J Comp Physiol A (1996) 179: 455–471

ORIGINAL PAPER

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The responses of central octavolateralis cells to moving sources

Accepted: 20 May 1996

Abstract Mechanosensory lateral line units recorded from the medulla (medial octavolateralis nucleus) and midbrain (torus semicircularis) of the bottom dwelling catfish *Ancistrus* sp. responded to water movements caused by an object that passed the fish laterally. In terms of peak spike rate or total number of spikes elicited responses increased with object speed and sometimes showed saturation (Figs. 7, 14). At sequentially greater distances the responses of most medullary lateral line units decayed with object distance (Fig. 11). Units tuned to a certain object speed or distance were not found. The signed directionality index of most lateral line units was between −50 and +50, i.e. these units were not or only slightly sensitive to the direction of object motion (Figs. 10, 17). However, some units were highly directionally sensitive in that the main features of the response histograms and/or peak spike rates clearly depended on the direction of object movement (e.g. Fig. 9C, D and Fig. 16).

Midbrain lateral line units of *Ancistrus* may receive input from more than one sensory modality. All bimodal lateral line units were OR units, i.e., the units were reliably driven by a unimodal stimulus of either modality. Units which receive bimodal input may show an extended speed range (e.g. Fig. 18).

Key words Lateral line · Teleost fish · Catfish · Mechanoreception

Abbreviations *MON* medial octavolateralis nucleus · *MSR* mean spike rate · *PSR* peak spike rate · *p-p* peak-to-peak · *SDI* signed directionality index

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Introduction

The mechanosensory lateral line of fishes is comprised of superficial and canal neuromasts (e.g. Münz 1979; Northcutt 1989; Webb 1989; Song 1989). Fish use the lateral line to detect hydrodynamic stimuli such as those generated by moving conspecifics, predators, or prey (e.g. Montgomery and McDonald 1987; Montgomery et al. 1988; Enger et al. 1989; Coombs and Janssen 1990; Blickhan et al. 1992; Coombs 1994). Some fish even use self induced flow fields to detect and identify stationary objects (e.g. von Campenhausen et al. 1981; Teyke 1985; Hassan 1989).

Lateral line neuromasts are "low-pass" sensors (<1 Hz up to about 150 Hz) that encode stimulus duration, amplitude, frequency, and phase (e.g. Bleckmann and Topp 1981; Topp 1983; Shangliang and Bullock 1984; Montgomery 1987; Münz 1989; Coombs and Janssen 1990; Coombs and Montgomery 1992; Wubbels 1992). In both cartilaginous and bony fish lateral line information is processed at all levels of the neuraxis, from medulla (e.g. Caird 1978; Claas 1980) to telencephalon (Finger and Bullock 1982; Echteler 1985; Bleckmann et al. 1987, 1989; McCormick 1989; Striedter 1991). In most central lateral line studies an electrical shock applied to the posterior lateral line nerve or a vibrating sphere placed close to a lateral line canal was used as a stimulus (review Bleckmann and Bullock 1989; Schellart and Kroese 1989; Bleckmann 1994). Although water movements caused by a vibrating sphere are well suited to drive peripheral (e.g. Münz 1985; Coombs et al. 1996) and central lateral line units (e.g. Caird 1978; Bleckmann et al. 1989), they do not simulate more natural, complex hydrodynamic stimuli, like the chain of vortex rings generated by a subundulatory swimming fish (Blickhan et al. 1992).

More natural complex hydrodynamic stimuli may, however, be more relevant to delineate central filter properties of the lateral line (Bleckmann et al. 1991a). The peripheral lateral line responds vigorously to water displacements caused by a moving object (Bleckmann and Zelick 1993). However, with the exception of one study (Bleckmann and Zelick 1993) there are no investigations which show how central lateral line units process the information contained in hydrodynamic stimuli caused by a nonvibrating, moving object.

A moving object has been used to stimulate peripheral and central high-frequency electrosensory (Bastian 1981a, b, 1983) and visual units (Tong and Bullock 1982) in fish. The present study describes the responses of medullary and midbrain lateral line units of the bottom dwelling catfish, *Ancistrus* sp., to hydrodynamic stimuli caused by such an object. Catfish were chosen because of their well developed acousticolateralis system, which includes a large low-frequency (ampullary) electroreceptive component (Knudsen 1976), in addition to the ordinary mechanoreceptive, auditory, and vestibular components (Knudsen 1976, 1977; Bleckmann et al. 1991b). Catfish have tactile receptors (Davenport and Caprio 1982; Marui et al. 1988; Lamb and Caprio 1993) which may also respond to large-amplitude water movements. For comparison the responses of some tactile, visual, ampullary, and acoustic units to a moving object were also analysed. Preliminary data were published as part of a conference report (Bleckmann et al. 1996).

Materials and methods

Experimental animals

For the experiments we used 18 (medullary recordings) and 39 (midbrain recordings) male and female catfish *Ancistrus* sp. (Loricariidae, Siluriformes), ranging in length from 6 to 12 cm. Animals were either from commercial dealers or laboratory bread. All fish were maintained in 200 l aquaria at 22–26°C on a daily 12–12 h light-dark cycle.

Surgical procedures

Prior to the experiments the animals were anaesthetised either by chilling to 2–4°C or with tricaine methansulfonate (MS 222, 1:15000). Xylocain (ASTRA-Chemicals) was used to anaesthetise the skin and/or muscles locally at the operation site. With a dental drill a $\leq 20\ \text{mm}^2$ portion of bone was removed in order to expose the medulla or the optic tectum. An injection of Pancuronium Bromide (Organon Teknika, 0.1–0.2 µg/g i.m.) was administered following surgery to block mobility of the animal for recording. With parts of the brain exposed the animal was transferred to the experimental tank (42 × 42 cm, water depth about 18 cm) and positioned on a Styrofoam support. In all medullary recordings and in some midbrain recordings the meniscus of the water was just below the opening in the skull. In most midbrain recordings the entire fish was covered with a water layer of about 2 mm. In order to prevent the water from making contact with the brain, a dam, which fitted the opening in the cranium, was glued on the head. In both cases the exposed brain was kept moist with Ringer's solution. In order to hold the fish in place, the caudalmost portion of the supraoccipital bone was fixed with a Plexiglas rod by gluing the tip of the rod, which was attached to a micro drive, with Histoacryl (Braun Melsungen) to the scull. Aerated fresh water was pumped at a rate of 50 to 70 ml/min over the fish's gills by use of polyethylene tubing inserted in the mouth. An outlet at one side of the experimental tank maintained the water level. The conductivity of the water in both, the holding tanks and the experimental tank, varied between 200 and 300 µS/cm.

Recordings

Single units and small groups of units ("few units") were recorded with indium metal electrodes (Dowben and Rose 1953) whose resistance were $\leq 1\ \text{M}\Omega$. Electrode penetrations were made from dorsal to ventral. The recording electrodes were positioned with aid of a nanostepper (HSS/1, Science products or SMS 87, TC-electronic) in the ipsilateral medulla or in the contralateral midbrain. Electrodes were advanced in steps of $\geq 1\ \mu\text{m}$. In eight successful cases (five in the medulla and three in the midbrain) lateral line recording sites were marked with an electrolytic lesion by passing 5 to 20 µA of cathodal current for 1 to 4 min through the recording electrode. After an experiment the fish was deeply reanesthetised and then perfused intracardially with freshwater teleost Ringer's solution followed by 5% glutaraldehyde solution in 0.1 *M* phosphate buffer (pH 7.3). All brains were subsequently dissected and sectioned at 10 (medulla) or 50 µm (midbrain). Brains were finally stained with cresyl violet for examination of the lesion site.

Stimulation

Moving object stimuli

A rectangular object (8 × 12 × 22 mm) with its long axis oriented vertically was moved past the fish in a circular orbit. Elevation of the moving object was such that the object extended across the entire dorsoventral extent of the fish. In order to exclude surface wave stimulation, some experiments were done with the water surface covered with a glass plate. In these experiments the moving object was completely submerged. The motion of the object was controlled by attaching it to an 8 cm arm which in turn was connected to a DC motor (Fig. 1, top). Object direction was either from anterior-to-posterior or from posterior-to-anterior. A DC-voltage controlled arm speed and thus the time it took the object to complete one orbit (e.g. 2.5 s at an arm speed of 20 cm/s). If not otherwise stated minimal lateral distance between fish and object was 1 or, in a few cases, up to 2 cm.

For stimulation of both, the mechanosensory lateral line and the ampullary eletroreceptors, a pair of 1.0 cm-spaced chlorided silver wire electrodes (diameter 0.3 mm) was glued onto the surface of the object. The wires were connected to a 1.5 V battery via a resistor. The actual voltage used during the experiments as a search stimulus for ampullary units was $< 1.5\ \text{mV/cm}$, measured at the smallest distance (1 cm) between fish and object used in our experiments. A DC-stimulus of this amplitude vigorously stimulates ampullary electroreceptors (Knudsen 1976) but is insufficient to elicit responses from primary lateral line afferents (e.g. Suga 1967; Bleckmann and Zelick 1993).

Vibrating sphere stimuli

In order to determine the approximate anterior/posterior position and size of the receptive field of a lateral line unit the animal was

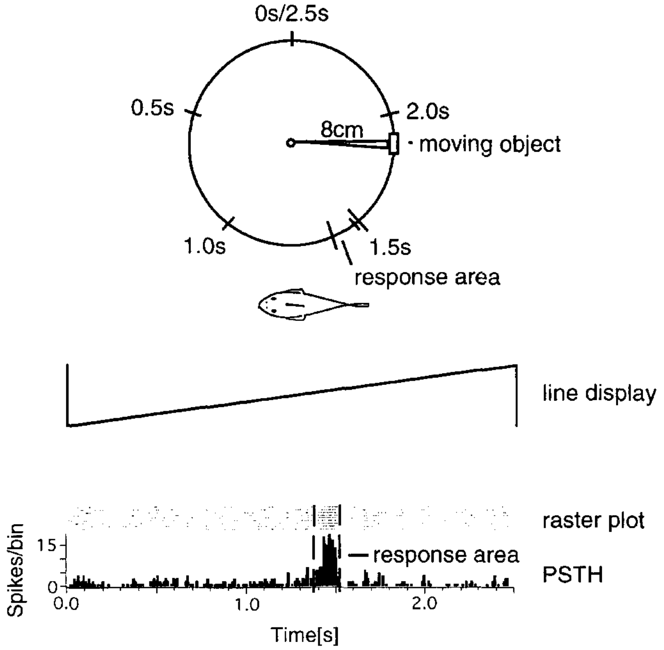


Fig. 1 *From top to bottom*: Object and orbit of moving object, position and size of fish relative to the orbit, and output of endless potentiometer (*line display*) attached to the DC-motor (one *sawtooth* corresponds to one orbit). Below the sawtooth are *raster plots* which indicate the arrival of each action potential by a *dot*. Below the raster plots the responses are shown as *peri-stimulus-time-histogram* in which the action potentials are integrated across stimulus repetitions. In the case shown the object needed 2.5 s to complete one orbit. The two *vertical dashed lines* indicate the boarders of the response area

stimulated with weak water jets or with local vibratory water movements produced with a small sphere (diameter 6.3 mm). The sphere was positioned under water close (about 1.5 cm) to the fish. With aid of a rod the sphere was connected to the membrane of a loudspeaker (BPSL 100/7, Isophon) which was driven by a digital sine wave generator. With aid of a microdrive the anterior-posterior position of the sphere could be adjusted. Axis of sphere vibration was approximately parallel to the long axis of the fish. Stimulus frequency was 5 Hz and varying peak-to-peak (p–p) displacement amplitudes of the sphere were obtained by means of an attenuator (total range 0–100 dB). Stimulus intensity was gradually reduced as increasingly sensitive body regions were found until no response could be elicited even at the region with the lowest threshold. Stimulus amplitude was than increased to threshold which was judged with aid of an audio-monitor and/or with aid of peri-stimulus-time histograms calculated On-line. The sphere was then moved in 10 mm steps in the anterior, thereafter in the posterior direction until no neural response could be recorded.

Electric dipole stimuli

For ampullary stimulation two wires were moved in the water without being attached to the object. Control experiments had shown that central units which received unimodal lateral line or tactile input did not respond to the water movements caused by the wires, provided object speed was low (2.3 cm/s). The responsiveness of an ampullary unit to dipole-field stimulation was also assayed by moving a hand-held dipole (1.5 mV/cm) around the fish.

Loudspeaker stimuli

Airborne sound was generated with a louspeaker (MB344, McBrown) suspended in air 150 cm above the fish. Sound intensity was measured with a sound level meter (Rhode and Schwartz) placed in air either directly above the fish or immediately below the loudspeaker. Stimulus duration was several seconds, the stimulus rise- and fall times of the constant frequency stimuli were 250 ms.

Vibratory stimuli

Vibratory stimuli were applied by tapping the edge of the experimental tank.

Tactile stimuli

Water displcements caused by a fast moving object may stimulate tactile receptors or receptors associated with barbels and extended fin rays. In order to test whether a given unit received tactile input we touched the skin of the fish with a soft brush, a hair, or a small glass filament (diameter 0.13 mm). The maximum pressure which could be applied was 1.5 g (hair) and 68 mg (glass filament), respectively.

Photic stimuli

Photic stimuli were applied with a flashlight or by switching on and off the room light.

To identify the nature of the input to a unit, stimulus regimes were such that the visual system, the acoustic system, the ampullary electroreceptors and the lateral line neuromasts could be stimulated nearly exclusively or in a combined fashion.

Measurements of subsurface water motion

The hydrodynamic stimuli caused by the moving object were measured with a hot-wire rheometer (custom made). With a fish absent the sensing element of the rheometer was placed in the water such that the moving object passed the sensor at a minimal distance of 1 cm. For the frequencies tested (5 and 20 Hz) the output of the rheometer increased linearly with p–p displacement amplitude of the vibrating sphere (Fig. 2, inset). If the amplitude was kept constant the output of the rheometer decreased exponentially with increasing frequency (Fig. 2). Therefore the hot-wire rheomometer was especially useful for measuring the low-frequency (≤ 10 Hz), transient water movements caused by the moving object. While the time course of the fast transient voltage change was comparable across stimulus presentations, the time course of the return to baseline was variable (Fig. 3A). The courses were similar for anterior-to-posterior and for posterior-to-anterior motion direction. Steepness and amplitude of the fast voltage change decreased with decreasing speed of the moving object (test range 2.5–23 cm/s) and with increasing minimal lateral distance (test range 1–7 cm) between object and fish.

Measurement of surface waves

Surface waves were recorded with a receiver electrode which was immersed about 0.8 mm into the water. A 20 cm long silver wire which was submerged into the water served as a reference electrode. The method of wave measurement is based on the principle that the

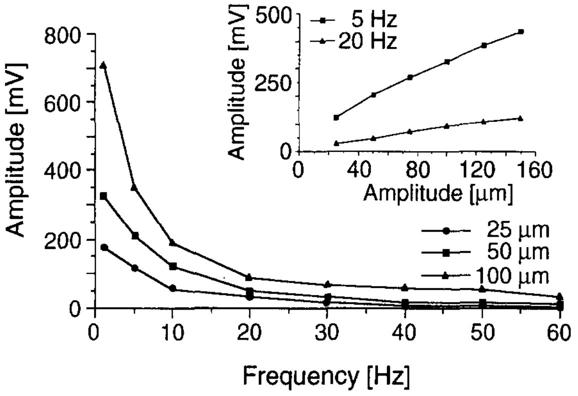


Fig. 2 Frequency response of the hot-wire rheometer used to measure the time course of subsurface water movements. The calibration curves were obtained by attaching the probe to the tip of a rod which was connected to the membrane of a loudspeaker. P-p vibration amplitudes of the loudspeaker were set to 25, 50, and 100 µm. *Inset*: Output of probe as function of P-p displacement amplitude for the vibration frequencies 5 and 20 Hz

electrical resistance between the emitter electrode inserted into the circuit of a Wheatstone bridge (custom-fabricated) and the receiver electrode depends on the immersion depth of the latter (Rudolph 1967). Calibration was done by sinusoidally moving the measuring electrode (which was attached to the cone of a loudspeaker) with a defined amplitude relative to the water surface. The frequency response of the measuring device is linear from DC up to at least 150 Hz (Bleckmann et al. 1994). For analysis the wave stimuli were digitalized (MacAdios board, sample interval 300 µs) and processed with a Computer (Power Macintosh) and the software SuperScope.

Data aquisition and analysis

Action potentials were amplified (Grass P15b or DAM 80, WPI), bandpass filtered (300–3000 Hz), displayed on an analog oscilloscope and stored on a digital tape recorder (Biologic, DTR 1200 or 1800). Units were isolated using a window discriminator (custom-fabricated) which delivered a TTL pulse for each action potential within or above the window. TTL pulses were digitized (GW Instruments MacAdios II and SuperScope II), stored on a computer (Apple Macintosh SE or IIci) and the time of occurrence of TTL pulses relative to the onset of object motion was calculated.

At all sites, ongoing activity was recorded in the absence of object movement. Responses to object movement were displayed as dot plots and peri-stimulus-time (PST) histograms that were computed across the 5 to 10 repetitions for each stimulus condition. Raster plots, PST histograms and ongoing activity were used to determine a response area. Peak spike rates (PSR) were determined from the bin in the peri-stimulus-time histogram (bindwidth 50 ms) with the greatest number of spikes and expressed in spikes/s. That part of a histogram where spike frequency clearly surpassed ongoing activity was defined as response area (see the two dashed vertical lines in Fig. 1, bottom). Mean spike rate was defined as the total number of spikes during the response divided by response duration and expressed in spikes/s. Per-second rates were normalized by subtracting the spontaneous (ongoing) rate of the unit. At high object speed the response area usually was well defined. However, at low and medium object speed the response area often could not be determined unequivocally. In order to compare the total number of spikes at different object speeds we first determined the response area (that part of an orbit where a clear excitatory response occurred) at high object speed. Thereafter the time windows during which the object passed this area at medium and low object speed were calculated and the number of spikes elicited within these time windows was determined.

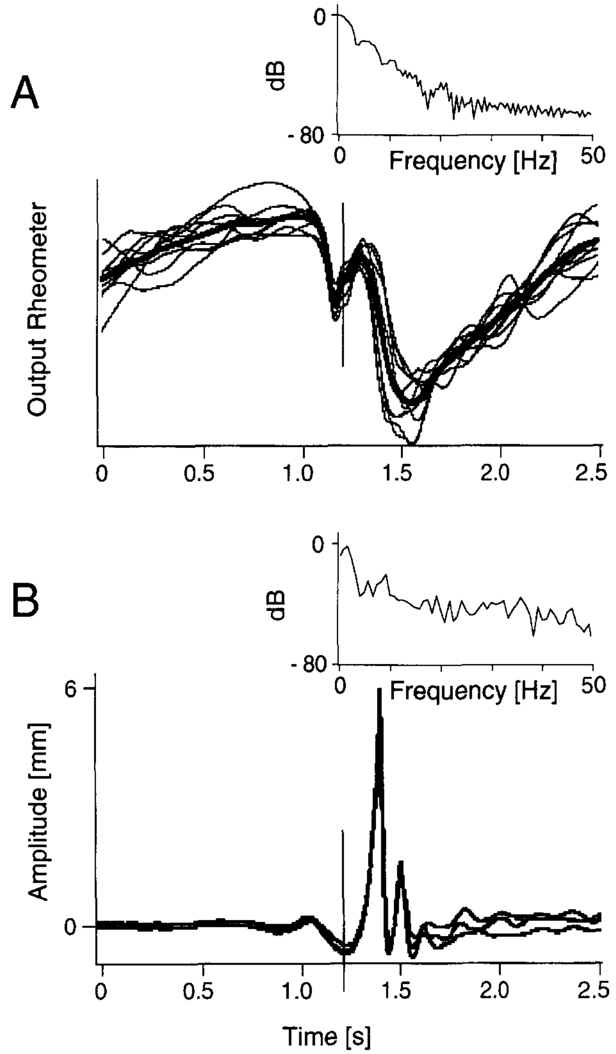


Fig. 3 **A** The time course of subsurface water movements caused by the moving object which passed the sensor of the hot-wire rheometer at a distance of 1 cm. Object speed was 23 cm/s. Ten measurements are superimposed. The *thick line* represents the mean of all measurements. **B** The time course of surface waves caused by the moving object which passed the wave measuring electrode at a distance of 1 cm. Object speed was 23 cm/s. Three measurements are superimposed. The *vertical lines* in **A** and **B** indicate the time when the object was closest to the wave measuring sensors. *Insets*: Amplitude spectra of the signals shown. Note that due to the low-pass filter properties of the rheometer (Fig. 2) the amplitudes of possible high-frequency components of subsurface waves produced by the moving object will be underestimated by a factor of up to 10

In series in which the responses were determined as function of object distance it became obvious that the response peaks shifted to later times with increasing object distances (e.g. Fig. 6A). To take these time shifts into account the occurrence of the largest response peak was determined for each distance tested. Thereafter the time span analysed around this response peaks was kept constant for each unit. In this way responses obtained at different object distances could be compared.

Object speed and distance were tested for the direction that yielded the strongest response. The signed directionality index (SDI) of a unit was defined as (see also Wagner and Takahashi 1992):

SDI =

$$100 * \left[1 - \left(\frac{\text{spike count in posterior-to-anterior direction}}{\text{spike count in anterior-to-posterior direction}} \right) \right]$$

if anterior/posterior was the preferred direction and

SDI =

$$100 * \left[\left(\frac{\text{spike count in anterior-to-posterior direction}}{\text{spike count in posterior-to-anterior direction}} \right) - 1 \right]$$

if posterior/anterior was the preferred direction. Units with a directionality index ≈ 0 do not exhibit a preference for a motion direction, whereas units with a strong directional preference have a value close to ±100.

N refers to the number of experimental animals and *n* to the number of recording sites. Mean values are given with their standard deviation.

Results

Anatomy

In eight animals, an electrolytic lesion was successfully placed at a physiologically characterised lateral line recording site. An example of a lesion in the medulla of *Ancistrus* is shown in Fig. 4. Medullary lesions were located either within the medial octavolateralis nucleus (MON) (2 cases) or on the border between MON and cerebellar crest (3 cases, one of which is shown in Fig. 4). The three midbrain lesions recovered were in the torus semicircularis.

Physiology

Units in the medulla and midbrain of the catfish *Ancistrus* sp. were tested for their responsiveness to the moving object, as well as for their responsiveness to vibratory, photic, tactile, electric field and loudspeaker stimuli. Medullary units classified as lateral line units responded to a weak water jet applied with a pipette, a falling water drop, or to water displacements caused by an object moving with 10 cm/s or more through the water. In contrast, units classified as receiving tactile input as well as units which innervated receptors associated with barbels or extended fin rays were fairly insensitive to water displacements caused by the moving object. Lateral line and tactile units were not sensitive to our electric field stimulus.

Medulla

Thirty-five single units and fourteen few-unit responses were recorded from the medulla of *Ancistrus*. These units were judged to receive either unimodal lateral line or unimodal tactile input. Units which responded to air-borne sound or to our electric field stimuli were not encountered.

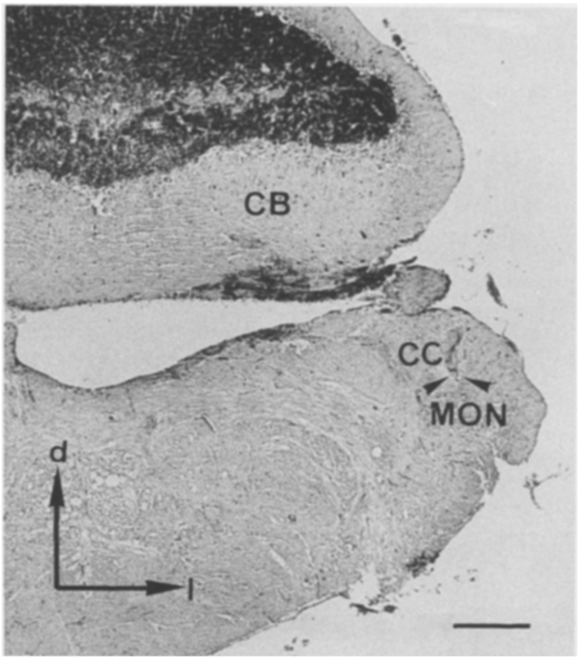


Fig. 4 Verification of a recording site in the medulla. The *arrowheads* point to the tip of an electrolytic lesion which is at the boarder between the cerebellar crest (*CC*) and the medial octavolateralis nucleus (*MON*). *CB* cerebellum; *d* dorsal; *l* lateral. *Scale bar* 200 µm

Ongoing activity. Ongoing activity was measured for at least 60 seconds with the DC motor switched off. Most medullary lateral line and tactile units showed ongoing activity. The distribution of interspike time intervals were usually asymmetrical (Poisson-like) but some units showed fairly symmetrical interspike time interval distributions. In lateral line units ($n = 26$) ongoing activity varied between 0 and 86 spikes/s (mean 15 ± 21 imp/s). The corresponding values for tactile units ($n = 8$) were 0 to 41 imp/s (mean 14 ± 20 imp/s).

Response types. At all speeds tested the moving object caused a low-frequency transient stimulus which was followed by some irregular higher-frequency water oscillations (e.g. Fig. 3A). Despite the uniform transient wave stimulus caused by the moving object several response types (object speed 23 cm/s, minimal distance between fish and object 1–2 cm) could be distinguished: 1) Units without ($n = 2$) and with ($n = 14$) ongoing activity which responded to the moving object with one or two excitatory peaks to either forward or backward movements. The duration of the main peak of the responses of these units varied between 80 and 700 ms; within this period peak-spike rates were up to 70 times above ongoing activity (Fig. 5A, B, C). Responses of this type were classified as type A responses. In single

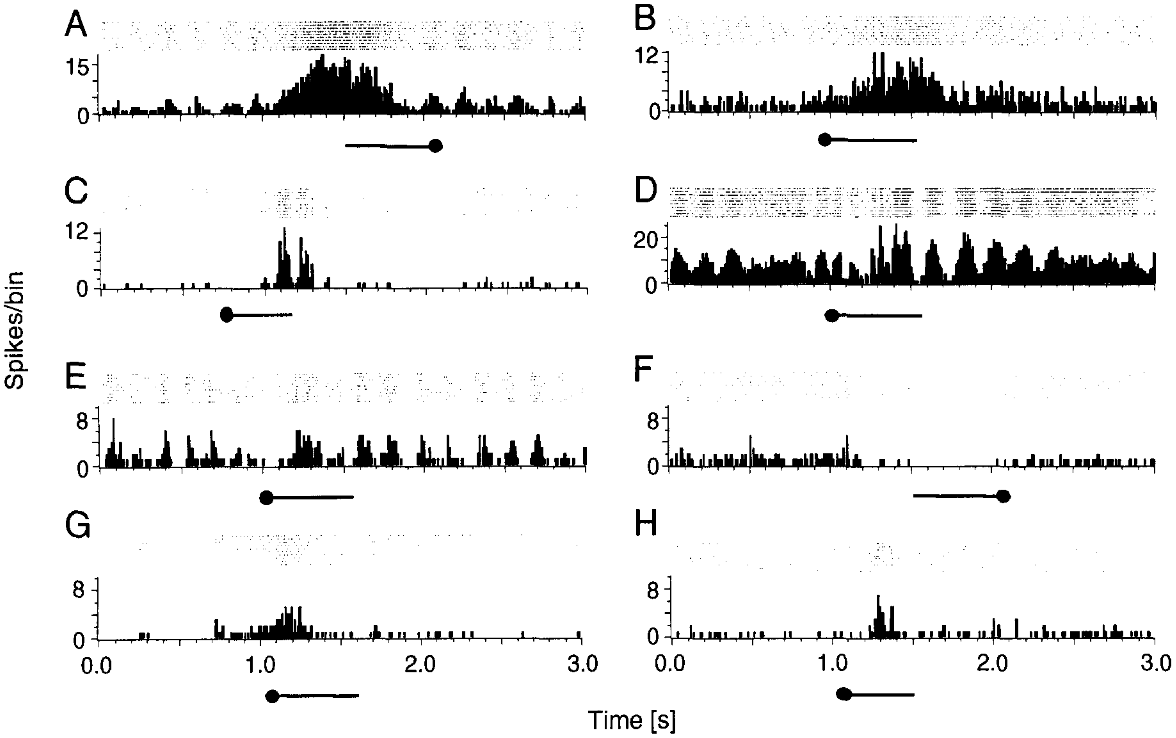


Fig. 5A–F Examples of responses of lateral line units recorded from the medial octavolateralis nucleus of *Ancistrus* to an object which passed the fish with a speed of 23 cm/s. Response histograms had either a dominant single broad peak (**A, B**), two peaks (**C**) or multiple peaks (**D, E**) of excitation. One unit responded exclusively with a decrease of neural activity while the object passed the fish (**F**). **G, H**: Responses of two medullary tactile units to the moving object. Object speed wa s 23 cm/s. In this figure and in Figs. 6, 9, 13 and 18 the *horizontal lines* below each histogram give size, position and orientation of the fish relative to one orbit. The *dot* indicates the position of the head

peaked type A responses the passing object may cause an excitation followed by inhibition or an inhibition followed by excitation. 2) Units which responded with multiple peaked spatial profiles to either forward or backward movement (type B responses, Fig. 5D, E and Fig. 6B). Peaks of increased spike activity usually were separated by periods in which neural activity was below ongoing activity. Type B responses appeared to be from the most sensitive units recorded from. In these units, which showed a high (26 ± 29 impulses/s) ongoing activity, responses became evident before the object reached the fish and often persisted for some time after the object had passed the animal (e.g. Fig. 5D, E). One medullary unit responded to the moving object with a short excitatory peak, sharply bordered on either side by zones of no neural activity (type C response, c.f. Fig. 9C). Another unit, whose ongoing activity was 13 impulses/s, responded exclusively with a decrease in neural activity while the object passed the fish, i.e. this unit showed neither an On- nor an Off-response (type D response, c.f. Fig. 5F). Type B responses resembled those of the most sensitive primary lateral line afferents recorded from the weakly electric fish *Eigenmannia* (c.f. Bleckmann and Zelick 1993). Type A and D responses were probably from second or higher order lateral line neurons. None of our medullary units which received lateral line input responded to any other stimulus modality, i.e. our acoustic and vibratory stimuli clearly did not stimulate the lateral line system of *Ancistrus*. In addition to the single units some few unit responses were recorded from the medulla. Five few-unit recordings resembled type A rsponses and eight type B responses. In the 39 units tested (25 single unit recordings and 14 few unit recordings), type A responses (11 [7]; values in square brackets refer to few unit recordings), type B responses (13 [6]) and type C responses (1) did not change with object distance (for examples see Fig. 6) nor did a given response type correlate with the anterior/posterior position of the center of the receptive field of the unit (determined with a vibrating sphere stimulus or with weak water jets applied to the animal).

In addition to the lateral line units we encountered eight medullary units which were judged to be unimodal tactile, i.e. these units responded to our tactile stimuli (see material and methods). Two of these units showed some responses to the moving object (Fig. 5G, H). Six units showed no or a weak response to the moving object, even if object speed was high. In two medullary units the input modality could not be determined.

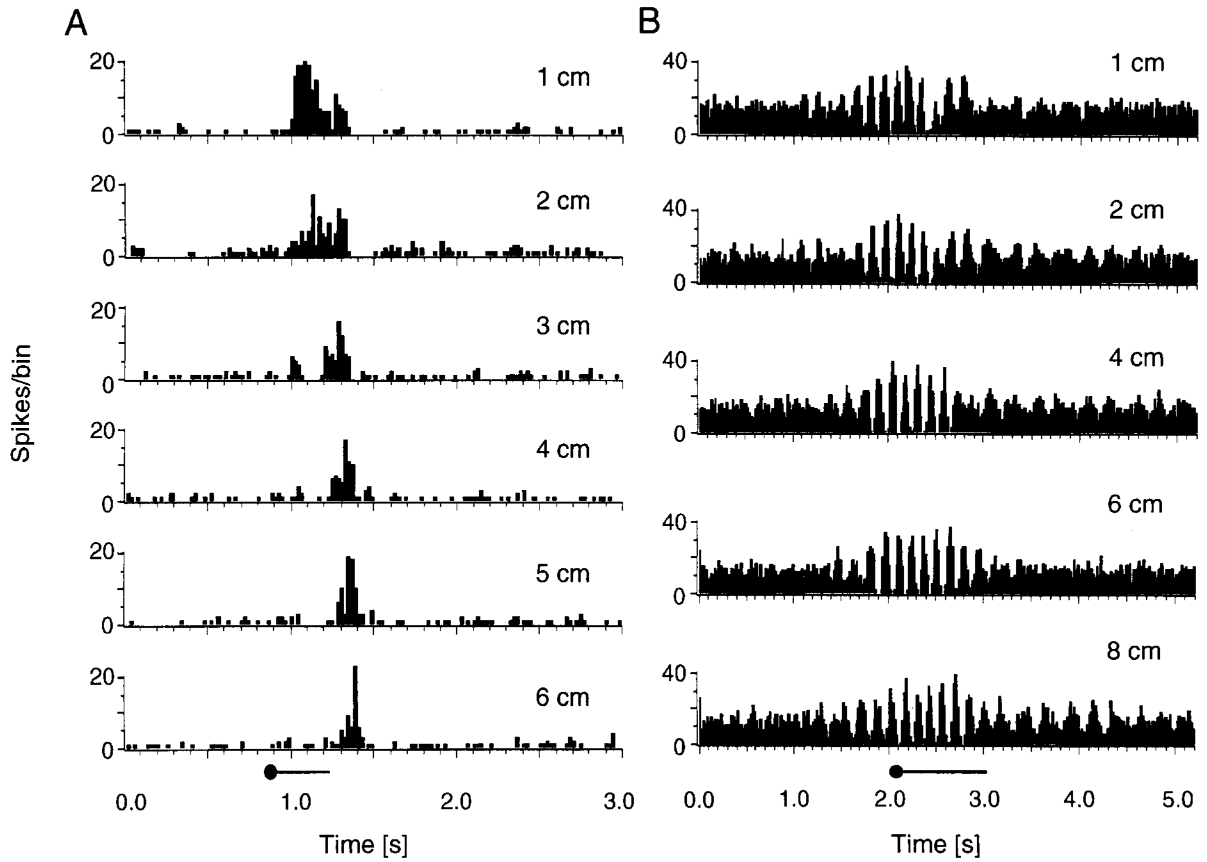


Fig. 6A, B Examples of a type A response (**A**) and a type B response (**B**) of lateral line units recorded from the medial octavolateralis nucleus of *Ancistrus* to an object which passed the fish laterally. Object speed was 23 cm/s in **A** and 10 cm/s in **B**. Note that response types do not change with object distance (indicated in the *upper right* of each histogram)

Effects of object speed. Three speeds were tested: low speed (2.5 cm/s), medium speed (10 cm/s), and fast speed (23 cm/s). The minimal distance between object and fish was 1 cm. Fourteen out of 15 medullary lateral line units responded at all object speeds tested, one unit responded only when object speed was ≥ 10 cm/s. With the exception of one unit which showed type B responses mean spike rates (MSR) significantly (Two-tailed correlation test after Spearman) increased with increasing object speed V (units with type A or type C responses: $MSR = 9.1 + 4.6\,V$; $r = 0.79$; $p < 0.001$; units with type B responses: $MSR = 15.7 + 3.3\,V$; $r = 0.75$; $p < 0.001$) (Fig. 7). Peak spike rates of units which showed type A or type C responses also increased significantly with increasing object speed ($p < 0.001$). In contrast peak spike rates of units which showed type B responses did not show a significant increase with increasing object speed ($p = 0.6$). Obviously even at low object speeds peak spike rates of units with type B responses are driven into saturation. Units sharply tuned to a distinct speed were not found.

Response decrement. Repeated stimulation may lead to a significant response decrement in higher order lateral line units (e.g. Bleckmann et al. 1989). Our data show that medullary lateral line units of *Ancistrus* did not experience a significant decrease in mean spike rate (MSR) if the object passed the fish in quick succession (Fig. 8). This contrasts tactile units which always showed some response decrement in a similar experimental situation. Consequently the MSR of tactile units were negatively correlated with orbit number ($MSR = -2.85 \times \text{orbit number} + 48.7$; $r = 0.29$; $p = 0.022$).

Directionality of medullary lateral line units. Some units were sensitive to the direction of object motion (e.g. Fig. 9). In order to test for directionality a unit was stimulated first with object motion starting in either the anterior/posterior or the posterior/anterior direction (object speed 23 cm/s; minimal distance between fish and object 1–2 cm). After completion of 5 to 10 orbits the motion direction of the object was reversed. In one medullary lateral line unit a change in stimulus direction caused a complete inversion of the main response features (Fig. 9C, D). When the object moved in one direction this unit responded with an excitatory peak that was bordered by periods of decreased neural activity. When the object moved in the other direction, the excitatory peak was replaced by a period of decreased activity that was bordered by small excitatory peaks.

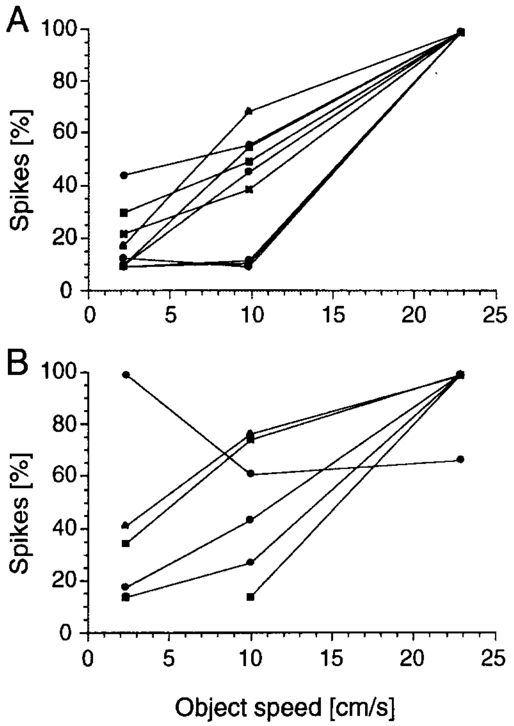


Fig. 7A, B Mean spike rates (percent of maximum) of single units which showed type A or C (**A**) or type B (**B**) responses as function of object speed. In each case the minimal object-to-fish distance was 1 cm

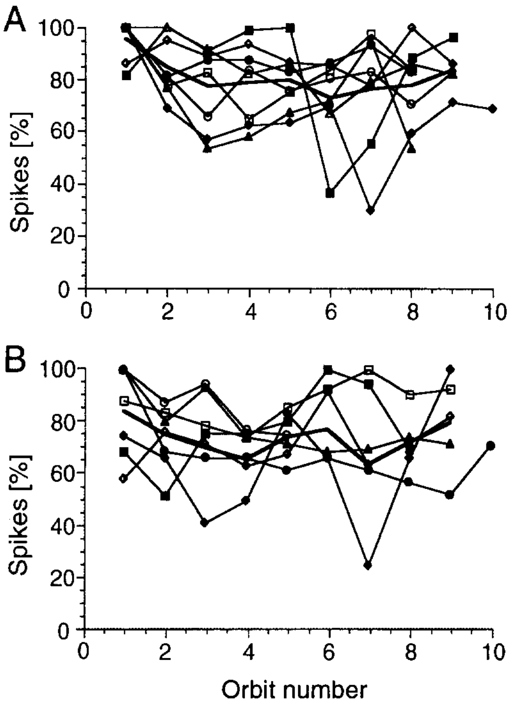


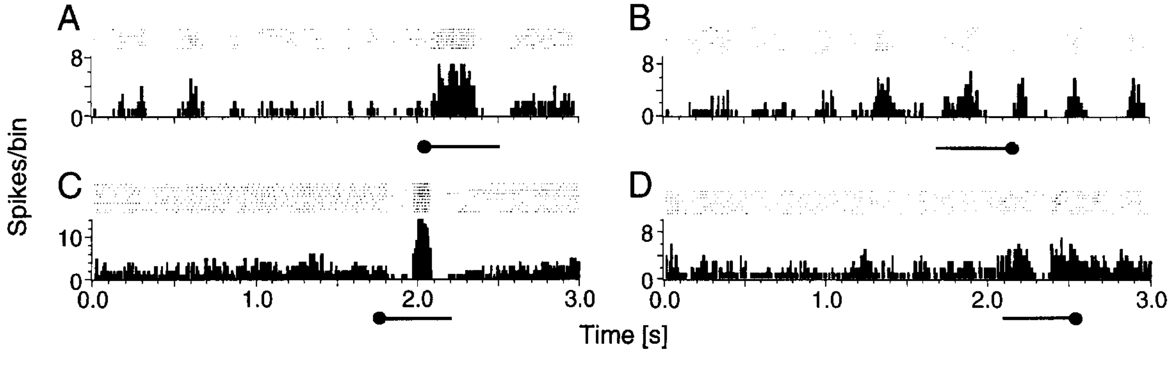
Fig. 8A, B Whole trial spike rates of type A responses (**A**) and type B responses (**B**) obtained by an object which passed the fish in a rostral-to-caudal or a caudal-to-rostral direction as function of orbit number. Object speed was 23 cm/s. For each unit the highest number of spikes obtained during one out of 10 consecutive orbits was set equal to 100%

Among the other 22 units, SDIs calculated for average and maximum discharge rates ranged from − 66.3 to + 65.2 (mean ± S.D. = − 6.4 ± 44.8, $n = 22$) and from − 63.6 to + 66.7 (mean ± S.D. = − 1.9 ± 33.9), respectively (Fig. 10). Units which responded only to one direction of object movement were not found. Nevertheless, for 8 units mean spike rates were significantly different (t-test, $p < 0.05$) for anterior/posterior and posterior/anterior direction of object motion.

Effects of object distance. With object speed 23 cm/s, the minimal distance between fish and object was varied between 1 and 7 cm. In all units mean spike rates elicited by the object on average decreased with increasing object distance D (type B responses: MSR = − 6.6 D + 49.5; $r = 0.51$; $p < 0.001$; type A, C, and D responses: MSR = − 8.1 D + 64.3; $r = 0.39$; $p < 0.001$) (Fig. 11). However, in two units which showed type B responses the responses increased up to a distance of 3 or 4 cm, thereafter they started to decrease.

Average peak spike rates of units which showed type B responses did not decrease with increasing object distance. However, in all other units PSR decreased

Fig. 9A–D Responses of two medullary lateral line units to an object which passed the fish at a minimal lateral distance of 1 cm in an anterior-to-posterior or posterior-to-anterior direction. Object speed was 23 cm/s. Note that a change in stimulus direction altered the time course of the responses of these units



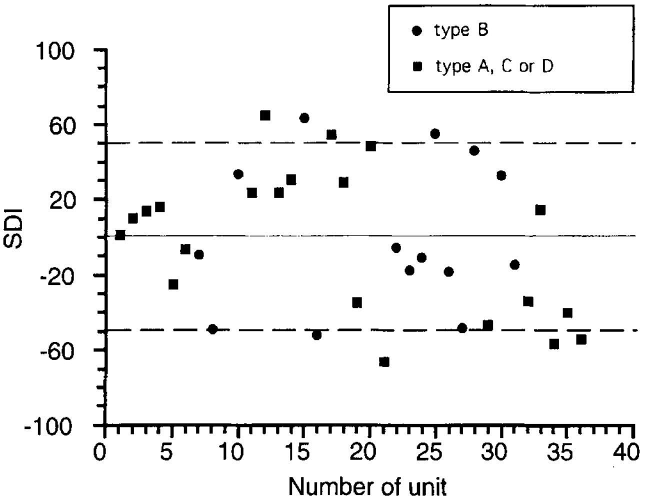


Fig. 10 The SDI value of medullary lateral line units. Object speed was 23 cm/s. Type B responses: (●), type A or C responses: (■). An SDI value < 0 indicates that anterior/posterior was the preferred direction. *Dashed lines* indicate an SDI of + 50 or − 50

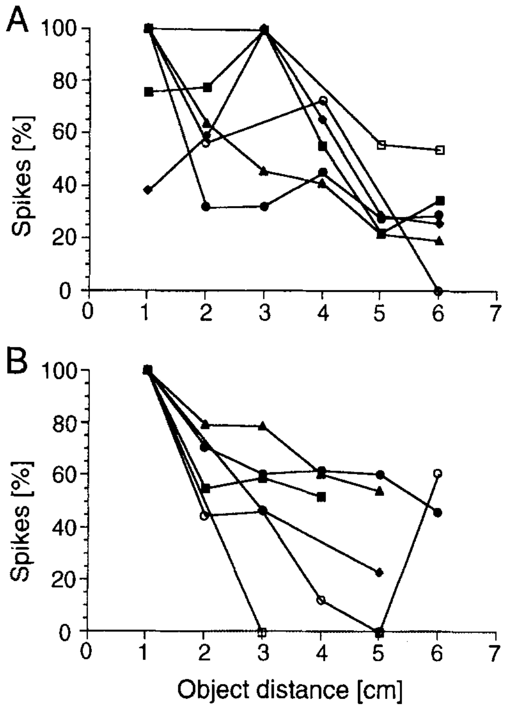


Fig. 11A, B Peak spike rates (percent of maximum) of single units which showed type B (**A**) or type A or C (**B**) responses as function of minimal object distance. Direction of object movement was the direction which caused the largest excitatory responses. Object speed 23 cm/s

significantly with increasing object distance (PSR = − 11.6 D + 112; $r = 0.38$; $p = 0.001$). If object speed was 10 cm/s, units which showed type B responses again responded with peak spike rates which were independent of object distance. However, units which showed type A, C, and D responses showed a significant decrease in the response (MSR and PSR) with increasing object distance (mean spike rates: MSR = − 3.8 D + 29.7; $r = 0.65$; $p = 0.003$; PSR = − 7.2 D + 81; $r = 0.52$; $p = 0.029$).

Midbrain

In the torus semicircularis of *Ancistrus* extracellular recordings were obtained from 71 units. Sixteen units were sensitive to air-borne sound, i.e. these units probably received acoustic input. Units classified as acoustic units responded vigorously to voice, claps, clicks and to feedback from the audiomonitor, but poorly to tones which usually elicited only an ON- and/or an Off-response. Acoustic units demonstrated little or no sensitivity to translatory movements of the object. In five acoustic units sensitivity to constant-frequency sound was tested. In these units best sensitivity to loudspeaker stimuli were in the frequency range 200–900 Hz, and high cut-off frequencies were around 2000–4000 Hz. In addition to the acoustic units we recorded nine units which responded vigorously to the moving object, provided the object was superimposed by a weak electric field (see Materials and methods). These units probably received ampullary input. Twenty units were judged to be unimodal lateral line, i.e. these units responded to the water movements caused by the moving object but not to air-borne sound, vibration, an electric field stimulus or a light flash. In addition to the above 45 units we found two toral units which responded only to visual input, three units which responded only to tactile stimuli and 21 units which were judged to be bimodal (see below). Unimodal visual units (for control we also recorded 7 visual units in the tectum) showed two clearly separated response peaks during each circular orbit of the object. One peak occurred when the object passed the visual field of the unit at close distance, the other when the object passed the visual field of the unit at large distance (c.f. Fig. 1; for an example of a neural response see Fig. 12, top). In contrast all non visual units responded only if the object moved through that half of the orbit which was closest to the fish. Six units did not respond to any of the stimuli applied to the fish.

Twenty-five of the 71 units recorded in the torus showed little (< 0.5 spikes/s) or no ongoing activity. In 15 units mean ongoing activity ranged between 1 and 7 spikes per second. The ongoing activity of the other units was not determined.

Response categories of midbrain lateral line units. At the level of the midbrain several response categories (object speed 20 cm/s, minimal distance between fish and object 1–2 cm) could be distinguished: 1) responses with short, sharply bordered single peaked spatial profiles, to both, forward and backward object movements (type MA responses; Fig. 13A, B). Some units which showed type MA responses consistently responded

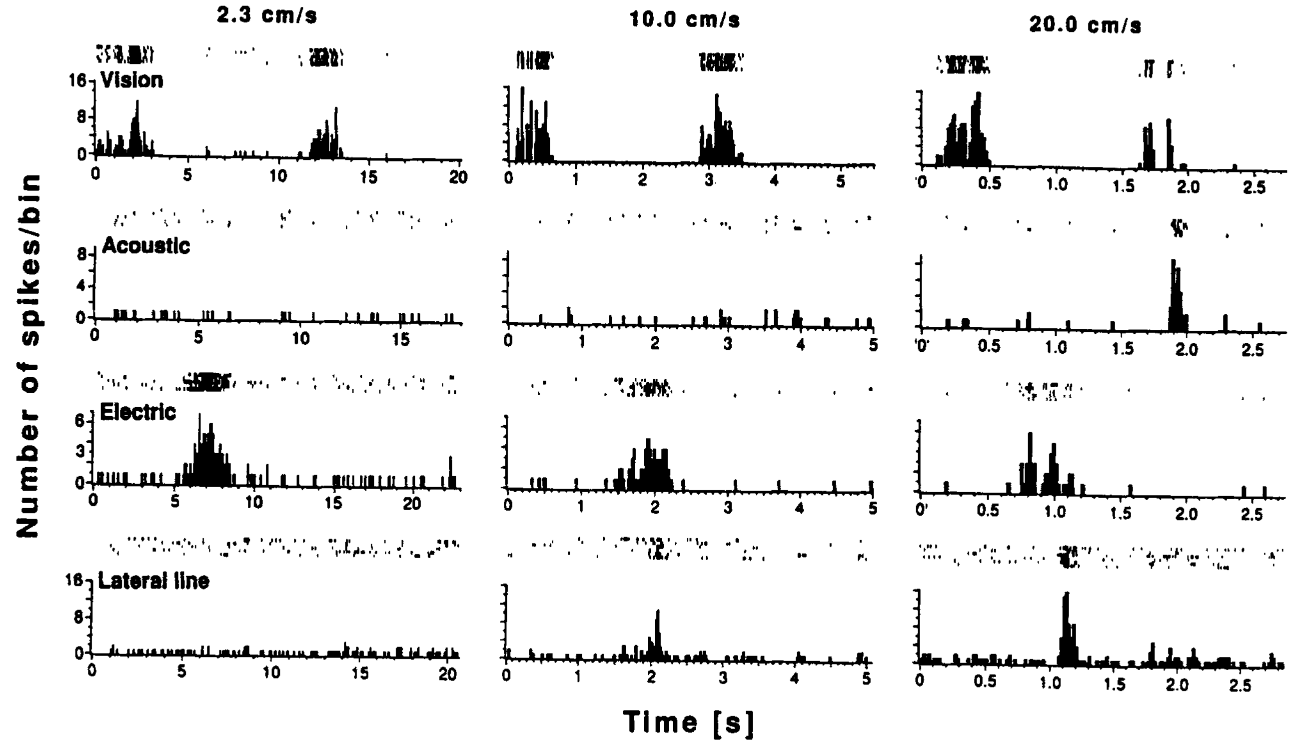


Fig. 12 Examples of midbrain-unit responses to an object which passed the fish with a speed of either 2.3 cm/s (*left*), 10 cm/s (*middle*), or 20 cm/s (*right*). *From top to bottom* responses are from units which were classified as unimodal visual, acoustic, ampullary (electric), and lateral line. In case of the ampullary unit the object was superimposed by a weak DC field

only with one spike while the object passed the fish; 2) responses with long, less sharply bordered single peaked spatial profiles, to both, forward and backward movements (type MB responses; Fig. 13E); and 3) responses with double or multiple peaked spatial profiles to either, or both, forward and backward movement (type MC responses; Fig. 13C, D). In units which were spontaneously active excitatory peaks could be bordered on one or on both sides by zones of decreased neural activity (e.g. Figs. 13B, D). In the midbrain of *Ancistrus* no lateral line units were found which responded solely with a decrease in neural activity to the moving object.

Effects of object speed. Three speeds (2.3, 10, and 20 cm/s) were tested. The minimal distance between fish and object was 1 or 2 cm. In terms of object speed midbrain units showed some range fractioning. Units which responded to air-borne sound ($n = 16$) either did not respond to the moving object at all (5 units) or they responded at medium and high (2 units) or at high object speed (9 units) only (e.g. Fig. 12, second series of histograms). All units which received ampullary input ($n = 25$) responded at all object speeds (e.g. Fig. 12, third series of histograms and Fig. 14C, D), provided the object was superimposed by a weak DC field. Most units classified as unimodal lateral line responded at both, medium and high object speed (e.g. Fig. 12, bottom), however, two unimodal lateral line units responded at all object speeds tested. In 5 lateral line units the responses did not increase when object speed was increased from 10 to 20 cm/s. In one unit there was a significant decrease in response if the object speed was changed from 10 to 20 cm/s (7.3 spikes at 10 cm/s vs 4.0 spikes at 20 cm/s). In those units which still showed a response increase between 10 and 20 cm/s the velocities at which the responses of the units would not further increase have not been established. From the 40 midbrain units tested, only one may have responded selectively to medium speed. The responses of some other lateral line units were slightly better at medium than at high object speed (c.f. Fig. 14A, B).

Response decrement. In contrast to medullary lateral line units some midbrain units showed a marked response decrement if the object passed the fish several times in quick succession (Fig. 15B). This response decrement also became obvious when the fish was stimulated with long lasting sinusoidal lateral line stimuli.

Directionality index of midbrain lateral line units. Midbrain lateral line units of *Ancistrus* may be highly directional (e.g. Fig. 16). In terms of mean or peak spike rate 15 of the 28 midbrain lateral line units tested for directional sensitivity (object speed 20 cm/s; minimal distance between fish and object 1 to 2 cm) had an SDI between − 50 and + 50. In eleven units the SDI was

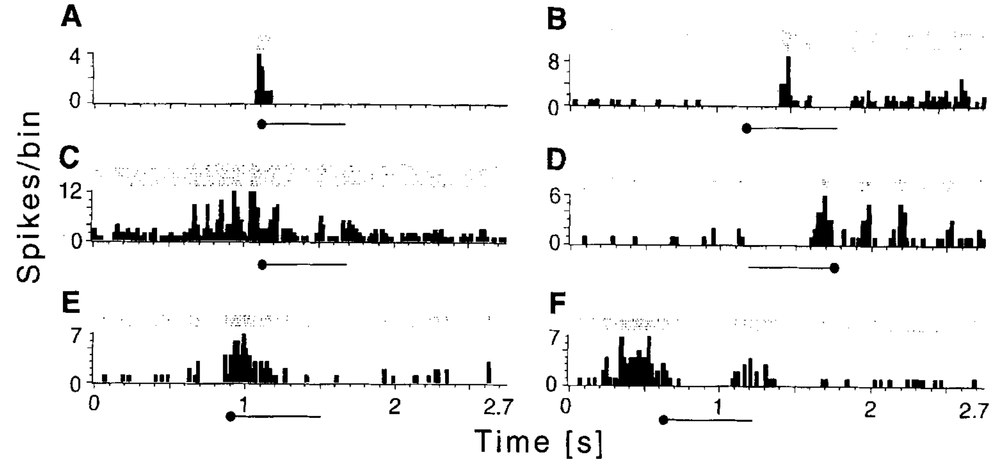


Fig. 13A–F Examples of single unit lateral line response to an object which passed the fish with a speed of 23 cm/s. Response histograms were single peaked (**A, B, E**), double peaked (**F**), or multiple peaked (**C, D**). In many units excitatory responses were bordered by zones of decreased neural activity (**B, D**)

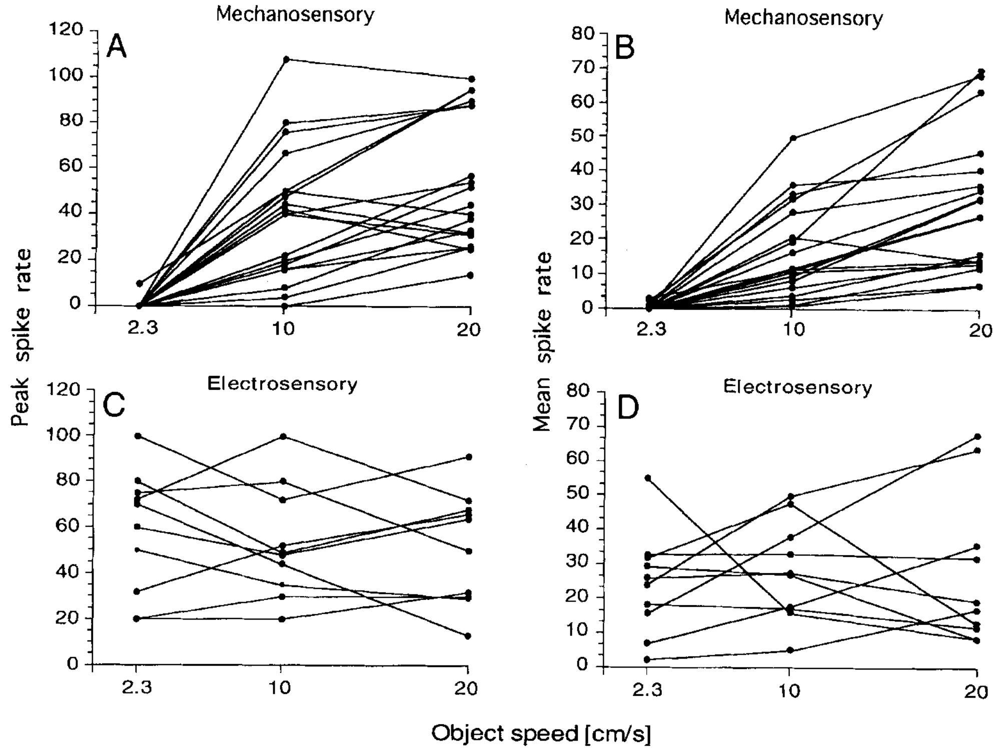


Fig. 14A–D Peak spike rate (**A, C**) and mean spike rate (spikes per trial per second) (**B, D**) of midbrain lateral line units as function of object speed. Direction of object movement was either anterior-to-posterior or posterior-to-anterior. In case of ampullary (*electrosensory*) units the moving object was superimposed by a weak DC-field

above + 50 or below − 50 and two units showed an SDI close to + 100 or − 100 (Fig. 17). In these two units a large response occurred when the object moved in one direction, while no response was evoked by the opposite direction of object motion (e.g. Fig. 16). In 17 out of the 28 midbrain units the responses to an object moving in an anterior-to-posterior direction were significantly different from the responses to an object moving in the opposite direction (t-test, $p \leq 0.05$). In these 17 units the SDI was also determined for medium object speed. In 6 of these units the SDI at medium speed was similar (± 10%) to the SDI obtained at high object speed. In 5 units the SDI was much higher at high object speed than at medium object speed, i.e. in these units the difference in SDI values was at least 30.

Multimodal interaction. Out of 71 toral units, 45 (63.4%) were classified as unimodal and 26 (36.6%) as bimodal. Sixteen (61.5%) bimodal units received mechano- and electrosensory input. These units had an

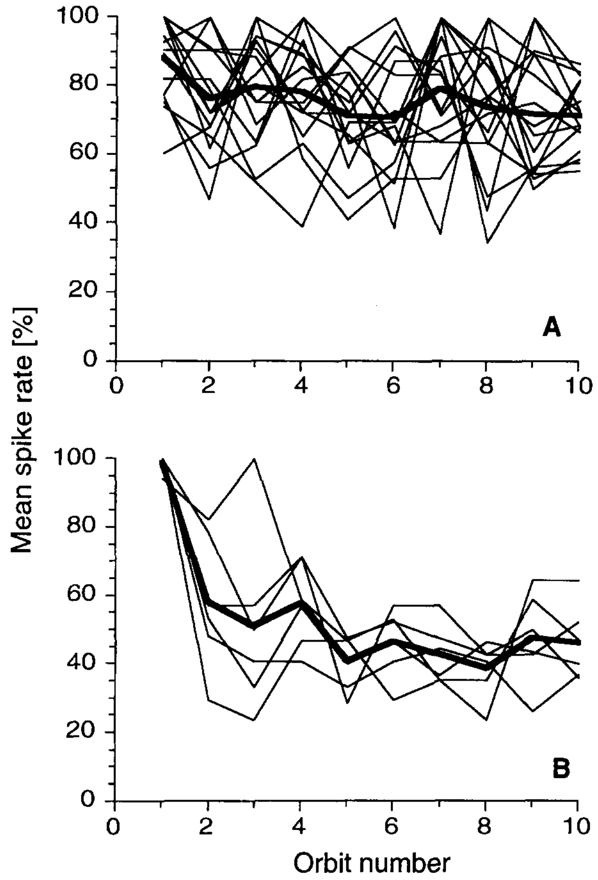


Fig. 15A, B Response as function of orbit number. The units presented in **A** did not show a response decrement, the units presented in **B** did

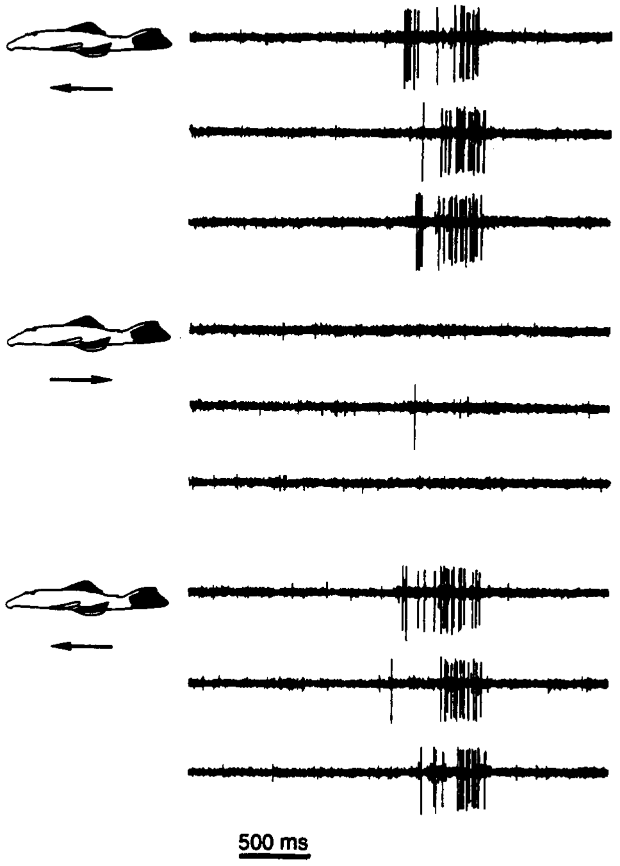


Fig. 16 Example of a unimodal directionally sensitive lateral line unit recorded in the torus semicircularis of *Ancistrus*. Note that the unit responded only if the object passed the fish in a posterior-to-anterior direction. Object speed was 10 cm/s, the smallest distance between object and fish was 1 cm

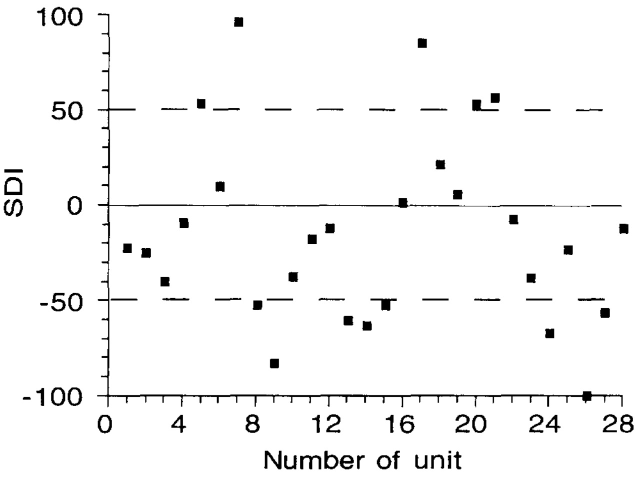


Fig. 17 The SDI value of midbrain lateral line units. Object speed was 10 cm/s. An SDI value < 0 indicates that anterior-to-posterior was the preferred direction. *Dashed lines* indicate an SDI of + 50 or − 50

extended velocity range to bimodal stimulation (e.g. Fig. 18). At high object speed the electrosensory input did not lead to an increase in neural response (88 spikes/s without electrosensory input vs. 80 spikes/s with electrosensory input) whereas at medium and low object speed the ampullary input caused a significant response increment (e.g. at low object speed we measured 1.8 spikes/s vs 70.6 spikes/s). Among different bimodal cells responses differed. If stimulated with both mechanosensory and electrosensory input, two bimodal units showed a strong response enhancement. In five units bimodal input did not alter the responses, and in seven units there was a significant response reduction when both stimulus modalities were presented. In two other units bimodal stimulation led to some spatial sharpening of the response. Two bimodal lateral line units were found that received visual input. One of these units responded with 14.1 ± 2.8 spikes/orbit under steady light conditions and with 6.9 ± 4.8 spikes/orbit in complete darkness. The corresponding peak spike rates were 2.8 ± 0.67 spikes/s and 1.5 ± 0.57 spikes/s, respectively. Two bimodal units received electrosensory and visual input. These units showed a strong reduction in the response when both modalities were presented.

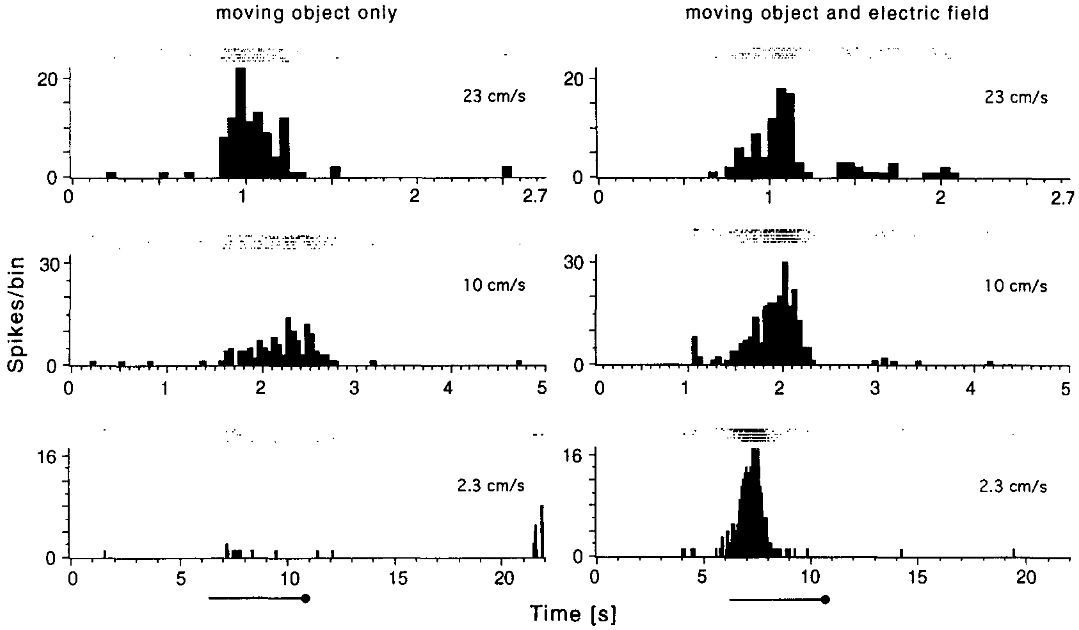


Fig. 18 Response of a bimodal midbrain unit which received input from the mechanosensory lateral line and the electrosensory system. Note the extended speed range if the object was superimposed by a weak electric field. Object speed 20 cm/s (*top*), 10 cm/s (*middle*) and 2.3 cm/s (*bottom*). Bin width 50 ms

Discussion

In this paper we present lateral line unit responses as a function of aspects of a moving object and not as a function of the water movements created by the object. One reason for this is that our wave measuring device was not sufficient to describe and quantify the complex water motions generated by the moving object. Our hypothesis is, however, that the central lateral line system of fishes encodes important aspects of a wave generator, e.g. its size, shape, speed, direction of movement, and distance.

The present study shows that most medullary and midbrain lateral line units of the bottom dwelling catfish *Ancistrus* sp. respond to a small object which passes the fish laterally with a speed of at least 10 cm/s. Transformations in response properties from medulla to midbrain (torus semicircularis) include a decrease in activity in the absence of the stimulus and an increase of response decrement in a repetitive stimulus regime. In addition units which responded to only one direction of object motion were so far only found in the midbrain.

The functional significance of response types

In both the medulla and midbrain several response types could be distinguished which did not appear to be part of a continuum (e.g. Figs. 5, 9 and 13). The question arises, however, whether these response types were mainly or exclusively due to central nervous integration mechanisms or whether they reflect – at least in part – peripheral effects. In primary lateral line afferents each wave cycle within a sinusoidal stimulus leads to an increase in neural activity followed by a decrease in neural activity (or vice versa). If a sinusoidally vibrating sphere is slowly moved along the trunk of a fish primary afferents which innervate canal neuromasts respond with a single peak of excitation which is bordered by two areas of decreased neural activity (Sand 1981; Coombs et al. 1996), a response type that can be predicted from the pressure gradient pattern across adjacent pores of the lateral line canal (Coombs et al. 1996). Thus both, the time course of a hydrodynamic stimulus and the peripheral design of the lateral line system influence or even determine the response patterns of primary afferents.

However, without further central processing one would not expect different response patterns in central lateral line units to a given hydrodynamic stimulus. One could argue that the structure of the subsurface waves was altered as the object passed *Ancistrus*. If so, neuromasts at different locations on the fish surface would experience different wave stimuli. There was, however, no correlation between response type and the anterior/posterior position of the receptive field of a unit. This argues against such an assumption. Also, control measurements showed that the time course of the wave stimuli caused by the moving object was so similar at various points along the rostro-caudal axis of the fish that spatial aspects most likely do not account for the observed differences in response patterns.

Another possible peripheral effect are surface waves generated by the moving object (Fig. 3B). Surface waves may interfere with subsurface waves and/or may stimulate neuromasts located close to the water-air interface. In most midbrain experiments the whole fish was covered by a water layer of about 2 mm. In medullary experiments only a small part of the fish's head was exposed to air. *Ancistrus* of the size we used have less than 10 free-standing neuromasts on each body side, most of which are situated close to the trunk lateral line canal (Fleck and Bleckmann, unpublished). In our experiments the trunk canal was 5 to 10 mm below the water surface. Due to physical reasons the depth impact of surface waves is small, i.e. at a depth of one wavelength (e.g. 23.6 mm at 10 Hz and 2.9 mm at 140 Hz) the movement of water particles has already diminished to less than one five-hundredth of that observed at the surface (Lighthill 1980). For all speeds and distances tested we measured the surface waves generated by the moving object. Although the moving object caused multiple peak surface waves (c.f. Fig. 3) the time course of these waves was different from the time course of type C responses (e.g. Fig. 6B).

In none of our eight control experiments did the coverage of the water surface with a glass plate alter the response type of a unit. Minor changes in response pattern did occur, however, indicating that the peripheral stimulus pattern had some influence on the responses of our central units. However, the changes were never sufficient to redefine the response type of a unit. Interestingly, if peripheral effects as those discussed above would be responsible for the various response types observed, *Ancistrus* could potentially obtain information about a moving object by analysing and comparing the response patterns generated through inputs from various neuromasts located at different parts of its body.

If a vibrating sphere of 6 mm diameter moves slowly along the side (anterior/posterior or posterior/anterior) of a fish, canal neuromast fibres respond with three consecutive peaks as the source moves past the neuromast. The pressure gradient stimulus field caused by the vibrating sphere predicts that the first and third (side) response peaks will be smaller than and 180° out of phase with the second (central) peak which will occur when the source is directly opposite the innervated neuromast (Coombs et al. 1996). Thus in case of a vibrating sphere the response pattern of a primary afferent indicates the position of the stimulus source. Rectangular objects which pass a fish with a speed of several cm/s may cause primary afferent responses which consist of several alternating peaks of increased and decreased neural activity (Bleckmann and Zelick 1993). Similar multiple peaked lateral line responses were also recorded in the medulla of *Ancistrus* (Fig. 5D, E). Units which respond with multiple peaks to a moving object signal to the brain that something is moving or vibrating in the water but they do to signal the exact position of the object. This was different in some of our medullary units which even at fast speed responded with only one peak as the object passed the fish (Fig. 5A, B). Like primary afferents (Bleckmann and Zelick 1993) and units which showed type B responses (this study) they did not encode the direction of object movement but they did signal the approximate position of the object. Other medullary and especially midbrain lateral line units seemed to encode the position of the object more precisely. The response pattern of some of these units had a narrow excitatory area in the centre flanked by symmetrical or asymmetrical inhibitory zones (or vice versa) (e.g. Fig. 9C). When the object moved in the other direction, the excitatory peak of one unit was replaced by a period of decreased activity that was bordered by small excitatory peaks. Recent recordings (Mogdans and Bleckmann, unpubl.) show that primary lateral line afferents of the goldfish *Carassius* can already respond to an object that passes the fish with such a reversal of the firing pattern. In any case, cells which most clearly encode the position of a moving object may be those which have no ongoing activity and which respond with only a few (in some cases with only one) spikes if the object passes the fish. Units with these response properties have been found thus far only in the midbrain (e.g. Fig. 13A).

Directional coding

In terms of MSR or PSR it was not until the midbrain that some units responded only if the object moved in a certain direction (e.g. Figs. 16 and 17). Two of our directionally sensitive units did not respond to a stationary vibrating sphere stimulus, therefore these units appeared to be especially suited to signal the direction of object motion. The directionality of midbrain units with a large positive or negative SDI most likely is due to central processing of lateral line information. In contrast we assume that an SDI unequal 0 but > -50 and $< +50$ may, at least in part, be due to peripheral hydrodynamic effects. From anterior to posterior the body of *Ancistrus* varies in width and shape. Thus even if object speed, shape, and size are identical, the hydrodynamic stimulus which reaches the lateral line of *Ancistrus* has some directional components.

Directional sensitive midbrain lateral line units have also been recorded from the weakly electric fish *Eigenmannia* (Bleckmann and Zelick 1993), the clawed frog *Xenopus*, and the axolotl *Ambystoma*. In *Xenopus* and *Ambystoma*, the direction of water surface waves is mapped in the tectum and the lateral line maps are in register with the visual (Zittlau et al. 1986; Claas et al. 1989), somatosensory (Stock et al. 1990), and – in *Ambystoma* – the electrosensory tectal map (Bertels et al. 1990). Whether a mapping of object direction is also present in the tectum of *Ancistrus* or other fish species is not known. Due to technical reasons our object could only be moved in two opposing (anterior/posterior and posterior/anterior) directions. Thus we cannot rule out that some of our units classified as non- or weakly-directional would have preferred directions other than the ones we tested. For a thorough discussion of this issue see Bleckmann and Zelick (1993).

Speed coding

Lateral line units in the medulla and midbrain were not tuned to a certain object speed. With increasing object speed, discharge rates of most units increased but did not saturate. Since conspecifics and other fish species may swim with speeds higher than 23 cm/s, this is not surprising. Higher object speeds than the ones we tested are probably needed to drive central lateral line units to their maximum discharge rates.

Other sensory modalities

Besides units which received lateral line input we found midbrain units which received visual, ampullary, acoustic, or tactile input. Our studies, although preliminary, indicate that sensory systems other than the lateral line encode for different aspects of the stimuli generated by a moving object. Two acoustic units responded at medium speed to the moving object. All other units ($n = 14$) which were sensitive to air-borne sound either did not respond to the moving object at all ($n = 6$) or only if object speed was high ($n = 8$). In contrast lateral line midbrain units already responded at low (2.5 cm/s) or medium object speed. Units which received ampullary or tectal visual input responded best at low object speed. Thus with respect to object speed there is some range fractioning in the different sensory systems of *Ancistrus*.

Central lateral line filters

In hydrodynamic sensory systems the animal's own movements create unwanted stimulation which may interfere with the detection of biologically meaningful signals. In addition a fish may be confronted with meaningless hydrodynamic noise. Besides the efferent lateral line system, which operates at the level of the neuromast hair cells (e.g. Roberts and Meredith 1989), there are at least three additional central filters in the mechanosensory lateral line. One filter cancels already at the level of the medulla identical input from the ipsi- and contralateral body side (Claas 1980; Plassmann 1980). Identical lateral line inputs are caused, for instance, by the animal's own gilling movements and therefore do not contain important sensory information. Another filter, which also operates at the level of the medulla, has a time constant of several minutes. This filter, which may be realised by a circuit which connects the cerebellum with the nucleus octavolateralis medialis of the hindbrain (Montgomery and Bodznick 1994), cancels any symmetric or asymmetric inputs consistently associated with the fish's gill movements (Montgomery and Bodznick 1994). Many of our midbrain lateral line units showed a substantial response decrement at either prolonged sinusoidal stimulation or in a repetitive stimulus regime (Fig. 15). This response decrement, which is even more pronounced in diencephalic and telencephalic lateral line centres (Bleckmann et al. 1987, 1989), depends neither on bilateral stimulation (common mode rejection) nor on inputs associated with the animal's gill or body movements. Thus there is a third filter which separates unwanted from meaningful hydrodynamic stimuli. The neural circuitry of this filter is unknown.

Multimodality

All sensory medullary units encountered in *Ancistrus* were unimodal. In contrast many midbrain units that responded to the moving object showed some degree of cross-modal interaction. For example, some of our midbrain units received input from the mechanosensory lateral line and either the visual or the ampullary system. All bimodal lateral line units recorded were OR units, i.e., these units were reliably driven by a unimodal stimulus of either modality. Some of the OR units had an extended velocity range (e.g. Fig. 18), i.e. these units responded well at all object speeds tested. Lateral line/acoustic OR units have been found in the midbrain of the trout. These units had an extended frequency range (Nederstigt and Schellart 1986).

Blind cave fish use the lateral line to detect and discriminate stationary objects (e.g. Weissert and von Campenhausen 1981; Hassan 1989). Unfortunately we do not know whether and to what precision any non-specialised midwater fish can discriminate with the lateral line objects that differ in speed and direction of motion, in size, shape, and distance. Behavioral experiments designed to solve these questions are clearly needed. The behavioral experiments should be complemented by physiological studies designed to learn how the parameters mentioned above are encoded by central lateral line centres.

Acknowledgements We thank Drs. T.H. Bullock, J. Mogdans and R. Zelick for comments on an early version of the manuscript. S. Coombs and an anonymous reviewer provided valuable suggestions. The experiments comply with the "Principles of animal care" Publication No. 85-23, revised 1985 of the National Institute of Health and also with the laws of Germany. Supported by grants of the Deutsche Forschungsgemeinschaft (Bl 242/2 and 3) and by the Bennigsen-Foerder-Preis of the State of Nordrhein-Westfalen to H.B.

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