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Phil. Trans. R. Soc. Lond. B 2000 **355**, 1321-1324
doi: 10.1098/rstb.2000.0692

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THE ROYAL SOCIETY

doi 10.1098/rstb.2000.0692

Multimodal sensory integration in the strike-feeding behaviour of predatory fishes

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The search for useful model systems for the study of sensory processing in vertebrate nervous systems has resulted in many neuroethological studies investigating the roles played by a single sensory modality in a given behaviour. However, behaviours relying solely upon information from one sensory modality are relatively rare. Animals behaving in a complex, three-dimensional environment receive a large amount of information from external and internal receptor arrays. Clearly, the integration of sensory afference arising from different modalities into a coherent 'gestalt' of the world is essential to the behaviours of most animals. In the last several years our laboratory team has examined the roles played by the visual and lateral line sensory systems in organizing the feeding behaviour of two species of predatory teleost fishes, the largemouth bass, *Micropterus salmoides*, and the muskellunge, *Esox masquinongy.* The free-field feeding behaviours of these fishes were studied quantitatively in intact animals and compared to animals in which the lateral line and visual systems had been selectively suppressed. All groups of animals continued to feed successfully, but significant differences were observed between each experimental group, providing strong clues as to the relative role played by each sensory system in the organization of the behaviour. Furthermore, significant differences exist between the two species. The differences in behaviour resulting when an animal is deprived of a given sensory modality reflect the nature of central integrative sensory processes, and these behavioural studies provide a foundation for further neuroanatomical and physiological studies of sensory integration in the vertebrate central nervous system.

Keywords: vision; lateral line; predatory behaviour; muskellunge; bass

1. INTRODUCTION

The search for useful model systems for the study of sensory processing in vertebrate nervous systems has resulted in numerous neuroethological studies investigating the roles played by a single sensory modality in a given behaviour. These studies have been useful in understanding the structure and function of nervous circuitry, but behaviours relying solely upon information from one sensory modality are rare. Animals behaving in a complex, three-dimensional environment receive a large amount of information from external and internal receptor arrays. All of this information is important in a general sense and some of it may, at any given moment, be useful or indeed vital to the accomplishment of a given behavioural objective. Clearly, the integration of sensory afference arising from different modalities into a coherent 'gestalt' of the world is essential to the behaviours of most animals. However, relatively few neuroethological studies exist that examine the manner in which sensory integration occurs during the course of a given behaviour. The purpose of this report is to provide a brief summary of the studies of multimodal integration that have been conducted in our laboratory.

Over the past several years, we have concerned ourselves with the roles played by the sensory systems of predatory teleost fishes in strike-feeding behaviour. Like all such behaviours, the organization and initiation of a strike at prey is part of a wider spectrum of activities and is dependent upon internal motivational states (i.e. hunger, curiosity) and external circumstances (possible presence of food or predators, environmental conditions, etc.). For the purposes of our studies, we have defined the 'strike-feeding' behaviour as that which occurs beginning with the initial orientation toward a prey, following through the approach and the eventual attempt to capture the prey. We thus have a clearly defined and easily observed behavioural sequence that we can repeatedly quantify.

Several previous studies have examined the relative roles of sensory systems in feeding behaviours (Enger *et al.* 1989; Janssen & Corcoran 1993; Von der Emde & Bleckmann 1998; Liang *et al.* 1998). However, these have generally not examined the successive phases of the behaviour in a quantitative manner and have limited themselves to measuring success rates or the time required to complete a search-and-acquisition task. Our studies have focused upon two species of freshwater predatory fishes, the muskellunge, *Esox masquinongy*, and the largemouth bass, *Micropterus salmoides*. Both of these euteleost fishes are apex predators in freshwater lakes and ponds of North America, but they are not closely related. The muskellunge is a member of the order Esociformes, which together with the orders Osmeriformes and Salmoniformes comprise the superorder Protacanthopterygii. The largemouth bass is a member of the Perciformes,

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which belong to the large and diverse superorder Acanthopterygii (Nelson 1994). However, as apex predators, both species are equipped with well-developed sensory systems for the detection and capture of prey. These include large eyes and correspondingly well-developed visual centres in the brain, particularly the midbrain optic tectum, and robust and well-developed lateral line systems characterized by wide cephalic and trunk canal systems. It is the role of these two systems in particular that we have focused upon in our studies. Previous studies in other fishes, as well as our own experience, have demonstrated that visually deprived and lateral-line-deprived animals do not attempt to capture free-swimming prey except rarely when the prey comes into actual contact with the predator (Enger *et al.* 1989; Liang *et al.* 1998).

2. STRIKE-FEEDING BEHAVIOURS

Our studies have involved the videotaping and quantitative analyses of thousands of strikes by muskellunge and bass at live fathead minnows (*Pimephales promelas*) in free-field conditions. From these observations we have reached conclusions about the general sequence of the behaviour common to both species (New *et al.* 2000). The initial orientation to the prey typically occurs with a brief, rapid 'start' or turning in the direction of the prey. We have termed this point the N-2 position and it is typically followed in both species by a slow 'stalk' towards the prey involving propulsion by the pectoral and caudal fins with relatively little motion of the body trunk. This continues until the animal reaches a position we have termed the N-1 position, which is typically greater than one body length of the predator away from the prey. At the N-1 position the predator initiates a rapid lunge towards the minnow, easily identifiable by the C- or S-shaped body posture coincident with the initiation of the lunge. The attack sequence ends with the attempt to capture the prey (the N position) either via ram feeding (grasping the minnow directly in the jaws) by muskellunge or via suction feeding (drawing the prey into the mouth via an inhalant current) by bass. Occasionally a fish will initiate a strike directly from the N-1 position, foregoing the preceding stalk phase. This sequence of events generally agrees with those previously reported for *Esox* (Webb & Skadsden 1980) and for *Siniperca* (Liang *et al.* 1998). The definition of sequential phases and position of the strike has allowed us to make quantitative measurements of distance and angular deviation between predator and prey at these positions. We have measured these under conditions where the animal is deprived of visual or lateral line systems, or both, and compared them with those of control animals.

3. EXPERIMENTAL METHODS

Bass or muskellunge were presented with fathead minnows in a test arena measuring 123 cm × 46 cm × 47 cm and the subsequent behaviour videotaped from lateral and top views simultaneously. The animals were separated into four groups: (i) a control group; (ii) a group in which the lateral line afference was suppressed (LLX group) by immersion in 0.1 mmol $CoCl_2$ prior to testing (Karlsen & Sand 1987); (iii) a group in which animals had been bilaterally blinded; and (iv) a group in which the lateral line system of bilaterally blinded animals was also suppressed. For all of these groups, the distances and angular deviations between predator and prey at the N-2 and N-1 positions were measured during subsequent videotape analysis. Distance was defined as the straight-line distance between the rostrum of the predator and the centre of mass of the prey. Angular deviation was determined as the angular measure between a line extending through the longitudinal midline axis of the predator and a line from the centre of mass of the predator to the centre of mass of the minnow. For complete details of the experimental procedures see New *et al.* (2000). All procedures in this study have been approved by the Loyola University Institutional Animal Care and Use Committee.

4. RESULTS

A quantitative comparison of the strike-feeding behaviours of blinded and/or lateral-line-deprived fishes provides insight into the relative roles of these sensory modalities at different stages of the behavioural sequence. Both control and LLX animals exhibited the complete strike behaviour as described in § 2, with clearly observable N-2 and N-1 positions. However, there were significant differences in distances and angles between these positions in the control and LLX groups. Lateral-line-suppressed muskellunge demonstrated an initial orientation to the prey (N-2) at angles and distances that were not significantly different from those of the control animals (table 1). The LLX animals also exhibited the rapid strike from the N-1 position, but at distances and angular deviations that were significantly smaller than those of the control animals. Thus, both lateral line and vision play a role in determining the optimal distance and range for the initiation of the strike. In the absence of lateral line afference, muskellunge approach to closer ranges and smaller angular deviations before initiating the lunge. Muskellunge that were blinded also initiated successful strikes at minnows, however, these fish never performed the N-2 to N-1 'stalking' portion of the feeding behaviour observed in the other experimental groups. Rather, these fish would initiate rapid lunging strikes at minnows only at very close ranges and angles, both significantly smaller than those of the other groups. Finally, muskellunge that were both blinded and lateral line suppressed would not feed at all, indicating that afference from vision or lateral line systems is necessary for the initiation and completion of strike behaviours.

Lateral line suppression and blinding did not significantly affect the rate of success of strikes in muskellunge. Control muskellunge in our studies were successful at capturing minnows 73% of the time, whereas LLX animals were successful in 84% of the observed strikes. Blinded muskellunge also demonstrated a success rate of 73%, these strikes were made from much smaller distances and angles. Frequency distributions of distances at the N-2 and N-1 positions demonstrated no clear differences in strike success with distance changes in any of these groups (figure 1*a*,*b*). However, control and LLX muskellunge did demonstrate clear differences in approach strategies and success under certain conditions. Attacks from the N-1 position in both groups that occurred from ranges greater than the mean plus one standard deviation

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Table 1. *Distances and angular deviations at N-2 and N-1 positions of strike-feeding behaviours in muskellunge and bass*

(Values are expressed as means ± s.e.m.; *indicates statistically significant differences from control values (ANOVA $p < 0.05$).)

	N-2	N-1
muskellunge (*Esox masquinongy*)		
control		
angular deviation	39° ± 3.8°	18.4° ± 2.2°
distance (cm)	25.4° ± 1.9	13.5 ± 0.9
lateral line suppressed		
angular deviation	34.4° ± 3.6°	11.5° ± 1.1°*
distance (cm)	22.7 ± 1.8	10.1 ± 0.8*
blind		
angular deviation	–	7.4° ± 0.7*
distance (cm)	–	3.2 ± 0.2*
largemouth bass (*Micropterus salmoides*)		
control		
angular deviation	65.7° ± 6.6°	26.5° ± 3.6°
distance (cm)	43.0 ± 1.7	17.0 ± 1.1
lateral line suppressed		
angular deviation	74.6° ± 6.6°	21.5° ± 3.2°
distance (cm)	36.9 ± 1.7*	11.4 ± 0.6*
blind		
angular deviation	–	18.8° ± 2.56°
distance (cm)	–	2.6 ± 0.2*

were arbitrarily designated as ‘far strikes’. In the control group these strikes were always initiated from angular deviations greater than 20° and in the majority of cases (82%) the minnow was moving in a direction away from the longitudinal midline axis of the muskellunge. Far strikes also occurred in LLX animals, however, these only occurred if the minnow was less than 20° from the midline axis and successful strikes occurred only when the minnow was directly ahead of the muskellunge.

Largemouth bass in our studies also struck regularly and enthusiastically at prey minnows, however, there exist significant quantitative differences between the strikes of control-group bass and control muskellunge. Bass initiated feeding behaviours from the N-2 position at much greater ranges and angular deviations than did the muskellunge (table 1). Furthermore, the removal of sensory input from the lateral line or visual systems (LLX group) produced significantly different results in *Micropterus* from those in *Esox*. In LLX bass there was no significant difference in the angular deviation at the N-2 position, however, the mean distance at N-2 was significantly smaller than in the controls (table 1). The same was true at the N-1 position: LLX bass struck from closer ranges than did the controls, but there was no significant difference between the angular deviation of control and LLX animals. In the LLX group, the distance for initiation of the lunge from N-1 was not significantly different from that of LLX muskellunge; all other values for control and LLX bass were significantly greater than the corresponding values for muskellunge. The data for blinded bass indicate that, like muskellunge, they only perform rapid lunges from the N-1 position at significantly closer ranges than the control or LLX animals (figure 1*c*,*d*). However, there are no significant differences between the angular deviations of blinded bass and those of control or LLX animals (table 1).

Unlike the muskellunge, suppression of lateral line afference slightly reduces the effectiveness of bass strikes, control bass were successful 79% of the time, whereas the success rate in LLX animals was 70% and that of blinded bass was 59%. Furthermore, the clear difference in preferred angular deviation between ‘far strikes’ in control and LLX muskellunge was not evident in bass.

5. MULTIMODAL INTEGRATION IN FEEDING BEHAVIOURS

The results described in this paper provide revealing insights into the relative roles of the visual and lateral line sensory systems during the course of a relatively complex behavioural task: the detection of, approach to and capture of free-swimming prey. The lateral line and visual systems each provide adequate information for successful feeding behaviours. Fishes in which the lateral line and visual systems were both suppressed either did not feed at all (muskellunge), or were generally unsuccessful when attempting to capture a prey item that came into actual physical contact with the predator (bass). However, the two systems studied play clearly different, though complementary, roles at different phases of the strike-feeding behaviour. Muskellunge hunt visually for their prey; there were no significant differences in the range or angular deviation of control and LLX fishes at the N-2 position. However, in the absence of lateral line afference muskellunge closed to smaller distances and angular deviations at the N-1 position, indicating that information from both modalities is used in determining the optimal position from which to strike. The lateral line system itself supplies sufficient information to guide the last portion of the strike, as demonstrated by the ability of blinded fishes to catch prey successfully at close range. Thus there exists a ‘sliding hierarchy’ of sensory modalities in muskellunge, with vision predominating in the early stages and the lateral line supplying more useful information as the behavioural sequence unfolds and the range decreases. Nevertheless, the visual system itself is also sufficient to guide the entire behaviour; LLX muskellunge were very successful at capturing prey. Finally, the conditions under which muskellunge will attempt long-range strikes are different in control and LLX fishes. In the former group, the angular deviation is greater than the mean, and the minnow is moving away from the midline axis. We interpret these as possible ‘desperation strikes’, the muskellunge making the best of a difficult situation. In LLX animals, successful long-range strikes never occurred unless the minnow was directly ahead of the muskellunge, in a region in which there is probable binocular overlap of the visual fields.

Multimodal integration during the strike-feeding behaviour in bass is similar in some respects to that in muskellunge but significant differences exist. Bass initially orientated to minnows at much greater ranges and angles than did muskellunge, suggesting that bass are foraging more actively than muskellunge, which employ an ‘ambush’ strategy. Furthermore, although the ranges at

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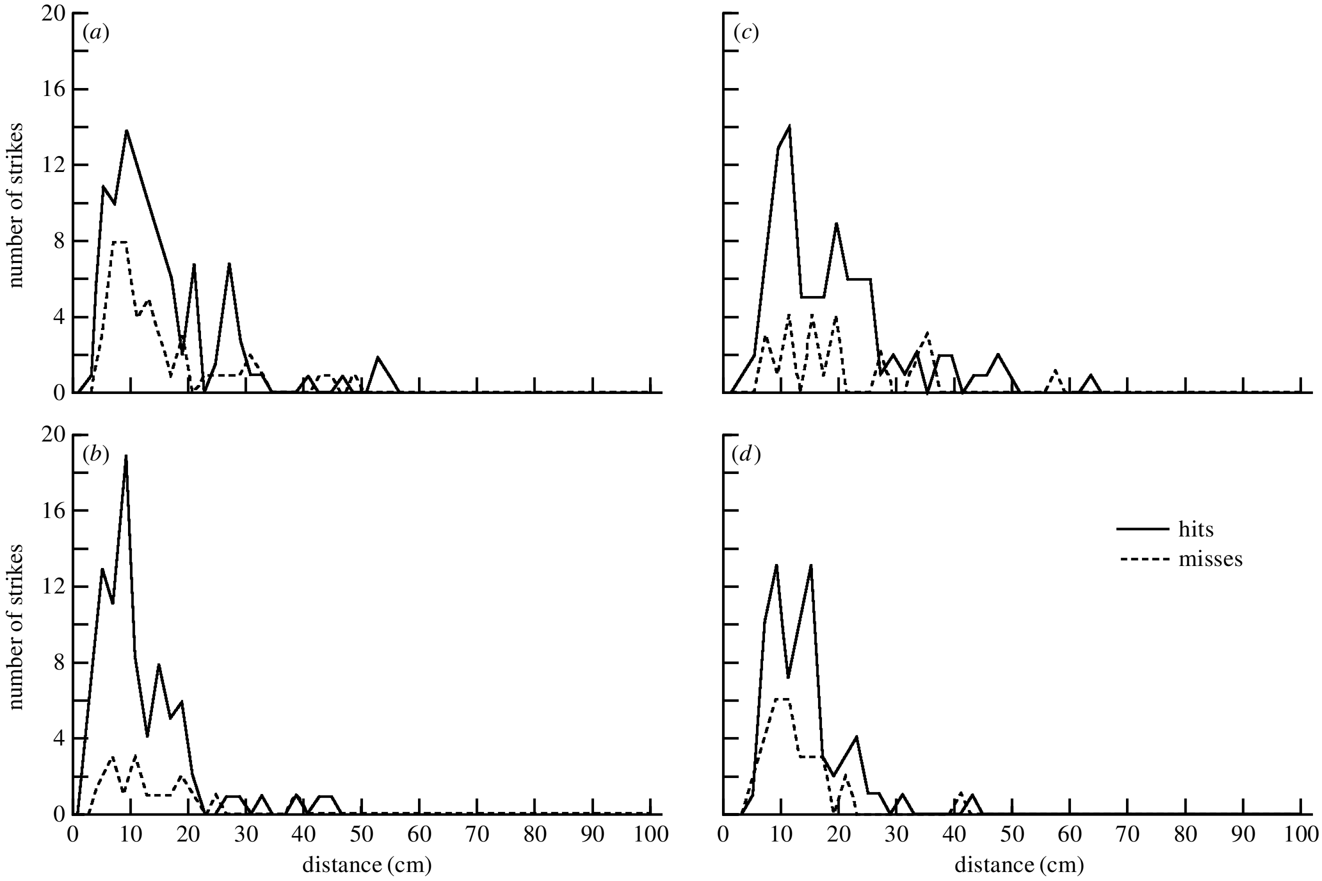

Figure 1. Frequency distributions of N-1 positions in control and cobalt-chloride treated (LLX) animals: (*a*,*b*) muskellunge, (*c*,*d*) largemouth bass; (*a*,*c*) control N-1, (*b*,*d*) $CoCl_2$-treated N-1.

different phases of the attack decrease with the removal of lateral line or visual information, the angular deviations show no significant differences between any of the treatment groups. Thus bass use whatever sensory information is available to approach prey at an 'optimal' mean angular deviation of *ca.* 22°. As in muskellunge, the different sensory systems play dominant roles at different times in the behavioural sequence. Unlike muskellunge, however, the mean N-2 range for LLX bass is significantly smaller than that of the control group. This is surprising, because at these long ranges the bass should not be receiving lateral line stimulation from the source. It is possible that the lack of afference raises the threshold at which the fish will respond with an orientation. This is clearly the case with the initiation of the strike from N-1 in both bass and muskellunge. Finally, the lateral line provides sufficient information at the closest ranges for the fish to make successful strikes.

Without visual or lateral line input, the fishes in our study did not respond to minnows, with rare exceptions when a minnow physically contacted a bass. This does not mean that other sensory modalities, such as audition or olfaction, were unable to detect the prey, however, they were unable, by themselves, to initiate and organize a feeding response.

REFERENCES

Enger, P. S., Kalmijn, A. J. & Sand, O. 1989 Behavioral identification of lateral line and inner ear function. In *The mechanosensory lateral line: neurobiology and evolution* (ed. S. Coombs, P. Gorner & H. Munz), pp. 575–590. New York: Springer.

Janssen, J. & Corcoran, J. 1993 Lateral line stimuli can override vision to determine sunfish strike trajectory. *J. Exp. Biol.* **176**, 299–305.

Karlsen, H. E. & Sand, O. 1987 Selective and reversible blocking of the lateral line in freshwater fish. *J. Exp. Biol.* **133**, 249–262.

Liang, X. F., Liu, J. K. & Huang, B. Y. 1998 The role of sense organs in the feeding behavior of Chinese perch. *J. Fish Biol.* **52**, 1058–1067.

Nelson, J. S. 1994 *Fishes of the world*, 3rd edn. New York: Wiley.

New, J. G., Fewkes, L. A. & Khan, A. N. 2000 Strike feeding behavior in the muskellunge, *Esox masquinongy*: contributions of lateral line and visual sensory systems. *J. Exp. Biol.* (Submitted.)

Von der Emde, G. & 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. & Skadsden, J. M. 1980 Strike tactics of *Esox*. *Can. J. Zool.* **58**, 1462–1469.