on both left and right flow-tank sidewalls begin moving either downstream (Optical-Pull) or upstream (Optical-Push), providing streamwise optic-flow to fish swimming against water current. We compare the swimming behavior of fish between the pre-stimulus ($t = -1$ to 0 s) and post-stimulus ($t = 0.5$ to 1.5 s) periods. We report data as mean $\pm$ SEM (standard error of the mean) and use a non-parametric Wilcoxon signed-rank test to compare paired observations, with a significance threshold of $p < 0.05$.

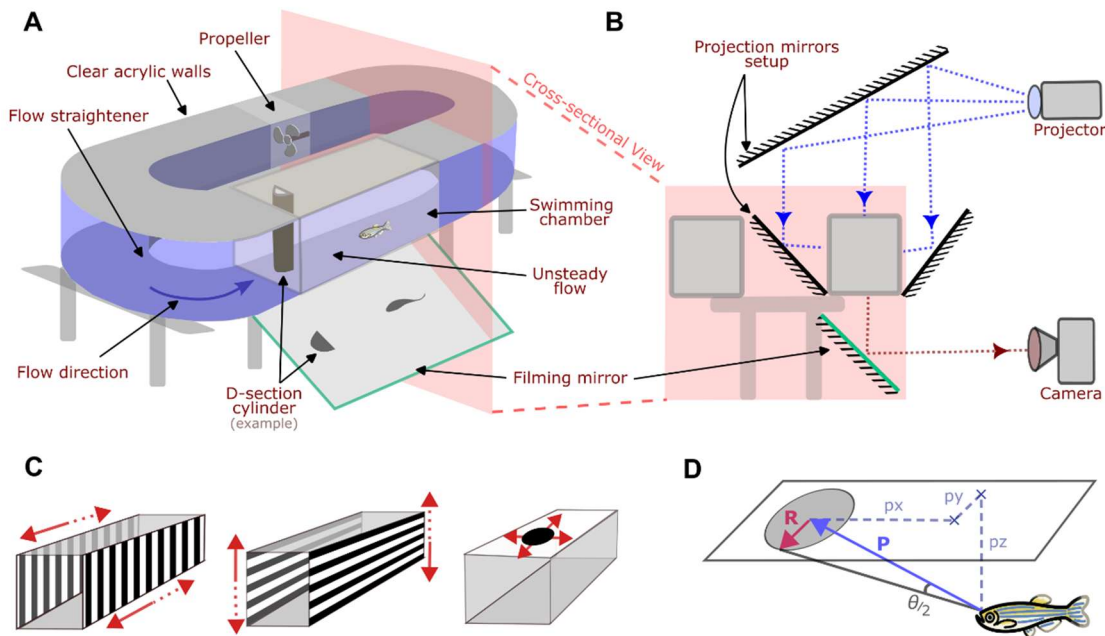


Figure 1 – Schematic of experimental setup and visual stimuli. (A) A transparent acrylic flow-tank with a front-surface mirror positioned underneath at 45° angle to capture the ventral view of the fish in the swimming chamber. (B) Cross-sectional schematic of the augmented reality flow-tank setup showing two side-mirrors and a top-mirror used for projecting visual stimuli on the flow-tank walls, alongside the filming mirror arrangement. (C) Schematic of visual stimuli projected on sidewalls (gratings) and ceiling (loom). Similarly styled arrows (solid or dashed) indicate the direction of optic-flow perturbations for each treatment. Vertical gratings move in the streamwise (Optical-Pull/Push) direction, horizontal gratings move in the cross-stream (Optical-Roll) direction, and the circular disk stimulus radially expands (Loom). (D) Calculation of the threshold stimulus angle (θ) as perceived by an escaping fish based on its position in the flow-tank and the instantaneous size of the loom stimulus. See also Figure S1.

Fish use wide-field optic-flow to maintain position in unsteady but not in steady flow

In steady flow, the swimming velocities of fish in the streamwise direction remain unchanged after the stimulus for both the Optical-Pull (pre-stim = -0.2 ± 1.2 cm/s; post-stim = 0.2 ± 1.2 cm/s; $p=0.90$, n.s.) and the Optical-Push (pre-stim = -0.1 ± 1.0 cm/s; post-stim = -0.9 ± 1.1 cm/s; $p=0.74$, n.s.) treatments (Figure-2 A,B). Conversely, presenting the same visual stimulus under unsteady flow elicits a stereotypical optomotor response (OMR), where swimming velocities in the streamwise directions reduces for the Optical-Pull (pre-stim = -0.2 ± 0.4 cm/s; post-stim = -4.2 ± 0.6 cm/s; $p=0.0004$) and increases for the Optical-Push (pre-stim = -0.3 ± 0.6 cm/s; post-stim = 2.3 ± 0.6 cm/s; $p=0.009$) treatments (Figure-2 C,D). This behavior represents a positive OMR, since the post-stimulus displacement of fish is in the same direction as the optic-flow moving on the sidewalls for both Optical-Pull and Optical-Push perturbations. A positive (compensatory) OMR may help station-holding fish to maintain their position using wide-field visual feedback in unsteady flow. Such an OMR is absent for both treatments in steady currents, suggesting that fish rely prominently on a sensory mechanism other than wide-field optic-flow to maintain position.

Fish move monotonically with wide-field optic-flow in unsteady flow

We quantify Spearman's correlation coefficient (ρ) between fish swimming trajectories and a theoretical linear motion, where $\rho = 1$ and $\rho = -1$ represent monotonic displacements in the forward and backward directions, respectively. Fish swimming in unsteady flow show statistically significant monotonic movements after visual stimulus onset. In unsteady flow, ρ increases for the Optical-Pull (pre-stim = -0.2 ± 0.2 ; post-stim = -0.8 ± 0.1 ; $p=0.009$), reflecting monotonic downstream drift, and for the Optical-Push (pre-stim = -0.2 ± 0.2 ; post-stim = 0.6 ± 0.1 , $p=0.04$), reflecting a largely monotonic upstream surge. This result suggests that fish continually update their position in response to a continued optic-flow. However, under steady flow, the ρ values are spread across the range with averages close to zero for both the Optical-Pull (pre-stim = 0.0 ± 0.2 ; post-stim = 0.0 ± 0.2 ; $p=0.99$, n.s.) and Optical-Push (pre-stim = 0.1 ± 0.2 ; post-stim = -0.1 ± 0.2 ; $p=0.74$), representing a lack of net monotonic displacement (Figure-2).

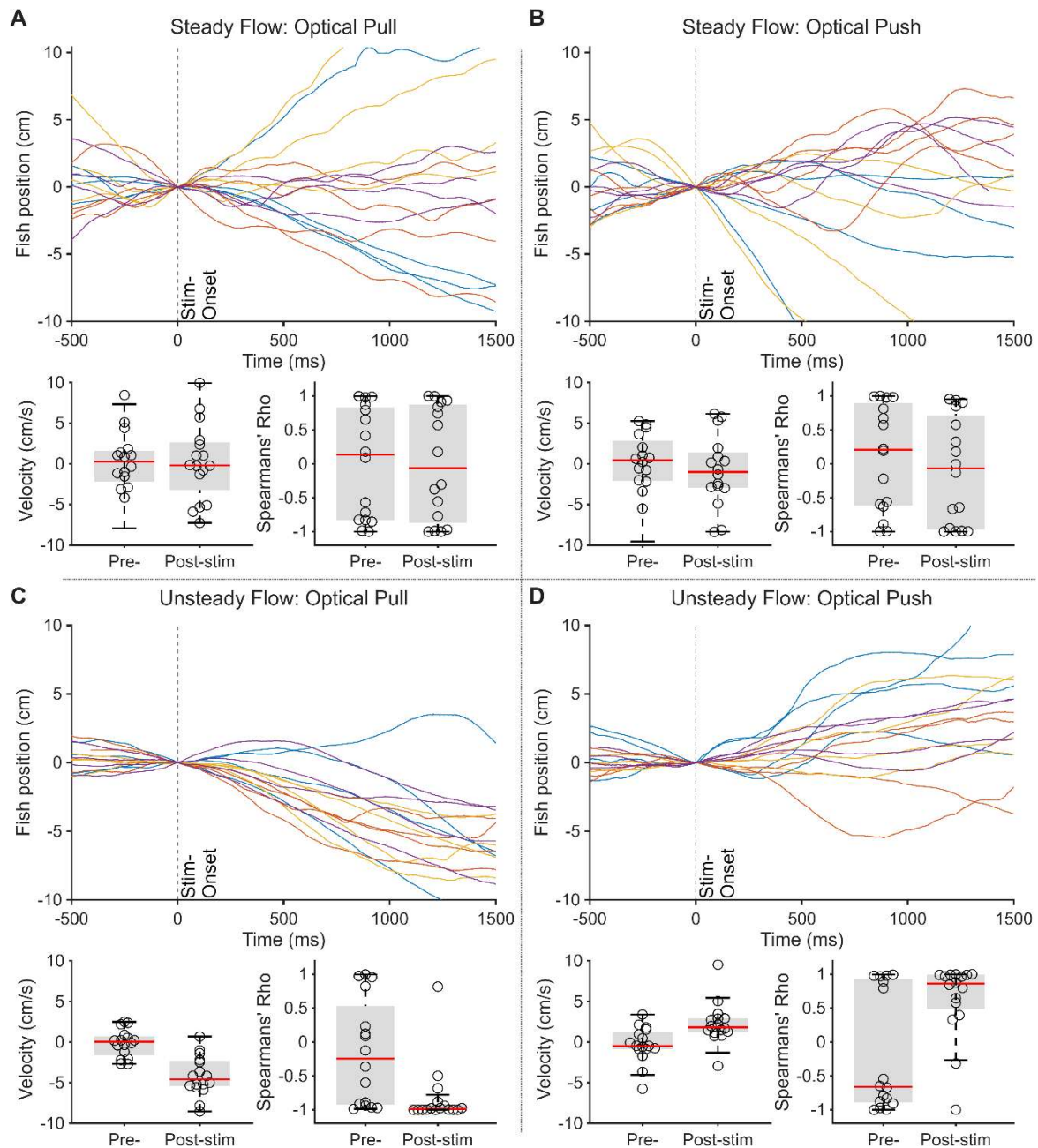


Figure 2 – Raw trajectories and quantification of station-holding behavior in the streamwise direction in response to the wide-field visual perturbations. (A-B) Steady flow trials and (C-D) unsteady flow trials. Top panel: Streamwise positions of fish over time, where positive and negative values indicate upstream and downstream positions, respectively, and each color represents an individual fish (n=4 fish, 4 trials each). Bottom panel: Comparison of swimming velocity and Spearman's correlation coefficient (ρ ; quantifying the degree of monotonic displacement) over a one-second window of pre-stimulus ($t = -1$ to 0 s) and post-stimulus ($t = 0.5$ to 1.5 s) data. See also Figure S2 and S4.

Compensatory OMR occurs only in the streamwise direction

For both steady and unsteady hydrodynamic conditions, any post-stimulus change in position occurs only in the streamwise direction, consistent with the streamwise direction of the visual stimulus (Figure-2). The displacement, velocity, and ρ values remain unchanged in the cross-stream direction (Figure-S2, Table-S1). We further find that Optical-Roll perturbations, providing optic-flow in the perpendicular direction to water-flow, do not elicit an OMR in either streamwise or cross-stream directions (Figure-S3). We also note that fish do not turn, change their swimming direction, or show an escape response (e.g., C-start) to any of our wide-field visual stimuli. Our results suggest that fish respond to optic-flow in the direction that is behaviorally relevant (i.e., along streamwise) rather than in arbitrary directions.

Next, we study the effect of hydrodynamic conditions on the escape response using an exponentially expanding visual stimulus (loom) projected onto the flow-tank ceiling. We find that the loom reliably elicits fast escape response (C-start). We compare escape behavior between trials in which fish hold station by swimming against a water current (Flow) and trials in still water (No-Flow), to understand behavior across habitats of varying hydrodynamical complexity. To assess whether the effect of external water flow on visual responsiveness is consistent across ecological contexts, the escape experiments include both individual (Single; 65 trials across 5 fish) and shoaling (Group; 18 trials of group of 3 and 12 trials of group of 5 fish) trials (Figure 3). We pool the Single and Group trials, unless noted otherwise, report data as mean $\pm$ SEM, and use a non-parametric Wilcoxon rank-sum test to compare fish escape responses between Flow and No-Flow treatments, with a significance threshold of $p < 0.05$.

Hydrodynamic conditions modulate the escape distance-delay relationship

Escape responses in both Single and Group trials show that escaping fish are positioned closer to the stimulus than non-escaping fish. This relationship between the presence of the escape response and distance from the stimulus is consistent across hydrodynamic conditions: Flow (Escape = 48.5 ± 6.3 mm, $n=36$; No-Escape = 93.7 ± 7.2 mm, $n=53$; $p=9.1e-6$) and No-Flow (Escape = 41.8 ± 4.2 mm, $n=41$; No-Escape = 60.3 ± 6.4 mm, $n=48$; $p=0.018$) (Figure-3A). Thus, in our subsequent analysis, we account for the position of fish when triggering a C-start. To determine whether the fish positioned closer to the stimulus also respond faster, we calculate the escape response delay from looming stimulus onset for each escaping fish across all trials and study its relationship with the distance of fish from the stimulus. Fish show a stronger positive distance-delay relationship in Flow trials (slope: Single = 0.22, Group=0.28) than in No-Flow trials (Single = 0.04, Group=0.03) (Figure-3B). To assess the strength and statistical significance of the linear relationship between distance and response

delay, we performed Pearson correlation analysis. We find a stronger positive distance-delay correlation for the Flow treatment (Pearson $R=0.67$, $n=36$, $p < 0.001$) than for No-Flow treatment (Pearson $R=0.21$, $n=41$, n.s.). This analysis shows that fish swimming against flow trigger a C-start sooner when positioned closer to, and later when positioned farther from, the stimulus. In contrast, fish in still water do not show such a distance-dependent response, suggesting they respond to the mere presence of the looming stimulus regardless of their position (Figure-3B).

Fish swimming in flow respond to visual looming stimuli sooner than in still water

The escape response is best characterized by quantifying the threshold stimulus angle for each escaping individual, as the angle accounts for both the distance of fish from the stimulus and response delay. We calculate the threshold stimulus angle of the looming stimulus in three-dimensional space at the time of escape (Figure-1D) to test whether station-holding fish in the Flow trials respond to the looming stimulus at a lower angle than fish in No-Flow trials, as it would be predicted by their distance-delay relationships (Figure-3B). To maintain consistency across all responses, we include only the trials in which the looming stimulus originates within their lateral-visual field (153° on each side, $n=50$), and exclude trials with stimulus originating within blind-spot (21° on the rear, $n=5$) or binocular field (33° on the front, $n=22$).¹⁷ This allows us to compare the escape response across Flow and No-Flow trials because the fish do not always face upstream in still water, unlike fish swimming against a water current. We plot the mean threshold stimulus angles (*theta*; Y-axis) for all treatments, along with their SEM as error bars, overlaid onto a typical looming stimulus from our trials with exponentially expanding angular size (Y-axis) over time (X-axis) (Figure-3C). We find a lower threshold angle to trigger a C-start for fish swimming against a water current than for fish in still water (Flow = $15.9^\circ \pm 3.9^\circ$, $n=21$; No-Flow = $32.6^\circ \pm 6.8^\circ$, $n=29$; $p=0.017$), suggesting increased responsiveness to visual looming stimuli in Flow trials (Figure-3D).

In summary, our results show that fish increase their reliance on wide-field optic-flow to maintain position when swimming against unsteady flow compared to steady flow, as studied using station-holding behavior, and increase their visual sensitivity to threat when swimming against steady water flow compared to still water, as studied using the escape response. Together, these findings indicate that fish increase visual responsiveness with increasing hydrodynamic complexity.

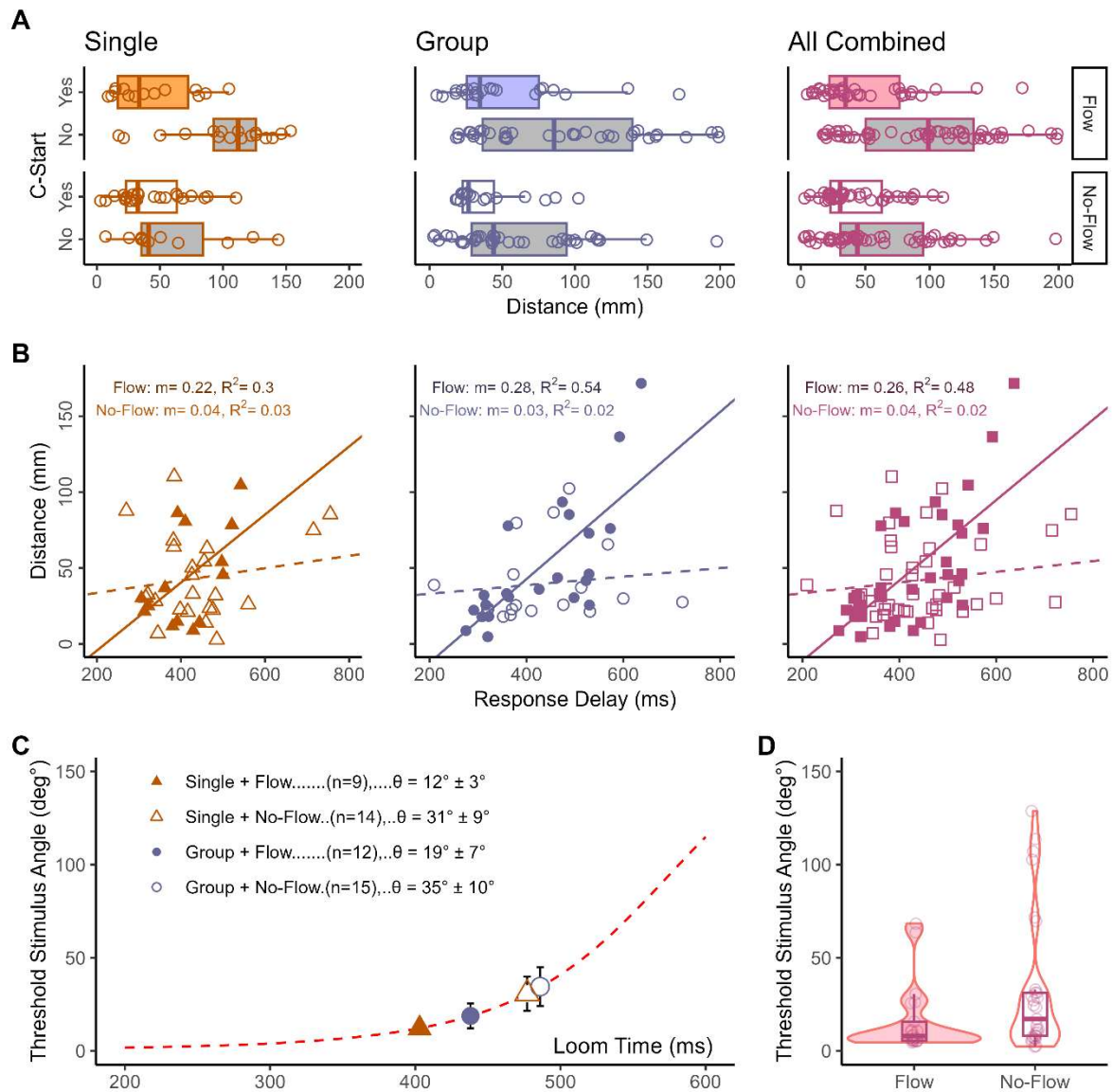


Figure 3 – Comparison of escape behavior (C-start) under Flow and No-Flow conditions in Single and Group trials. (A) The distance between the looming stimulus origin and the fish's position, compared between the trials in which fish did and did not trigger a C-start, for Flow and No-Flow conditions. (B) Relationship between the fish's distance from the stimulus and escape response delay for all the escaping fish, across Flow and No-Flow conditions. (C) Comparison of the threshold stimulus angle (θ) across all eligible trials in which the looming stimulus originated from the lateral visual field of the escaping fish. Means and SEMs (shown as error bars) for each treatment are shown overlaid on a representative looming stimulus (dashed line). (D) Comparison of threshold stimulus angles across all Flow and No-Flow trials, where a lower angle represents a quicker escape response. See also Figure S4.

DISCUSSION

Our results provide direct evidence that adult zebrafish dynamically shift their reliance between visual and mechanosensory cues during locomotion, depending on the complexity and predictability of the surrounding flow.

Developmental and Hydrodynamic Influences on OMR

The OMR has long been recognized as essential for visual position maintenance in terrestrial animals.^{18–20} In dynamic aquatic environments, where light is attenuated and currents can be forceful, the OMR is much less understood. For fishes, the hydrodynamic environment itself shapes sensory processing demands. Unlike small larval fish operating at low Reynolds numbers ($Re < 100$) where viscosity facilitates predictable flow, larger adults operate in high Reynolds numbers ($Re > 1000$) where vortices across a range of spatial scales can create unpredictable, turbulent flow.²¹ The presence of these vortices may degrade lateral line reliability as an indicator of self-motion.^{22–24,14} If this were true, swimming at high Reynolds numbers may prompt a shift toward vision, analogous to the ambient luminance-dependent sensory reweighting in hawkmoths.^{10,12,25} Ontogenetic shifts also accompany increases in body size. Unlike newly hatched larvae, adults have had the time to develop calibrated expectations of the lateral line and vestibular inputs to visual feedback during flow,²⁶ as well as accumulate error-driven motor learning experiences.^{14,27} Perhaps reflecting these changes, adult zebrafish have been observed to display opposite behaviors to larvae. Specifically, adults swim against optic-flow (negative OMR) in still water,¹⁰ while larvae swim with optic-flow (positive OMR).²⁵ We study adult zebrafish swimming against water flow and find that they perform positive OMR to maintain position in turbulence, indicating an adaptive sensory prioritization, rather than fixed integration, that may represent a widespread solution to aquatic environmental uncertainty. Our findings suggest that, across diverse riverine and coastal ecosystems where flow is inherently unpredictable, vision often becomes the dominant cue fish use to maintain their position relative to the Earth's frame of reference.

Energetic Imperatives and Adaptive Sensory Prioritization

The diminished reliability of lateral-line input in turbulent flow, combined with the strong drive to conserve energy, may force fish to depend more heavily on visual cues to stay within low-cost wake zones. During station-holding, fish can exploit vortical wakes by swimming in specific regions behind bluff bodies to reduce swimming costs.^{15,23,28–30} However, even small displacements can eject fishes into the surrounding freestream flow and lead to substantial increases in swimming energetics.^{30–32} Vision becomes exceedingly consequential in this situation, where actively maintaining position in a

specific, energetically favorable region of the wake (or returning to it if displaced), is crucial to optimizing locomotory efficiency. By contrast, the absence of compensatory OMR in steady flow suggests that the lateral line input is a more reliable sensory modality given efferent feedback loops.³³ Concurrently, it could also suggest a role for energy conservation, given the significantly higher metabolic cost associated with visual processing in animal behavior.³⁴

Vision-Dependent Escape Responses in Flow

The relationship between the lateral line and vision in flow remains unexplored for adult fishes performing escape responses, despite over a century of research on this canonical behavior and its ecological relevance. Previous studies focused on understanding this behavior in still water or using purely mechanical stimulation, a necessity for disentangling the underlying biomechanics and physiology.^{9,35,36} However, unlike in still water, where escape speeds and energetic costs are equal in all directions, upstream escapes likely result in slower bursts and higher energetic costs compared to downstream or cross-stream escapes.^{26,36,37} Therefore, escapes in flowing water do not operate under the same constraints as in still water, prompting animals to adaptively tune their sensory sensitivity. By employing a purely visual stimulus to eliminate confounding hydrodynamic cues, we find that fish respond faster when swimming in flow than in still water. This supports the hypothesis that fish increase on visual cues when relative mechanosensory reliability decreases.

Schooling is a common anti-predator strategy,^{38–40} and individuals must process predatory threats as well as hydrodynamic and visual cues from conspecifics. We find that escape sensitivity for both solitary and grouped fish increased when swimming in steady flow, though the shoaling fish required a larger angular expansion before initiating a C-start. This is supported by field observations where wild schools favor stimulus robustness over maximal sensitivity.⁴¹ However, grouped fish show reduced visual sensitivity compared to solitary fish, revealing a trade-off that favors collective detection reliability over individual responsiveness. We contend that this dynamic has significant, yet largely unexplored, implications for the study of collective behavior.

Role of the Efferent System and Sensory Conflict

We propose that the lateral-line efferent system gates the weighting of visual inputs via corollary discharge.³³ In predictable (steady) flow, this gating suppresses responses to wide-field optic-flow, allowing fish to ignore such perturbations while relying on the faster, more reliable mechanosensory feedback. When flow becomes turbulent, lateral-line signals become unreliable;¹⁴ the efferent gating is disengaged and visual cues dominate, producing the compensatory optomotor responses we observe. Consistent with this mechanism, station-holding fish do not stop swimming or turn

downstream after a visual perturbation. Instead, they drift downstream but remain swimming in an upstream orientation, keeping the corollary discharge signal active. Hence, active swimming provides the corollary discharge that calibrates expected flow signals along the lateral line, enabling a rapid switch from mechanosensory to visual control when environmental predictability declines. We predict that fish lacking a functional lateral line (i.e. both afferent *and efferent* signals blocked) would show a compensatory OMR under steady flow, in contrast to the fish in this study.

Our hypothesis that the efferent system gates the weighting of visual inputs is further supported by our sensory-conflict experiments. Our Optical-Roll experiments reveal that conflicting optic-flow becomes less influential when lateral line input better aligns with the fish's expected hydrodynamic environment. This suggests that continuous hydrodynamic input to the lateral line, coupled with semicircular canal inputs that do not align with rolling movements, overrides sudden visual inputs, causing fish to disregard cross-stream moving visual stimulus.¹⁰ This intricate multisensory interplay likely constitutes a fundamental behavioral mechanism that privileges robust, rapid lateral line signals over slower visual processing, serving as a key survival strategy for ancestral vertebrates that concurrently evolved these two systems.^{3,4}

Rethinking the Lateral Line: Towards Integrated Flow Detection

Our findings inspire new avenues of investigation towards characterizing parameters that govern how hydrodynamic conditions shape sensory prioritization. Since the turbulent flow in our experiments was strong enough to displace the body, evoking both lateral line and vestibular signals, future work may employ unpredictable flow with reduced vortex strength sufficient to stimulate the lateral line without displacing the fish. For example, turbulence intensity can be varied independently of flow velocity.^{42,43} This would be preferable to pharmacological lateral line ablations that compromise the afferent system but leave the efferent system intact, which likely alters proprioceptive abilities and therefore complicates behavioral interpretations.

Overall, our work demonstrates that fishes dynamically prioritize modalities according to the flow regime they inhabit, rather than simply integrate sensory inputs. Dynamically re-weighting sensory cues highlights the adaptive flexibility of fishes in the complex habitats that shaped their evolution. By showing that vision becomes the principal reference for maintaining position in unpredictable flow, our naturalistic experiments uncover a principle with far-reaching relevance for neuroscience, collective behavior, ecology, evolution, and bio-inspired robotics.

269 **STAR★METHODS**

270

271 **KEY RESOURCES TABLE**

REAGENT OR RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and processed data from this paper	Mendeley Data	DOI: 10.17632/jkssdtkmjm.1 (preview-link)
Experimental models: Organisms/strains		
Adult zebrafish	University of California, Santa Barbara	Wild-type (AB strain)
Software and algorithms		
MATLAB (R2025a)	MathWorks	RRID:SCR_001622
R (4.5.1)	The R Foundation	RRID:SCR_001905
RStudio (2025.05.1+513)	Posit Software, PBC	RRID: SCR_000432
PsychoPy Standalone	PsychoPy	RRID:SCR_006571

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273 **EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS**

274 ***Animals***

275 We used adult male zebrafish, *Danio rerio* (wild-type AB strain; >90 dpf; mean±SEM: body-length =
276 38.6±0.7 mm, weight = 599.8±40.4 mg; n=20), which were raised at the University of California, Santa
277 Barbara zebrafish facility in accordance with all ethical regulations and protocols approved by the
278 University Institutional Animal Care and Use Committee (IACUC). Fish were transferred to the
279 experimental room two weeks prior to the experiments and housed in two 10 L freshwater tanks
280 maintained at 23±0.5 °C with a commercial aquarium heater (Eheim Co.). Fish were kept on a 12:12
281 light:dark cycle and fed commercial pellets *ad libitum*. All trials were conducted in the afternoon
282 (12:00-17:00 PST) in a room enclosed by blackout curtains. Fish were randomly assigned to the
283 experimental groups. On experimental days, single-trial fish were housed individually, and group-trial
284 fish were kept in groups of three and five in 1.5 L freshwater containers. Fish were introduced into the
285 flow tank from the containers and allowed 10 minutes to acclimatize before trials began. Following

data collection across different water-flow conditions (i.e., Steady and Unsteady, or Flow and No-Flow), the fish were euthanized with an overdose of MS-222.

METHOD DETAILS

Flow tank

All experiments were conducted using a custom-built 5 L recirculating flow tank (Figure-1A) with a working section (i.e., swimming chamber) of 22 x 7 x 7 cm (length x width x depth). The cross-sectional area of the fish was less than 5% of the cross-sectional area of the flow tank, minimizing any solid blocking effects.⁴⁴ Water was filtered, aerated, and maintained at room temperature of 22.1 ± 0.1 °C throughout the experiment. Water flow was generated by a variable-speed AC-DC series motor (Dayton model 2MO37A, 115V 1.5A, Lake Forest Illinois USA) driving a propeller that circulated water through 2 sets of honeycomb collimators (1/8" aperture diameter) to generate uniform (Steady) flow. Flow velocity was set at 10 cm/s and verified by tracking suspended plastic particles within the working section of the flow tank. This flow velocity elicited the most reliable station-holding response for our setup. Three D-section cylinders (diameter = 0.5 to 1 cm) were placed at the upstream end of the working section (Figure-S1C) to create a distinct flow refuge and generate suitable turbulent (Unsteady) flow.¹⁵ Water flow was turned off during No-Flow trials and fish were allowed to freely move through the working section of the flow-tank.

Filming and digitization

A monochromatic Chronos 1.4-HD high-speed video camera (1024 x 1024, 1000 frames/s, Burnaby BC Canada) was aimed at a front-surface mirror angled at 45° and placed directly below the working section to film the swimming kinematics and position of zebrafish (Figure-1B). An LED panel with white lights and an overlaid diffuser were used to optimize the image contrast of the fish. In loom experiments, this panel was replaced with a projection screen for the top-projected loom stimulus against a uniform background illumination. We used a semi-supervised machine-learning based tool, DeepLabCut,⁴⁵ that allowed us to reliably track 4 points on the fish (head-tip, tail-tip, right- and left-pectoral fin base). To create a training set, we manually labelled these 4 points in a total of 800 frames, randomly selected from 40 videos, and trained a neural network model for ~1 million iterations to minimize the tracking error. We subsequently used this model to track points on more than 400,000 frames from 80 video recordings. The videos tracked using DeepLabCut were visually verified and approved before further analysis.

317 **Visual perturbations**

318 We used a system of mirrors (Figure-1B) to project visual stimuli on customized rear-projection
319 screens mounted to the flow tank walls. Fish were acclimatized for 5 minutes before each trial using
320 either horizontal or vertical gratings on sidewalls for station-holding trials, or a plain white background
321 on the top wall for escape trials, during which video data from the previous trial were manually
322 downloaded and saved from the high-speed camera. The treatment order was randomized to evoke a
323 reflexive response and minimize any contribution from learning and memory. For wide-field grating
324 patterns on the sidewalls, we varied orientation and motion (vertical gratings moving
325 downstream/upstream; horizontal gratings moving up/down) and set the optic-flow speed at ca. 10
326 cm/s (spatial period = 1.8 cm/cycle, temporal frequency = 5.5 cycles/s) to match hydrodynamic flow
327 velocity.⁴⁶ We recorded these moving projection patterns using a high-speed camera at 1000 frames/s
328 to verify the optic-flow rates. For the visual looming stimulus, we used an exponentially expanding
329 (doubling-time: diameter=50ms, area=25ms) dark-circle with a bright background presented on the
330 top-wall (Figure-1C).

331 **Optic-flow terminology**

332 **Streamwise optic-flow – Optical-Pull and Optical-Push.** As the fish swim against water-flow, we
333 externally provide wide-field optic-flow by suddenly moving the surroundings (i.e., vertically oriented
334 visual gratings) in the forward (upstream) or the backward (downstream) directions. The fish typically
335 experience optic-flow either during self-movements or when external factors (such as water-flow)
336 move them. Since our treatments induce optic-flow analogous to that experienced by fish displaced by
337 external factors, we call them 'Optical-Pull' and 'Optical-Push', based on the direction of optic-flow
338 generated. The prefix 'Optical' here refers to the fact that they are purely visual perturbations, rather
339 than changing water-flow speed to move the fish. Optical-Push involves moving the visual
340 surroundings from the back to the front of the fish, mimicking the optic-flow direction as if the fish were
341 pushed backward externally (e.g., sudden increase of water-flow speeds). Similarly, the Optical-Pull
342 treatment suddenly moves wide-field visual patterns from the front to the back (i.e., in a downstream
343 direction) mimicking a scenario in which a station-holding fish is pulled forward due to external factors
344 (e.g., sudden decrease of water-flow speeds).

345 **Rotational optic-flow – Optical-Roll.** We move the visual surroundings (i.e., horizontally oriented
346 visual gratings) in the opposite directions on both sidewalls simultaneously (e.g., optic-flow moving up
347 on the right wall and down on the left), at the same spatial and temporal frequencies used for
348 streamwise optic-flow. Thus, the optic-flow direction remains orthogonal to the water-flow direction,
349 creating a sensory conflict and mimicking the optic-flow patterns encountered as if the fish were

undergoing rotation. Optical-Roll is either clockwise (CW: right-side moving down, left moving up) or counterclockwise (CCW: right-side moving up, left moving down), defined from the fish's perspective.

QUANTIFICATION AND STATISTICAL ANALYSIS

Effect of wide-field visual perturbation during station-holding behavior

We studied fish swimming performance for each treatment (Figure-2, S2, S3) by tracking fish-head position over time and aligning all the trajectories ($n=16$) at the stimulus onset ($t = 0$ s). For each trajectory, we compared a one-second window of pre-stimulus data ($t = -1$ to 0 s) to post-stimulus data ($t = 0.5$ to 1.5 s) and quantified changes in body position, swimming velocity, and trajectory pattern. Note that we excluded the first half-second of data immediately after the stimulus onset from this analysis to account for any transient behavior and sensory processing delay. We quantified the components of swimming behavior in the streamwise direction (along with the water flow; e.g. Figure-2) and the cross-stream direction (perpendicular to flow; e.g., Figure-S2) to better explain the behavioral observations in each directional component. The trajectory patterns were quantified by comparing fish displacements with a theoretical linear motion using Spearman's correlation coefficient (ρ), which measures monotonic changes in position. A fish showing a monotonic upstream displacement would yield $\rho = 1$, and similarly $\rho = -1$ for downstream displacement. We used a non-parametric statistical test, the Wilcoxon signed-rank test, to compare two paired observations (i.e., pre-stimulus and post-stimulus quantity for each trajectory), with a significance threshold of $p < 0.05$ (Figure-2, S4). Rather than directly comparing swimming performance across different conditions (e.g., Steady and Unsteady flow), we first identified the behavioral changes due to the visual stimulus as compared to the baseline pre-stimulus behavior for the given treatment. Then, we reported whether we found such changes across different hydrodynamic conditions.

Escape response analysis

We quantified the fast escape responses of fish (C-start), involving reflexive bending of the body triggered by a purely visual looming stimulus, for single and group trials during Flow and No-Flow conditions (Figure-3). For all the trials, we first found the positions of fish at the onset of the looming stimulus and calculated their horizontal distance from the stimulus (Figure-3A). Comparing the distance between escaping and non-escaping fish allowed us to determine that the distance from the stimulus is a factor in a successful escape response. We then excluded the trials that did not result in a C-start and quantified the response delay for all escaping fish events in the remaining trials. From all

the events in Single and Group trials, we quantified the strength and significance of the linear relationship between the distance and the response delay using Pearson correlation analysis, with a significance threshold of $p < 0.05$ (Figure-3B). A strong linear relationship between distance and response delay would suggest the need to calculate an angular threshold to account for both the quantities before comparing the behavior across the flow treatments. Thus, we used the instantaneous radius (R) of the looming stimulus (as a proxy of the response delay) and the three-dimensional distance (P) of the escaping fish to calculate the threshold stimulus angle (*theta*) as perceived from the escaping fish's position (Figure-1D), using the formula: $\theta = 2 * \arctan(R / \text{Norm}(P))$. To maintain consistency in our comparison, we first determined the angle at which the looming stimulus originated with respect to the heading direction of the fish (found from the vector between the fish head and body-center points), and excluded all events where the looming stimulus originated outside of the lateral-visual field (153° on the right and left side).¹⁷ We showed a representative looming stimulus, and overlaid the mean threshold stimulus angles of each treatment, along with their SEM shown as error bars (Figure-3C). We used a non-parametric Wilcoxon rank-sum test (also known as the Mann-Whitney U test) to compare the threshold stimulus angles across all the trials of Flow and No-Flow treatments (i.e., single and group trials combined), with a significance threshold of $p < 0.05$ (Figure-3D,S4). We also perform a leave-P-out sensitivity analysis to evaluate whether our statistical outcomes are heavily influenced by any single or combination of data points. We find that all reported statistical comparisons remain robust, retaining their significance across all iterations (Figure-S4).

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, James C. Liao (jliao@whitney.ufl.edu).

Materials availability

This study did not generate new unique reagents.

Data and code availability

Raw and processed data have been deposited at Mendeley Data and are publicly available as of the date of publication at DOI: 10.17632/jkssdtkmjm.1 ([preview-link](#)). This paper does not report original

411 code. Any additional information required to reanalyze the data reported in this paper is available from
412 the lead contact upon request.

413 **ACKNOWLEDGEMENTS**

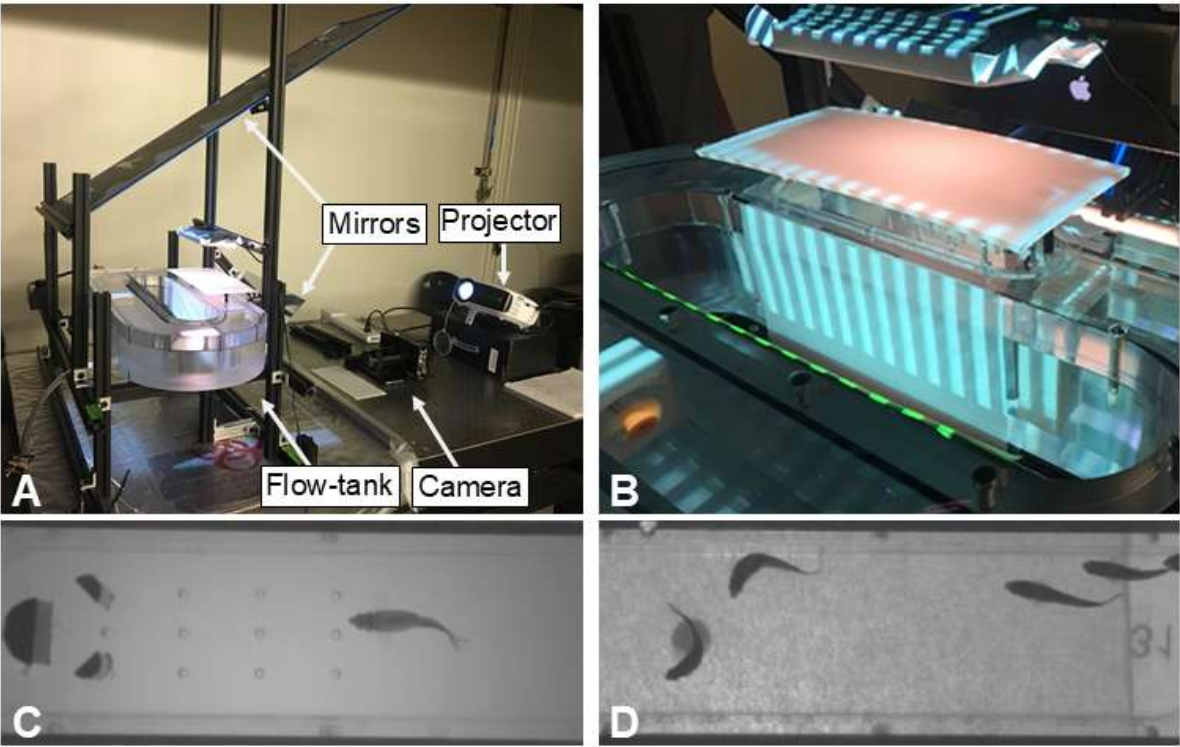
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423 **AUTHOR CONTRIBUTIONS**

424 Conceptualization: J.C.L., S.D. Methodology: J.C.L., S.D.; Software: S.D. Validation: J.C.L., S.D.;
425 Formal analysis: S.D.; Investigation: J.C.L., S.D.; Resources: J.C.L.; Data curation: J.C.L., S.D.;
426 Writing - original draft: J.C.L., S.D.; Writing - review & editing: J.C.L., S.D.; Supervision: J.C.L.; Project
427 administration: J.C.L.; Funding acquisition: J.C.L.

428 **DECLARATION OF INTERESTS**

429 The authors declare no competing interests.



431

432 **Figure S1 – Images of the experimental setup. Related to Figure 1.** (A) Augmented reality setup consisting
433 of the flow-tank, visual stimulus projection system, and the behavior recording camera. (B) Vertical gratings
434 projected on the sidewalls of the swimming chamber, as employed in Optical-Pull/Push perturbations. (C)
435 Representative image showing a station-holding fish swimming behind three D-section cylinders (bluff bodies)
436 arranged to produce unsteady flow. (D) A group of fish swimming under an expanding looming stimulus, with the
437 two fish (on the left) triggering a C-start.

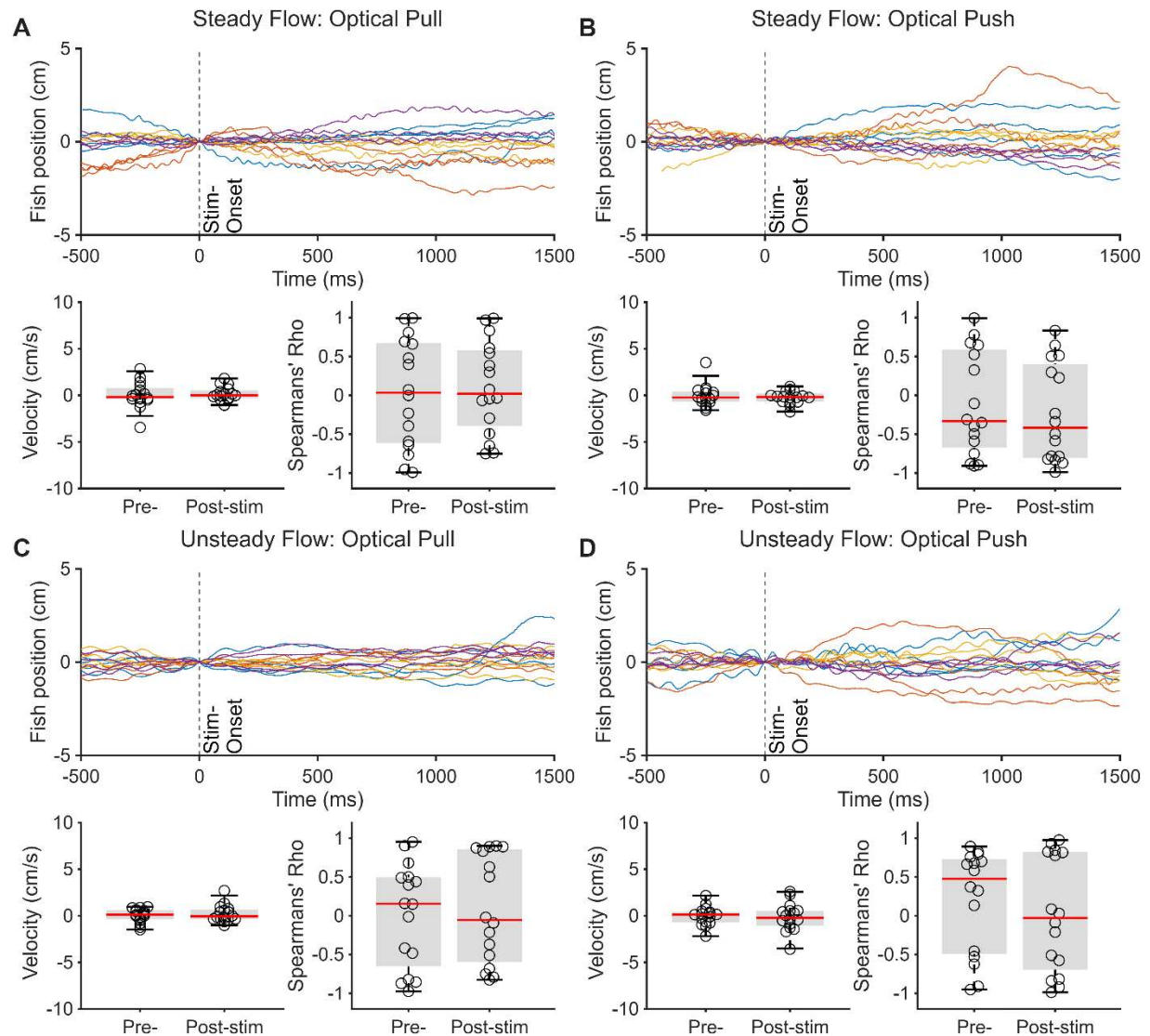


Figure S2 – Raw trajectories and quantification of station-holding behavior in the cross-stream direction in response to the wide-field visual perturbations. Related to Figure 2. (A-B) Steady flow trials and (C-D) unsteady flow trials. **Top panel:** Streamwise positions of fish over time, where positive and negative values indicate upstream and downstream positions, respectively, and each color represents an individual fish ($n=4$ fish, 4 trials each). **Bottom panel:** Comparison of swimming velocity and Spearman's correlation coefficient (ρ ; quantifying the degree of monotonic displacement) over a one-second window of pre-stimulus ($t = -1$ to 0 s) and post-stimulus ($t = 0.5$ to 1.5 s) data. See also Table S1.

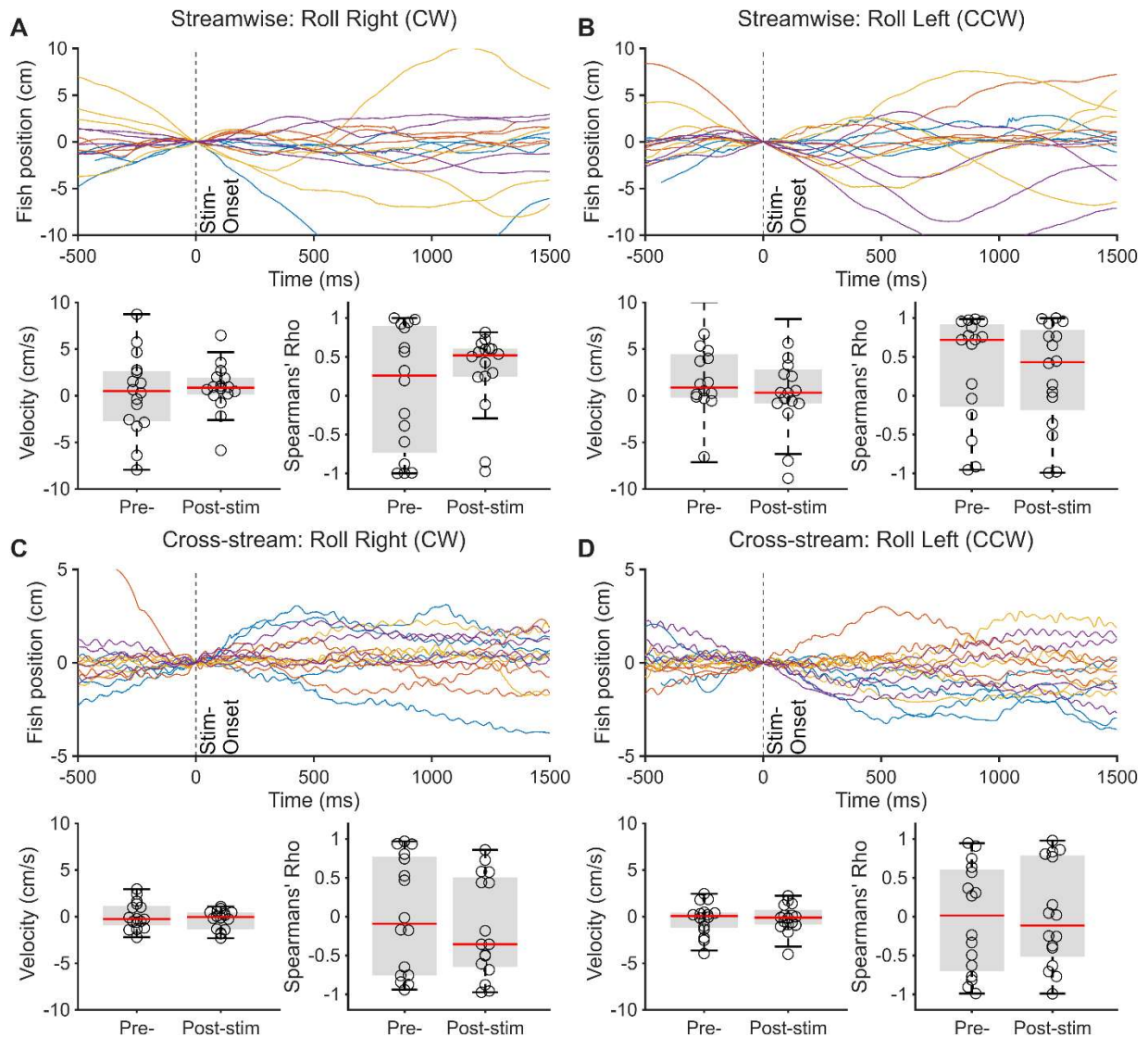


Figure S3 – Raw trajectories and quantification of station-holding behavior in response to the wide-field visual perturbations that conflict with unsteady water-flow direction (Optical-Roll). Related to STAR Methods. (A-B) Streamwise component and (C-D) cross-stream component of the behavior. **Top panel:** Positions of fish over time, where positive and negative values indicate upstream and downstream positions, respectively, and each color represents an individual fish (n=4 fish, 4 trials each). **Bottom panel:** Comparison of swimming velocity and Spearman's correlation coefficient (rho; quantifying the degree of monotonic displacement) over a one-second window of pre-stimulus (t = -1 to 0 s) and post-stimulus (t = 0.5 to 1.5 s) data. See also Table S1.

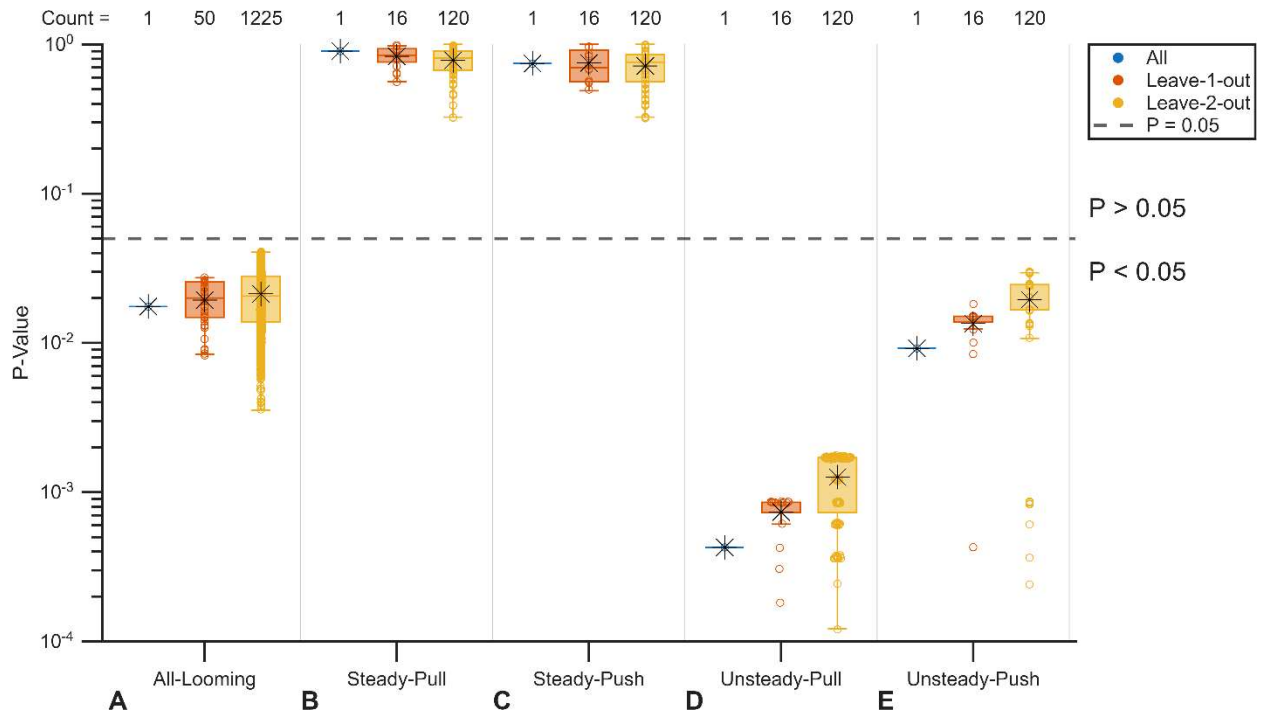


Figure S4 – Sensitivity analysis for key statistical comparisons using a leave-P-out approach. Related to Figure 2 and 3. Each data point represents the p-value resulted from rerunning the statistical test after excluding zero, one or two trials, plotted on a log-scale and overlaid on the boxplots. (A) Sensitivity of the threshold stimulus angle for escape response between Flow and No-Flow conditions (Wilcoxon rank-sum test; see Figure 3D). (B-E) Sensitivity of the station-holding velocity changes between pre-stimulus and post-stimulus data (Wilcoxon signed-rank test; see Figure 2).

Quantity Treatment	Velocity mean±SEM (cm/s)		P-val	<i>rho</i> mean±SEM		P-val
	Pre-stimulus	Post-stimulus	Pre vs Post	Pre-stimulus	Post-stimulus	Pre vs Post
Optical-Pull (Steady)	4.2E-04 ± 3.5E-03	1.5E-03 ± 2.0E-03	0.98 (n.s.)	3.2E-02 ± 1.8E-01	1.0E-01 ± 1.5E-01	0.82 (n.s.)
Optical-Push (Steady)	-3.7E-04 ± 2.9E-03	-2.2E-03 ± 1.7E-03	0.63 (n.s.)	-1.1E-01 ± 1.7E-01	-2.3E-01 ± 1.6E-01	0.60 (n.s.)
Optical-Pull (Unsteady)	3.6E-04 ± 1.8E-03	2.3E-03 ± 2.3E-03	0.67 (n.s.)	1.5E-02 ± 1.7E-01	8.0E-02 ± 1.7E-01	0.86 (n.s.)
Optical-Push (Unsteady)	-1.6E-04 ± 2.5E-03	-1.6E-03 ± 3.8E-03	0.74 (n.s.)	2.0E-01 ± 1.7E-01	2.1E-02 ± 1.9E-01	0.46 (n.s.)
Optical-Roll (cw)	-2.5E-03 ± 4.2E-03	-1.8E-03 ± 3.7E-03	0.98 (n.s.)	-2.6E-02 ± 1.7E-01	6.0E-03 ± 1.7E-01	0.90 (n.s.)
Optical-Roll (ccw)	1.2E-03 ± 3.6E-03	-3.3E-03 ± 2.6E-03	0.74 (n.s.)	1.4E-02 ± 1.9E-01	-1.5E-01 ± 1.6E-01	0.86 (n.s.)

Table S1 – Statistical summary of cross-stream-only motion in response to visual perturbation. Related to Figure S2 and S3.

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