

STRIKE FEEDING BEHAVIOR IN THE MUSKELLUNGE, *ESOX MASQUINONGY*: CONTRIBUTIONS OF THE LATERAL LINE AND VISUAL SENSORY SYSTEMS

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Summary

The muskellunge, *Esox masquinongy*, is a predatory esocid fish with well-developed visual and lateral line systems. The purpose of this study was to determine the relative roles of these two sensory modalities in organizing the strike behavior of the animal. Subadult muskellunge were videotaped in a test arena while feeding on fathead minnows (*Pimephales promelas*). Animals were tested under five conditions: (i) control animals in which the visual and lateral line systems were intact; (ii) animals with lateral line afference suppressed by immersion for 12–24 h in 0.1 mmol l^{-1} CoCl_2 ; (iii) animals blinded by bilateral optic nerve transection; (iv) animals that had been unilaterally blinded; and (v) animals in which the lateral line system had been unilaterally denervated.

The feeding behavior of the muskellunge consists of two phases: a slow stalk of the prey with minimal body movement followed by an explosive C- or S-start lunge at the prey. Quantitative comparisons of animals in the five test groups indicate that, although vision is used in the

initial acquisition of the prey, both vision and the lateral line system play important roles in determining the initiation of the rapid strike. The lateral line system may play a critical role in the final capture of the prey at the end of the strike. In addition, lateral-line-suppressed muskellunge strongly alter their approaches to more distant prey. Bilaterally blinded muskellunge do not stalk their prey, but will lunge only at prey that are at close range. Unilaterally blinded or denervated muskellunge also alter their detection of and approach to prey, attending to a wider region of the intact sensory hemisphere.

Our data suggest not only that the visual and lateral line systems play complementary roles in the feeding behavior sequence but also that each system plays a more or less dominant role during consecutive phases of the behavior.

Key words: fish, muskellunge, *Esox masquinongy*, predator, prey, multimodal, sensory integration, sensorimotor.

Introduction

Animals use information from a variety of different sensory systems to accomplish behavioral objectives. Occasionally, information encoded within a single sensory modality alone may be sufficient to accomplish a task, such as in the jamming avoidance response of weakly electric fishes (for a review, see Heiligenberg, 1991). More commonly, however, input from several different sensory modalities is integrated within the central nervous system to supply a richer depth of information. Such integration of sensory information may take the form of a quasi-hierarchical arrangement of responses to different cues that take varying precedence during the changing phases of a behavioral sequence. The organization of such hierarchies and the integration of information from different sensory modalities within a behavioral program are fundamental issues in attempts to understand sensorimotor integration in the vertebrate central nervous system and the functional relationship between brain and behavior.

The purpose of this study was to evaluate the roles played by the visual and lateral line sensory systems in the strike

feeding behavior of the muskellunge *Esox masquinongy*. Muskellunge are large, predatory fishes of the family Esocidae and are apex predators in many freshwater lakes and ponds in the northern United States and Canada. They are typically ambush predators that remain relatively still in the water and rely upon a rapid, directed lunge to catch their prey (Webb and Skadsden, 1980; Rand and Lauder, 1981). They possess well-developed visual and lateral line senses, each of which is likely to play a role in predatory behavior. Our study examines quantitatively the role of the visual and lateral line systems at different defined phases of the feeding behavior of the muskellunge. We demonstrate that, although each sensory system is sufficient by itself to enable the fish successfully to localize and attack prey, the two modalities play different and complementary roles in organizing the intact behavior.

Materials and methods

Subadult muskellunge *Esox masquinongy* (Mitchell 1824),

15–25 cm in standard length, were obtained from a commercial hatchery. Fish were housed in 9081 freshwater aquaria maintained at approximately 18 °C and fed weekly upon a diet of live fathead minnows (*Pimephales promelas*) obtained from local suppliers. All the protocols for handling, surgery and experimentation employed in this study have been approved by the Loyola University Institutional Animal Care and Use Committee.

In the first set of behavioral experiments, the experimental animals were separated into four groups. The first of these was a control group ($N=9$) in which the animal's lateral line and visual systems were unperturbed and which provided a baseline of normal behavior. In the second group of animals ($N=5$), the lateral line was suppressed by immersion of the fish in 0.01 mmol l^{-1} CoCl_2 in deionized water for 24 h immediately prior to testing. Such treatment has been demonstrated to suppress the activity of the lateral line neuromast organs in teleost fishes for a period of at least several days (Karlsen and Sand, 1987). The test animals showed no evidence of stress following this procedure and fed vigorously following a brief acclimation period (approximately 30 min) in the test arena tank immediately following treatment. Animals in the third group ($N=6$) were blinded by bilateral transection of the optic nerves. The animals were anesthetized with approximately 0.025 % tricaine methanesulfonate (MS-222; Sigma, St Louis, MO, USA), and a semicircular incision was made through the epithelial tissue connecting the eye to the edge of the orbit. The eye was then gently deflected to expose the optic nerve and blood vessels supplying the retina. These were transected with iridectomy scissors, and the wound was closed using cyanoacrylate adhesive. In these animals, the destruction of the arterial blood supply to the eye caused the eye to atrophy and the pupil to take on a characteristic opaque appearance. These symptoms, in addition to the dark coloration of these animals post-surgery and their lack of visual responses to stimuli (e.g. a net in the tank), provided a degree of confidence that they were profoundly blinded. In the fourth group of animals ($N=3$), muskellunge were blinded by the method described above and subsequently immersed, prior to testing, for 24 h in 0.01 mmol l^{-1} CoCl_2 to additionally suppress the lateral line system.

In the second set of experiments, the animals were deprived unilaterally of visual or lateral line sensory input. In these experiments, new animals were separated into two groups. In the first group ($N=4$), the lateral line system was suppressed unilaterally by transection of the principal branches of the anterior (ALLN) and posterior (PLLN) lateral line nerves. The animals were anesthetized with 0.025 % tricaine methanesulfonate as described above, and the branches of the lateral line nerves were exposed. The superficial ophthalmic and buccal branches of the ALLN were exposed in the orbit *via* a semicircular incision made through the epithelial tissue between the eye and the edge of the orbit, and the eye was gently deflected to expose the nerves. A section of nerve approximately 5–6 mm in length was removed, and a small piece of dry gelfoam (Upjohn Inc.) was placed between the

transected nerve endings to serve as a physical barrier to nerve regeneration. The wound was then closed using cyanoacrylate adhesive. Care was taken to prevent any of the adhesive from contacting the cornea of the eye, which might decrease the visual acuity of the animal. The hyomandibular branch of the ALLN was exposed by drilling through the preopercular bone to expose a 1–2 mm length of the nerve proximal to its emergence through the foramen. The segment of nerve was then removed, and a small piece of dry gelfoam was again placed in the space between the nerve endings to serve as a barrier to regeneration. The wound was then closed with dental acrylic, which dropped off after a period of several weeks following the normal healing of the wound. The posterior lateral line nerve (PLLN) was exposed just caudal to the operculum, and a section of nerve was removed and replaced with gelfoam as described above. The wound was closed using cyanoacrylate adhesive and healed normally in all animals. Although some minor branches of the lateral line nerves may have survived our surgical incursions, we are confident that the majority of lateral line neuromasts were denervated by these techniques. The nerves were all transected as proximal to the brain and as deeply as possible, and all were removed deep to the emergence of the nerves towards the positions of the neuromasts on the skin. We examined these transected nerves surgically in the animals after 1–2 months. In no cases had the nerves regenerated, and the proximal ends had retracted and the distal ends degenerated completely, so we considered these animals to be permanently unilaterally deprived of lateral line input from these branches. Two of the fish in this group were denervated on the right side of the animal and the other two on the left.

In the second group of animals ($N=4$), the subjects were unilaterally blinded by optic nerve transection using the methods described above. Two of these fish were blinded on the right side of the animal and the other two on the left.

Behavioral experiments

Behavioral experiments took place in an acrylic test arena tank measuring $123 \text{ cm} \times 45.5 \text{ cm} \times 47 \text{ cm}$ (length \times width \times depth). A $4 \text{ cm} \times 4 \text{ cm}$ grid was drawn on the back and bottom of the tank to facilitate distance measurement. Above the tank, a mirror was positioned in a wooden frame at an angle of 45° , providing a top view of the arena. A video camera (Panasonic, model WV-1460) was positioned lateral to the tank to record both side and top views of the animals in the tank. Behavior was recorded during natural daylight conditions on VHS tape at a speed of 66 frames s^{-1} for subsequent analysis.

Prior to testing, the muskellunge were deprived of food for a period of 7–14 days to ensure that they would be hungry and ready to feed. Individual muskellunge were transferred from their home tank into a holding section of the experimental tank measuring $53 \text{ cm} \times 45.5 \text{ cm} \times 47 \text{ cm}$ (length \times width \times depth), which was partitioned from the rest of the tank by an opaque sliding panel. The animals were allowed to acclimate within this holding area for at least 15–20 min. A fathead minnow (*Pimephales promelas*) was then introduced into the main

portion of the experimental arena, and the opaque door was raised. As the muskellunge proceeded into the experimental arena and eventually attacked the minnow, the strike feeding behavior was recorded on video tape. Only rarely did the muskellunge immediately attack the minnow upon removal of the panel and, because the minnow was allowed to swim freely about within the experimental arena, there was an element of randomness between the positions of the muskellunge and minnow at the initiation of the feeding behavior. Following a successful strike, the animal was returned to the holding area behind the opaque screen, a new minnow was introduced and the experiment repeated until the animal ceased feeding, after which it was returned to the home aquarium.

Initial feeding studies using the bilaterally blinded muskellunge demonstrated that these animals struck only at minnows that were at very close range. Because of the large size of the tank compared with the fishes, such tests consumed large amounts of time before a minnow happened to stray within the range at which a muskellunge would make a strike. Consequently, in later tests using these bilaterally blinded fishes, several minnows were introduced at the same time to increase the likelihood of a strike at a minnow.

Data analysis

A frame-by-frame analysis of the video recordings was used to define and measure distances and angles between the muskellunge and the minnow at discrete defined positions during the strike feeding behavior (see Results for a description of these positions). Video playback from a Panasonic AG-7350 video cassette recorder (VCR) was displayed on a Sony HR-Trinitron video display monitor. The positions of the muskellunge and the minnow were drawn onto a transparent acetate sheet placed on the video monitor screen. The distance between the fishes was defined as the straight-line distance from the snout of the muskellunge to the center of mass of the minnow (Fig. 1). Distance was measured from both the lateral and top views of the tank either by hand on the video screen or by using a digitizing pad and measurement software (SigmaScan, Jandel Inc.). The horizontal displacement (h) of the muskellunge and minnow was then measured against the grid drawn on the bottom of the tank from the top view, whereas the vertical displacement (v) was measured against the grid on the side of the tank from the lateral view. The actual distance (D) between the muskellunge and minnow was calculated as:

$$D = \sqrt{(v^2 + h^2)}. \quad (1)$$

The angles between the muskellunge and minnow were measured by drawing a line originating at the middle of the caudal peduncle of the muskellunge and extending through the longitudinal midline of the fish. A second line defining the angle was then drawn from the same origin extending to the approximate center of mass of the minnow (Fig. 1). The caudal peduncle of the muskellunge was used as the origin in these measurements because the elongate shape of the muskellunge

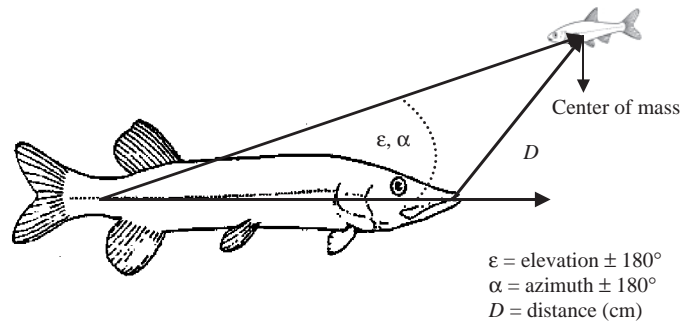


Fig. 1. Schematic diagram indicating the manner in which the measurements described in this study were performed. Elevation ϵ and azimuth α angles were plotted independently from the lateral and top views, respectively, as described in the text. Fish are not depicted to scale.

made a consistent visual determination of the muskellunge's center of mass difficult. Angles were measured from the lateral and top views to provide relative angular elevation (ϵ) and azimuth (α) respectively. By convention, angles of elevation for which the minnow was above the longitudinal midline axis of the muskellunge were scored as positive values, and angles for which the minnow was below the muskellunge's midline were scored as negative values. Similarly, azimuth angles for which the minnow was to the right of the longitudinal midline axis were scored as positive values, whereas those to the left were scored as negative values. The angular deviation in three-dimensional space (δ) between the muskellunge's longitudinal axis and the position of the minnow in space was then calculated as:

$$\delta = \sqrt{(\epsilon^2 + \alpha^2)}. \quad (2)$$

The measurement error caused by parallax resulting from differences in the fish's position within the arena was determined to be insignificant because of the distance between the recording camera and the test tank. The mean values of the data obtained from each fish were calculated. The significance of differences between the distances and the transformed (square root) angular deviations at defined phases of the strike feeding behavior in each of the three groups was tested using t -tests comparing the mean values obtained from each fish in each group.

Values are presented as means \pm S.E.M. unless stated otherwise.

Results

Strike feeding behavior of muskellunge

Having watched hundreds of repeated trials, we have divided the strike feeding behavior of muskellunge into two distinct phases demarcated by three points. The point at which the muskellunge first orients to the prey will be referred to as N-2 (Fig. 2). This point is characterized by a brief turning of the head or a momentary quick 'start' that is quite noticeable and is the

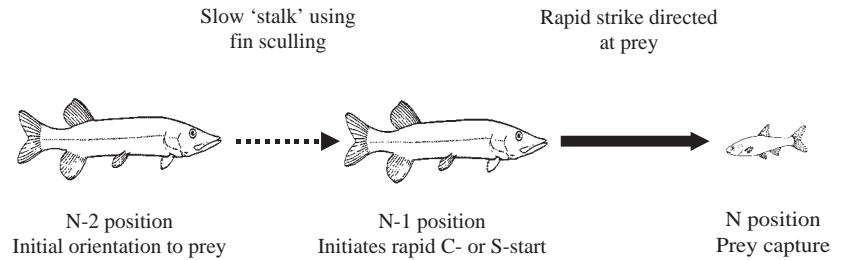


Fig. 2. The typical strike feeding behavior of muskellunge as described in this study. Fish are not depicted to scale.

moment when the muskellunge first overtly responds to the minnow. This is immediately followed by the first phase of the feeding behavior, which consists of a slow, directed 'stalk' towards the prey, generally using pectoral and caudal fin sculling movements but relatively little bending of the body trunk. Eventually, the muskellunge reaches a point in relation to the minnow's position that we have called N-1, at which the muskellunge initiates an explosive C- or S-start with waves of muscular contractions characteristically bending the fish's body. This results in a very rapid lunge directed at the target, culminating (if successful) in prey capture, during which the prey item is either seized in the jaws or missed (the N position). In 22% of the control cases ($N=37$), the initial portion of the behavioral sequence (N-2 to N-1) was absent and the only observable behavior was a rapid lunge directly at a minnow. In these cases, only the latter portion of the attack had been deemed to occur, and only N-1 distances and angles were measured.

The control group of muskellunge possessed intact visual and lateral line systems and served as the baseline standard for comparison with the other experimental conditions. All results are summarized in Table 1. In total, 166 feeding strikes were recorded from the control muskellunge. The mean distance between the muskellunge and the minnow at the N-2 point in each of these animals was 25.5 ± 1.8 cm. The mean of the absolute value of the angles of elevation at N-2 was $25.7 \pm 2.2^\circ$ (Fig. 3A), and the mean of the absolute value of the azimuth angle was $24.0 \pm 3.6^\circ$. The mean angular deviation between the muskellunge and the minnow at N-2 was $40 \pm 3.8^\circ$ from the longitudinal midline axis of the muskellunge. The correlation coefficient r for distance *versus* angular deviation was 0.08, indicating that the detection threshold did not change systematically with increasing angular deviation. Muskellunge had a similar threshold distance of N-2 orientation at all recorded angles surrounding the fish (Fig. 4A), although the majority (mean +1 S.D.) of the N-2 point orientations were within a cone subtending 54° forward of the animal (Fig. 4A).

As muskellunge progressed from the N-2 to the N-1 point, the distances and angles between predator and prey decreased. The mean distance of the N-1 point for control muskellunge was significantly closer to the prey minnow (mean 13.5 ± 0.9 cm, $P < 0.05$) (Fig. 4B; Table 1). Furthermore, the means of the absolute values of the angles of elevation and azimuth at N-1 decreased to $11.3 \pm 1.7^\circ$ and $11.8 \pm 1.7^\circ$, respectively (Fig. 3B). The mean angular deviation between the prey and the longitudinal body axis of the muskellunge decreased significantly to $18.4 \pm 2.3^\circ$ ($P < 0.05$) (Fig. 4B;

Table 1). Muskellunge in the control group were generally very successful at catching prey, with a success rate of 73.4%. A frequency distribution of the number of successful (hits) and unsuccessful (misses) strikes as a function of distance revealed no clear advantage in terms of success of prey capture across the range of distances recorded at the N-1 point from which the strike was initiated (see Fig. 7A). Although the majority of the strikes occurred within 1 S.D. of the mean, a number of strikes occurred at much greater distances. We use the term 'far strikes' to indicate any of these at which the N-1 position occurred at distances greater than the mean N-1 point for all strikes +1 S.D. (mean + S.D. = 24.4 cm). The angular deviation at which both successful and unsuccessful far strikes were initiated by the control muskellunge was always greater than 20° (mean value 35.3°) (see Fig. 8A). We also determined the direction of the minnow's movement with respect to the muskellunge during far strikes and found that, in the vast majority of cases (82%), the minnow was moving away from the midline axis of the muskellunge. Thus, for the majority of the N-1 locations that resulted in the initiation of far strikes, the prey was located at an angular deviation greater than 20° from the longitudinal axis of the muskellunge and was also

Table 1. Summary of data

	N-2	N-1
Control ($N=166$)		
Mean angular deviation (degrees)	40 ± 3.8	18.4 ± 2.3
Mean distance (cm)	25.5 ± 1.8	13.5 ± 0.9
Lateral-line-suppressed ($N=109$)		
Mean angular deviation (degrees)	34.4 ± 3.6	7.4 ± 0.7
Mean distance (cm)	22.8 ± 1.8	10.1 ± 0.8
Blinded ($N=114$)		
Mean angular deviation (degrees)	N/A	7.4 ± 0.7
Mean distance (cm)	N/A	3.2 ± 0.2
Unilaterally blinded ($N=224$)		
Mean angular deviation (degrees)	62.7 ± 4.0	10.9 ± 0.9
Mean distance (cm)	27.4 ± 1.2	7.8 ± 0.4
Unilaterally lateral-line-denervated ($N=204$)		
Mean angular deviation (degrees)	73 ± 4.4	13.7 ± 1.1
Mean distance (cm)	22.2 ± 1.2	7.42 ± 0.4

Values are means \pm S.E.M.

N/A, not applicable.

N-2, position of initial orientation to prey; N-1, position at initiation of strike.

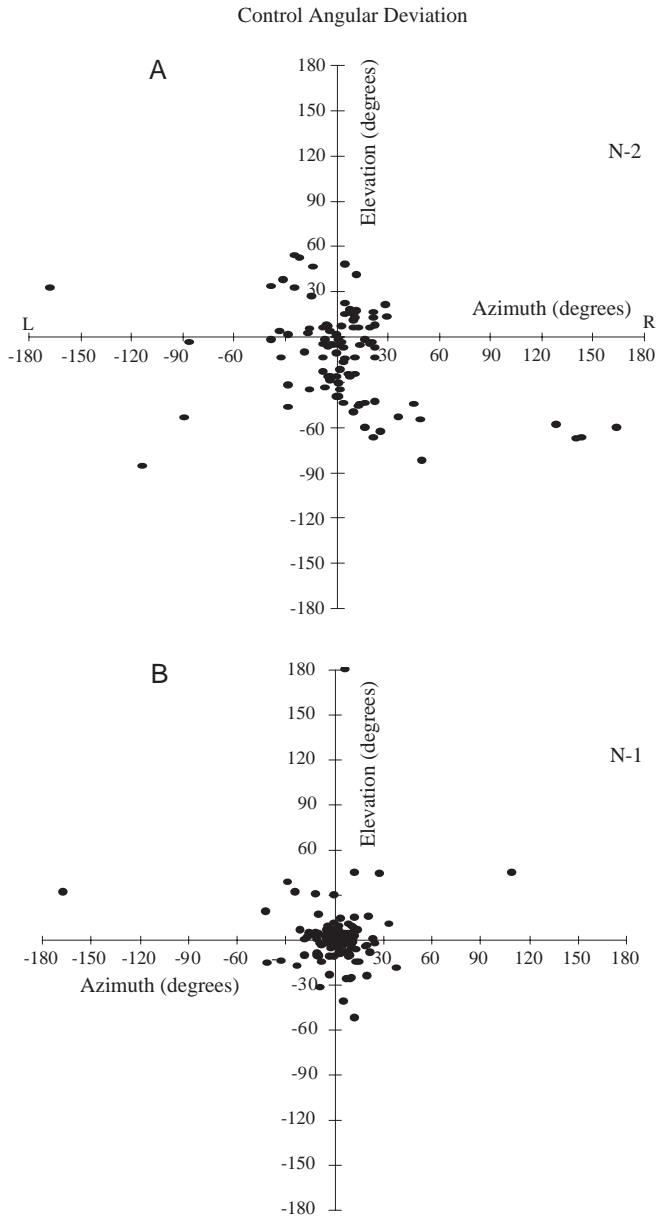


Fig. 3. Polar coordinate plots illustrating angular deviations of individual strikes at the N-2 (first orientation to prey) and N-1 (initiation of strike) positions in control animals. The plot is oriented so that the rostrum of the muskellunge is fixed at the origin and the axes curve around in space converging at the animal's tail, the whole describing a sphere surrounding the fish. Angular deviation is defined as the distance from the origin to a given point measured in degrees (see equation 2). (A) Measurements made at the N-2 position. (B) Measurements made at the N-1 position. L, left; R, right.

increasing that angle by swimming away from the midline axis of the muskellunge.

For muskellunge in which the initial strike from the N-1 point was unsuccessful (that is, in which the prey was not successfully captured), the usual result was that the muskellunge repeated the strike feeding behavior by remaining

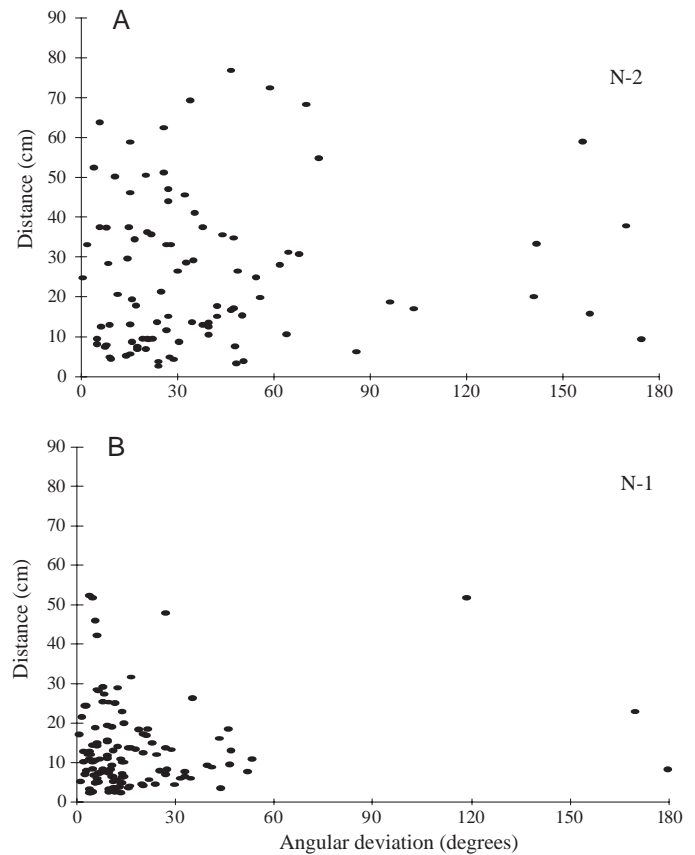


Fig. 4. Plots of distance *versus* angular deviation for individual trials at the N-2 (first orientation to prey) and N-1 (initiation of strike) positions of control animals. The filled circles are the data from individual trials. (A) N-2 position. (B) N-1 position.

relatively still until it had re-identified the prey. The muskellunge then initiated another rapid lunge, which was often preceded by a short stalk (the N-2 to N-1 phase). Only rarely did the muskellunge actively chase a minnow that it had missed.

Lateral-line-suppressed group

Muskellunge in which the lateral line system had been suppressed by immersion in CoCl_2 demonstrated normal and robust strike feeding behavior with both phases of the behavior intact and clearly definable N-2 and N-1 points. In total, 109 feeding strikes were recorded from fishes in this group. The mean absolute value of the azimuth for these attempts was $23.4 \pm 2.3^\circ$, the mean absolute value of the elevation was 21.3 ± 3.1 and the mean angular deviation from the longitudinal midline axis was $34.4 \pm 3.6^\circ$ (Fig. 5A; Table 1). The mean distance between the muskellunge and the minnow at N-2 in this group was 22.8 ± 1.8 cm (Fig. 6A). These values for distance and angular deviation at the N-2 point were not significantly different from those of the control animals (distance $P > 0.2$, angular deviation $P > 0.18$). The coefficient of correlation r between angular deviation and distance was 0.11, indicating that the threshold detection range around the

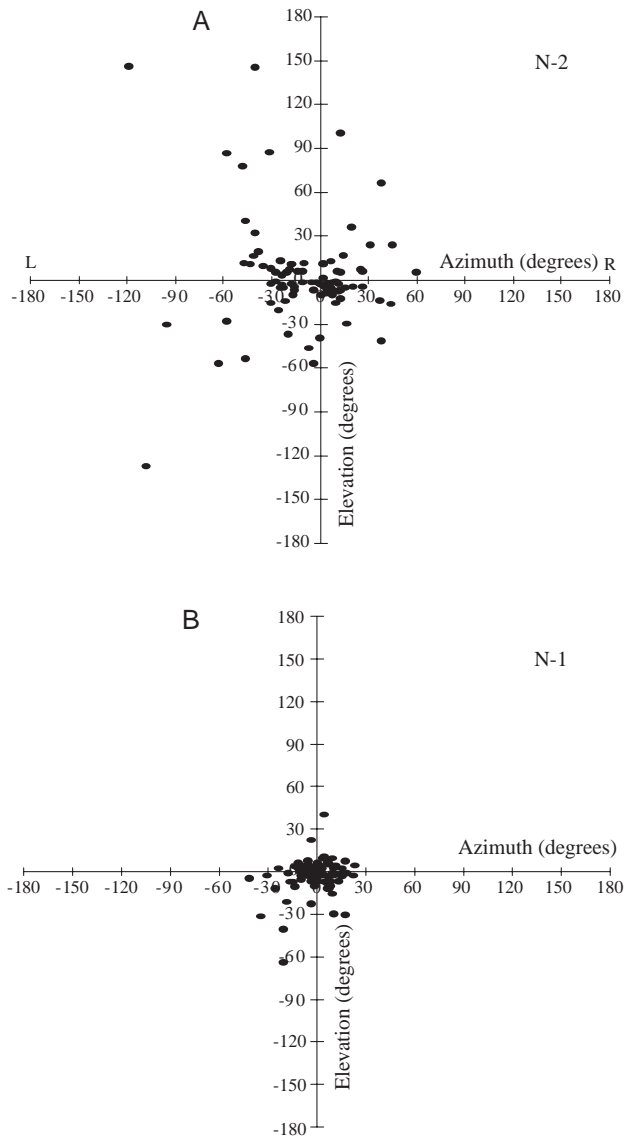


Fig. 5. Polar coordinate plots illustrating angular deviations of individual strikes at the N-2 (first orientation to prey) and N-1 (initiation of strike) positions in animals with lateral line activity suppressed by treatment with CoCl_2 . (A) Measurements made at the N-2 position. (B) Measurements made at the N-1 position. L, left; R, right.

muskellunge's body did not change systematically with increasing angular deviation (Fig. 6A).

However, the angular deviation and distance calculated from the N-1 point in the feeding behavior of lateral-line-deprived muskellunge were significantly different from those of the control animals at the N-1 point. The muskellunge in this group closed to significantly smaller distances and angles before initiating a rapid lunge towards the minnow (distance $P < 0.01$, angular deviation $P < 0.02$). The mean distance at N-1 in these animals was 10.1 ± 0.8 cm (Fig. 6B), and the mean angular deviation was $11.6 \pm 1.1^\circ$ (Fig. 5B). The mean of the absolute value of the azimuth was $8.1 \pm 0.7^\circ$, and the mean of the absolute value of elevation was $6.5 \pm 0.9^\circ$.

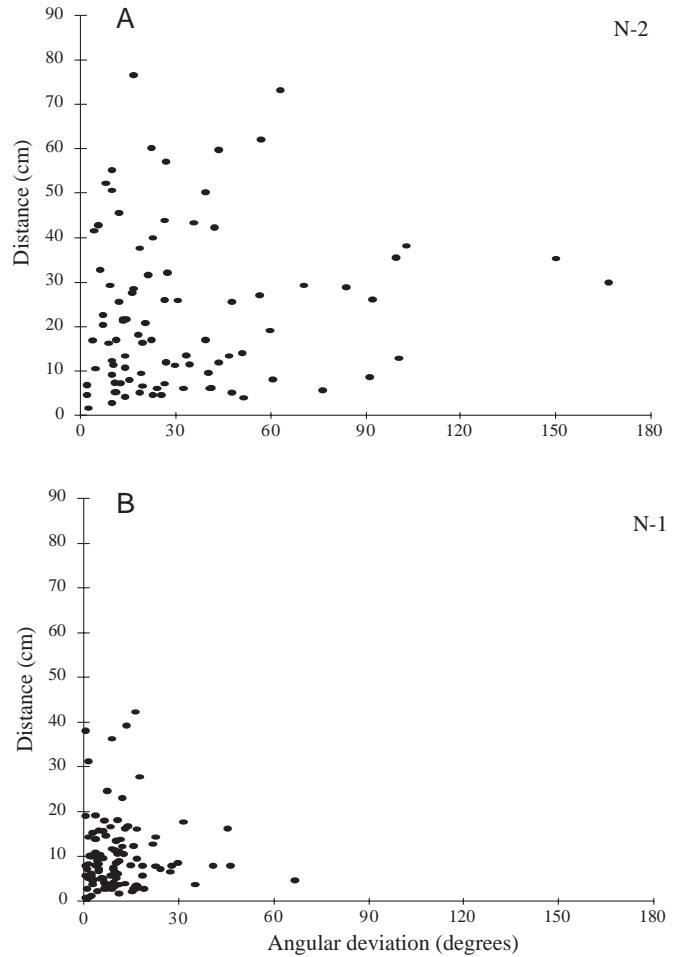


Fig. 6. Plots of distance *versus* angular deviation for individual trials at the N-2 (first orientation to prey) and N-1 (initiation of strike) positions of CoCl_2 -treated animals. (A) N-2 position. (B) N-1 position.

The lateral-line-suppressed muskellunge were even more successful at prey capture than were the control animals, with a success rate of 84.4%, although this difference was not significant. This result may have been because the muskellunge were closing to smaller distances and angles before initiating the strike. A frequency distribution of successful and unsuccessful strikes *versus* distance demonstrated a similar distribution pattern to that of the control animals (albeit with a smaller mean distance), with the majority of hits falling within 1 S.D. of the mean and a smaller number of hits occurring at greater ranges (Fig. 7B). Far strikes initiated by this group (N-1 at greater than the mean +1 S.D., i.e. >18.1 cm) were analyzed and revealed differences from the control group. Far strikes were initiated in these lateral-line-suppressed animals only when the angular deviation between the minnow and the longitudinal axis of the muskellunge was less than 20° , and successful strikes were initiated only when the angular deviation was less than 5° from the longitudinal midline axis (Fig. 8B). However, as with the control animals, 80% of these far

strikes were initiated when the minnow was moving away from the midline axis of the muskellunge.

Blinded group

Muskellunge that had been blinded bilaterally by optic nerve transection were able to feed on minnows, although they did not display the full strike feeding behavior seen in control and lateral-line-suppressed animals. In total, 114 feeding strikes were recorded for the muskellunge in this group, and all were initiated directly from the N-1 position without a preceding N-2 to N-1 'stalk'. Typically, these fish remained relatively motionless in the tank until a minnow approached within a fairly small distance. The muskellunge then initiated a rapid lunge directed at the minnow, similar to those described at the N-1 point in the control and lateral-line-suppressed animals. Hence, the initial orientation and 'stalking' behavior (between points N-2 and N-1) were not observed in blinded fish. The mean distance of the N-1 point in these fish was 3.2 ± 0.2 cm (Fig. 9B) and the mean angular deviation was $7.4 \pm 0.7^\circ$ (Fig. 9A; Table 1). The mean of the absolute value of elevation was $5.2 \pm 0.7^\circ$ and the mean of the absolute value of azimuth

was $4.3 \pm 0.3^\circ$ (Fig. 9A). These angles and distances were all significantly smaller than those in both the control and lateral-line-suppressed groups (blind *versus* control and blind *versus* CoCl_2 -treated; distances and angular deviations $P < 0.005$). The muskellunge were generally as successful in these strikes as were the control animals (73%); however, since these attempts all occurred within a small range of distances from the muskellunge, we did not consider any of them to be far strikes as defined for the other experimental groups (Fig. 10).

Blinded and lateral-line-suppressed group

The fourth group consisted of animals ($N=3$) that had been both bilaterally blinded and lateral-line-suppressed. No feeding behavior was observed in these animals despite prolonged observations and the presence of one, several or many minnows. The animals remained relatively motionless, although with normal posture, for long periods and consistently ignored minnows swimming even at very close distances.

Unilaterally blinded animals

Unilaterally blinded animals also pursued and captured prey

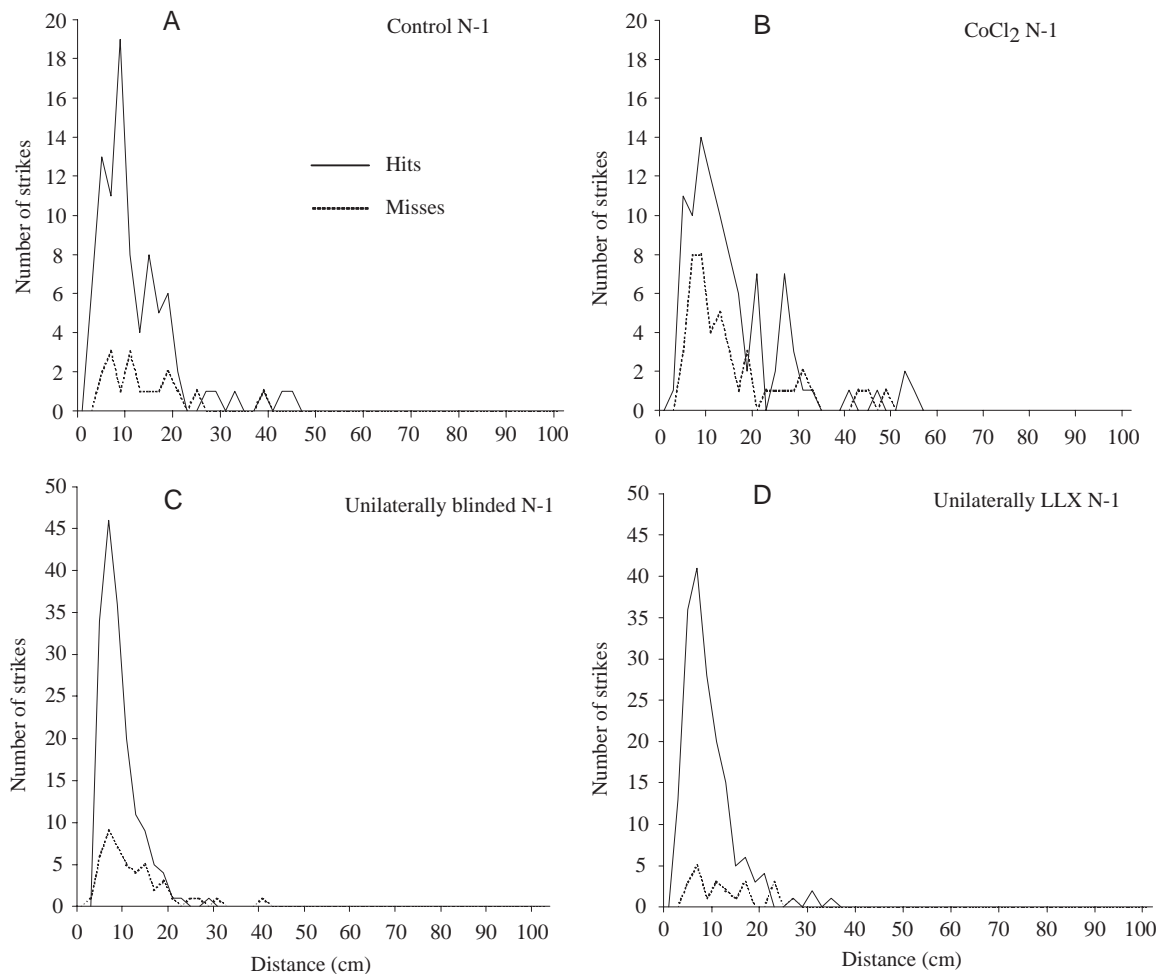


Fig. 7. Frequency distribution of feeding strikes as a function of distance at the N-1 (initiation of strike) position in (A) control, (B) CoCl_2 -treated, (C) unilaterally blinded and (D) unilaterally lateral-line-nerve denervated (LLX) animals. The solid lines indicate successful attempts at prey capture, and the broken lines indicate failed attempts.

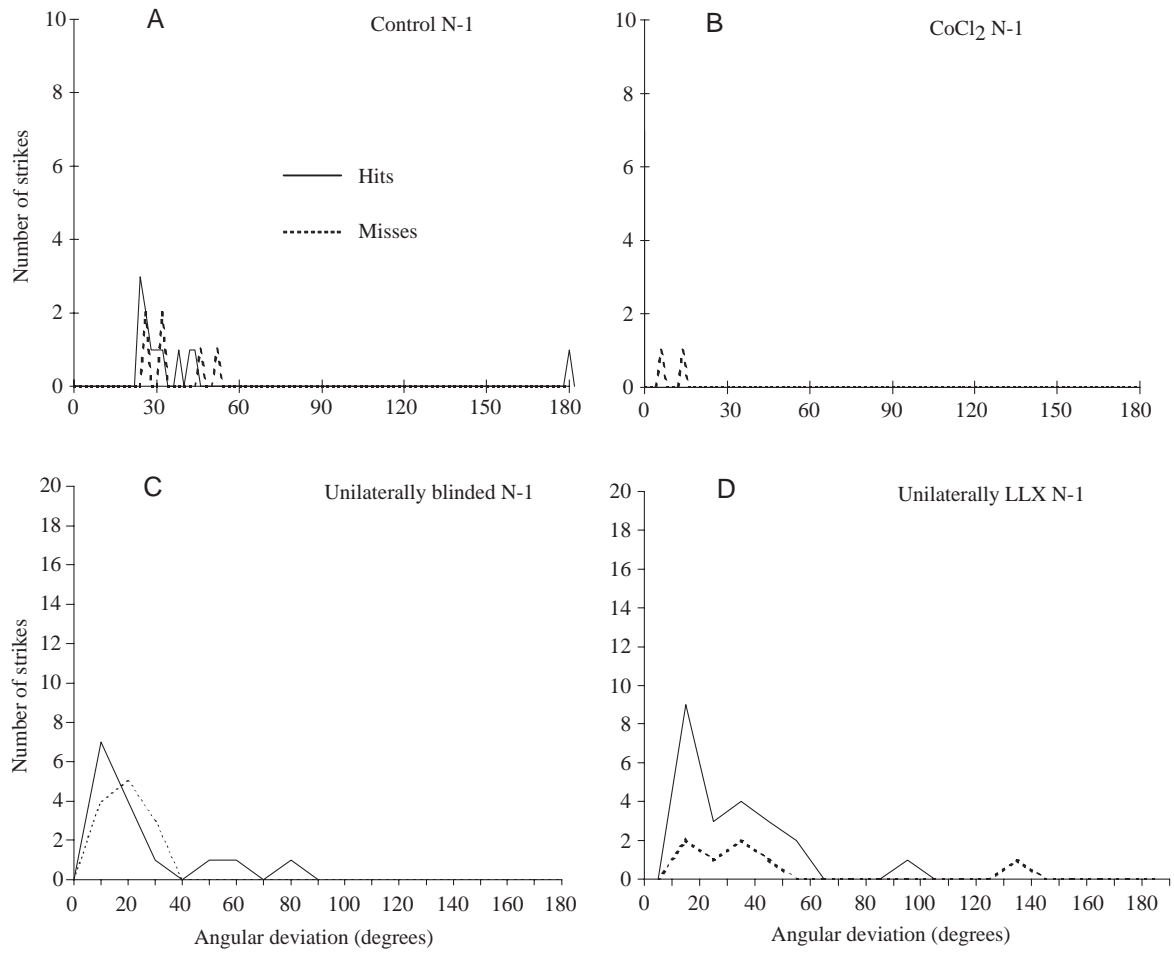


Fig. 8. Frequency distribution of angular deviations at the N-1 (initiation of strike) strike position for far strikes. 'Far strikes' are those that occur at N-1 distances greater than the mean +1 s.d. from the prey. (A) Control animals, (B) CoCl₂-treated fishes, (C) unilaterally blinded fishes and (D) unilaterally lateral-line-denervated (LLX) animals (D).

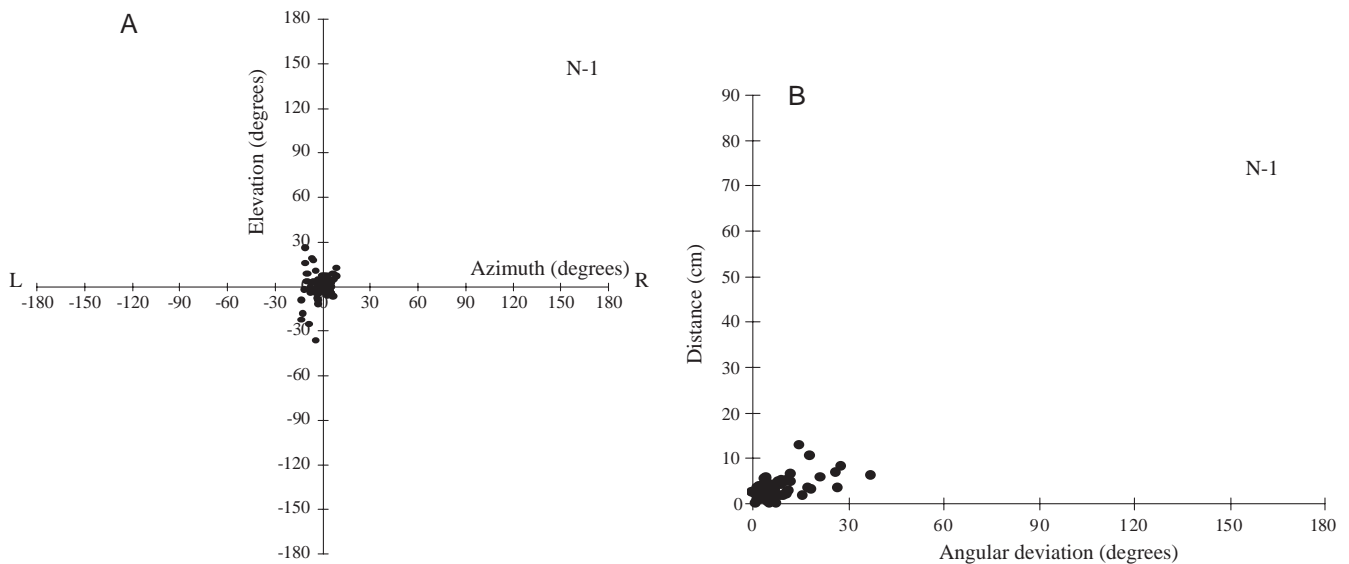


Fig. 9. (A) Polar coordinate plots illustrating angular deviations of individual strikes at the N-1 (initiation of strike) position in blinded muskellunge. L, left; R, right. (B) Plot of distance *versus* angular deviation for individual trials at the N-1 position of blinded animals.

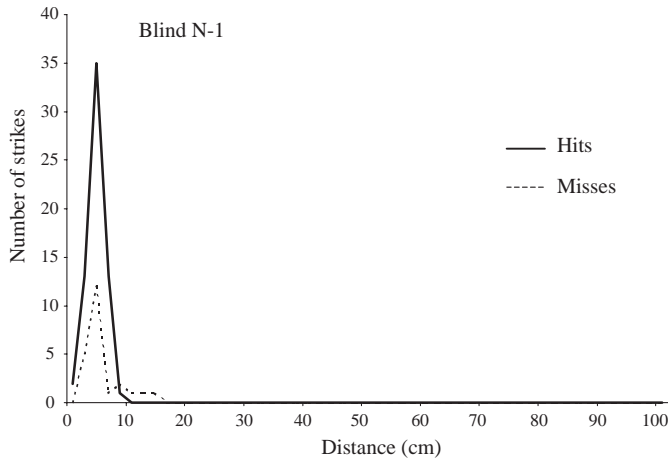


Fig. 10. Frequency distribution of feeding strikes as a function of distance at the N-1 (initiation of strike) position in blinded muskellunge. The solid line indicates successful attempts at prey capture and the broken line indicates failed attempts.

following the same sequence of behaviors as described for the control fishes, i.e. an N-2 to N-1 stalk followed by a rapid lunge directed at the prey. In total, 224 strikes were recorded in these animals, all but two of these involving both N-2 and N-1 positions during the strike at the prey. In these fishes, the initial orientation to the prey at the N-2 position was generally on the sighted side of the animal, and no N-2 orientations were observed to minnows on the blinded side at azimuth angles of greater than 20° from the rostral midline axis (Fig. 11A). The mean distance to the prey at the N-2 position in these fish was $27.41.2 \pm \text{cm}$ (Fig. 12A), which was not significantly different from the N-2 distance in control animals ($P > 0.5$) or from that of the bilaterally lateral-line-suppressed animals ($P > 0.5$). However, the mean angular deviation between the muskellunge and the prey minnow ($62.7 \pm 4.0^\circ$) (Fig. 11A; Table 1) was much larger than that of the control animals ($P < 0.001$) and of the bilaterally lateral-line-suppressed animals ($P < 0.01$). The mean of the absolute values of the angles of elevation was $42.6 \pm 3.3^\circ$, and the mean of the absolute values of the azimuth angles was $38.2 \pm 3.3^\circ$.

The mean angular deviation at the N-1 position was $10.9 \pm 0.9^\circ$ (Fig. 11B). As at the N-2 position, these angles were almost uniformly on the sighted side of the animal; the maximum azimuth angle on the blinded side in the relatively few cases in which such angles occurred was less than 20° from the rostral midline. The mean angular deviation was not significantly smaller than the control N-1 angular deviation ($P > 0.1$), but was significantly greater than that of the bilaterally lateral-line-suppressed animals ($P < 0.05$) and that of the bilaterally blinded animals ($P < 0.01$). The mean of the absolute values of the elevation angles was $6.5 \pm 0.5^\circ$ and that of the angles of azimuth was $6.3 \pm 0.4^\circ$. The mean distance at the N-1 position in unilaterally blinded fish was $7.8 \pm 0.4 \text{ cm}$ (Fig. 12B), which was significantly shorter than that of the control animals at the N-1 position ($P < 0.01$) and the bilaterally

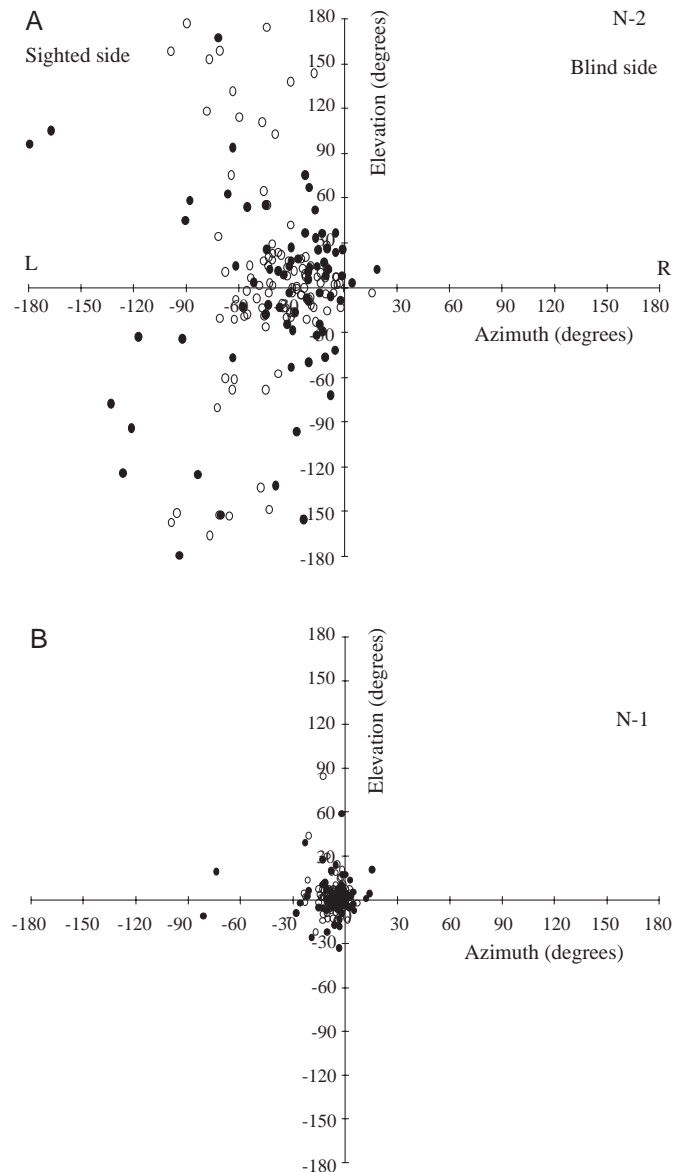


Fig. 11. Polar coordinate plots illustrating angular deviations of individual strikes at the N-2 (first orientation to prey) and N-1 (initiation of strike) positions in unilaterally blinded muskellunge. The left side of each plot represents the side of the animal with intact vision and the right side represents the blinded side. Filled circles represent animals blinded in the right eye, and open circles represent animals blinded in the left eye. (A) Measurements made at the N-2 position. (B) Measurements made at the N-1 position. L, left; R, right.

lateral-line-suppressed animals ($P < 0.01$) and significantly greater than that of the bilaterally blinded animals ($P < 0.001$).

A frequency distribution of strikes as a function of distance at the N-1 position demonstrated a unimodal distribution with no clear relationship between the distance at which the strike was initiated and the success of the strike (Fig. 7C). There were relatively fewer far strikes than in the control or CoCl_2 -treated animals and, unlike those animals, there was a broader distribution of angles from which these far strikes were

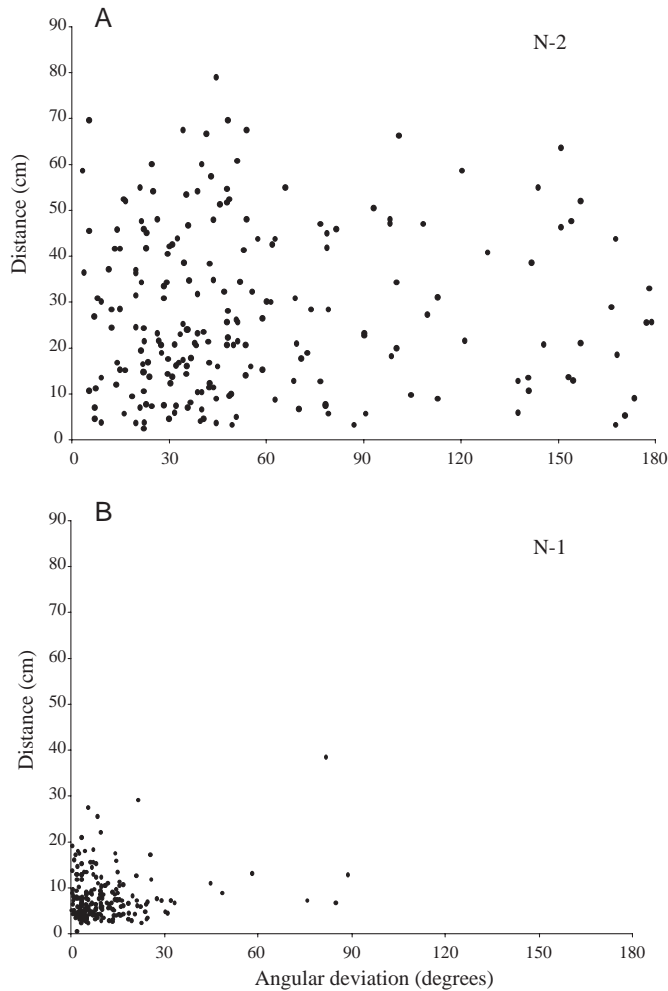


Fig. 12. Plots of distance *versus* angular deviation for individual trials at the N-2 (first orientation to prey) and N-1 (initiation of strike) positions of unilaterally blinded muskellunge. (A) N-2 position. (B) N-1 position.

initiated (Fig. 8C). The range of N-1 angular deviations of these far strikes encompassed those of both the control and CoCl_2 -treated animals.

Unilaterally lateral-line-denervated animals

Animals in which the lateral line system had been suppressed by unilateral lateral line nerve transection also exhibited the normal pattern of strike feeding proceeding from N-2 orientation to N-1 strike and capture of the prey. In total, 204 strikes were analyzed in these animals, all except one of these involved both the N-2 and N-1 positions during the course of the strike. Muskellunge that had been unilaterally denervated were successful at catching minnow prey 86% of the time. The mean angular deviation in these animals at the N-2 position was $73 \pm 4.4^\circ$ (Fig. 13A), which was significantly greater than that of control animals ($P < 0.01$) and of animals in which the lateral line had been suppressed bilaterally with CoCl_2 ($P < 0.01$). The mean of the absolute values for the angles of elevation was $55.9 \pm 4.3^\circ$, and that of the angles of azimuth

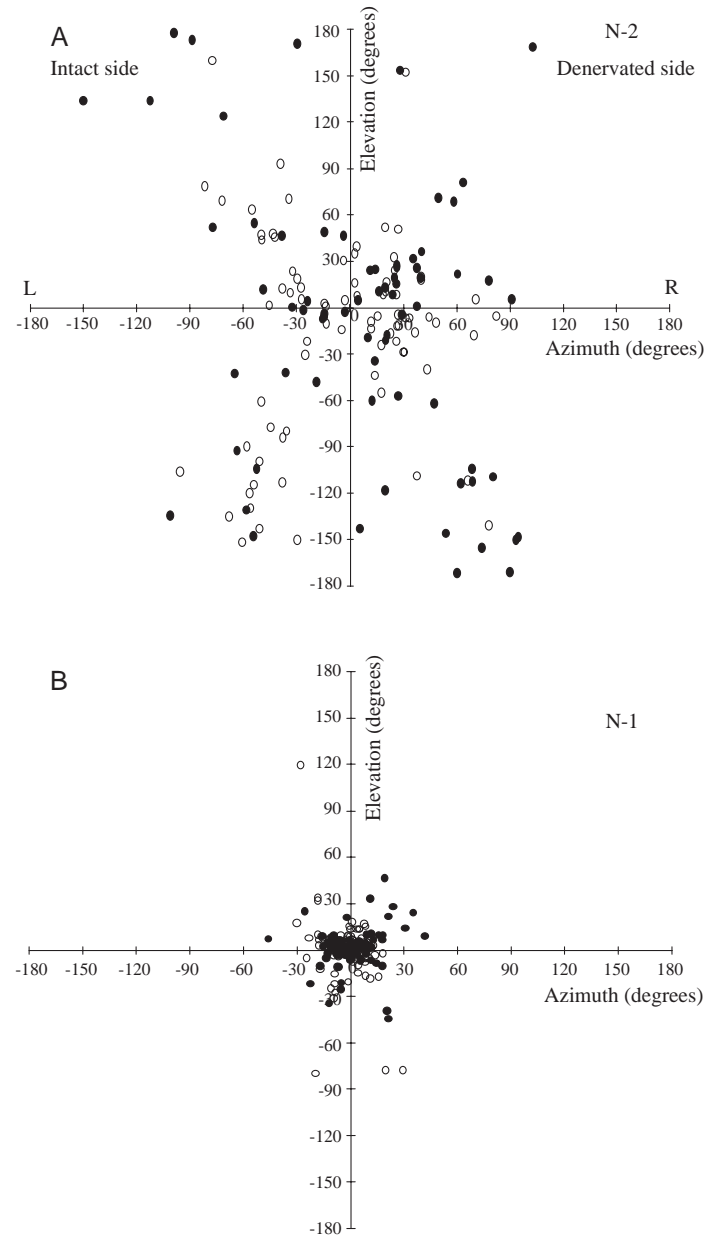


Fig. 13. Polar coordinate plots illustrating angular deviations of individual strikes at the N-2 (first orientation to prey) and N-1 (initiation of strike) positions in muskellunge in which the lateral line system had been unilaterally denervated as described in the text. The left side of each plot represents the side of the animal with an intact lateral line, and the right side represents the denervated side. Filled circles represent animals denervated on the right side, and open circles represent animals denervated on the left side. (A) Measurements made at the N-2 position. (B) Measurements made at the N-1 position. L, left; R, right.

was $40.1 \pm 2.2^\circ$ (Fig. 13A). The mean angular deviation at N-2 in these fishes was not significantly different from that of the unilaterally blinded animals ($P > 0.05$). Unlike the unilaterally blinded animals, however, the N-2 angles in these fishes were equally distributed on either side of the midline irrespective of

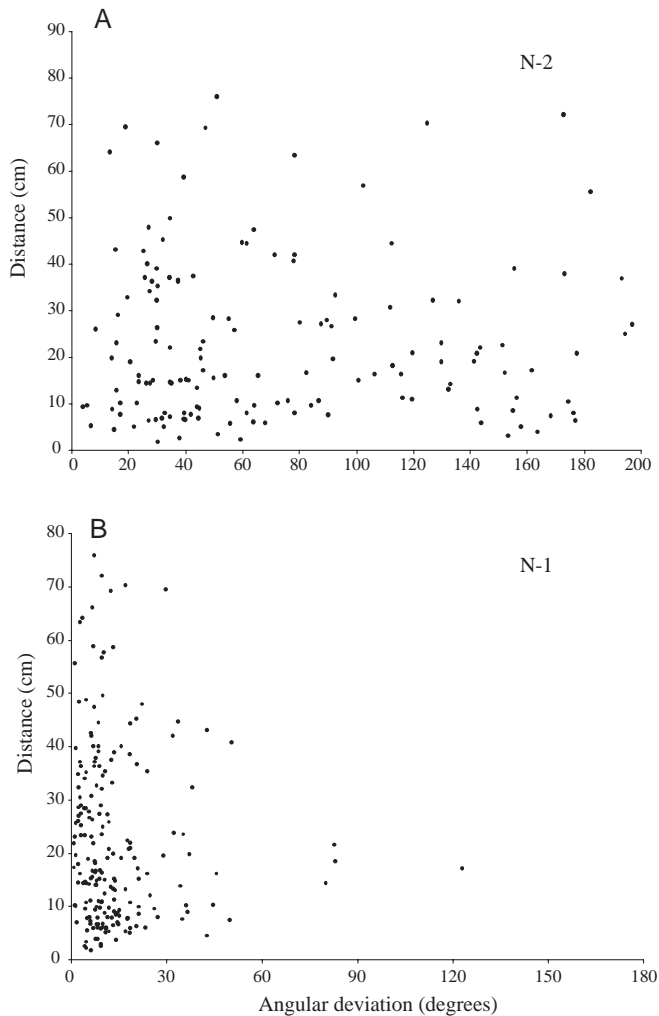


Fig. 14. Plots of distance *versus* angular deviation for individual trials at the N-2 (first orientation to prey) and N-1 (initiation of strike) positions of unilaterally lateral-line-denervated muskellunge. The filled circles are the data from individual trials. (A) N-2 position. (B) N-1 position.

which side had been denervated. The mean distance at the N-2 position was 22.2 ± 1.2 cm (Fig. 14A). This was not significantly different from the values for either the control or the CoCl_2 -treated animals ($P > 0.5$ for both), nor was it significantly smaller than the mean N-2 distance for unilaterally blinded animals ($P > 0.6$).

The mean of the absolute values of the elevation angles at the N-1 position was $8.8 \pm 1.0^\circ$, and the mean of the absolute values of the angles of azimuth was $8.7 \pm 0.6^\circ$. The mean angular deviation calculated from these values was $13.7 \pm 1.1^\circ$ (Fig. 13B; Table 1). This was not significantly different from the angular deviations for the control animals ($P > 0.1$), for the bilaterally lateral-line-suppressed group ($P > 0.05$) or for the unilaterally blinded group ($P > 0.3$), but was significantly greater than that of both the bilaterally blinded group ($P < 0.01$) and the unilaterally lateral-line-suppressed group ($P > 0.01$). The mean distance at the N-1 position was 7.4 ± 0.4 cm

(Fig. 14B), which was significantly smaller than those of the control and the CoCl_2 -treated groups ($P < 0.01$ for both groups), but not significantly different from that of the unilaterally blinded group ($P > 0.4$). The mean N-1 distance for this group was also significantly greater than that of the bilaterally blinded animals ($P < 0.01$).

The frequency distribution of successful and unsuccessful capture attempts as a function of the N-1 distance exhibited a similar pattern to those seen in the control animals (Fig. 7D), with no clear relationship between the distance at which the strike was initiated and the success or failure of the strike. However, an analysis of the far strikes (those initiated at distances greater than the mean $+1$ s.d.; > 12.8 cm) demonstrated that, as in the unilaterally blinded animals, the range of angles at which far strikes were initiated was greater than that for either control or lateral-line-suppressed animals and encompassed the range of both of the latter (Fig. 8D).

Discussion

Our study demonstrates that the relative importance, or role, of a given sensory system may change during different portions of a behavioral sequence. In muskellunge, vision is of primary importance in the initial location of, and orientation to, the prey. Both vision and the lateral line system play a role in determining the optimal distance and angle from which to launch the rapid strike at the prey. The lateral line system may be of principal importance in the capture of the prey in the final stages of the strike. Hence, there is a 'sliding hierarchy' of sensory system dominance during each consecutive portion of the strike, with each system playing a more or less important role during each phase.

This study has demonstrated significant and important differences in the roles played by the visual and lateral line sensory systems during the successive stages of the strike feeding behavior in muskellunge. In general, data from control animals agree with those of Webb and Skadsden (Webb and Skadsden, 1980) for tiger muskellunge (a muskellunge:northern pike hybrid) with only a few exceptions. Unlike Webb and Skadsden (Webb and Skadsden, 1980), we did not discriminate between what they described as pattern A and pattern B initiations of the strike. They describe a 'stalk', the equivalent of our progression from the N-2 to N-1 positions, in only 20% of their cases leading to a strike, whereas we observed the stalk in the majority of our control cases (78%). However, they do mention an 'initial orientation using paired and median fins' that may be equivalent to our initial stalk. The frequency distribution of their observed strike distances (Webb and Skadsden, 1980) corresponds well with our own N-1 distances, although their measurements were made only in the horizontal plane, whereas we measured actual distance, including both vertical and horizontal displacements. The angular measurements they provided were between the longitudinal midline axes of the predator and the prey in the horizontal plane, so it is not possible to compare their data

directly with our own. The success rate of 73 % they observed corresponds to the rate of success of our control animals.

The visual system clearly plays the dominant role in the initial localization of, and orientation to, the prey. There were no significant differences between the mean distance of detection at the N-2 position in control, CoCl₂-treated, unilaterally blinded or lateral-line-denervated animals, indicating that muskellunge are hunting for their prey visually. The lack of a significant difference in the N-2 angular deviation between control and CoCl₂-treated animals further strengthens this idea. Behavioral studies of visual acuity in the larval pomacentrid reef fish *Pinnaeus biaculaetus* have demonstrated a tendency to prefer prey in the anterior visual field (Job and Bellwood, 1996). Subadult muskellunge also demonstrate this tendency; in bilaterally sighted animals, there was no significant increase in the mean N-2 orientation distance through all angular deviations, but the majority of these orientations were to animals in the anterior portion of the visual field. Blinded muskellunge did not exhibit the N-2 orientation and slow approach to the N-1 position observed routinely in sighted fish, but instead remained relatively motionless in the water and appeared to strike opportunistically at minnows that moved close to their head.

Both visual and lateral line systems play a role in the determination of the optimum distance and angle at which to initiate the rapid strike portion of the behavior from the N-1 position. Muskellunge typically decrease the distance and angular deviation between their midline body axis and the prey between the N-2 and N-1 positions, but control muskellunge typically attack from greater distances and angles than do those in which the lateral line system has been suppressed by CoCl₂ treatment. Without lateral line afference, muskellunge attack from significantly closer distances and with smaller angular deviations. The reason for this difference may lie in the differing natures of the visual and lateral line stimuli and in the orientations of the visual and lateral line systems. Modeling of hydrodynamic flow and lateral line systems has demonstrated that the azimuth of a stimulus source is encoded by the location of the maximum pressure gradient amplitude upon the spatially distributed array of lateral line receptors. Source distance, in contrast, is determined by the spread of the excitation pattern: the greater the distance from the source, the greater the spread of excitation across the receptor array. This is in contrast to the visual system, in which the visual arc subtended by a given stimulus, and hence the spread of receptor activation, decreases with distance (Coombs and Conley, 1997a; Coombs and Conley, 1997b; Conley and Coombs, 1998). Behavioral studies in blinded mottled sculpin (*Cottus bairdi*) have shown that these fish employ an approach strategy in which a source stimulus is approached at an angle rather than along a straight path (Coombs and Conley, 1997a). In this manner, lateral line information may be maximized across the neuromasts of the head and trunk. Similarly, control muskellunge tend to approach prey at an angle (the angular deviations at the N-2 and N-1 positions). However, muskellunge in which the lateral line system has been suppressed by CoCl₂ significantly

decrease their angular deviation at N-1, approaching the prey in a more directly 'head-on' fashion. These data suggest that the visual system may be directed more towards stimuli located ahead of the animal, whereas the lateral line system, which is distributed along the sides of the head and body, is more laterally directed.

Further evidence for this may be observed in the differences in 'far strike' approaches between control and lateral-line-suppressed muskellunge. Lateral-line-suppressed muskellunge employ a different strategy when attempting 'far strikes' at prey (from distances greater than the mean distance +1 S.D. of all strikes). In the control muskellunge, the fish attempted far strikes at prey that were invariably at angular deviations greater than 20° from the midline and were, in the majority of cases, moving away from the midline axis of the animal. We suggest that this relative minority of cases may represent a 'desperation strike' in which the muskellunge finds itself with a difficult approach to a prey moving away from the preferred orientation and commits itself to an early attack at a range greater than the normal distribution of ranges.

In muskellunge in which the lateral line has been suppressed by CoCl₂ treatment, the strategy that appears to motivate far strikes is the opposite of that in the controls. In these animals, strikes are initiated only when the prey is less than 20° from the midline axis in the frontal visual field and, in the majority of cases, is swimming away from the midline. Successful far strikes in these animals were recorded only when the prey was directly ahead of the subject fish. We suggest that what may motivate these attacks is the lack of lateral line afference and, simultaneously, a target located at the distance and orientation for which the bilateral visual fields of the muskellunge overlap ahead of the animal.

The retinotectal projections of esocids are entirely contralateral, so information from a single retina projects only to a single tectal hemisphere (Reperant et al., 1976; Bazer and Ebbeson, 1987; J. G. New and D. E. Kolak, unpublished observations). A moving image on regions of the paired tectal hemispheres that represent the anterior overlap of the visual fields in these cases may result in release of the strike behavior. It is interesting in this context to observe that, in our unilaterally blinded animals, far strikes were very uncommon compared with the control or CoCl₂-treated animals, further suggesting that the rostral overlap of the bilateral visual fields may influence far strike behaviors.

Blinded muskellunge are quite capable of successfully striking at and capturing prey minnows, although from significantly smaller distances and angular deviations than the N-1 positions recorded from control or CoCl₂-treated animals. This suggests that, although the lateral line provides useful information in determining the optimum distance and angle at which to initiate the strike from the N-1 position, the threshold for the release of a strike behavior on the basis of lateral line afference alone is considerably higher than it is when visual input is also present. Lateral line afference may provide useful information concerning the location of the prey during the final stages of the attack as the muskellunge completes its lunge

towards the minnow. The blinded muskellunge were, in general, as successful at catching prey as the sighted muskellunge, suggesting that lateral line afference conveys all the critical information required by the muskellunge to catch the prey at close range.

In the unilaterally blinded and lateral-line-denervated fishes employed in this study, the mean distance at the N-2 position was not significantly different from those of the control or CoCl₂-treated animals. This lack of difference in the N-2 orientation distance in all sighted muskellunge suggests that there is a mean minimum threshold for visually guided orientation to prey. The mean length of the fathead minnows employed in this study was approximately 5 cm. At a distance of 25.5 cm (the mean N-2 distance in the control animals), a 5 cm minnow subtends a maximum angle of approximately 11° within the visual field. This may represent the minimum size of an object moving within the visual field required to release the initial orientation of a strike feeding sequence. Teleosts have been demonstrated to display size constancy in their visual behavior, which allows the animal to determine the size of an object on the basis of the visual angle and the distance to the target (Douglas et al., 1988). In some cases, however, fishes tend to rely solely upon the visual angle subtended by a target (Douglas and Hawryshyn, 1990). Thus, any moving object subtending a given critical angle within the visual field may serve as a 'releaser' initiating an approach.

The unilaterally deprived animals did not behave simply as 'half-animals' in their orientation or approach to the prey. The angular deviations for both unilaterally blinded and lateral-line-denervated muskellunge at the N-2 positions were significantly larger than those of the control or CoCl₂-treated groups. Although it is not possible to determine precisely what the muskellunge were experiencing, the data suggest that unilaterally deprived animals attend more to regions of the intact field that are of lesser importance to the control animals. Thus, unilaterally blinded muskellunge are more likely to detect prey at greater angles within the remaining intact portions of the visual field than are sighted muskellunge. Similarly, the deprivation of unilateral lateral line afference may result in the muskellunge attending more to a wider region of the visual field than do control fishes. If this is the case, it is then not clear why there was no significant difference between the N-2 angular deviations of control muskellunge and of fishes in which the lateral line system had been bilaterally suppressed with CoCl₂. It is possible that, in denervating these animals *via* an approach to the anterior lateral line nerves through the orbit, some damage may have been done to the visual system on that side. However, there was no significant difference in N-2 range or angular deviation between the intact and denervated sides in these animals, indicating that the visual system was intact and functioning.

In the unilaterally blinded animals, the angular deviation at the position at which the strike was initiated (N-1) was significantly greater than that of the bilaterally blinded animals, as was the distance between the muskellunge and the prey. It

is possible that, in closing the distance and angular deviation between the N-2 and N-1 positions, some useful visual information was lost to the fish as a result of the minnow moving relative to the anteromedial boundary of the visual field. With the minnow at the very edge of the visual field, and perhaps moving out of it, the muskellunge may have relied more on lateral line input in judging the optimal distance and angle from which to launch the strike.

The unilaterally lateral-line-denervated animals initiated the N-1 strike at angular deviations that overlapped those of the control and CoCl₂-treated animals, although the range from which strikes were initiated was significantly less in the denervated animals than in the control group. In these animals, a degree of lateral line input was removed by denervation but some necessarily remained intact, at the least from the side contralateral to denervation. It is possible that, in the denervated animals, spatial information was still provided to the rest of the lateral line system, permitting a 'normal' approach to the N-1 position. However, the decreased sensitivity resulting from unilateral denervation may have caused the animal to overestimate the range to the prey and to move closer before achieving sufficient lateral line input to release the behavior. The data from the unilaterally blinded and denervated animals are complex and difficult to interpret, and our interpretations of the relative roles of the sensory systems in these cases are necessarily speculative.

Other sensory systems did not seem to play an important role in the direct orientation towards, or strike at, the minnow prey. We assume that the fish's auditory system remained intact; physiological studies have demonstrated that CoCl₂ immersion has little effect upon the activity of the inner ear endorgans in fishes (Karlsen and Sand, 1987). Furthermore, the CoCl₂-treated muskellunge maintained normal balance and swimming postures, suggesting that the inner ear hair cell systems were unaffected by the treatment. Moreover, although the immersion treatment may have produced a degree of physiological stress as a result of osmoregulatory considerations, the muskellunge did not appear to be significantly affected by the treatment and fed actively and enthusiastically after a brief period of adaptation to the test arena. It is likely that the blinded and CoCl₂-treated animals were capable of hearing minnows swimming nearby, and it is possible that such information plays a role in the strike feeding behavior. However, in the absence of visual and lateral line input, auditory afference by itself is insufficient to elicit a feeding response in these fish. Olfaction may also play an important role in the feeding behavior of muskellunge, which are well equipped with olfactory apparatus. However, olfactory cues diffusing through the water column are unlikely candidates for organizing a well-directed and rapid strike at a small, rapidly moving prey item. It seems more likely that olfaction may play a role in potentiating feeding behavior, mediating arousal cues that result in the animal searching for prey.

Behavioral studies conducted early in this century (Hofer, 1908) demonstrated that blinded pike (*Esox lucius*) were able

successfully to strike at minnows and that this ability disappeared after bilateral denervation of the lateral line. Other studies of feeding behavior in esocids and other teleost fishes (e.g. Alexander, 1970; Webb and Skadsden, 1980; Rand and Lauder, 1981; Lauder, 1983; Lauder, 1986; van Leeuwen, 1983; Cooper et al., 1985; Muller et al., 1985; Nyberg, 1986; Norton, 1993; Brown et al., 1995) have focused principally upon the kinematics of feeding strikes, foraging strategies and mechanisms of prey capture. A number of studies have focused on the use of the lateral line system in feeding and swimming behaviors (Montgomery and Saunders, 1985; Saunders and Montgomery, 1985; Bleckmann et al., 1989; Montgomery, 1989; Montgomery and Milton, 1993; Montgomery et al., 1997). A brief report (Enger et al., 1989) demonstrated that the feeding behavior of bluegill sunfish (*Lepomis macrochirus*) in the dark was impaired after suppression of the lateral line system with CoCl_2 . Under these conditions, bluegills struck only at prey goldfish (*Carassius auratus*) following direct contact; their ability to strike from even a short distance ($<0.2\text{ cm}$) was abolished. Studies by Janssen and his collaborators (Janssen et al., 1995; Janssen, 1996; Janssen, 1997) have demonstrated that planktivorous fishes rely upon their lateral line systems to localize and obtain prey in the absence of visual input. Coombs and Conley (Coombs and Conley, 1997a; Coombs and Conley, 1997b) have demonstrated that blinded mottled sculpin (*Cottus bairdi*) use their lateral line system in detecting, orienting to and striking at vibratory sources that apparently mimic prey. Furthermore, Conley and Coombs (Conley and Coombs, 1998) demonstrated that unilateral denervation of branches of the lateral line nerves in blinded sculpin produced site-specific deficits in the animal's ability to localize a vibrating sphere. All these studies have indicated that the spatial array of neuromasts across the body surface provides sufficient information for the localization of and orientation to the vibrating source. Janssen (Janssen, 1997) further suggests that the elaborated canal system of the ruffe, *Gymnocephalus cernuus*, provides increased sensitivity for this species, which typically inhabits environments in which visibility is reduced.

There is a large literature on the visual systems and capabilities of teleost fishes (for a review, see Douglas and Djamgoz, 1990) but relatively fewer studies relating visual processing to feeding behavior using behaviorally relevant stimuli. Studies of visual acuity and performance in fish have generally relied upon behavioral or anatomical techniques. A brief study by Janssen and Corcoran (Janssen and Corcoran, 1993) demonstrated that lateral line stimuli can override visual input in directing the feeding strikes of centrarchid fishes. In this study, green sunfish (*Lepomis cyanellus*) and largemouth bass (*Micropterus salmoides*) trained to feed from a feeding tube tended to strike at a simultaneously presented water jet in preference to the visually presented food source. More recently, von der Emde and Bleckmann (von der Emde and Bleckmann, 1998) have examined the roles of a number of sensory modalities including vision and low- and high-frequency-sensitive electrosensory systems in

the ability of the weakly electric mormyrid fish *Gnathonemus petersii* to locate prey. In that study, the principal measurement was the time required by the subject fish to locate a worm hidden in a test arena. In addition, the investigators were unable to determine the role of the lateral line system because of the sensitivity of the animals to CoCl_2 . These studies emphasize the complementarity of sensory systems in prey capture behavior and their hierarchical organization.

A recent study (Liang et al., 1998) examined the roles of vision, olfaction and the lateral line system in the Chinese perch *Siniperca chuatsi*. The results indicated no significant differences in the number of prey captures within a fixed interval between control fish and test fish with either the lateral line or the visual system blocked. Perch with both systems blocked, however, demonstrated greatly reduced feeding in a manner similar to the muskellunge in our study. Since the study by Liang et al. (Liang et al., 1998) did not employ the same quantitative approach as our study does, it is difficult to draw extensive comparisons between their results and our own. It is our belief, on the basis of experience, that blinded muskellunge would not capture prey at the same rate as control or lateral-line-suppressed animals. This may be because muskellunge employ an 'ambush' strategy rather than a more active foraging strategy. We can say, however, that in Chinese perch, as in muskellunge, both vision and the lateral line system provide adequate information for the capture of prey, but that suppression of both systems strongly inhibits the animal's ability to feed successfully.

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References

- Alexander, R. McN. (1970). Mechanisms of the feeding action of various teleost fishes. *J. Zool., Lond.* **160**, 145–156.
- Bazer, G. T. and Ebbesson, S. O. E. (1987). Retinal projections in the chain pickerel (*Esox niger* LeSueur). *Cell Tissue Res.* **248**, 227–229.
- Bleckmann, H., Tittel, G. and Blübaum-Grönau, E. (1989). Lateral line system of surface feeding fish: anatomy, physiology and behavior. In *The Mechanosensory Lateral Line: Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 501–526. New York: Springer-Verlag.
- Brown, G. E., Chivers, D. P. and Smith, R. J. F. (1995). Localized defecation by pike: a response to labelling by cyprinid alarm pheromone? *Behav. Ecol. Sociobiol.* **36**, 105–110.
- Conley, R. A. and Coombs, S. (1998). Dipole source localization by mottled sculpin. III. Orientation after site-specific, unilateral denervation of the lateral line system. *J. Comp. Physiol.* **183**, 335–344.
- Coombs, S. and Conley, R. A. (1997a). Dipole source localization by mottled sculpin. I. Approach strategies. *J. Comp. Physiol.* **180**, 387–399.
- Coombs, S. and Conley, R. A. (1997b). Dipole source localization

- by the mottled sculpin. II. The role of lateral line excitation patterns. *J. Comp. Physiol.* **180**, 401–415.
- Cooper, S. D., Smith, D. W. and Bence, J. R.** (1985). Prey selection by freshwater predators with different foraging strategies. *Can. J. Fish. Aquat. Sci.* **85**, 42.
- Douglas, R. H. and Djamgoz, M. B. A.** (1990). *The Visual System of Fish*. New York: Chapman & Hall. 526pp.
- Douglas, R. H. and Hawryshyn, C. W.** (1990). Behavioral studies of fish vision: an analysis of visual capabilities. In *The Visual System of Fish* (ed. R. H. Douglas and M. B. A. Djamgoz), pp. 373–418. New York: Chapman & Hall.
- Douglas, R. H., Eva, J. and Guttridge** (1998). Size constancy in goldfish (*Calassius auratus*). *Behav. Brain Res.* **30**, 37–42.
- Enger, P. S., Kalmijn, A. J. and Sand, O.** (1989). Behavioral identification of lateral line and inner ear function. In *The Mechanosensory Lateral Line: Neurobiology and Evolution* (ed. Coombs, S., Görner, D. and Münz, H.), pp. 575–590. New York: Springer-Verlag.
- Heiligenberg, W. F.** (1991). *Neural Nets in Electric Fish*. Cambridge, MA: MIT Press. 179pp.
- Hofer, B.** (1908). Studien über die Hautsinnesorgane der Fische. I. Die Funktion der Seitenorgane bei den Fischen. *Ber. Kgl. Bayer. Biol. Versuchsstation München* **1**, 115–164.
- Janssen, J.** (1996). Use of the lateral line and tactile senses in feeding in four Antarctic notothenoid fishes. *Env. Biol. Fish.* **47**, 51–64.
- Janssen, J.** (1997). Comparison of response distance to prey via the lateral line in the ruffe and the yellow perch. *J. Fish Biol.* **51**, 921–930.
- Janssen, J. and Corcoran, J.** (1993). Lateral line stimuli can override vision to determine sunfish strike trajectory. *J. Exp. Biol.* **176**, 299–305.
- Janssen, J., Jones, W. R., Whang, A. and Oshel, P. E.** (1995). Use of the lateral line in particulate feeding in the dark by juvenile alewife (*Alosa pseudoharengus*). *Can. J. Fish. Aquat. Sci.* **52**, 358–363.
- Job, S. D. and Bellwood, D. R.** (1996). Visual acuity and feeding in larval *Pemnas biaculatus*. *J. Fish Biol.* **48**, 952–963.
- Karlsen, H. E. and Sand, O.** (1987). Selective and reversible blocking of the lateral line in freshwater fish. *J. Exp. Biol.* **133**, 249–262.
- Lauder, G. V.** (1983). Prey capture hydrodynamics in fishes: experimental tests of two models. *J. Exp. Biol.* **104**, 1–13.
- Lauder, G. V.** (1986). Aquatic prey capture in fishes: experimental and theoretical approaches. *J. Exp. Biol.* **125**, 411–416.
- Liang, X. F., Liu, J. K. and Huang, B. Y.** (1998). The role of sense organs in the feeding behavior of Chinese perch. *J. Fish Biol.* **52**, 1058–1067.
- Montgomery, J. C.** (1989). Lateral line detection of planktonic prey. In *The Mechanosensory Lateral Line: Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 561–574. New York: Springer-Verlag.
- Montgomery, J. C., Baker, C. F. and Carton, A. G.** (1997). The lateral line can mediate rheotaxis in fish. *Nature* **389**, 960–963.
- Montgomery, J. C. and Milton, R. C.** (1993). Use of the lateral line for feeding in the torrentfish (*Cheimarrichthys fosteri*). *N.Z. J. Zool.* **20**, 121–125.
- Montgomery, J. C. and Saunders, A. J.** (1985). Functional morphology of the piper *Hyporhamphus ihi* with reference to the role of the lateral line in feeding. *Proc. R. Soc. Lond. B* **224**, 197–208.
- Müller, M., van Leeuwen, J. L., Osse, J. W. M. and Drost, M. R.** (1985). Prey capture hydrodynamics in fishes: two approaches. *J. Exp. Biol.* **119**, 389–394.
- Norton, S. F.** (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.* **176**, 11–29.
- Nyberg, D. W.** (1971). Prey capture in the largemouth bass. *Am. Midl. Nat.* **86**, 128–144.
- Rand, D. M. and Lauder, G. V.** (1981). Prey capture in the chain pickerel, *Esox niger*: correlations between feeding and locomotor behavior. *Can. J. Zool.* **59**, 1072–1078.
- Reperant, J., Lemire, J., Miceli, D. and Peyrichoux, J.** (1976). A radioautographic study of the visual system in freshwater teleosts following intraocular injection of tritiated fucose and proline. *Brain Res.* **118**, 123–131.
- Saunders, A. J. and Montgomery, J. C.** (1985). Field and laboratory studies of the feeding behaviour of the piper *Hyporhamphus ihi* with reference to the lateral line in feeding. *Proc. R. Soc. B* **224**, 209–221.
- van Leeuwen, J. L.** (1984). A quantitative study of flow in prey capture by rainbow trout, *Salmo gairdneri* with general consideration of the actinopterygian feeding mechanism. *Trans. Zool. Soc. Lond.* **37**, 171–227.
- von der Emde, G. and Bleckmann, H.** (1998). Finding food: Senses involved in foraging for insect larvae in the electric fish *Gnathonemus petersii*. *J. Exp. Biol.* **201**, 969–980.
- Webb, P. F. and Skadsen, J. M.** (1980). Strike tactics of *Esox*. *Can. J. Zool.* **58**, 1462–1469.