

## SHORT COMMUNICATION

# LATERAL LINE STIMULI CAN OVERRIDE VISION TO DETERMINE SUNFISH STRIKE TRAJECTORY

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Although all fishes have a mechanosensory lateral line system – a system of water flow detectors (neuromasts) in canals or free on the skin's surface – particular behavioral functions are documented for only a few species. Work on lateral line use for feeding has focused on either cavefishes or night-active species (Montgomery, 1989). While surface-feeding fishes with well-developed eyes do use the lateral line to locate prey (Müller and Schwartz, 1982), it is generally assumed that diurnal/crepuscular fishes are visual predators. We show that a hydromechanical stimulus detected by the cephalic lateral line system in two sunfishes (Centrarchidae) can be the sole determinant of a strike trajectory. The response occurs without reinforcement and appears to be an unconditioned response.

Green sunfish (*Lepomis cyanellus* Rafinesque) and largemouth bass (*Micropterus salmoides* Lacépède) are North American sunfishes that inhabit ponds, lakes and slow streams. Both species have diverse diets, including invertebrates and fishes (Carlander, 1977). These species and their congeners are active during the day; at night in field and laboratory they lie near or on the bottom and are lethargic (Neill and Magnuson, 1974; Helfman, 1981). Both species have cones and rods in the retina; the green sunfish visual pigments are characteristic of crepuscular mid-water fishes (Dearry and Barlow, 1987; Lythgoe and Partridge, 1989). Visual feeding of a congener of the green sunfish (*L. macrochirus*) has been studied previously (Li *et al.* 1985).

The visual stimulus for this experiment was food presented through a feeding tube; the lateral line stimulus was a water jet (Fig. 1). The visual stimulus was sometimes given with the lateral line stimulus but mostly without the lateral line stimulus (see next paragraph). Green sunfish (four, 111–115mm) were housed individually in 19l rectangular glass aquaria on one side of a vertical acrylic partition. The single largemouth bass was in a similar 38l aquarium. The white plastic feeding tube (12.3mm i.d.) penetrated the partition and to either side of it were single 10ml water-filled pipette 'jet nozzles', extending 5–6cm horizontally from the partition (Fig. 1). The visual stimulus (a piece of squid mantle) was presented on a wire pushed through the feeding tube. The lateral line stimulus, one or the other water jet, was activated *via* air pressure from a pump to one pipette by closing a bleed valve. Jet velocities, measured along the jet axis by hot-

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film anemometry (Janssen *et al.* 1990), ranged from  $115\text{mm s}^{-1}$  at 80mm to  $680\text{mm s}^{-1}$  at 6mm from the nozzle. Anemometry showed no evidence of turbulence in the jet stream and the radius (distance from the axis to where there was no detectable flow) was about 8mm at 80mm from the nozzle and less than 2mm at 6mm from the nozzle. Measurements of dye released from the nozzle revealed similar radii. The time for the flow to increase from 20% to 80% of maximum ranged from about 5ms (at 6mm from the nozzle) to 40ms (at 80mm). The flow along the jet axis was equal to or slightly greater than hydromechanical signals from small swimming fishes (Bleckmann *et al.* 1991).

Each session (one per day per fish) began with feeding a fish through the tube one to five times (randomly determined), followed by one unrewarded trial, videotaped from above, with the jet activated as the fish watched the food oscillate in the tube. Fish had been trained to wait in front of the tube by oscillating the food within the tube near the tube mouth for several seconds before positioning it so the fish could seize it. For the jet trial, the food was presented as before but, as the fish watched the food it was stimulated with a water-jet to the head *via* one pipette, randomly chosen. The jet was delivered when the fish's head was positioned so the jet would strike it, using a side mirror (also on video) to monitor the fish's elevation. While the fish were trained to feed from the tube, biting at the water jet was never reinforced either during training or during the trials. In preliminary work, we found that after several sequential water jets the fish would hover too far away from the jet axis. Because of this, we only had one jet trial per day, which was preceded by one to several feedings from the tube. In aggregation for the series of experiments, each green sunfish had 10 trials and the largemouth bass had 20 trials.

We quantified signal characteristics by the position and angle of jet impact on the fish's head and nozzle distance (Fig. 1C) determined from the video frame just prior to the response. Impact angle was the angle between the jet axis and fish axis and impact position was the distance between two parallel lines orthogonal to the fish axis with one parallel line intersecting the snout and the other intersecting the point at which the jet axis met the fish. Jet distance was the distance from the pipette tip to the fish along the jet axis. The response of the fish was characterized by the polar coordinates of the snout trajectory relative to the fish's initial body axis (Fig. 1C). The distance between the snout positions in the two video frames was the snout trajectory distance and the snout trajectory angle was the angle between the snout trajectory distance line and the fish's axis. The water jet always elicited a combined orientation movement and bite (100%,  $N=10$  for each green sunfish; 100%,  $N=20$  for the largemouth bass). Statistical analysis for both the green sunfish and largemouth bass showed that strike trajectory angle was best predicted by where the jet impacted the fish (impact position), not by either the direction of the source (impact angle) or the jet distance (Table 1). Both species turned more to bite when the impact positions were more posterior (Fig. 2). The snout trajectory distance was statistically less with an impact at the snout than for a more posterior impact for the largemouth bass, but there was no significant effect for the green sunfish (Table 1). The only bites approximately towards the visual cue were in response to stimuli impacting at the snout, in which case the jet impact and food were both approximately along the initial fish axis. No bite in response to a water jet resulted in the fish obtaining the food,

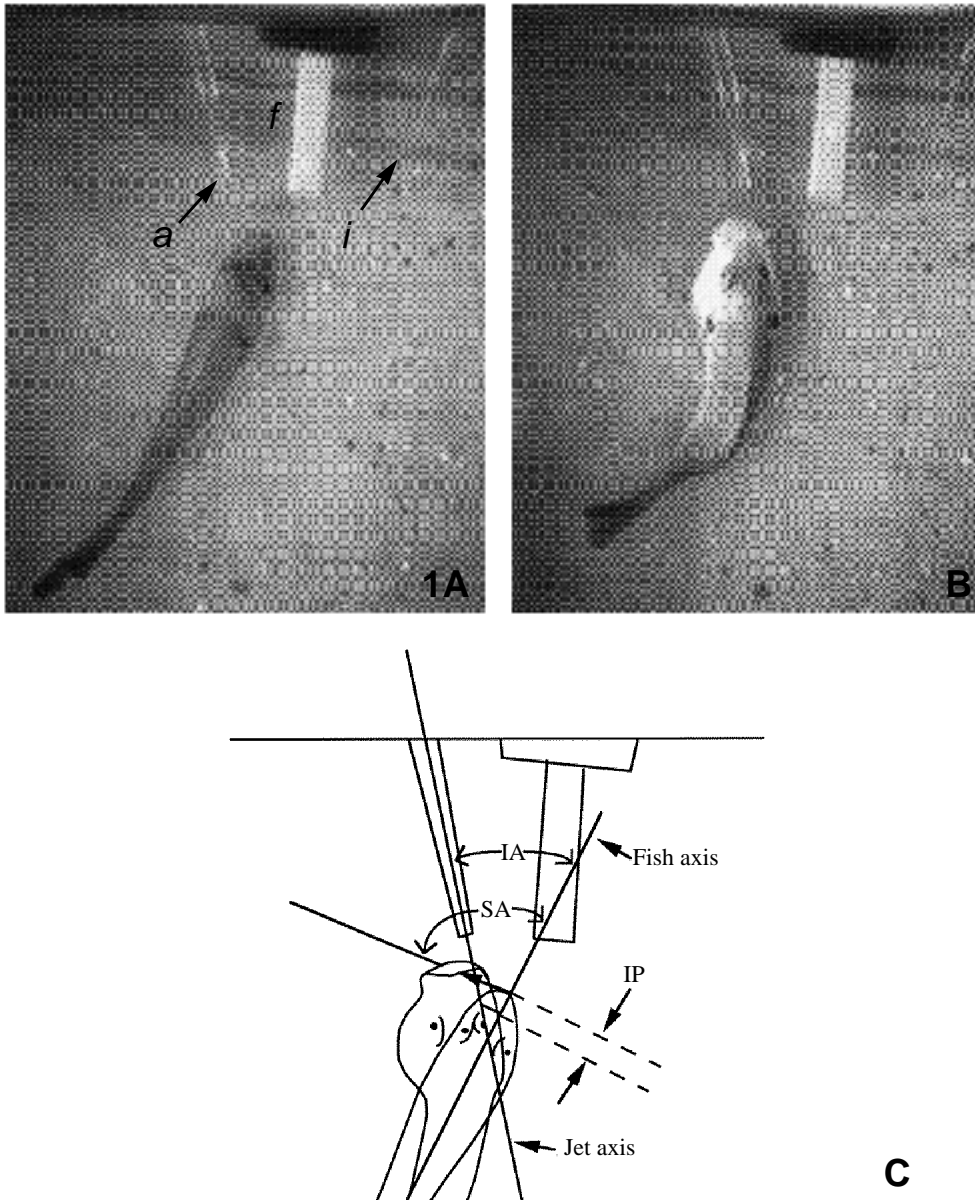


Fig. 1. Experimental apparatus and the response of a green sunfish to a water jet trial. A and B are sequential single frames from the overhead video system,  $1/500\text{s}$  shutter speed,  $30\text{frames s}^{-1}$ . *f*, feeding tube; *a*, active nozzle; *i*, inactive nozzle. (C) Measurements from the video frames in A and B. Impact angle (IA): the angle between the jet axis and fish axis. Impact position (IP): the distance between two parallel lines orthogonal to the fish axis; one parallel line intersects the snout and the other intersects the point at which the jet axis meets the fish. Jet distance (not shown): the distance from the pipette tip to the fish along the jet axis. The arrow connecting the snout positions in the two frames is the snout trajectory composed of the snout trajectory distance (arrow's length) and the snout trajectory angle (SA: the angle between the arrow and the fish's axis).

Table 1. *Summary statistics for the four green sunfish and single largemouth bass*

Source	Green sunfish			Largemouth bass		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Dependent variable: snout trajectory angle						
Fish	1.6	3,33	>0.20	–	–	–
Impact position	30.6	1,33	<0.0001	18.3	1,16	<0.001
Impact angle	0.2	1,33	>0.80	3.1	1,16	>0.09
Jet distance	0.2	1,33	>0.90	0.7	1,16	>0.40
Dependent variable: snout trajectory distance						
Fish	1.0	3,33	>0.39	–	–	–
Impact position	2.8	1,33	>0.10	25.5	1,16	<0.001
Impact angle	1.4	1,33	>0.24	0.3	1,16	>0.60
Jet distance	1.1	1,33	>0.30	1.3	1,16	>0.27

Degrees of freedom (d.f.) are (source d.f., error d.f.) corresponding to the *F* ratio.

The green sunfish analysis was an analysis of covariance with fish as a group variable and impact position, snout distance and nozzle distance as covariates.

The largemouth bass analysis was a multiple regression with impact position, snout distance and nozzle distance as covariates; fish was not a group variable because there was only one largemouth bass.

Degrees of freedom (d.f.) are (source d.f., error d.f.) corresponding to the *F* ratio.

including those in which the impact position and food were in the same direction (0% for all green sunfish and bass trials). All bites in response to the water jet fell short of seizing the nozzle. For all bites to food delivered without a jet the fish seized the food or feeding tube (100%,  $N=127$  for all green sunfish; 100%,  $N=56$  for the largemouth bass).

The strong effect of the impact position on snout trajectory suggests that the orientation movement was determined by that part of the cephalic lateral line which received the stimulus. We showed that the lateral line is necessary because neither the four green sunfish nor the largemouth bass responded to a water jet when the lateral line was (reversibly) pharmacologically ablated with streptomycin (Kaus, 1987) or calcium-free water with  $\text{Co}^{2+}$  inhibitor (Karlsen and Sand, 1987). Trials were run as with unablated fish, i.e. one jet trial per day preceded by a random number of feedings from the tube. There were five trials per fish per ablation treatment type. The ablated fish continued to seize food from the feeding tube but did not respond to the jet.

Canal neuromasts appeared to be more important for feeding than superficial neuromasts, as the latter are confined to the posterior of the head (Fig. 2). It has been shown theoretically that different stimulus positions produce different patterns of fluid flow in lateral line canals, which would be useful in determining source direction (Gray and Best, 1989). A relationship between an orientation response to surface waves and stimulated neuromasts has been shown for blinded topminnows (*Aplocheilichthys lineatus*) (Müller and Schwartz, 1982). The otolithic organs of the inner ear can also provide directional information in response to a displacement of the head (Fay, 1984). This would depend on the impact angle, which ranged from 4 to 63°. The direction of acceleration of the fish's head would be detected by the otoliths, and therefore the impact angle's lack of a statistically significant effect on snout trajectory angle would suggest that the ear is not involved.

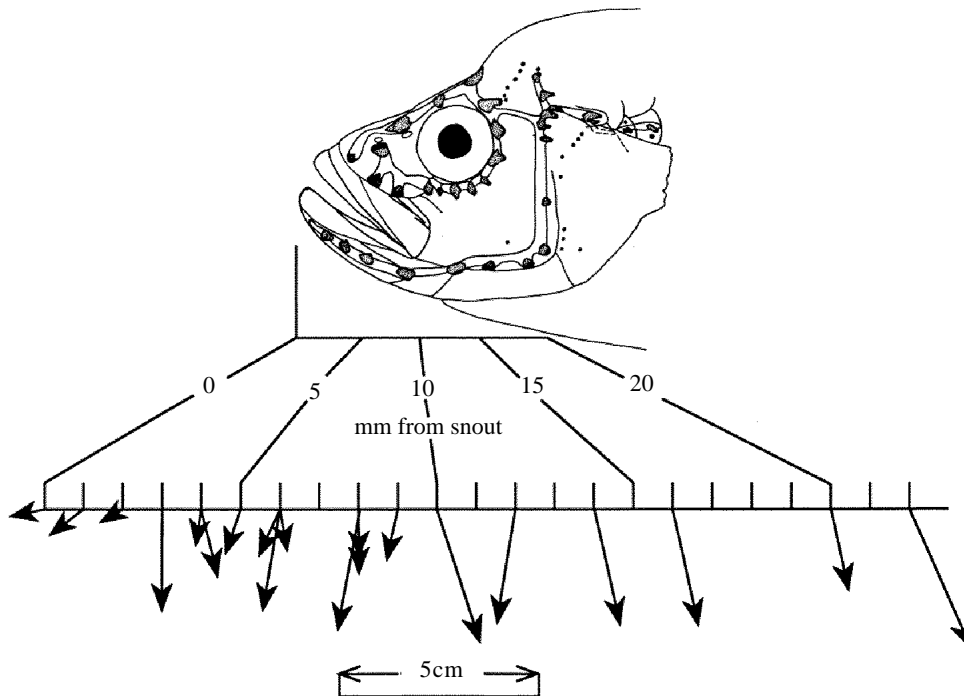


Fig. 2. Lateral view (rotated  $90^\circ$  from the camera view to show the lateral line canals) of a green sunfish head showing the lateral line canals (reprinted with permission from Branson and Moore, 1962) (above) and snout trajectories (below, scaled line with arrows). Stippled areas on the head indicate the fleshy areas surrounding pores; the connecting lines indicate canals. There is usually a neuromast between each pair of pores. Superficial neuromasts are indicated by black dots. The scaled line denotes jet impact positions projected onto the fish axis (same dorsal view as Fig. 1C). Lines extending from below the fish head to the scaled line indicate anatomical positions that correspond to particular impact positions (all green sunfish heads were nearly the same size). Arrows originating on the scaled line indicate snout trajectories from the two 'worst correlation' green sunfish (impact position vs snout angle correlations:  $r=0.80$  and  $r=0.82$ ). Each arrow originates at the impact position for a trial; its angle is the snout trajectory angle and its length is the snout trajectory distance (Fig. 1C). Responses to stimuli to the fishes' right have been reflected to the left to consolidate. Snout trajectory distances are on a different scale (5cm scale bar) from that of the fish head.

We interpret the hydrodynamically elicited bite as an unconditioned feeding response because the behavior was easily elicited from naive fish with a hand-held pipette applied to fish feeding on adult brine shrimp (*Artemia salina*), but could not be evoked in frightened or well-fed fish. The fish appeared not to be frightened by the jet because after a single water jet trial the fish returned to its position in front of the feeding tube and fish stimulated with a water jet while feeding on live prey continued to feed.

It is possible that the lateral line is either less sensitive or more sensitive when the visual system is activated. In *Opsanus tau* L., visual stimuli inhibit certain lateral line afferent neurons whilst others are unaffected (Tricas and Highstein, 1990). If the inhibited class of neurons is involved in prey detection then sensitivity to prey may decrease, but if that class is not involved in feeding then the fish may be more sensitive to

prey because unaffected neurons responsive to prey signals become relatively more important.

This experiment does not demonstrate that the lateral line is either more or less important than vision. The fish fed readily when the lateral line was pharmacologically eliminated and bit at food presented to the exterior glass surface of the aquarium. This experiment demonstrates that the lateral line provides significant input to enhance the efficiency of fish predators. Natural conditions are seldom visually optimal for sunfishes because waters can be quite turbid (Vinyard and O'Brien, 1976), some species tend to feed at dawn and dusk (Helfman, 1981) and because prey are cryptic and blocked from view by litter or vegetation. A movement blocked from the fish's eyes may register as a hydromechanical signal on the more spatially distributed lateral line. Our apparatus may simulate the essentials of a natural situation in which the fish is initially visually aware of food which cannot be reached or has hidden itself, but the prey reveals itself hydromechanically by a swimming, crawling or respiratory movement. To understand the sensory basis of fish predation requires an understanding of how fish integrate sensory modalities.

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