

The importance of the lateral line in nocturnal predation of piscivorous catfish

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Summary

In a previous study we showed that nocturnal piscivorous catfish track the wake left by a swimming prey fish to locate it, following past locations to detect the present location of the prey. In a wake there are hydrodynamic as well as chemical signatures that both contain information on location and suitability of the prey. In order to determine how these two wake stimuli are utilised in prey tracking, we conducted experiments in catfish in which either the lateral line or the external gustation was ablated. We found that a functional lateral line is indispensable for following the wake of swimming prey. The frequency of attack and capture was greatly diminished and the attacks that did occur were

considerably delayed when the lateral line was ablated. In contrast, catfish with ablated external taste still followed the wakes of their prey prior to attacking, albeit their attacks were delayed. The external taste sense, which was reported earlier to be necessary for finding stationary (dead) food, seems to play a minor role in the localisation of moving prey. Our finding suggests that an important function of the lateral line is to mediate wake-tracking in predatory fish.

Key words: catfish, lateral line, gustation, non-visual predation, prey wake.

Introduction

Trophic relationships have a major influence on activity patterns and sensory systems in fish (Hobson et al., 1981). Although sensory aspects of predator–prey interactions have been extensively studied in fish, the major focus has been on visual predators (Abrahams and Kattenfeld, 1997; Ryer and Olla, 1999; Thetmeyer and Kils, 1995; Utne-Palm, 2002; Vogel and Beauchamp, 1999). This is especially true for piscivorous fish (Beauchamp et al., 1999; Mazur and Beauchamp, 2003; Petersen and Gadomski, 1994). Little is known about strategies and senses that non-visual aquatic piscivores use to detect and locate their prey. Information on fish activity at night is often inferred from static observation of their distribution or from stomach content analyses; most information comes from coral reefs where vision is still feasible at night (Helfman, 1993; Hobson et al., 1981). In temperate aquatic systems, however, vision is often limited due to turbidity and structures such as macrophytes. At night and at greater depths light is scarce and there are frequently conditions of total darkness. A few predatory fish have been specialising on these low-light niches where prey fish are less evasive and there is limited competition as well as risk from other visual predators. These nocturnal predators provide good models to investigate ecologically relevant non-visual interactions in fish.

In a recent study we found that European catfish *Silurus glanis* follow the wakes of piscine prey prior to attacking them in the absence of visible light (Pohlmann et al., 2001). In tracking wakes the predator is following past locations of prey in more or less convoluted trails over several prey-body lengths, which finally lead to the prey's present location. This tracking is clearly different from the direct approach behaviour expected from the detection of the instantaneous position of the prey through electrical, visual, or acoustic cues emitted by the prey. Wakes contain hydrodynamic and chemical information about the sender that persists after the sender has moved on and thus considerably increases the 'active space' in which the prey is detectable (Westerberg, 1990). Directional information in wakes and other plumes can be provided both by chemical and hydrodynamic gradients (Atema, 1996; Webster and Weissburg, 2001). The hydrodynamic information is estimated to be detectable in trail lengths of several decimeters to meters and over several seconds, depending on flow conditions and the size of the fish (Bleckmann, 1993). The chemical directional information is present for at least one order of magnitude longer, both in time and space (Westerberg, 1990). We found catfish utilised wakes as old as 10 s and followed 2.5 cm long fish over distances of up to 40 cm for about 55 prey-body lengths, even in our

confined experimental tank with high background turbulence due to the catfish's own movement (Pohlmann et al., 2001).

Wakes of moving animals are distinct flow patterns in which fine structure depends on the size, swimming velocity and the mode of swimming of their creator. The guppies *Poecilia reticulata* used in our study swim in the push-and-coast mode, where each tail beat creates a disturbance including a vortex ring, followed by a coast phase without fin movements dragging water behind (Breithaupt and Ayers, 1996; McCutchen, 1977; Müller et al., 2000). Wake height and the lateral distance between vortices correspond to the size of the tail fin and thus of the fish. The specific structure of the wake provides information about swimming style. The sense of rotation and travelling direction of the vortices and the direction of the dragged water give information on swimming direction of the prey. A wake shows distinct structural changes when ageing (Hanke et al., 2000; Westerberg, 1990). Thus the hydrodynamic structure could inform a predator if the creator of the wake is suitable prey (size, swimming speed), in which direction it went and if the wake is fresh enough to be worth following (Bleckmann, 1993).

Fish can detect hydrodynamic structures with their lateral line organs (Kalmijn, 1988; Dijkgraaf, 1933). These consist of free standing neuromasts and canal neuromasts that detect the velocity or acceleration components and the direction of water movements. In European catfish these neuromasts are sufficiently numerous on the body surface, and especially in the head region (Herrick, 1901), to enable the detection and spatial resolution of fine scale structures. The sensitivity of lateral line neuromasts covers the amplitude and frequency range found in wakes of small fish (Bleckmann, 1993; Bleckmann et al., 1991).

There is also chemical information in the wake. Substances are constantly and involuntarily released by all fish and are distributed with the water movements. Westerberg describes the evolution of a chemical trail in three stages: the initial mixing produced by a source, a stretching and deformation by shear and a final stage in which molecular diffusion becomes important (Westerberg, 1990). In the wake there is incomplete mixing before the velocity fluctuations lose their momentum to viscosity. Molecular diffusion of chemical substances is about 1000 times slower than the viscous dampening. Thus the wake will contain small scale 'frozen' filamentous and patchy structures of odour even after the hydrodynamic disturbance that caused them is dampened out by viscosity. At the time when the distinct hydrodynamic signature of a wake is lost the diameter of the chemical trail will be about 10 times larger than the source. With increasing age of the chemical trail, molecular diffusion and shear will remove its remaining spatial structure and dilute its concentration into a uniform background.

In a chemical trail a predator could use the degree to which small-scale concentration fluctuations have been smoothed out within the trail to determine the distance and direction to the source, independent of flow conditions (Atema, 1996; Westerberg, 1990).

Fish are known to have extraordinarily sensitive chemical

senses enabling them to distinguish between different species and even individuals (Brown and Smith, 1994; Kleerekoper, 1969; Mann et al., 2003). Olfaction in fish is located exclusively in the nose, while gustation is perceived inside the mouth and, in some fish, also on parts of the body surface. In catfish there are high numbers of taste receptors on the whole body surface, with highest densities on the barbels and in the head region (Atema, 1971). In catfish gustation is the major chemical sense involved in foraging and feeding (Atema, 1971; Todd, 1971; Wunder, 1927). Bullheads (*Ictalurus natalis* and *I. nebulosus*) are able to locate stationary food by their chemical sense alone using true gradient search (Bardach et al., 1967; Johnsen and Teeter, 1980); when locating dead meat the external taste sense is used exclusively (Atema, 1971).

In the present study we compared the foraging behaviour of catfish with ablated lateral lines or ablated external gustation to that of intact catfish, in order to study the involvement of these senses in wake following. We used a video-based infrared (IR) illuminated system allowing 3-D evaluation of the animal behaviour with the exclusion of visible light.

Materials and methods

Experimental techniques and protocol

In order to observe fish behaviour in the dark by non-invasive means we used a glass tank (120 cm long × 60 cm wide × filled to a height of 40 cm) that was illuminated by infrared back illumination. Interactions were recorded by IR-sensitive cameras from two directions on digital video (Sony GV-D 900E, Tokyo, Japan). The recordings of the two views were synchronised with single frame accuracy.

Guppies *Poecilia reticulata* (Peters 1859) were chosen for their slow swimming behaviour and for their low tendency to thigmotactic (wall hugging) behaviour, minimising wall effects. They mostly use push-and-coast swimming, the hydrodynamics of which are well described (Müller et al., 2000; Videler et al., 1999). Guppies (total length 2.0–5.1 cm) were obtained from a local aquarium fish supplier. Four different catfish *Silurus glanis* (Linnaeus 1758) were used as predators, total lengths 20–31 cm. They were obtained from an aquaculture facility (Ahrenhorster Edelfisch, Badbergen, Germany) 7 weeks prior to the first trials and had been fed with live fish ever since to ensure their familiarity with living piscine prey. All fish were kept in holding tanks in the experimental room so they were subjected to the same temperature (18°C) and light regime (12 h:12 h light:dark cycle with dawn and dusk periods simulated by 30 min of lower light intensity). Catfish were kept individually in holding tanks and returned to these tanks after each trial. Between trials each individual catfish spent at least one day unfed in its holding tank. Guppies were kept in one large holding tank as a group of about 100 fish.

The experimental tank was cleaned and filled with aged, non-chlorinated tapwater at ambient temperature before each trial, because catfish are known to deploy aggressive territorial behaviour to the chemical stimulus of another catfish (Todd et

al., 1967). After the catfish was acclimated in the experimental tank for at least 1 h in darkness each trial started with the introduction of a single guppy. For this, the investigator entered the experimental room through a double curtain to ensure total darkness and added one individual guppy with a small amount of water (<50 ml) into the middle of the experimental tank. 5 min after the prey had been consumed (viewed on monitors next door) the next guppy was added. To avoid satiation a trial ended when 10 guppies had been eaten. A trial was aborted when the added prey fish was not consumed within 20 min. Thus, in each trial 0–10 guppies could be consumed.

We ran 16 trials for each of three treatments: intact catfish (control), catfish with ablated lateral lines, and catfish with ablated external taste. Each trial consisted of the subsequent addition of 1–10 guppies, depending on the number of captures.

We compared the behavioural performance after the two ablations with the behaviour of the same fish before ablations. The control data were part of the data reported previously (Pohlmann et al., 2001).

Ablations

Ablation of the lateral line using CoCl_2 is reversible. We used the same four catfish as in the control trials. A single catfish was put into an incubation tank containing calcium-free artificial freshwater with $0.5 \text{ mmol l}^{-1} \text{ CoCl}_2$ (Karlsen and Sand, 1987). Calcium counteracts the effect of CoCl_2 by competitively displacing it. Added to Ca^{2+} -free water, cobalt ions fully suppress the lateral line function without affecting the inner ear (Karlsen and Sand, 1987). Co^{2+} is thought to block the hair cell sensitivity by competitively inhibiting Ca^{2+} flux through membrane channels, thus inhibiting the receptor current in lateral line hair cells or by modifying the permeability of the transducer membranes to other ions.

The artificial freshwater was made by adding stock solution ($1.78 \text{ mmol l}^{-1} \text{ KCl}$, $3.57 \text{ mmol l}^{-1} \text{ KNO}_3$, $3.57 \text{ mmol l}^{-1} \text{ NaH}_2\text{PO}_4$, $7.14 \text{ mmol l}^{-1} \text{ MgSO}_4$ and $14.28 \text{ mmol l}^{-1} \text{ NaCl}$) to deionized water until the conductivity had reached $350 \mu\text{S cm}^{-1}$, matching the conductivity in the catfish holding tanks; NaOH was added to match the pH at 7.6 (modified after Karlsen and Sand, 1987). Catfish were kept in the CoCl_2 solution for 6 h prior to transfer into the test tank filled with artificial calcium-free freshwater. The catfish was left to acclimate there for 1 h prior to the start of a trial. The maximum time a catfish spent in the test tank was 3 h, which is well within the time (over 24 h) that the total ablation of the lateral line persists in calcium-free water (Karlsen and Sand, 1987). To evaluate if lacking motivation was the reason that catfish did not attack prey in some trials, we offered those catfish a fresh guppy directly in front of their mouth after each trial without captures. For data analysis only, trials were included in which the catfish subsequently readily took this fish. To test for possible effects of the calcium-free artificial freshwater we ran one trial similar to the lateral line ablation trials but without CoCl_2 in the incubation tank. The feeding

behaviour was similar to that of the control trials (data not shown).

The ablation of the external taste is invasive and irreversible. It was done 2 months after the end of the lateral line ablations. We only taste-ablated animals that had been used in the control and (reversible) lateral line ablation experiments to have comparable data for individual animals motivated to track. We removed the dorsal (chemosensory) area of the bilateral facial lobes in the dorsal medulla oblongata using the method developed earlier (Atema, 1971). This brain lesion was developed for a related species, *Ictalurus nebulosus*, where this external taste system is necessary to localise dead meat (non-moving, odorous food) and to trigger food pick up. It remains the only procedure to eliminate exclusively this one chemosensory system that guides the catfish's localisation behaviour for dead meat. The taste system of fish consists of two distinct parts. The one that we ablated is innervated by the facial nerve (VII), subserving all taste buds on the body skin, lips, and anterior part of the mouth and ends in the facial lobe in the dorsal medulla oblongata. We did not ablate the other taste system that contains the taste buds on the posterior part of the mouth and on the gill arches, and is innervated through nerves IX and X ending in bilateral vagal lobes in the dorsal medulla oblongata, because vagal lobe ablation blocks swallowing, not locating behaviour (Atema, 1971).

We evaluated the success of the ablation after surgery and after every other trial by offering the catfish a piece of liver in the experimental tank. Liver was our catfish's favourite food and intact fish show strong searching behaviour immediately after introduction of liver to the tank finding and consuming it within seconds. Catfish with ablated external taste, both *Ictalurus nebulosus* and *Silurus glanis*, took a long time to locate the food despite repeated chance contacts and close passes.

According to these criteria the taste ablation was successful in 2 of the 4 animals used earlier. By running 16 trials between both animals we ensured sufficient sample size.

Again, after each trial without attacks we put a fresh guppy onto the catfish's lips to evaluate hunger /motivation. In all these tests the guppy was immediately consumed.

Parameters and evaluation

We determined all attacks by reviewing the video recordings of top and side view. Attacks consisted of successful captures and of snaps not leading to capture but directed at the guppy from a distance of less than 2 cm. Both unsuccessful attacks and captures show that the prey had been accurately localised by the predator. For each trial we recorded the time between introduction of prey and first attack and the time from introduction to capture (further referred to as 'time-to-first-attack' and 'time-to-capture'). From the video recordings we further determined if the guppy was moving prior to the attack. All attacks were categorised based on the video recordings as one of three types: (1) wake-following: the predator swam along the same path as the moving prey, eventually attacking it; (2) head-on encounters: the predator encountered moving

prey without prior path similarity; (3) attacks on stationary guppies. In a previous study we showed that our categorisation was justified by quantitatively analysing a sub-sample of the swim paths, calculating similarity indices between swim paths of predator and prey, and cross-validating our classification on the basis of these similarity indices (Pohlmann et al., 2001).

To determine the time spent close (within 4 cm) to prey while tracking we analysed all tracking events leading to attacks in both ablation treatments as well as 22 sequences of tracking in the control trials. Those latter were the same sequences used earlier to quantitatively confirm the categorisation of capture behaviour (see Pohlmann et al., 2001).

Two wake-tracking sequences, one control sequence and one sequence of taste-ablated catfish, were digitized (at 25 Hz; Adobe Premiere 5.1, Adobe Systems, Mountain View, CA, USA) and the positions of the tips of the heads of both predator and prey were manually tracked using motion analysis software (Winanalyze 1.1, Weinberger, Karlsruhe, Germany). The resulting three-dimensional swim paths of predator and prey were plotted after smoothing with a running average of 5 points to eliminate tracking inaccuracies (see Fig. 1).

We used logistic regression analyses with *post-hoc* contrast

analyses for pairwise comparison (JMP 4.02) to determine differences across treatments in ‘time-to-first-attack’, ‘time-to-capture’, ‘time spent close to prey while tracking’ and in ‘time spent hovering’. Hovering was a behaviour observed particularly in catfish with ablated lateral lines, in which their elongated confluent fins were undulating while the fish stayed in place.

Results

We ran 16 trials for each of the three treatments (control, lateral line ablated, external taste-ablated). In each trial, 1–10 guppies were added sequentially, depending on the number of captures. A trial was ended if the prey fish was not captured within 20 min. In the control trials, 74 prey fish elicited 99 attacks of which 65 were successful (see Table 1). Due to video recording errors five attacks had to be excluded from further analysis. Of the analysed 94 attacks, 55% were categorised as wake-following, 30% as head-on encounters and only 15% of all attacks were directed toward stationary prey, although prey fish were stationary 67% of the time (averaged from eight arbitrarily chosen sequences; total time 31 min).

In trials with lateral-line ablated fish, 18 guppies elicited 18

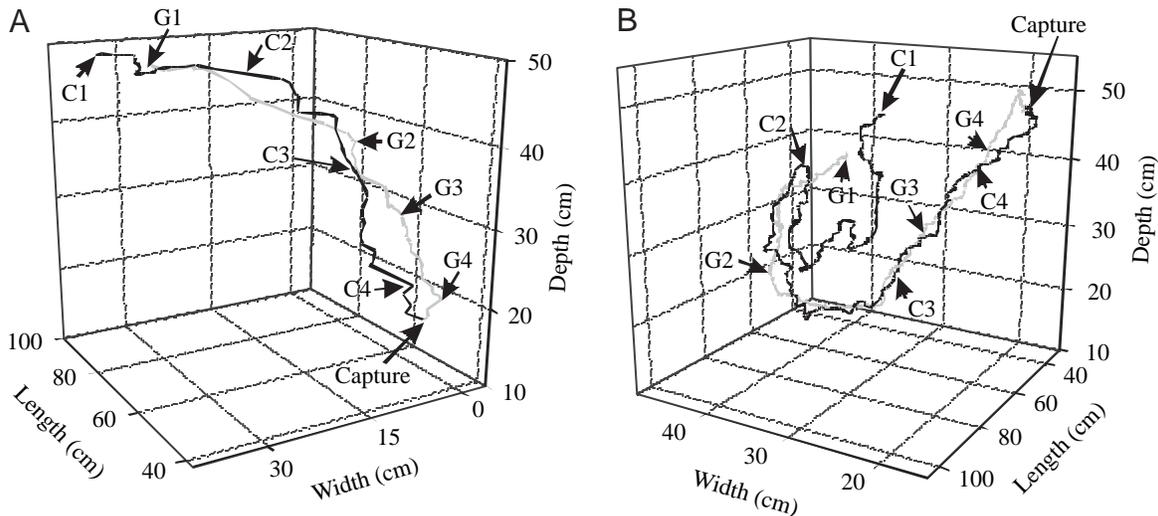


Fig. 1. Wake following paths of (A) intact and (B) taste-ablated catfish. C, catfish; G, guppy. Numbers mark track points at similar times (e.g. at the time the catfish was in position C3 the guppy was at G3). Time points were: (1) 24.1 s prior to attack in A and 30.2 s in B, (2) 18 s, (3) 12 s, (4) 7 s in A and B. Distances between predator and prey at these different times in A were 17 cm (time 1), 29 cm (time 2), 21 cm (time 3), 9 cm (time 4); in B, 13 cm (time 1), 22 cm (time 2), 9 cm (time 3), 5 cm (time 4). Note that the ablated catfish, while already in its proximity, follows the prey for a longer distance before attacking (time 3, time 4).

Table 1. Attacks by treatment and category; summary of all trials

Treatment	Number of guppies added	Number of all attacks (number of captures)	% of attacks		
			Wake-following	Head-on encounters	Stationary guppies
Intact	74	99 (65)	55	30	15
Lateral line ablated	18	18 (3)	6	88	6
External taste ablated	56	67 (40)	27	58	15

attacks of which only three were successful (see Table 1). Almost all attacks (88%) in the lateral line ablation trials were categorised as head-on encounters; one attack (6%) was directed toward a stationary guppy and one attack was categorised as wake following. The latter, however, occurred close to a wall and the path similarity was short so that it may have been incidental. In comparison to the control trials, lateral line-ablated animals showed a somewhat altered swimming behaviour: they spent significantly more time hovering in one place than control or taste-ablated animals (Fig. 2D). They also pushed their heads more strongly into the aquarium corners without the forward probing with their maxillary barbels, typical of intact catfish.

When the external taste was ablated, 56 guppies elicited 67 attacks of which 40 were successful. We categorised 27% of all attacks as wake-following, 58% as head-on encounters and 15% as attacks on stationary guppies (Table 1). The capture success rates (captures/all attacks) were similar in the control and the taste ablation trials (0.66 and 0.6, respectively), but much lower in the lateral line ablation trials (0.17).

The percentage of wake-following was highest in the control, intermediate in the taste ablation and lowest in the lateral line ablation trials (see Table 1). When following wakes, taste-ablated catfish spent significantly more time close to the guppies (within 5 cm of the prey) before attacking than

intact animals (Fig. 2C; $P=0.0119$, $d.f.=1$, $F=6.988$; Fig. 1: compare shorter distances indicating close following between C3 and G3 in A with C3 and G3 in B). In the taste ablation trials there were an additional 12 sequences of obvious wake-following which did not lead to an attack. This was observed only twice in the control trials and never in the lateral line ablation trials. Finally, in the control and lateral line ablation trials but not in the taste ablation trials the catfish showed an interest (spending time and repeated returning) in places where the guppy had hung out recently, indicating the possible detection of chemical traces from the prey.

With all three treatments, stationary guppies were attacked less frequently than expected from the (high) percentage of time they spent resting compared to the time they spent swimming.

The time-to-first-attack was significantly longer in the lateral line ablation trials than in the control trials, while there were no significant differences between the taste ablation and the control trials (Fig. 2A). The time-to-capture was significantly longer in the lateral line ablation trials than in both the control and the taste ablation trials, but there was no significant difference between control and taste ablations (Fig. 2B). Note that in the lateral line ablation trials the number of observations was very low because without a functional lateral line only three guppies were captured successfully.

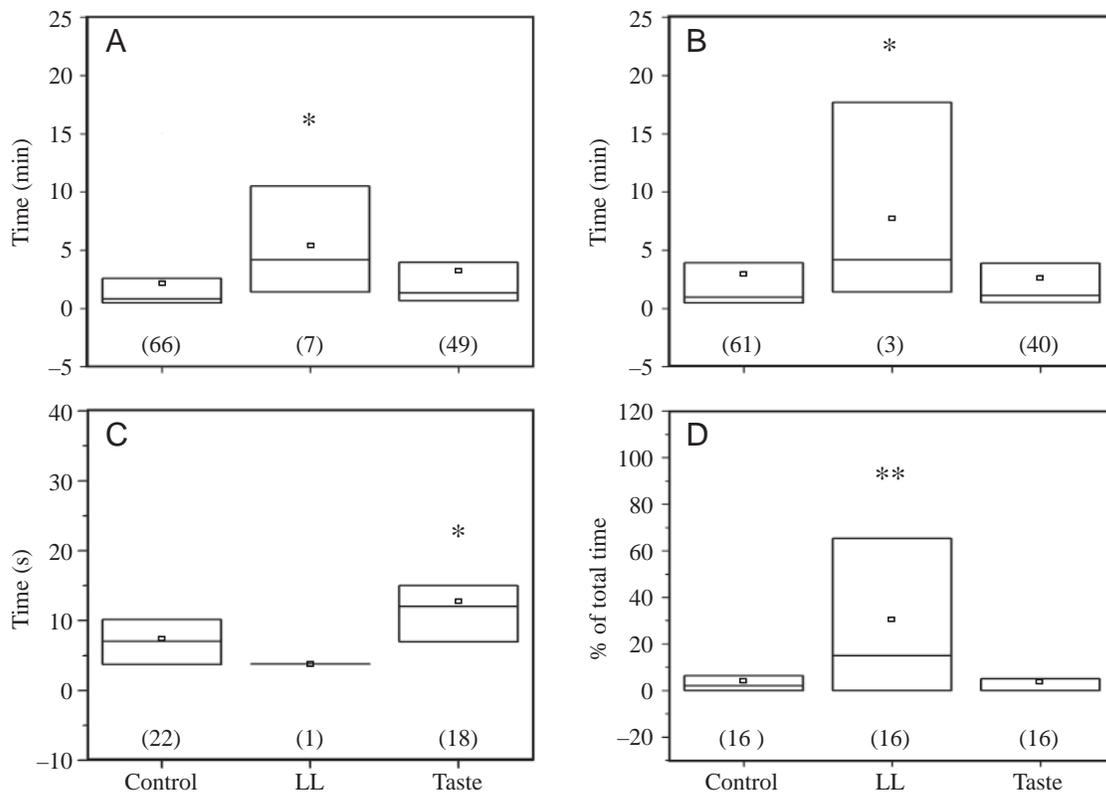


Fig. 2. Temporal parameters characterizing predatory behaviour of unrestrained and of lateral-line (LL) and taste-ablated catfish. (A) Time to first attack; (B) time to capture; (C) time spent close to a prey; (D) time spent hovering. Each box chart indicates mean (square) and percentiles: 75% (box upper frame), median (box mid line), 25% (box lower frame). Asterisks indicate treatment groups that were significantly different from their respective control group (logistic regression followed by contrast analysis: * $P<0.05$; ** $P<0.01$); N values are given for each box.

Discussion

Our results show that the lateral line is indispensable for the catfish to be able to track the wakes of piscine prey and localise swimming fish, while external gustation is not. Catfish with dysfunctional lateral lines were unable to locate swimming prey by following their trails. The only instance in which corresponding swim paths preceded an attack by a catfish with an ablated lateral line was a short path overlap that occurred close to a wall, suggesting that this one case of path similarity may well have been incidental. Hydrodynamic stimuli appear to be important in all attack modes, not just in wake-following, since catfish with ablated lateral lines showed considerably diminished frequencies of attack and capture, reflected also in the significantly extended time-to-first-attack and time-to-capture. The importance of hydrodynamic stimuli is further supported by our finding that in all treatments stationary guppies, which only give weak hydrodynamic signals caused by their respiratory movements, were attacked less often than expected from the total amount of time they spent resting. In other words, prey swimming provided the significant hydrodynamic stimulus to allow wake-tracking and attack in general. In addition, taste ablation did not alter the percentage of attacks on stationary guppies, pointing to the importance of hydrodynamic stimuli (e.g. local gill currents) and not gustatory stimuli for detection of the (live) prey. Catfish were earlier reported to be able to locate stationary dead prey on the basis of external gustation alone (Atema, 1971; Bardach et al., 1967; Johnsen and Teeter, 1980).

The lateral line may also play a role in feedback about the catfish's own locomotion. The ability of trout to hold station behind a solid object in fast flowing water requires an intact lateral line organ (Montgomery et al., 2003). In our study, lateral line-ablated catfish altered their swimming behaviour in the absence of visual information, with extended instances of hovering in one place. However, the altered swimming behaviour of the catfish predator cannot be the reason for the observed predation differences, because even in trials with little or no hovering (7 or 4 out of 16 trials, respectively) the numbers of attacks and captures were considerably diminished compared to the controls and no wake-tracking occurred.

Our CoCl_2 concentrations (0.5 mmol l^{-1}) and exposure time (9 h) were well below the toxic level reported by Karlsen and Sand (1987) for roach (1 mmol l^{-1} , 1–2 weeks exposure) and by Janssen (2000) for Mexican blind cavefish (2 mmol l^{-1} , 10–17 h). In addition, toxicity is always a function of body mass and our catfish were much larger than those utilised in the above-mentioned studies. Janssen (2000) found an increased swimming activity, change of spatial use and strong mucus excretion prior to the death of the cobalt-exposed fish. Our catfish, in contrast, decreased their movement and did not alter their spatial use of the test tank; neither in the incubation tank nor in the test tank did they show any enhanced mucus production. None of our catfish died during the entire study and their behaviour after recovery in tapwater was unchanged. The fact that lateral line-ablated catfish readily consumed dead fish confirm findings by Enger et al. that cobalt treatment does

not noticeably reduce feeding motivation (Enger et al., 1989). Cobalt does not impair olfaction in the sublethal concentrations applied in this study (Brown et al., 1982). Altogether, this gives us confidence that the altered swimming and prey-following behaviour was not caused by cobalt toxicity.

We do not exclude the possibility that internal gustation or olfaction were involved in the decision to follow a detected wake or to trigger an attack. But those senses alone did not suffice to follow wakes or readily attack prey, as shown by the lateral line ablation trials. Despite the obvious importance of the lateral line for finding the prey, we recorded 18 attacks of lateral line-ablated animals on guppies. These attacks were in general (88% of all attacks; Table 1) head-on encounters that could have occurred by chance or been elicited by chemical, electro- or auditory receptors. All these alternative receptors, however, could not compensate for the lack of wake-tracking performance caused by lateral line ablation (see also Pohlmann et al., 2001).

External taste on the other hand, while critical for locating dead meat, does not seem to be mandatory for recognising and following wakes, since catfish with their external taste ablated still showed a considerable percentage of wake-following prior to attacks and no delay in time-to-first-attack or time-to-capture. That the percentage of wake-following here was lower than in the control is the result of our decision to exclude instances of apparent wake-following that did not lead to attacks (Table 1). These were excluded because we could not be certain if any overlap of trajectories not leading to attacks, particularly short segments, were accidental or the result of the predator's recognising the wake of the prey. Including the 12 obvious instances would bring the percentage of wake-following to 50%, comparable to that of the control experiments. This and the observation that prey fish were attacked after a longer period of closely following the prey suggests that external gustation may normally help trigger the actual attack, as described for the pick-up response of non-moving food items in bullhead catfish (Atema, 1971). Perhaps olfaction, or internal taste stimulated by odour entering the mouth cavity with the respiratory flow, partially supplemented the missing external taste before the – delayed – final strike. This trigger delay in taste-ablated animals is seen both in the significantly extended time spent close to prey when tracking (Fig. 2C) and in the instances when wake-following catfish did not strike at all. Apart from the longer hesitation before the actual attack and the resulting extended tracking distance, the wake-tracking behaviour of taste-ablated animals did not differ in terms of swim path resemblance or swimming behaviour from that of intact catfish we described earlier (Pohlmann et al., 2001). No casting movements of the catfish across the guppy's swim path were observed in any of the treatments (see Fig. 1B), but one has to keep in mind that the catfish head including barbules is wide enough to cover an even somewhat aged trail of a small guppy.

The physiological and morphological properties of the lateral line sensory system and its neuronal processing have been studied in detail (Bleckmann, 1993, 1994). Sensitivity,

frequency resolution and directionality have been investigated with artificial stimuli (mostly vibrating spheres). The biological significance of lateral line systems, however, can only be recognised by studying the behaviour in its natural context (Bleckmann, 1993). The lateral line system has been shown to be involved in many different behaviours such as detection and localisation of stationary objects (Abdel-Latif et al., 1990), obstacle entrainment and rheotaxis in fast-flowing streams (Baker and Montgomery, 1999; Montgomery et al., 1997, 2003; Sutterlin and Waddy, 1975) and intraspecific communication such as schooling (Partridge and Pitcher, 1980; Pitcher et al., 1976) and mating (Satou et al., 1993, 1994). Lateral line involvement was also shown in different feeding behaviours of fish. Surface feeding by topminnows, *Aplocheilichthys lineatus*, on struggling prey is mediated by the head lateral line (Bleckmann, 1980; Bleckmann and Schwartz, 1982). Here distance determination by lateral line analysis of water surface waves requires only one intact canal organ, while determination of source direction depends on the spatial interaction of several organs (Bleckmann and Schwartz, 1982). The lateral line is further involved in detection and localisation of live zooplankton and crustaceans (Hoekstra and Janssen, 1985; Montgomery et al., 1995; Montgomery, 1989; Montgomery and Hamilton, 1997). Blinded sculpins *Cottus bairdi* consume live prey and react to other moving objects but ignore dead prey. Inactivation of the lateral line eliminates the feeding response to live prey (Hoekstra and Janssen, 1985). The spatial integrity of lateral line organs also seems to be necessary for correct directional response in the sculpin.

There are only two studies in which the involvement of the lateral line was tested in piscivorous fish, both using diurnal visual predators. Blinded pike *Esox lucius*, which are visual ambush predators, attack live fish from distances of up to 10 cm only if their lateral line is intact (Wunder, 1927). Intact bluegills *Lepomis macrochirus* attack live fish in the absence of visible light when it is moving or after touch (Enger et al., 1989). When their lateral line is ablated they attack prey only after touch. We made similar observations with rather non-visual catfish.

Montgomery et al. hypothesise that deteriorating visual conditions may increase the importance of lateral line cues (Montgomery et al., 1995). They report an observation on estuarine star-gazers *Leptoscopus macropygus*, which initiated a strike in complete darkness when the front of the prey had just barely passed over the mouth without touch. This rapid strike mechanism is activated by lateral line input. They argue that the short range of the lateral line system is often seen as a disadvantage, but in terms of initiating a strike it does have the benefit of indicating the close proximity of the prey without the need for sophisticated central processing to determine target range. This is clearly different in the wake-following we observed: here, catfish follow a series of past locations constituting the trail that leads to the prey, thus deriving directional information. Even in our spatially limited tank we found wake-tracking over distances as long as 120 cm. Our study shows for the first time that fish evolutionarily adapted

to conditions of limited visibility are utilising the lateral line to detect and follow the trails left by their prey. Using the hydrodynamic trail will considerably enhance the encounter probability under natural circumstances. Trail following was also reported for copepods following the trails of their mating partners (Doall et al., 1998). However, copepods were found to use chemical and not hydrodynamic cues in the wakes (Weissburg et al., 1998).

Our finding that nocturnal piscivores follow hydrodynamic cues in the wake of potential prey fish extends the classical definition of predation tactics in fish. Wake-tracking can be categorised as stalking behaviour, which is normally considered to have a major visual component (Keenleyside, 1979).

Fish behaviour and predation strategies are plastic and catfish can deploy a variety of strategies, depending on the environmental conditions and the nature of their prey. Wake-following is not the only predatory strategy, as shown in our ablation experiments, but certainly important under natural conditions, because being able to utilise wakes dramatically extends the space in which the presence and location of prey is detectable. Catfish are slow predators that have little chance to capture prey in light conditions when prey are aware of their approach (J.A. and K.P., personal observation). Both *Silurus glanis* and *Ictalurus nebulosus* do not even respond to the visual presence of small goldfish in well-lit tanks but attack the prey after chemically or hydrodynamically detecting their presence (J.A. and K.P., personal observation). Thus capture success of a slow predator should improve by searching for and tracking prey in the dark when the prey is visually less defended, and approaching from behind where all sensory systems of the prey (e.g. lateral line, olfaction) are less likely to detect the predator's approach.

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