

SHORT COMMUNICATION

Single target acuity in the common sunfish (*Lepomis gibbosus*)

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ABSTRACT

Vision contributes to foraging, territorial and reproductive behavior in sunfish. In these contexts, sunfish need to perceive single targets, such as prey items or body markings from either conspecifics or individuals of other sunfish species, from some distance. We determined the single target acuity of six common sunfish in a behavioral experiment to assess whether the visual abilities of sunfish correspond with behavioral observations or reactive distance measures, and thus assessed the limits of vision for the mentioned behaviors. Single target acuity for full-contrast single targets amounted to 0.17 deg (0.13–0.32 deg). When contrast was reduced to Weber contrasts of 0.67 and 0.41, single target acuity dropped to 0.34 deg (0.31–0.37 deg), and finally to 0.42 deg (0.34–0.54 deg). Single target acuity would thus allow common sunfish to perceive biologically relevant stimuli at reasonable distances even when contrast is reduced.

KEY WORDS: Vision, Fish, Resolution, Target detection, Contrast sensitivity

INTRODUCTION

Members of the genus *Lepomis* are found in ponds, lakes and streams of eastern and middle North America. The common sunfish (*Lepomis gibbosus*) prefers clear, quiet waters with sparse vegetation (Miller, 1963), but is also found in other habitats (Keast, 1978). It is a diurnal forager that preys upon a range of species (Miller, 1963; Keast, 1978). Previous studies have suggested that hunting, territorial and courtship behavior are based on visual signals (Miller, 1963; Stacey and Chiszar, 1978). During hunting, sunfish hover motionless, searching for prey, and seem to be attracted to their prey by its movement (Miller, 1963; Kieffer and Colgan, 1991).

During territorial and courtship behaviors, body patterns convey information on dominance or *Lepomis* species. Each species of *Lepomis* has a unique combination of markings. During aggressive encounters and during the reproductive season, enhanced coloration and intensity of body patterns, especially on the opercular flap or the iris, express dominance to other males (Stacey and Chiszar, 1978; Guthrie, 1986). In subordinate fish, these features fade (Stacey and Chiszar, 1978). This fading, along with the appearance of dark stripes, is characteristic of female common sunfish when in the male's nest, and reduces male aggressiveness (Miller, 1963; Stacey and Chiszar, 1978). Moreover, the dorsal fin ray spot of bluegill sunfish elicits aggressive behavior in the common sunfish (Stacey and Chiszar, 1978). Together, these observations imply that visual perception in general and the perception of single objects in particular

are crucial for the behavioral repertoire of common sunfish. Therefore, the present study was conceived to assess the limits of single target acuity (STA), the minimum size of a single object that can be perceived by a sunfish.

Among fishes, STA has only been determined for the archerfish (*Toxotes jaculatrix*) (Ben-Simon et al., 2012) and the triggerfish (*Rhinecanthus aculeatus*) (Champ et al., 2014). For the archerfish, Ben-Simon et al. (2012) determined STA as 0.075 to 0.15 deg. Champ et al. (2014) reported thresholds in the triggerfish ranging between 0.4 and 0.8 deg only.

For common sunfish, only one study reporting reactive distances can be related to vision (Confer et al., 1978). These estimates suggest that common sunfish can perceive objects at least subtending a visual angle of 0.5 deg or larger.

In contrast, vision is well characterized for bluegill sunfish (*Lepomis macrochirus*). Visual acuity was assessed as 3–5.5 cycles deg^{−1} in behavioral experiments as well as on the basis of the cone mosaic (Northmore et al., 2007); retinal resolution was determined as 2.8–11 cycles deg^{−1} (Williamson and Keast, 1988; Gomi and Miyazaki, 2015). Minimum contrast thresholds amounted to 0.03 at 0.4–0.5 cycles deg^{−1} (Northmore et al., 2007), whereas Hawryshyn et al. (1988) reported contrast thresholds even lower than 0.01. As bluegill sunfish grow larger, visual acuity increases (Hairston et al., 1982; Breck and Gitter, 1983). Hairston et al. (1982) and Guthrie (1986) concluded that this improvement was related to increases in the lens' focal length during growth while cone spacing remaining constant.

Vision can vary considerably even between closely related species, thus the acuity of the bluegill sunfish cannot be presumed for the common sunfish. As visual abilities reflect features of the habitat, which can differ in *Lepomis* (Werner et al., 1977; Keast, 1978; Mittelbach, 1984), we may find differences in the visual systems in the sunfish species. Lastly, grating acuity is not a reliable indicator of the minimum object size perceptible, as different physical mechanisms determine how fine grids and how small objects can be, to still be resolved. Although the resolution of stripe patterns is mainly limited by the retinal sampling density (most likely the ganglion cell density; Collin and Pettigrew, 1989), the limiting factor for the detection of single objects is contrast sensitivity (O'Carroll and Wiederman, 2014). Therefore, it is possible that an object even smaller than the retinal resolution can still be detected, provided that the contrast between the object's border and the background is sufficient.

In this study, STA was determined in the common sunfish to describe the limits of vision with respect to single objects in different behavioral contexts. STA was assessed for ecologically relevant, low contrast stimuli, thereby extending previous STA studies on fishes, which used only high-contrast single targets for threshold determination.


MATERIALS AND METHODS

Experimental animals

Six common sunfish [*Lepomis gibbosus* (Linnaeus 1758)], 11 to 12 years old, and with body lengths of 8–11 cm, were used as

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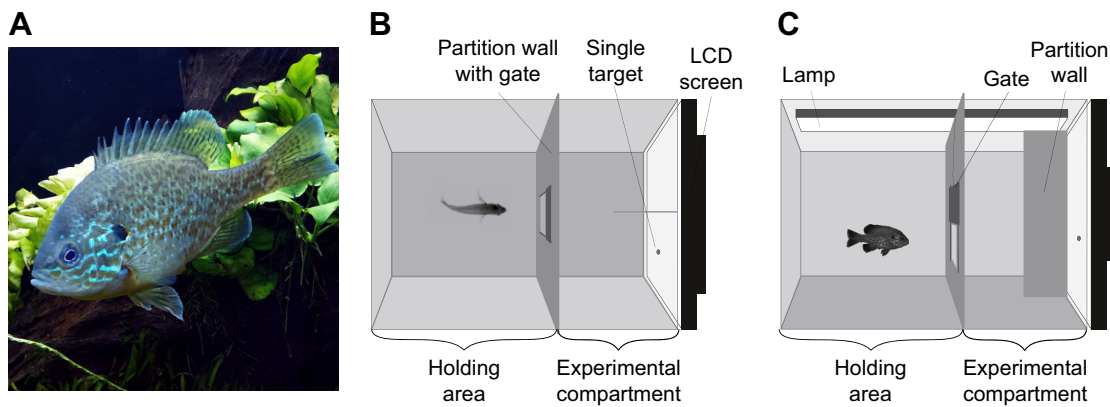


Fig. 1. Study species and experimental setup. (A) Experimental animal, the common sunfish (*Lepomis gibbosus*). Experimental setup from (B) the top and (C) the side. The gate in the partition wall was opened, allowing the fish to enter the experimental compartment, where it had to choose between two stimulus fields on an LCD screen, only one containing a single target. The stimulus fields were separated by a partition wall. The aquarium was illuminated from above by lamps.

experimental animals (Fig. 1A). Two of these animals were males and four were females. All animals had already participated in previous visual cognitive experiments (Bauer, 2016; Schnermann, 2019). The animals were kept individually in 240 l aquaria (120×40×55 cm) at a water temperature of 20–24°C. Water quality was regularly tested with JBL ProScan water analysis strips (JBL, Neuhofen, Germany). The aquarium was cleaned regularly, and a quarter of the water volume was exchanged weekly. The animals were rewarded with red mosquito larvae during the experiments.

All experiments were carried out in accordance with the European Communities Council Directive of 24 November 1986 (86/609/EEC). The individuals used in the study were not subject to pain, suffering or injury; therefore, no approval or notification was required. Maintenance was approved by local authorities (Landesministerium für Landwirtschaft, Lebensmittelsicherheit und Fischerei Mecklenburg-Vorpommern).

Experimental setup

The experiment took place in the holding tank of the fish (Fig. 1B,C). For the experiment, a vertical gray plastic board with a gate that could be opened and closed was inserted into the aquarium and divided the aquarium into two areas: an experimental compartment in front of the monitor, and the holding area. The experimental compartment into which the animal swam during each trial had an LCD screen (model no. 1907FPf, Dell, Round Rock, TX, USA) attached from outside to the glass wall of the aquarium’s short side. The LCD screen served to present the stimuli. The stimulus fields, covering an area of 15×38 cm, and which either included a single target or not (see Stimuli, below), were separated by a partitioning wall, which assured that the animal’s responses were clearly either to the right or left stimulus field (Fig. 1B). A 40 cm long partition wall was selected for full contrast targets and a 16 cm long partition wall for lower contrast targets; partition walls of two different lengths were necessary to be able to use the same stimulus sizes for all contrast levels.

The aquarium was lit from above by two lamps (Juwel Aquarium, LED Day 9000K, LED Nature 6500K; Fig. 1C). During experiments, the aquarium was shielded from all sides to prevent unintentional cueing by the experimenter.

Stimuli

A dot served as the single target. It was presented in the right or left stimulus field (background luminance 131.83 cd m⁻²) according to a pseudorandom schedule after Gellermann (1933). The single

target was positioned at the height of the gate, through which the fish entered the experimental compartment (Fig. 1C). Thus the fish could directly see and swim towards the single target after passing the board.

The stimuli used during pretraining were generated and presented in Microsoft PowerPoint (Microsoft Office Professional Plus 2010 v. 14.0.7258.5000, Microsoft Corporation, Redmond WA, USA), and the stimuli used during data collection were generated and displayed with MATLAB (v. R2018b, The MathWorks, Natick, MA, USA) and the Psychophysics Toolbox 3.0 (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007).

Detection thresholds were determined for dots with three different contrasts (C1–C3) to the background. Table 1 indicates Weber as well as Michelson contrasts for the contrast levels. These contrasts were calculated from luminance measurements conducted with a luminance meter (LS-110, Minolta, Langenhagen, Germany).

The size of the single target is given as full width at half amplitude. To determine the size of the single target, photographs of the monitor with single target were taken from the inside of the aquarium with an underwater camera (WP5 2020 outdoor Smartphone, OUKITEL, Guanlan Silicon Valley, China). These photos were imported into ImageJ (1.53a, Wayne Rasband, National Institutes of Health, Bethesda, MD, USA) in order to extract the gray values along the midline of the single target.

Table 1. Single target acuity for six common sunfish depicted as averages (deg) calculated from the three thresholds with which threshold determination was ended, and as mean single target acuity (deg) plus standard deviation for single targets with different contrast (C1, C2, C3) to the background

	Single target acuity (deg)		
	C1	C2	C3
Weber contrast $(I_0 - I_b)/I_b$	0.98	0.67	0.41
Michelson contrast $(L_{max} - L_{min})/(L_{max} + L_{min})$	0.97	0.50	0.25
Fish			
Roy	0.14±0.02	0.32±0.02	0.34±0.02
Hanna	0.13±0.01	0.35±0.01	0.42±0.02
Anna	0.32±0.02	0.35±0.02	0.47±0.03
Frida	0.13±0.01	0.35±0.02	0.38±0.02
Luigi	0.18±0.01	0.37±0.00	0.54±0.02
Lina	0.13±0.00	0.31±0.00	0.34±0.01
Mean	0.17±0.08	0.34±0.02	0.42±0.08

These gray values were used to calculate the amplitude and thus the width at half amplitude within Origin Pro 2018b (b9.5.5.409, OriginLab Corporation, Northampton, MA, USA). Millimeter paper attached to the monitor served as scale. Altogether, three photographs were recorded per single target, and the size of the single target was measured three times for each photograph. Thus the final value indicated is the mean of three independent measures, each of which was sampled three times, for a single target of a particular size.

Experimental procedure

At the beginning of each trial, the stimulus was presented and the gate was opened. The fish was allowed to swim into the experimental compartment, where it could decide to move to the right or left side of the partition wall, thus selecting the right or left stimulus field. A decision was considered to be made when the fish swam to one side of the partition wall beyond its pectoral fins. If the fish responded correctly, i.e. it swam into the compartment with the stimulus field containing the single target, often touching it in the final end, it was fed two to three red mosquito larvae applied with the help of a syringe (see Movie 1). The monitor turned black as soon as the fish had eaten the reward. If the fish swam to the stimulus field on which no stimulus was presented, the screen immediately turned black, and no food reward was given. The trial ended once the fish had returned to the holding area voluntarily, upon which the gate was closed.

Pre-training

During pre-training, the fish became familiar with the experimental procedure. It was first presented with a single, supra-threshold target. Once the fish had learned to swim towards the stimulus field containing the single target, the number of supra-threshold single targets varying in size displayed in one session was increased from one to three, then to five and finally to six. Sessions consisted of 30 trials and then 36 trials when six differently sized targets were included in one session. Each of these pre-training steps was considered completed once the fish had reached the learning criterion of $\geq 80\%$ correct choices in two consecutive sessions.

During pre-training, only single targets with a Weber contrast of 0.97 to the background were used. Four fish, Roy, Hanna, Anna and Frida, required only two pre-training sessions prior to testing. The fish Luigi and Lina required 23 and 60 sessions with different stimuli as well as specific training steps to overcome their strong side preferences.

Data collection

After pre-training, thresholds were determined by presenting a predefined set of six stimuli 30 times each over five 36-trial sessions, according to the method of constant stimuli. Single targets with sizes between 0.72 and 2.93 mm were used for threshold determination. The average performance of the experimental animal per stimulus over 30 stimulus presentations was used to determine the threshold (see Analysis, below). For each contrast, the threshold was determined numerous times as the performance of the fish improved over threshold determinations (see Table S1). The threshold was considered to have been reached once the threshold values did not improve over three consecutive threshold determinations.

Analysis

The 75% threshold was determined by linear interpolation of the last supra-threshold value and the first sub-threshold value. The

threshold was finally expressed as minimum visual angle α taking the viewing distance from the point of decision into account.

All analysis steps including statistical analyses (see details in results) was performed in Microsoft Excel (Microsoft Office Professional Plus 2010 v. 14.0.7258.5000) and SPSS Statistics (version 27.0.0.0, IBM, New York, NY, USA).

RESULTS AND DISCUSSION

The performance of each fish improved over two to three and four to eight threshold determinations before it reached a constant level for C1/C2 and C3 single targets (see Table S1). STA for C1 stimuli varied between 0.13 and 0.32 deg (Table 1, Fig. 2). One fish, Anna, had a significantly higher threshold of 0.32 deg (indicating a poorer performance; Games–Howell *post hoc* test, $P < 0.01$), although it was neither obviously unmotivated – having learnt the task as rapidly as the fastest of the other fishes, nor was there clear evidence of ocular impediments – the fish's target acuity for C2/C3 stimuli did not deviate from that of the other fish.

STA for the five other fish ranged between 0.13 and 0.18 deg with a mean \pm s.d. value of 0.14 ± 0.02 deg corresponding to a grating resolution of 3.6 ± 0.5 cycles deg^{-1} with no significant difference among individuals (Kruskal–Wallis test, $P > 0.05$). This mean value is intermediate to the STA reported for archerfish (Ben-Simon et al., 2012) and for triggerfish (Champ et al., 2014). The archerfish's high STA most likely reflects the larger aerial viewing distances overseen by an eye that experiences high light levels at the water's surface (Temple et al., 2010). Triggerfish are generalist feeders, and also graze on non-moving algae (Chen et al., 2001), which would not require high resolution vision. The perception of the body patterns of triggerfish might also not require excellent STA, as their body patterns are probably only perceptible at short ranges (Champ et al., 2014). These body patterns most likely become blurred over longer distance and may camouflage the fish rather than playing any role in long-range communication, for which better STA would be required. The STA of the archerfish and the common sunfish might be superior to that of the triggerfish because they are predatory fishes. Indeed, the viewing axis was shown to be directed

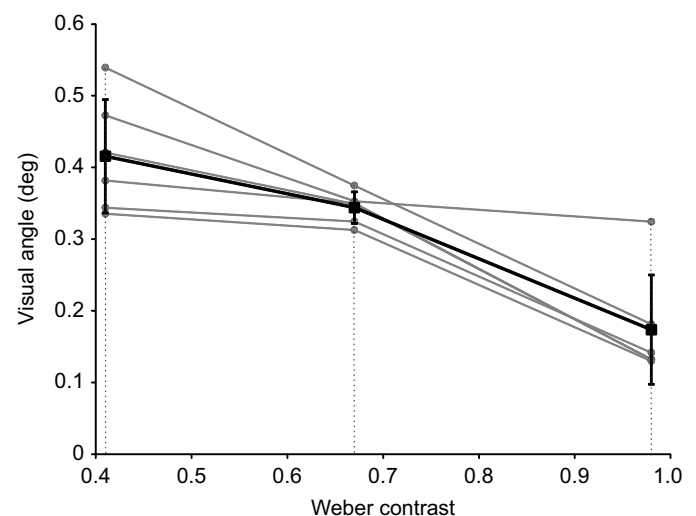


Fig. 2. Single target acuity as visual angle (in deg, average of last three threshold determinations) for single targets of different Weber contrast (C1=0.98, C2=0.67, C3=0.41) to the background for six common sunfish individually as well as the mean \pm s.d. single target acuity (bold black line). Single target acuity was greatest for C1 stimuli, but decreased with contrast; interindividual variability was largest for C3 single targets.

to the front in bluegill sunfish (Gomi and Miyazaki, 2015). More comparative studies are necessary to assess how acuity correlates with lifestyle in fishes (Collin and Pettigrew, 1989).

The greatest STA in common sunfish corresponds well with the grating acuity assessed in the bluegill sunfish (Northmore et al., 2007). Future studies on visual resolution in common sunfish, also including younger sunfish individuals, might help to assess whether STA is indeed comparable to grating acuity. Interspecific comparison with other vertebrates revealed a good correspondence between the two acuity measures (Haller et al., 2014; Mitkus et al., 2014; Chaib et al., 2019). In contrast, STA might be superior to grating acuity, as in humans (Hecht et al., 1947), lizards (Ehrenhardt, 1937) and some insects (see, for example, Somanathan et al., 2017), or inferior as in the triggerfish (Champ et al., 2014).

When the contrast of the single target was reduced to C2, the STA dropped to values of 0.31–0.37 deg (mean±s.d. 0.34±0.02 deg or 1.5±0.1 cycles deg⁻¹; Table 1, Fig. 2). With C2 single targets, thresholds varied the least interindividually, with only those of Luigi and Lina being significantly different from one another (Games–Howell *post hoc* test, $P<0.01$). The STA for C2 single targets was significantly lower than for C1 single targets (Games–Howell *post hoc* test, C1–C2, $P=0.01$; C1–C3, $P=0.001$).

A further reduction of the contrast of the single target to C3 resulted in thresholds between 0.34 and 0.54 deg (Table 1, Fig. 2). The mean thresholds for C2 and C3 (0.42±0.08 deg or 1.2±0.2 cycles deg⁻¹) single targets did not differ significantly (Games–Howell *post hoc* test, $P>0.05$). A comparable effect was found in budgerigars (Chaib et al., 2019). Our results from common sunfish suggest that its contrast sensitivity is low, as reported for the budgerigar. Future studies will help to contextualize our findings with reference to the high contrast sensitivity reported for bluegill sunfish (Hawryshyn et al., 1988; Northmore et al., 2007).

The common sunfish should be able to detect prey at a distance of 70–120 cm when contrast to the background is high, when vegetation does not limit viewing distance, and in consideration of prey sizes as in Confer et al. (1978). The common sunfish prefers clear waters with slight vegetation (Miller, 1963), which would provide the visual conditions necessary to detect prey at the viewing distances determined on the basis of high contrast STA. With reduced contrast levels, the common sunfish should be able to detect prey items at a distance of 25–40 cm, which corresponds well with the reactive distances obtained in *Lepomis* under various experimental conditions (Vinyard and O'Brien, 1976; Confer et al., 1978). Because these fish are attracted by the movement of their prey (Miller, 1963; Kieffer and Colgan, 1991), we would like to assess STA for moving targets, which can be easily done with our LCD screen, presuming STA is better for moving than for stationary stimuli.

In the context of intraspecific interactions, the perception of the opercular flap and body patterns is crucial. Under full contrast conditions, this spot, ranging from 0.17 to 0.24 cm² in our experimental animals, could thus be detected from at least 65 cm distance, allowing the common sunfish to assess the status of the conspecific at some distance. As suggested by Stacey and Chiszar (1978), the red color of the opercular flap spot is the most important element in the pattern. Thus, color vision, still to be studied in common sunfish, most likely contributes to the ability to distinguish the opercular flap spot from the background (Hawryshyn et al., 1988).

In the context of interspecific interactions, body patterns, which are unique to every species of *Lepomis*, most likely play an

important role in species identification and reproductive isolation. Stacey and Chiszar (1978) found that the common sunfish reacts with increased aggression to the dorsal fin ray spot that is typical of bluegill sunfish, which breed in the same regions. When fully darkened, the dorsal fin ray spot of the bluegill sunfish reaches a size of 1.0 cm² in large animals (Stacey and Chiszar, 1975). Thus, the common sunfish can detect this spot from 1.5 to 4.5 m distance depending on contrast. Indeed, common sunfish were found to react to other fish at approximately 1 m distance (Clark and Keenleyside, 1967).

To conclude, STA allows the predatory common sunfish with their frontal-directed viewing axis to recognize prey, and identify body markings on conspecifics or related species from distances in the range of tens of centimeters to a few meters depending on contrast; these viewing distances seem to be plausible in their underwater habitat. Our results thus define the dimension of visual acuity for foraging, territorial and courtship behaviors.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: C.S., F.D.H.; Methodology: C.S., J.S.S., F.D.H.; Software: C.S., L.-M.S., F.D.H.; Validation: C.S., F.D.H.; Formal analysis: C.S., L.-M.S.; Investigation: C.S.; Resources: F.D.H.; Writing - original draft: C.S.; Writing - review & editing: L.-M.S., J.S.S., F.D.H.; Visualization: C.S.; Supervision: F.D.H.; Project administration: F.D.H.; Funding acquisition: F.D.H.

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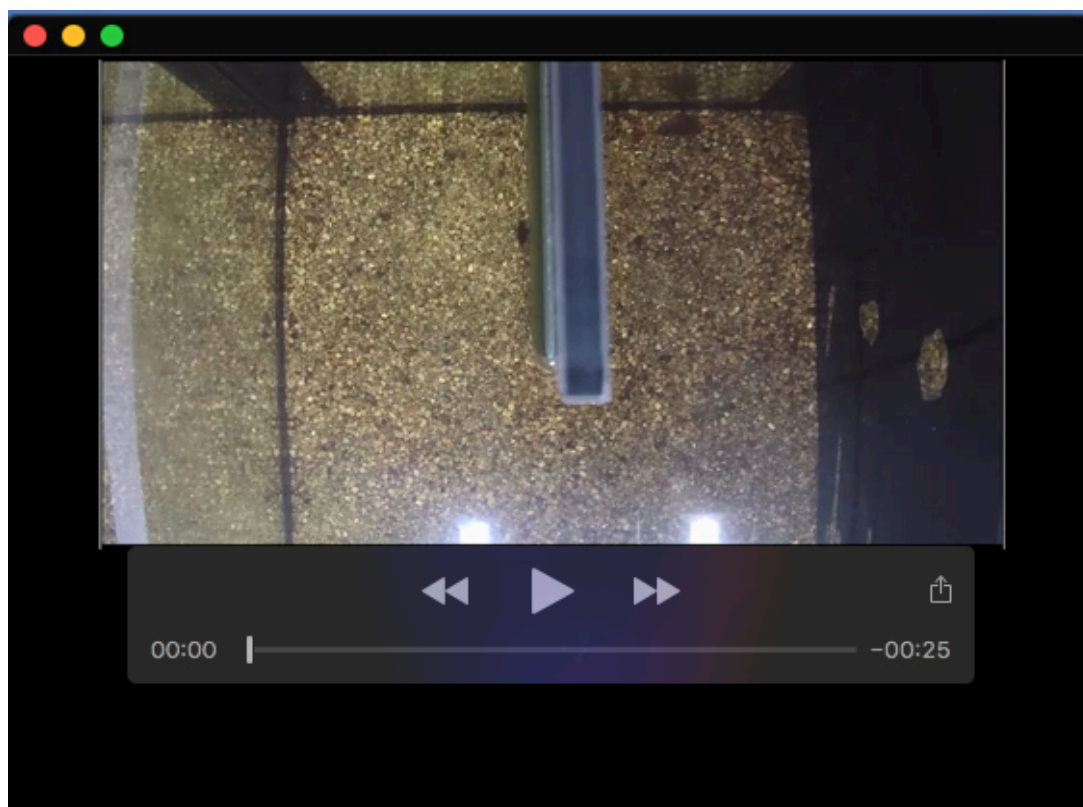
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Table S1. Threshold determinations for single target acuity with different contrast levels to background for each individual fish.

Single target acuity [deg]					
for single targets with Weber/Michelson contrast of					
C1 = 0.98/0.97					
Threshold determination	1	2	3	4	
Roy	0.24	0.13	0.13	0.16	
Hanna	0.13	0.13	0.14	0.13	
Anna	0.32	0.31	0.32	0.34	
Frida	0.15	0.12	0.13	0.13	
Luigi	0.17	0.19	0.19	0.19	
Lina	0.15	0.12	0.12	0.12	
Single target acuity [deg]					
for single targets with Weber/Michelson contrast of					
C2 = 0.67/0.5					
Threshold determination	1	2	3	4	5
Roy	0.51	0.32	0.31	0.35	
Hanna	0.40	0.36	0.36	0.34	0.35
Anna	0.35	0.34	0.37	0.36	
Frida	0.65	0.36	0.33	0.37	
Luigi	0.99	0.64	0.37	0.37	0.37
Lina	0.35	0.31	0.31	0.31	

Single target acuity [deg]								
for single targets with Weber/Michelson contrast of								
C3 = 0.41/0.25								
Threshold determination	1	2	3	4	5	6	7	8
Roy	1.01	0.67	0.65	0.40	0.34	0.33	0.36	
Hanna	0.62	0.59	0.40	0.44	0.43			
Anna	0.55	0.48	0.45	0.50	0.56			
Frida	0.55	0.51	0.58	0.54	0.45	0.37	0.37	0.40
Luigi	1.06	0.65	0.67	0.56	0.51	0.55		
Lina	0.55	0.34	0.32	0.34				



Movie 1. Experimental trials.