Fish Avoid Visually Noisy Environments
Where Prey Targeting Is Reduced

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ABSTRACT: The environment contains different forms of ecological noise that can reduce the ability of animals to detect information. Here, we ask whether animals adapt their behavior to either exploit or avoid areas of their environment with increased dynamic visual noise. Three-spined sticklebacks (Gasterosteus aculeatus) were immersed in environments with a simulated form of naturally occurring visual noise—moving light bands that form on underwater substrates caused by the refraction of light through surface waves. We tested whether this form of visual noise affected fish’s habitat selection, movements, and prey-targeting behavior. Fish avoided areas of the environment with increased visual noise and achieved this by increasing their activity as a function of the locally perceived noise level. Fish were less likely to respond to virtual prey in environments with increased visual noise, highlighting a potential impact that visual noise has on their perceptual abilities. Fish did not increase or decrease their refuge use in environments with increased visual noise, providing no evidence that visual noise increased either exploratory or risk-aversive behavior. Our results indicate that animals can use simple behavioral strategies to avoid visually noisy environments, thereby mitigating the impacts that these environments appear to have on their perceptual abilities.

Keywords: perception, virtual prey, Gasterosteus aculeatus, caustics, environmental noise.

Introduction

Animals live in inherently noisy environments, where noise can be defined as any environmental stimulus that interferes with the ability of animals to detect or respond to biologically meaningful cues (Bremm 2013; Corcoran and Moss 2017; Cuthill et al. 2017). Noise can take acoustic, chemical, or visual forms and can vary dynamically in the environment. For example, windblown vegetation, turbidity (Chamberlain and Ioannou 2019), and the refraction and scattering of light through water (Matchette et al. 2018, 2020) can create backgrounds with dynamically changing illumination, while weather, traffic, and other human activities can generate varying intensities of background acoustic noise (Vasconcelos et al. 2007; Slabbe Koorn and Rijmeester 2008; Tasker et al. 2010; Lampe et al. 2012; Morris-Drake et al. 2016). These forms of noise can reduce the likelihood of animals detecting information in their environment through two processes. First, by adding statistical error to the sensory modality being utilized, noise can make detection of a stimulus within that sensory channel more difficult because of masking effects. Alternatively, by distracting an animal, noise may limit its ability to detect or respond to information across sensory modalities (Morris-Drake et al. 2016). Through these processes, noise can reduce the ability of animals to communicate with conspecifics (Fleshman 1986; Ord et al. 2007; Peters et al. 2007; Vasconcelos et al. 2007; Slabbe Koorn and Rijmeester 2008; Lampe et al. 2012; Herbert-Read et al. 2017), detect moving targets (Matchette et al. 2018), forage efficiently (Purser and Radford 2011; Party et al. 2013; Wale et al. 2013; Azeem et al. 2015; Evans et al. 2018; Matchette et al. 2019), and respond to predatory attacks (Wale et al. 2013; Morris-Drake et al. 2016), all of which have significant survival and fitness consequences for individuals.

Because noise can reduce the ability of animals to detect or respond to information in their environment, prey and predators may use behavioral strategies to either exploit or avoid noisy environments, thereby increasing their likelihood of detecting information or avoiding being detected themselves. For example, if attempting to remain undetected, some species may preferentially select noisier environments or increase their exploration of the environment during times of increased environmental noise. Indeed, fathead

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minnows (Pimephales promelas), three-spined sticklebacks (Gasterosteus aculeatus), and larval pike (Esox lucius) show decreased antipredator behavior in more turbid water (Abrahams and Kattenfeld 1997; Lehtiniemi et al. 2005; Sohle and Lindstrom 2015), suggesting that they may exploit times of high turbidity to avoid being detected by visual predators (although see Chamberlain and Ioannou 2019). On the other hand, some species may attempt to avoid noisy environments as gathering information in those environments becomes more difficult. Indeed, some species of bats avoid areas of their environment with higher levels of acoustic noise (Bennett and Zurcher 2013), and others spend more time foraging in areas with lower levels of acoustic noise (Schaub et al. 2008; but see Bonsen et al. 2015). When avoidance of noisy areas is impossible, however, some species may adapt their behavior to compensate for reduced information detection. Zebra finches (Taeniopygia guttata), for example, spend more time being vigilant in noisier acoustic environments, but this comes at the cost of decreased foraging rates (Evans et al. 2018). While animals’ behavioral responses to noise, in particular acoustic noise, have been relatively well documented (Kunc et al. 2016; Shannon et al. 2016), whether animals adapt their behavior in response to noise in other sensory channels, in particular dynamic visual noise, has received far less attention. Moreover, whether these changes to behavior represent adaptive behavioral decisions to exploit or avoid noisy environments remains unclear.

Shallow aquatic environments are particularly prone to one form of naturally occurring dynamic visual noise—caustics. Caustics are formed from the refraction and reflection of light from the disturbance of surface waves that is projected through the water column onto the substrate below (Lock and Andrews 1992). This form of dynamic illumination can reduce the likelihood of humans detecting a target on a computer-animated display (Matchette et al. 2018) and can increase the latency of triggerfish (Rhinecanthus aculeatus) to attack a moving target (Matchette et al. 2020). Because caustics appear to reduce the ability of animals to detect or respond to information, animals could try to mitigate the impacts of or exploit these visually noisy environments. For example, species might avoid areas with higher levels of visual noise to increase the likelihood of detecting information themselves, or alternatively, they could preferentially associate with visually noisy environments to reduce their own likelihood of being detected.

Here, we ask how visual noise affects the movements, refuge use, and prey targeting of three-spined sticklebacks (G. aculeatus). Sticklebacks are a small (~2–6 cm) fish found in both shallow marine and freshwater environments where caustics are prevalent. They feed on small insects, fish fry, and crustaceans by actively searching for prey among the substrate and in the water column and are themselves predominantly predated by birds and larger fishes, such as pike (E. lucius). To understand whether sticklebacks exploit or avoid these visually noisy areas, we performed a series of three experiments. We first asked whether sticklebacks avoided or spent more time in areas of the environment with increased levels of visual noise. In this experiment, we also determined whether fish were actively or passively avoiding areas of the environment with different levels of visual noise. We did this by quantifying their activity (speed and time spent stationary) in response to the locally perceived level of noise and by asking whether there was directed movement toward or away from noisier areas. Second, we tested whether the fish increased or decreased refuge use in different levels of visual noise. Last, we tested whether visually noisy environments affected the ability of sticklebacks to respond to prey in their environment by quantifying the likelihood that individual sticklebacks targeted virtual prey in environments with different levels of visual noise.

**Methods**

*Playbacks*

For each of the three experiments, we projected video playbacks of simulated caustics into an experimental arena (fig. 1a). These refracted patterns of light naturally vary in their spatial distribution, intensity, and velocity as a function of the water depth and the properties of the surface waves (Lock and Andrews 1992). To produce the playbacks, we first generated a series of 600 images of caustic patterns using the software Caustics Generator Pro (Dual Heights 2018), cropped to an aspect ratio of 3,840 × 2,159 pixels (see software settings in table S1; tables S1–S5 are available online). We created animations of these images in MATLAB (2018), where the images were stitched together sequentially (see video S1; videos S1, S2 are available online). The animations were designed so that they could be looped without the caustics appearing to spatially or temporally “jump.” To create six different levels of visual noise, we wanted to ensure that we manipulated only one property of the caustic patterns. For example, if we had manipulated the spatial fractal nature of the caustic patterns, this would have also changed the total light intensity within our animations. Therefore, we chose to manipulate the speed that the caustics moved while maintaining their spatial properties. To do this, we created videos where the images looped through at different speeds, so that the slowest to fastest animations took 80, 40, 20, 10, 5, and 2.5 s, respectively, to complete a full loop. We classified faster-moving playbacks as having higher levels of visual noise. We ensured that the speed at which the caustics moved in the arena and the light levels in the arena were representative of those found in nature (see the supplemental PDF and fig. S1; figs. S1–S8 are...
Furthermore, we chose to not include a treatment of a static projected image of the caustic patterns, as we were specifically interested in how different levels of visual noise affect behavior and static caustics are ecologically unrealistic in aquatic environments.

Study Subjects and Experimental Arena

Three-spined sticklebacks (n = 204) were caught from River Cary in Somerton, Somerset, United Kingdom (lat. 51.069990, long. −2.758014), and we observed that caustics were present where the fish were caught. Fish used in experiment 1 were caught in November 2017, and fish used in experiments 2 and 3 were caught in March 2019. All fish were in nonbreeding condition when used in experiments. All fish were housed for at least 2 weeks before experimentation. The fish were housed in glass housing tanks (40 cm × 70 cm × 35 cm; height × length × width) on a flow-through recirculating freshwater system with plastic plants and tubes for environmental enrichment. The fish were held

Figure 1: Experimental arena and choice test in experiment 1. a, Schematic of the experimental setup. b, Still image from a video of a choice trial depicting a section of the trajectory of a fish superimposed in blue. The red dashed line shows the virtual boundary between the two choice areas. c, Proportion of time the fish spent on the side of the arena with more or less visual noise (ignoring absolute differences in noise level). Fish spent more time on the side of the arena with less visual noise. The central line of each box shows the median value, while the upper and lower lines of the box show the upper and lower quartiles of the data, with the whiskers extending to the most extreme data point within 1.5 times the interquartile range. Jittered dots represent raw data points. d, Matrix showing the mean proportion of time across trials (the heat) that fish spent on the left-hand side (LHS) of the arena, where each cell represents the choice a fish was given between two levels of visual noise. One through six correspond to the lowest to highest levels of noise, respectively. Fish avoided areas with high levels of visual noise. When the noise level was lower on the left side of the arena (upper-right corner of the plot), the fish spent more time on that side. When the noise level was higher on the left side of the arena (lower-left corner of the plot), the fish spent less time on that side. Note that one minus this matrix would give the proportion of time spent on the right-hand side of the arena.
at 14°C under a 11L:13D cycle. Each tank housed approximately 40 individuals, and fish were fed bloodworms once per day, 6 days per week.

The experimental tank for all three experiments consisted of a test arena (1.46 m × 0.84 m; length × width) and a holding area (0.84 m × 0.34 m; length × width) separated by white opaque plastic (fig. 1a). Both sections were filled to a depth of 15 cm with water from the recirculating freshwater system. Water was filtered within the tank using an Eheim classic 600 external filter and chilled to between 14.2° and 15.2°C using a D-D DC-300 chiller. The holding area contained plastic plants and tubes for environmental enrichment. Water was changed in the experimental tank after each day of trials, all fish that would be tested in the subsequent day were placed in the holding area together overnight, allowing them to acclimate to the conditions of the tank. Fish were not fed for 24 h before each experiment.

A camera (Panasonic HC-VX870) located 2.15 m above the center of the test arena filmed the trials at 4K resolution (3,840 × 2,160 pixels) at 25 frames per second. The camera was controlled remotely using the Panasonic image app operated by an experimenter outside the room. The experimenter was not present in the room while the trials were run. A BenQ W1700/HT2550 digital projector with 4K resolution operating at a 60-Hz vertical scan rate located 2.19 m above the arena (fig. 1a) projected the playbacks into the arena. The projections were played using a Dell Inspiron 15 notebook connected to the projector via a 4K HDMI cable located outside the experimental room. The arena was surrounded by blackout curtains to minimize any external light source entering.

**Experiment 1: Do Fish Prefer to Associate with More or Less Visually Noisy Environments?**

To determine whether fish avoided or preferred to associate with more or less visually noisy environments, individual fish were presented with a binary choice, where on one side of the arena we projected one level of visual noise and on the other side we projected a different level of visual noise. As there were six different levels of noise, this gave 15 possible combinations of noise pairings. We constructed six different playbacks, where each playback contained all 15 different noise pairings, played one after the other. Each choice (noise pairing) was presented for 320 s, with the total length of each playback equaling 80 min. Across the different playbacks (n = 6), each noise level was presented evenly on each side of the test arena to control for any potential side biases (table S2). The ordering of the noise pairings within a playback was also assorted (see table S2) between the six playbacks so that there was no systematic bias in their ordering across the trials. For each trial, a single fish was exposed to one of these six playbacks. The order of the six playbacks was randomized within each day, with each playback being used a maximum of once per day.

For each trial (n = 48), an individual fish (5.4 ± 0.7 cm; mean ± SD) was moved from the holding area to the test arena and left to acclimate for 10 min. During this period, the first frame of the playback was projected into the test arena as a static image, but the video playback was not started. After 10 min, we started the video playback remotely. After each trial, the fish was removed, placed in a separate housing tank, and fed. No fish were reused between trials.

Fish were tracked using an adapted version of DIDSON tracking software (Handegard and Williams 2008) in MATLAB (2018; fig. 1b). Because the fish were darker than the arena or moving projections, we took a grayscale threshold of each frame to isolate the fish within the videos without requiring any background subtraction. The X- and Y-coordinates of the fish were smoothed using a rolling average of 12 frames (approximately half a second). Tracks were smoothed only if at least 50% of the track was present within these 12 frames (using the function nanfastsmooth in MATLAB); otherwise, these segments of the tracks were removed (replaced with NaN). Smoothing is a standard procedure used in trajectory analysis, allowing spurious errors in point estimates to be reduced (Calenge et al. 2009; Chachet et al. 2011; Katz et al. 2011; Lacey et al. 2011; Gautrais et al. 2012; Spitzen et al. 2013; Tunstrom et al. 2013; Pérez-Escudero et al. 2014; MacGregor et al. 2020). In the supplementary material, we provide a visualization of this smoothing (fig. S2).

In addition to plotting and manually inspecting the tracks for accuracy, we calculated that fish were tracked for 88.2% of all frames (see below). The tracking accuracy was not systematically affected by different levels of visual noise (see the supplemental PDF and fig. S3). There was also not a difference in the tracking accuracy between different sides of the arena (figs. S3, S4).

From the trajectories of each fish, we calculated the amount of time the fish spent on each side of the test arena in each paired choice. To do this, we used the inpolygon function in MATLAB to determine when a fish’s track was on either the left or right side of the arena. We then calculated the proportion of time that the fish spent in the noisier side of the arena for each noise pairing. We also calculated the amount of time the fish spent stationary and the speed that they adopted when they were moving in different levels of noise. To do this, the instantaneous speed of the fish was calculated as the displacement in their position between two consecutive frames. We defined a fish as being stationary when its speed was less than 2 mm s⁻¹, informed
by plotting a histogram of all the fish’s speeds across all trials (see fig. S5). The mean speed of a fish was calculated excluding the times when they were stationary (i.e., when speeds were >2 mm s⁻¹) and was calculated when the fish was on each side of the arena separately.

Experiment 2: Do Fish Use a Refuge More or Less in Increased Levels of Visual Noise?

To determine whether the fish were more or less likely to use a refuge in different levels of visual noise, two plastic plants (each 5 cm × 2 cm × 15 cm; length × width × height at the base) were placed as a refuge in the middle of the test arena (see fig. S6). For each trial (n = 48), an individual fish (4 ± 0.5 cm; mean standard length ± SD) was exposed to six different levels of visual noise, with each level of noise being projected throughout the entire arena (unlike in experiment 1) and each level of noise projected sequentially one after the other. To ensure that each noise level was presented in a different order within trials, we again created six playbacks, where each playback contained each level of noise, but each noise level occurred in a different order within each playback (referred to as “order within trial”) in a Latin square design (see table S3). Each trial, therefore, consisted of six levels of noise, each presented for 320 s, with the total running length of the playbacks equaling 32 min. Every playback was presented once per day (between 9:00 a.m. and 5:00 p.m.) and in a random order on different days. As in the choice tests, individual fish were moved from the holding area and placed in the test arena for 10 min of acclimation time (while a static caustic image was projected into the arena) before the playback was started remotely. Experimented fish were removed, placed in a separate housing tank, and later fed. Used fish were kept separately from unused fish, and fish were not reused between trials. Fish that were used in this experiment had not been used in experiment 1.

We scored the amount of time (in seconds) that the fish spent under the refuge during each level of noise. To do this, videos were imported into the software BORIS (ver. 7.9.15; Friard et al. 2016), where we defined the fish to be under the refuge when any part of its body was under any of the fronds of the plastic plant (see fig. S6). Each fish could therefore be under the refuge for a minimum of 0 s to a maximum of 320 s in each level of visual noise.

Experiment 3: Does Visual Noise Affect the Likelihood That Fish Respond to Virtual Prey?

To determine whether visual noise affected whether fish responded to prey in their environment, we created playbacks of the six different levels of visual noise (as in experiment 2, played sequentially and throughout the entire arena) that included virtual prey that appeared and disappeared in random locations. In particular, the prey appeared as moving uniform red dots (similar to the virtual prey experiments in Duffield and Ioannou [2017] and Ioannou et al. [2012, 2019]) on top of the caustic patterns (see video S2). Because the sticklebacks were fed red bloodworms in their housing tanks, they were highly responsive to these red dots, often attempting to peck at them if in range, mimicking natural feeding behavior. Therefore, the fish did not need to be trained to attack the virtual prey. Each virtual prey appeared at a random location within the arena as a looming stimulus, increasing in size from 0 to 12.5 mm in diameter within three-fourths of a second, maintaining a 12.5-mm diameter for ~1 s, and then shrinking to 6 mm before disappearing. Each prey was visible in the arena for a total of 2 s, moving on a correlated random walk at 7 cm s⁻¹. Playbacks of the caustics and prey were created in MATLAB (2018).

The limited presentation time of each prey (2 s) was designed to allow the fish to detect and start swimming toward the prey while reducing the likelihood of the fish sampling the prey and learning that the prey were not edible. Because of the short presentation times, the large size of the arena, and the prey appearing in random locations, the prey would often appear far from the fish’s position. To increase the potential for the fish to detect the prey, therefore, each level of noise contained 50 individual prey presentations (300 presentations within a single trial), with 4 s between the end of one prey presentation and the start of another.

As in experiment 2, for each trial (n = 108), individual fish (3.3 ± 0.4 cm; mean standard length ± SD) were exposed to six different levels of visual noise but here in combination with virtual prey. To control for order effects, six different playbacks were created, where each playback contained each level of noise, with each noise level occurring at different times (order within trial) in the playbacks in a Latin square design (table S3). Controlling for order effects was particularly important here, as there was the potential for the fish to become habituated to the prey over time. In these playbacks, we also added transitions between the different levels of noise so that the change in speed of the moving caustics between different noise levels was smooth. This involved creating animations that increased or decreased in speed from one noise level to another, which were subsequently placed between the respective animations of visual noise with the prey. Within these transition periods, no prey were projected. As in the other experiments, each level of noise lasted 320 s, with each transition period lasting between 70 and 90 s. Each playback in total, therefore, lasted ~50 min and 45 s. Each playback was presented once per day and at different times of the day (between 9:00 a.m. and 5:00 p.m.) on different days. As in the previous two experiments, individual fish were moved from the holding
area to the test arena and allowed 10 min of acclimation time. During this time, the lowest level of noise was projected into the test arena for 10 min before transitioning to the start of the playback. Experimented fish were removed, placed in a separate housing tank, and fed. No fish used in experiment 1 or 2 were used in this experiment, and fish were not reused between trials.

Videos of the trials were manually inspected to determine whether the fish responded to the virtual prey. A response to the prey was defined as when there was a noticeable change in the speed or direction of the fish toward the prey (for examples, see video S2). Therefore, if the fish accelerated or decelerated while moving toward the prey, this counted as a response. We quantified how many prey (out of a maximum of 50) the fish responded to in each level of noise within each trial. These changes in speed or direction could be misclassified as a response if by chance the fish changed its speed or direction toward the prey without detecting it (i.e., false positives). To quantify the likelihood of false positives, for each experimental trial, we simulated the appearance of a single simulated prey within a random location in the arena at a random time when there were no prey presented within each level of noise in the trial (i.e., 648 simulated prey events, 108 events for each noise level). In these events, we asked whether our classification method would have scored the fish as responding to these prey (even though the prey were not there). This method allowed us to estimate the baseline level of false positives as a function of noise level.

**Statistics**

All statistics were performed in R (ver. 3.5.1; R Development Core Team 2018). The package lme4 (Bates et al. 2015) was used for all mixed models. Assumptions for all linear mixed models (LMMs) were checked using standard diagnostic plots (quantile-quantile normal plots and residuals plotted against fitted values). Models were also checked for collinearity. Assumptions for all generalized linear mixed models (GLMMs) were checked using the DHARMA package (Hartig 2019), including checking the dispersion and the distribution of the residuals. The full models were simplified by removal of nonsignificant terms. We used the anova function in R (ver. 3.5.1; R Development Core Team 2018) to compare pairs of models using the $\chi^2$ statistic. The estimates and effect sizes (Cohen’s $D$) are presented in Table S4. All R graphs were created using ggplot2 (Wickham 2016). All data used here have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.rf6q577x; Attwell 2021).

**Experiment 1.** To test whether fish spent more or less time in areas with more or less visual noise (regardless of absolute noise level), we subtracted 0.5 from the proportion of time they spent on the noisier side of the arena separately for each of the 15 noise pairings per trial. We tested whether the intercept of an LMM predicting those proportions, with trial included as a random effect, differed from zero (i.e., proportion of time on the noisier side $-0.5 \sim 1 + (1 | \text{Trial})$ in lme4 nomenclature). We then asked whether the absolute difference in noise level within a choice affected the amount of time the fish spent on the noisier side of the arena. To do this, we calculated the difference between noise levels on each side of the arena for each noise pairing. For example, the difference between a choice of noise levels 1 and 5 was calculated as 4. We then used an LMM to ask whether this difference could predict the proportion of time the fish spent on the noisier side of the arena. In this model, the difference in noise was treated as a discrete numeric variable, trial (fish identity) was included as a random intercept, and difference in noise levels was included as a random slope. We also checked that including times when fish did not visit both sides of the arena during a single choice did not qualitatively affect the interpretation of our results (see the supplemental PDF).

We then asked whether a fish changed its movements depending on the level of noise on each side of the arena. To investigate this, we used LMMs to predict whether a fish’s mean speed and, in a separate model, its time spent stationary on the side of the arena the fish was on could be predicted on the basis of the level of noise on each side of the arena (modeled as separate fixed effects: noise level on the side occupied by the fish and noise level on the unoccupied side). Mean speed and the proportion of time stationary were square root transformed because of a positive skew in these data. Order within trial (1–6) was also added as a fixed effect, trial (fish identity) was included as a random intercept, and noise level on the side occupied by the fish was included as a random slope.

Because a fish’s speed and time spent stationary were dependent on the noise level they were in (but not dependent on the noise level on the other side of the arena; see below), we asked whether these differences in speed and time spent stationary could explain the amount of time fish spent in the corresponding levels of visual noise. To test this, the mean speed that the fish adopted in different levels of noise and the proportion of time spent stationary were added as covariates to the model investigating the proportion of time spent on the side of the arena with more visual noise. We also tested whether the fish showed any evidence of directed movement toward or away from the sides of the arena with more or less visual noise (for full details, see the supplemental PDF).

**Experiment 2.** We tested whether the level of visual noise had a significant influence on the time the fish spent...
under refuge. We initially attempted to model the time spent in the refuge as a binomial response (time in vs. time out of refuge); however, these models were overdispersed. Therefore, because of the relatively bimodal distribution of the response variable (fig. S7a), we transformed the time spent in refuge into a binary response variable, where fish that spent more than 50% of their time in the refuge were given a value of 1 and fish that spent less than or equal to 50% of their time in the refuge were given a value of 0. This binary response variable was modeled using a GLMM with a binomial error structure. Noise level was included as a fixed effect (discrete numeric as before) along with order within trial, and trial (fish identity) was added as a random intercept. We did not include noise as a random slope in this experiment because there was no effect of noise on the response variable.

Experiment 3. To test whether the level of visual noise affected the likelihood that fish responded to the virtual prey, we used a GLMM with a Poisson family error structure. The response variable was the number of responses to prey at each level of noise, and fixed effects were the level of visual noise and order within trial. Trial (fish identity) was added as a random intercept, but noise was not added as a random slope in this case because the model did not converge when this term was included.

Results

Experiment 1: Do Fish Prefer to Associate with More or Less Visually Noisy Environments?

Fish spent more time on the side of the arena with less visual noise (fig. 1c; LMM: \( t = -7.8, P < .001 \)). Furthermore, the relative difference between the noise levels on each side of the arena affected the time the fish spent in the noisier side of the arena. As the relative difference in noise between the two sides of the arena increased, fish spent less time on the side of arena with more visual noise (fig. 1d; LMM: \( \chi^2 = 9.77, df = 7, P = .002 \); for 95% confidence intervals, see table S5).

The fish’s movements were affected by the level of visual noise on the side of the arena they were in. Fish moved faster (fig. 2a; LMM: \( \chi^2 = 52.3, df = 8, P < .001 \)) and spent less time stationary when on the side of the arena with more visual noise (fig. 2b; LMM: \( \chi^2 = 90.8, df = 8, P < .001 \)). The noise level on the other side of the arena (across from the side the fish was on) did not affect the fish’s speed (fig. 2c; LMM: \( \chi^2 = 0.35, df = 8, P = .55 \)), and the noise level on the other side also did not affect the proportion of time the fish spent stationary (fig. 2d; LMM: \( \chi^2 = 0.34, df = 8, P = .56 \)). When these movement variables were added as covariates to the model, the difference in noise level between the two sides of the arena was no longer a significant predictor of the time the fish spent on the noisier side (LMM: \( \chi^2 = 1.61, df = 11, P = .20 \)). Therefore, how a fish adapted its movements to the locally perceived level of noise determined the amount of time it spent in that region. There was no evidence, however, that the fish were more likely to show directed movement toward or away from the side of the arena with more or less visual noise (see the supplemental PDF).

Experiment 2: Do Fish Use a Refuge More or Less in Increased Levels of Visual Noise?

There was no evidence that the level of visual noise affected whether the fish spent the majority of time under the refuge (fig. S7b; GLMM: \( \chi^2 = 1.75, df = 4, P = .19 \)). However, fish spent less time under the refuge as the trial progressed (GLMM: \( \chi^2 = 7.07, df = 4, P = .0079 \)).

Experiment 3: Does Visual Noise Affect the Likelihood That Fish Respond to Virtual Prey?

Fish were less likely to respond to the virtual prey in higher levels of visual noise (fig. 3; GLMM: \( \chi^2 = 155.3, df = 4, P < .01 \)). There was an effect of the order within trial on the number of responses to prey by the fish (GLMM: \( \chi^2 = 451.3, df = 4, P < .01 \)); fish became less likely to respond to the prey over the course of the trial. Our estimations of the number of false positives (classification of the fish responding to the prey even if the prey had not been detected) were far below that observed in the responses to the real virtual prey (fig. 3).

Discussion

Fish spent less time in areas with more visual noise, and this reduction in time could be attributed to how the fish adapted their movements in response to noise. In particular, fish increased their speed and spent less time stationary in areas with more visual noise. There was no evidence, however, that the level of visual noise on the other side of the arena affected their movements or that fish directed their movement toward less noisy areas, suggesting that the fish were responding only to the level of noise in their local vicinity. While increases in speed and decreases in time spent stationary could be interpreted as the fish exploiting these environments to increase exploration during times of increased environmental noise, our second experiment provided evidence against this explanation. If fish were exploiting times of higher visual noise to avoid being detected themselves, we would have expected the fish to spend less time in the refuge in higher levels of visual noise (as refuge use is a key measure of risk taking in sticklebacks; Bevan...
et al. 2018). In fact, we found no evidence that fish altered their risk-taking behavior depending on noise level. Furthermore, it is unlikely that fish were increasing their activity in noisier areas to match their swim speed with the movements of the caustics, as the optical flow produced by the caustics did not move in a consistent direction (see fig. S1a, video S1). Instead, we suggest that fish use a simple mechanism, namely, increasing their speed and activity, to avoid areas of their environment with higher levels of visual noise. This mechanism was first termed “orthokinesis” by Fraenkel and Gunn (1961), whereby an animal’s movements change depending on the intensity of an environment stimulus. Fraenkel and Gunn (1961) found that wood lice move faster in areas of low humidity compared with areas of high

Figure 2: How fish movements were affected by visual noise in experiment 1. a, Square root of the mean speed of fish as a function of the visual noise level they were in. Fish swam faster in more visually noisy areas. b, Square root of the proportion of time the fish spent stationary as a function of the noise level they were in. Fish spent less time stationary in noisier areas. In a and b, the central line of each box shows the median value, while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the most extreme data point within 1.5 times the interquartile range. Jittered points represent raw data points. c, Mean speed of fish (the heat) as a function of the noise level the fish was in (columns) and the noise level on the other side of the arena (rows). d, Mean proportion of time the fish spent stationary as a function of the noise level the fish was in (columns) and the noise level on the other side of the arena (rows). One through six correspond to the lowest to highest levels of noise, respectively. The presence of a trend from left to right, but not top to bottom, in these heat plots indicates that the fish moved faster and spent less time stationary in higher levels of visual noise, but the noise level on the other side of the arena did not affect their movements.
humidty, leading to the wood lice spending more time in humid areas. Similarly, the estuarine fish *Micropogon undulates* moves faster in environments with changing salinity compared with environments with fixed salinity, leading them to aggregate in areas of fixed salinity (Perez 1969). Similar mechanisms have been proposed for how groups of animals collectively track resources in their environment (Berdahl et al. 2013; Hein et al. 2015). In our case, this mechanism could lead fish to passively move out of areas with more visual noise and toward regions of the environment with lower visual noise. This could provide a simple, yet effective mechanism to move toward or away from particular regions of the environment without detecting where more favorable regions of the environment are located.

Our final experiment suggests a functional reason why these visually noisy environments might be avoided by sticklebacks, with increased visual noise reducing the number of responses to virtual prey. Fish were less likely to respond to the virtual prey in these environments, consistent with other systems where humans, chicks, and triggerfish took longer to detect prey on backgrounds with dynamic visual noise as opposed to static controls (Matchette et al. 2018, 2019, 2020). Because animals have finite time and energy reserves and limited attention (Cuthill et al. 2019), they are expected to make optimal foraging decisions that increase the rate or efficiency at which they gather resources (Schoener 1971; Stephens and Krebs 1986; Ydenberg et al. 1994). This allows them to devote more time and energy to other fitness-related activities (Planka 1988; Schmid-Hempel 1991). Much like how animals choose foraging patches according to their profitability (Krebs 1979; Milinski 1979, 1987), we might expect animals to selectively choose where to forage in their environment according not only to the resource profitability of a patch but also to the likelihood of detecting those resources given the perceptual constraints imposed by that environment. Indeed, there is large natural variation in both the temporal and spatial distribution of caustics in the aquatic environment, as well as other forms of environmental noise. Caustics, for example, are affected by ambient light levels, water depth and speed, and the size of surface waves. Such variation may lead foragers to select habitats on the basis of the environmental noise determined by the local ecological conditions (e.g., Schaub et al. 2008; Bennett and Zurcher 2013).

While we interpret our results as the visually noisy environments acting as a perceptual constraint on the fish, reducing their ability to detect the prey, we cannot exclude the possibility that in increased levels of visual noise, the fish were less motivated to attack the prey despite those prey being detected. This could occur, for example, if increased levels of visual noise resulted in higher levels of stress or increased vigilance behavior for threats. While our second experiment argues against this explanation, as fish were not more likely to increase refuge use in increased levels of visual noise, the possibility that increased visual noise decreases motivation or increases stress remains. Future experiments measuring cortisol levels in these fish could test this possibility, and more detailed tracking data regarding whether and where individuals respond to prey in their visual field could help quantify potential reductions in visual perceptual abilities in increased visual noise.

While fish avoided visually noisier environments, we may also expect individuals’ behavioral responses to environmental visual noise to vary as a function of other factors. For example, sticklebacks have been shown to both decrease (Sohel and Lindstrom 2015) and increase (Ajemian et al. 2015; Chamberlain and Ioannou 2019) their anti-predator behavior and refuge use in more turbid water (a form of static visual noise). This suggests that their response to visual noise could vary depending on context or state. Indeed, 15-spined sticklebacks (*Spinachia spinachia*) are less risk averse when hungry, but when partially satiated, they choose less productive areas where they can spend more time being vigilant (Croy and Hughes 1991). In our trials, we did not feed the fish for 24 h before the experiments to induce exploratory behavior and to promote search and targeting of the virtual prey. However, since sticklebacks are both predators and prey, it would be valuable to test whether the fish also avoid visually noisy environments when they

*Figure 3:* Responses to virtual prey in experiment 3. Proportion of responses to the virtual prey out of the possible 50 prey presentations in each level of visual noise per fish (*n* = 108 fish). The violin represents a mirrored probability density function, and each black marker represents an individual data point (responses for each fish within a noise level) jittered for clarity. Fish were less likely to respond to the virtual prey in higher levels of visual noise. The lines show the proportion of false positives (false classifications) that were checked using the simulated prey presentations.
are satiated or when the level of risk in the environment is greater. Indeed, we might expect animals to choose noisier areas of the environment when satiated or when faced with greater risk. While not measured here, animals might also switch to relying on other sensory modalities in visually noisy environments when their vision is compromised (Partan 2017; Suriyampola et al. 2018). For example, female three-spined sticklebacks rely more on visual cues when choosing a mate in clear water, but in turbid water, where vision is compromised, they rely more on olfactory cues (Heuschele et al. 2009). When habitats consistently differ in their ecological noise, this could have sweeping effects on populations. For example, gray squirrels (Sciurus carolinensis) from acoustically noisy urban habitats respond more to visual alarm signals than squirrels from rural habitats, which instead rely more on acoustic alarm signals (Partan et al. 2010). Hence, animals from different populations may show different behavioral responses, highlighting the need for cross-population comparisons. We might also expect animals to rely more heavily on social information in sensory-demanding environments. Indeed, animals in groups often benefit from pooling imperfect estimates of the world around them in order to make more accurate decisions collectively (Dall et al. 2005; Ward et al. 2011; Ioannou 2017; Berdahl et al. 2018). Using playbacks of caustic visual noise, it would be possible to test how reliance on social information changes when individuals are exposed to an ecologically relevant form of environmental noise that reduces their visual perceptual abilities.

Conclusion

Our results demonstrate that natural forms of ecological noise reduce the likelihood of animals responding to information in their environment. To combat this, animals can update their behavior to avoid noisy areas, which could lead to an increased likelihood of gathering information and thereby compensate for the potential negative impacts of environmental noise on their perception.

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Statement of Authorship

J.R.A. and J.E.H.-R. were involved in the conceptualization, all authors were involved in the experimental design, and J.R.A. collected the data, performed the data analysis, and wrote the original draft of the manuscript. All authors were involved in editing the manuscript.

Data and Code Availability

All data used in this article have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.rf6q577x; Attwell et al. 2021).

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Sketch of a three-spined stickleback in caustics. Artist: David Clarke.