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Response properties of diencephalic neurons to visual, acoustic and hydrodynamic stimulation in the goldfish, *Carassius auratus*

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Summary

We studied the responses to sensory stimulation of three diencephalic areas, the central posterior nucleus of the dorsal thalamus, the anterior tuberal nucleus of the hypothalamus, and the preglomerular complex. Units sensitive to acoustic (500 Hz tone burst), hydrodynamic (25 Hz dipole stimulus) and visual (640 nm light flash) stimuli were found in both the central posterior and anterior tuberal nucleus. In contrast, unit responses or large robust evoked potentials confined to the preglomerular complex were not found. In the central posterior nucleus, most units were unimodal. Many units responded exclusively to visual stimulation and exhibited a variety of temporal response patterns to light stimuli. In the anterior tuberal nucleus of the hypothalamus, most units responded to more than one modality and showed a stronger response decrement to stimulus repetitions than units in the central posterior nucleus. Our data suggest that units in the central posterior nucleus are primarily involved in the unimodal processing of sensory information whereas units in the anterior tuberal nucleus of the hypothalamus may be involved in multisensory integration.

Key words: teleost fish, thalamus, hypothalamus, preglomerular complex, sensory processing

Introduction

For a long time it was assumed that nonolfactory sensory pathways reaching the telencephalon occur only in amniotes. However, recent anatomical and physiological studies clearly show that all sensory modalities reach the telencephalon of anamniotes (Ebbesson and Schroeder, 1971; Ito and Kishida, 1978; Ebbesson, 1980; Finger, 1980; Wullimann, 1998). Anatomical studies suggest that in teleosts ascending sensory information is relayed to the telencephalon via two main diencephalic pathways: the dorsal thalamus and the preglomerular complex of the posterior tubercle (PG; Murakami et al., 1986a, b; Striedter, 1991, 1992; Wong, 1997; Zupanc, 1997; Wullimann, 1998). Although numerous tract tracing studies exist (e.g., Echteler and Saidel, 1981; Echteler, 1984; Murakami et al., 1986 a, b; Striedter, 1990a, b, 1991), physiological data which confirm that certain diencephalic areas of teleosts receive and process sensory information are sparse. Echteler (1985) mapped the brain of the teleost, *Cyprinus carpio*, while exposing the animal to acoustic and/or lateral line stimuli. He found auditory activity within the central posterior thalamic nucleus (CP), one of the three nuclei comprising the dorsal thalamus, but did not demonstrate auditory responses in the preglomerular complex (PG). Lu and Fay (1995) recorded single unit responses in the CP of goldfish to acoustic stimuli. They found a nonuniform distribution of characteristic frequencies, phasic or tonic temporal response patterns and weak or no phase-locking to pure tones. Finger and Bullock (1982) described responses to mechanical stimuli in an area which later was identified by Striedter (1990a) as the anterior tuberal nucleus (TA) of the hypothalamus. Besides Echteler (1985), no one has attempted to record responses to sensory stimuli in the preglomerular complex. Also, little is known about putative diencephalic visual areas. The few recordings which do exist demonstrate that visual neurons in the dorsal thalamus have large receptive fields, are best stimulated by stationary stimuli, do not selectively respond to stimulus direction, and show only

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weak habituation (Friedlander, 1983). According to Friedlander (1983) bimodal visual-somatosensory neurons are present in the ventral but not in the dorsal thalamus of teleosts. None of the above studies attempted to investigate whether diencephalic sensory areas of teleosts are unimodal, as in mammals, or relay exclusively bi- or even multimodal information to the telencephalon. This is the first study which systematically investigates the responses of both medial diencephalic sensory areas and the PG to hydrodynamic, acoustic and visual stimuli. While the PG barely responded to any of the stimulus modalities applied to diencephalic areas, the CP and the TA clearly processed uni- and multimodal sensory information.

Materials and methods

Data were were collected from 32 goldfish, *Carassius auratus*, ranging from 8 to 10 cm body length. The animals were acquired from local commercial dealers and were maintained in 200 liter aquaria at 20 °C on a daily 10–14 h light-dark cycle.

Animal preparation

Animals were anaesthetized in ice water (0 °C) and immobilized by injection of 0.2–0.3 µl/g Pancuronium bromide (Organon Teknika). In addition, Xylocaine (ASTRA Chemicals) was administered to the skin at the preparation site. A small opening (about 3 mm × 3 mm) was drilled in the scull near the midline of the head, above the optic tectum and the torus longitudinalis. Fatty tissue was removed with small tweezers. After surgery the fish were transferred to the experimental tank (29 cm × 48 cm × 20 cm) filled with aged tap water of room temperature (about 20 °C). The tank rested on a pneumatic vibration-isolation table (Micro-g, TMC). Fish were positioned in a stainless steel holder which consisted of a mouth piece for artificial respiration with freshwater (flow rate about 45 ml/min) and two screws by which the head was kept in a fixed and stable position. The fish were placed in the tank with the dorsal surface of the head just above the water surface. The exposed brain was kept moist with a physiological salt solution (Oakley and Schafer, 1978).

Stimulation

A series of three stimuli, separated by 700 ms intervals, was presented. This sequence was repeated 10 times every 30 or 40 s. The first stimulus was a sinusoidal water motion generated by a vibrating sphere (diameter 8 mm). The sphere was attached to a vibrator (Ling Dynamic Systems, Model V101) by a stainless steel rod (length 13 cm, diameter 3 mm). The vibrator was mounted on a separate holder, ensuring that no unwanted vibrations were transmitted indirectly to the animal via the ground and experimental tank. The electronic signal driving the vibrator was a 200 ms sine wave with rise/fall times of 50 ms. Stimulus frequency was 25 Hz, displacement amplitude of the sphere was 360 µm peak-to-peak (p-p). For calibration the movement of the vibrating sphere was monitored under a microscope. To avoid boundary layer effects (Kalmijn, 1988), the distance between the surface of the fish and the sphere was no less than 5 mm. The sphere was elevated to approximately the level of the trunk lateral line canal. The second stimulus was a tone burst generated by a loudspeaker (ACL) placed in air but close to the water surface at a position 50 cm caudal and lateral to the fish. The loudspeaker was driven with a 140 ms sine wave with rise/fall times of 20 ms. Stimulus frequency was 500 Hz, sound pressure was 1.27 Pa. Sound pressure was measured with a hydrophone (Brüell and Kjær 8103; 9 mm diameter) positioned at the location in the experimental tank where the fish would normally reside. In some experiments a click (sound pressure 1.7 Pa) was used to stimulate the acoustic system. The third stimulus was a 20 ms light flash (light intensity 2 mcd) emitted from a red (640 nm) light-emitting diode placed 1-2 mm in front of the right eye. The electronic signals for the three stimuli were generated with a self-written Turbo Pascal program (PC 386) and read out of a 16 bit D/A-converter at a conversion rate of 10 kHz. To characterize unit responses in more detail stimuli of 1 s duration were used.

Data recording and analysis

Units and evoked potentials (EP) were recorded in the left diencephalon contralateral to the stimulation side using glass micropipettes filled with an indium alloy (Small Parts Inc.). The electrode tips had a diameter of about 4 µm and were plated with platinum (H_2PtCl_6) until an impedance <2 MΩ was reached. The electrodes were mounted in a plexiglass holder which was attached to a microdrive (HS6; WPI), used to manually adjust the electrode position in the horizontal plane. Electrodes were advanced through the brain in 1 µm steps with a motorized microdrive (Model 607W, Kopf Instr.). Recordings were amplified (DAM 80, WPI), bandpass filtered (evoked potentials: 1–3000 Hz; unit responses 300–3000 Hz), fed through a noise eliminator (Hum Bug, Quest Scientific) which eliminated 50 Hz noise and harmonics, and displayed on an oscilloscope (Hameg HM 205-3). Recordings were digitized (GWI instrunet 100B, sampling rate 20 kHz, 14 bit resolution) and stored in a computer (Apple Macintosh G3) with the software SuperScope II (GWI). Unit re-

sponses were analyzed using the software Igor Pro (WaveMetrics). With self-written macros (M. Kettler), raster diagrams and peri stimulus time (PST) histograms (binwidth 10 ms) were computed across all repetitions of a stimulus condition.

Characterization of unit responses

Single units were discriminated from multi-unit recordings on the basis of spike amplitudes. Data for ongoing activity, modality, temporal response patterns and paired stimuli responses are based on single unit recordings. Units were defined as unimodal lateral line, auditory or visual if responses were repeatedly and unambiguously elicited only by the hydrodynamic, the acoustic or the visual stimulus, respectively. Units were described as bi- or trimodal if the responses were elicited by two or three of the applied stimuli, respectively. Latencies were measured from stimulus onset to the maximum of the PST histogram (binwidth 10 ms). Units were further characterized by their responses to paired stimuli.

Histology

In 25 cases the location of the recording site was marked with a small electrolytic lesion by passing a 2–3 µA DC current (15 s positive and 15 s negative) through the electrode tip. Fish were deeply anesthetized with 0.05% MS 222 and perfused intracardially with 0.1 M phosphatebuffer (pH 7.4 with 0.1% EDTA) followed by 4% paraformaldehyde solution (in 0.1 M phosphatebuffer with 0.1% EDTA). Brains were removed, postfixed and cut at 20 µm in a transverse plane parallel to the electrode penetration. Sections were stained with cresylviolet and analyzed under a microscope. Sections which contained lesions were photographed with a digital camera (Nikon Coolpix E950).

Lists of abbreviations

Cer = Cerebellum; CP = Central posterior thalamic nucleus; DP = Dorsal posterior thalamic nucleus; "G" = Nucleus glomerulosus; ND = Nucleus diffusus; PC = Posterior commissure; PG = Preglomerular complex; PGa = Anterior preglomerular nucleus; PGl = Lateral preglomerular nucleus; PT = Posterior tubercle; PTec = Pretectum; PVH = Periventricular hypothalamus; TA = Anterior tuberal hypothalamic nucleus; Tel = Telencephalon; TO = Tectum opticum; ToLa = Torus lateralis; Val = Valvula cerebelli; VL = Ventrolateral thalamic nucleus; Vlo = Vagal lobe; VM = Ventromedial thalamic nucleus

Results

Recording sites

A total of 27 electrolytic lesions were made to verify the location of recording sites. In addition, the depth of

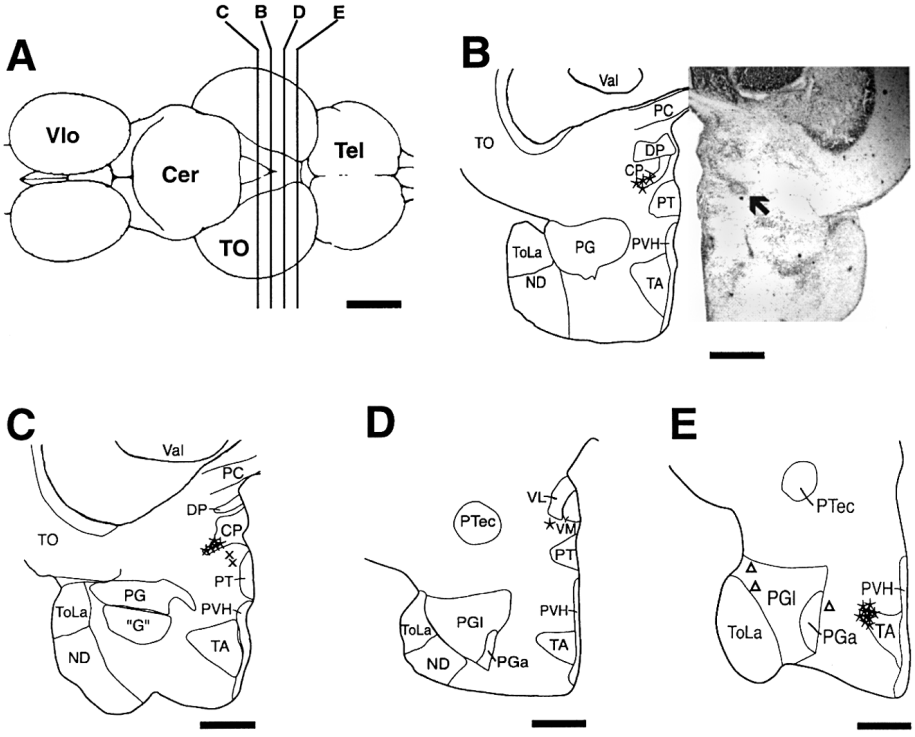

Fig. 1. Dorsal view of the goldfish brain **(A)** and chartings of cross sections through the goldfish brain **(B–E)** at the levels indicated in A. Scale bar in A = 1000 µm, in B to E scale bar = 400 µm. In B a cresylviolet stained hemisection is shown on the right, the arrow points to an electrolytic lesion. Asterisks in the line drawings indicate the location of electrolytic lesions in the dorsal thalamus **(B–D)** and the hypothalamus **(E)**. In the dorsal thalamus most lesions were in the ventrolateral CP (asterisks in **B**, **C**). Two lesions were, as expected from micrometer readings, slightly ventral to the medial CP (crosses in **C**). Only one was located in the transition rostrally to CP between the ventral thalamic nuclei (VL and VM) and the posterior tubercle (PT) **(D)**. Lesions in the hypothalamus were exclusively in the anterior tuberal nucleus **(E)**. Three lesions were in the PG (triangles in **E**). In the line drawings in **B** to **E** dorsal is up and lateral is left.

the electrode penetration was monitored during the recordings. Thirteen lesions were recovered at depths above 1700 µm. Nine of these lesions were located in the CP and were distributed from the center of the CP to its rostro-lateral end (Fig. 1 B, C). Two lesions were found in the medial part of CP or, as expected from micrometer readings, slightly ventral to the CP (Fig. 1C). One lesion was located rostral to the CP in a region between ventrolateral thalamic nucleus (VL) and posterior tubercle (PT; Fig. 1D). Thirteen lesions were recovered when electrode depth exceeded 2300 µm. Ten lesions were located in the TA (Fig. 1E) and 3 lesions were in the PG (Fig. 1E). Two lesions (not shown) were at intermediate depths between 1700 and 2300 µm. These lesions were located in the vicinity of the lateral and medial forebrain bundles and could not be assigned to specific cell groups. Hence, data from recordings at depths between 1700 and 2300 µm were excluded from further analysis.

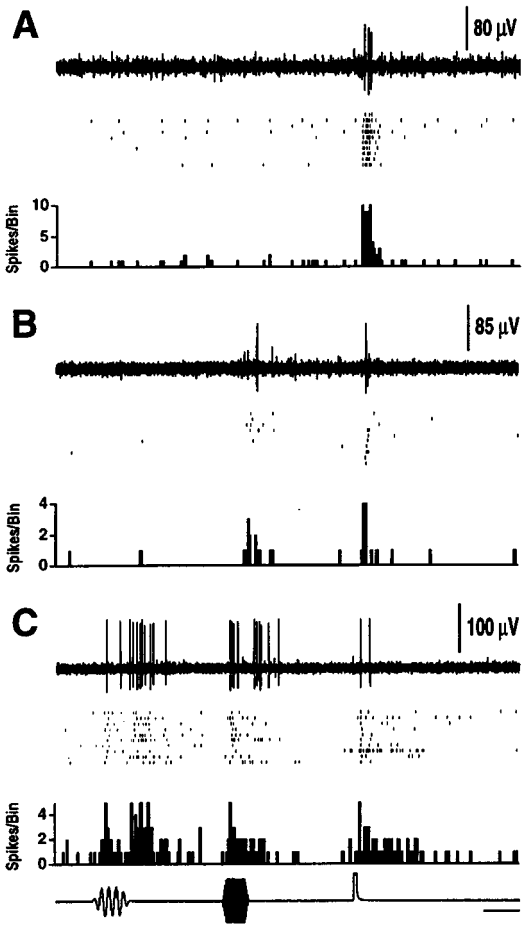

Fig. 2. Examples of a unimodal, bimodal and trimodal unit recorded in the diencephalon. In this figure and in Figs. 4 to 7 each part shows from top to bottom an original recording, a raster diagram of the responses to ten repetitions of a sequence of stimuli (see Materials and Methods) and a peri-stimulus-time histogram (binwidth 10 ms). Stimulus traces are shown on the bottom. Responses to a hydrodynamic, an acoustic and a visual stimulus (see stimulus trace) of units classified as unimodal visual recorded in the CP **(A)**, as bimodal acoustic and visual recorded in the TA **(B)**, and as trimodal recorded in the TA **(C)**. Horizontal scale bar represents 200 ms.

Physiology

In initial mapping experiments more than 200 electrode tracks were made through the diencephalon of goldfish, *Carassius auratus*. To do so the electrode was positioned on the surface of the rostral tectum at 100 µm mediolateral and 100 µm rostro-caudal intervals, and the EPs elicited by stimulation of the lateral line, the acoustic and the visual system were recorded at depth intervals of 100 µm within each track. The form, size and latency of the EPs, as well as the occurrence of massed unit activity ("hash") and few or single unit responses, varied according to the position of the track on the brain surface, the electrode depth within each track and the type of stimulus delivered. Robust EPs and unit responses were reliably obtained in the CP and TA. In the 18 tracks made through the PG, as confirmed by lesions, only small EPs were found which were not local. In one penetration we got local EPs from the PG while stimulating the animal with the vibrating sphere. However, units responsive to our lateral line stimulus or to any other of the applied stimuli were never encountered.

Outside the PG a total of 194 diencephalic units were encountered. Because units could only be reliably recorded in the CP and TA we present data from these two nuclei only. In the CP 58 out of 83 units, and in the TA 34 out of 58 units responded to either one or a combination of the applied stimuli, 49 units were unresponsive.

Ongoing activity

Ongoing activity, i.e., activity without a stimulus being present, was determined for 16 single CP and 6 single

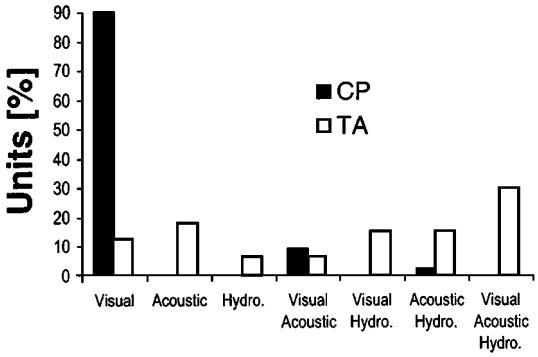

Fig. 3. Frequency distribution of unimodal (visual, acoustic and hydrodynamic), bimodal (visual/acoustic, acoustic/hydrodynamic and visual/hydrodynamic) and trimodal (visual/acoustic/hydrodynamic) CP and TA units.

TA units. Among units in the CP, average ongoing activity was 6.6 ± 4.5 spikes/s (mean ± S.D., range 0.4–17 spikes/s). Average ongoing activity of TA units was 5.0 ± 1.7 spikes/s (range 1.4–9.9 spikes/s). These values were not significantly different (Mann-Whitney U-test, p = 0.4).

Unit modality

Responses to sensory stimuli were recorded in both the CP and TA. Figure 2A shows data from a CP unit classified as unimodal visual. The unit responded with a short increase in discharge rate to a 20 ms light flash but not to acoustic or hydrodynamic stimuli. Data from a bimodal TA unit are exemplified in Fig. 2B. This unit responded to both the acoustic and the visual stimulus with a transient increase in discharge rate, but did not respond to the hydrodynamic stimulus. Figure 2C shows data from a trimodal TA unit which responded to each of the three test stimuli with an increase in discharge rate.

The frequency of unimodal, bimodal and trimodal units in the CP differed from that in the TA (Fig. 3). Most single CP units (n = 52, 90%) were unimodal visual. Unimodal acoustic or lateral line units were not found. Ten percent of the single units recorded in the CP were bimodal and responded either to the visual and the acoustic stimulus (n = 5, 9%), or to the acoustic and the hydrodynamic stimulus (n = 1, 2%). Trimodal units were not found.

In the TA 36% of the single units were unimodal. Four of these units (12%) received visual, 6 units (18%) acoustic, and 2 units (6%) lateral line input. Most single TA units responded, however, to more than one modality. Twelve units (36%) were bimodal and 10 units (28%) were trimodal. Bimodal units responded to visual and acoustic, visual and hydrodynamic, and acoustic and hydrodynamic stimuli.

Latency

Mean latencies of CP units were 17 ± 9 ms (range 10–30 ms, acoustic stimulation, n = 6), and 57 ± 48 ms (range 20–260 ms, visual stimulation, n = 57). The only unit sensitive to the vibrating sphere stimulus had a latency of 70 ms. Mean latencies for TA units were 77 ± 61 ms (range 20–270 ms, lateral line, n = 20), 33 ± 29 ms (range 10–140 ms, audition, n = 23) and 40 ± 20 ms (range 20–100 ms, vision, n = 21). Due to the occurrence of very long latencies the most frequent latency (main latency) was usually shorter than the mean latency. Main latencies of CP units were 10 ms (acoustic stimulation, n = 4) and 30 ms (visual stimulation, n = 20). Main latencies of TA units were 30 ms for hydrodynamic stimulation (n = 5), 10 ms for acoustic stimulation (n = 7) and 30 ms for visual stimulation (n = 13). Visual and acoustic response latencies of CP and TA units were not different (Mann-Whitney U-test, p = 0.31 (visual) and 0.12 (acoustic).

Temporal response patterns

A variety of temporal response patterns was found. Among CP units three response types were distinguished. Units responded either with a transient increase in discharge rate (n = 30, 58%; Fig. 4A), with a decrease in discharge rate (n = 16, 30%; e.g., Fig. 4B), or with two or more increases and/or decreases in discharge rate (n = 6, 12%; e.g., Fig. 4C). The first type was observed in response to acoustic, hydrodynamic and visual stimuli. The latter two types of responses were observed only if visual stimuli were applied. TA

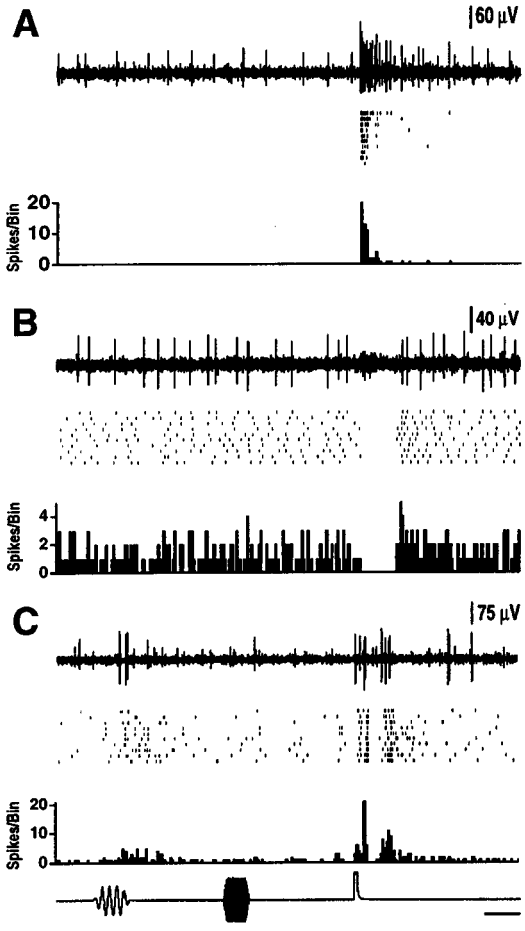

Fig. 4. Temporal patterns of dorsal thalamus unit responses to sensory stimuli. **(A)** Example of a unit which responded with an increase in discharge rate to the visual stimulus. **(B)** Example of a unit which responded with a decrease in discharge rate to the visual stimulus. **(C)** Example of a unit which exhibited a complex response pattern to the visual stimulus. Horizontal scale bar represents 200 ms.

units (n = 34) always responded with an increase in discharge rate, irrespective of stimulus modality and stimulus duration.

The responses of 14 CP and 12 TA units were further characterized by presenting stimuli of 1 s duration. In response to a 1 s visual stimulus, the discharges of two CP units were suppressed, in one unit for the duration of the stimulus (Fig. 5A) and in one unit transiently after stimulus onset (Fig. 5B). Five units responded with phasic or phasic-tonic increases in discharge rate

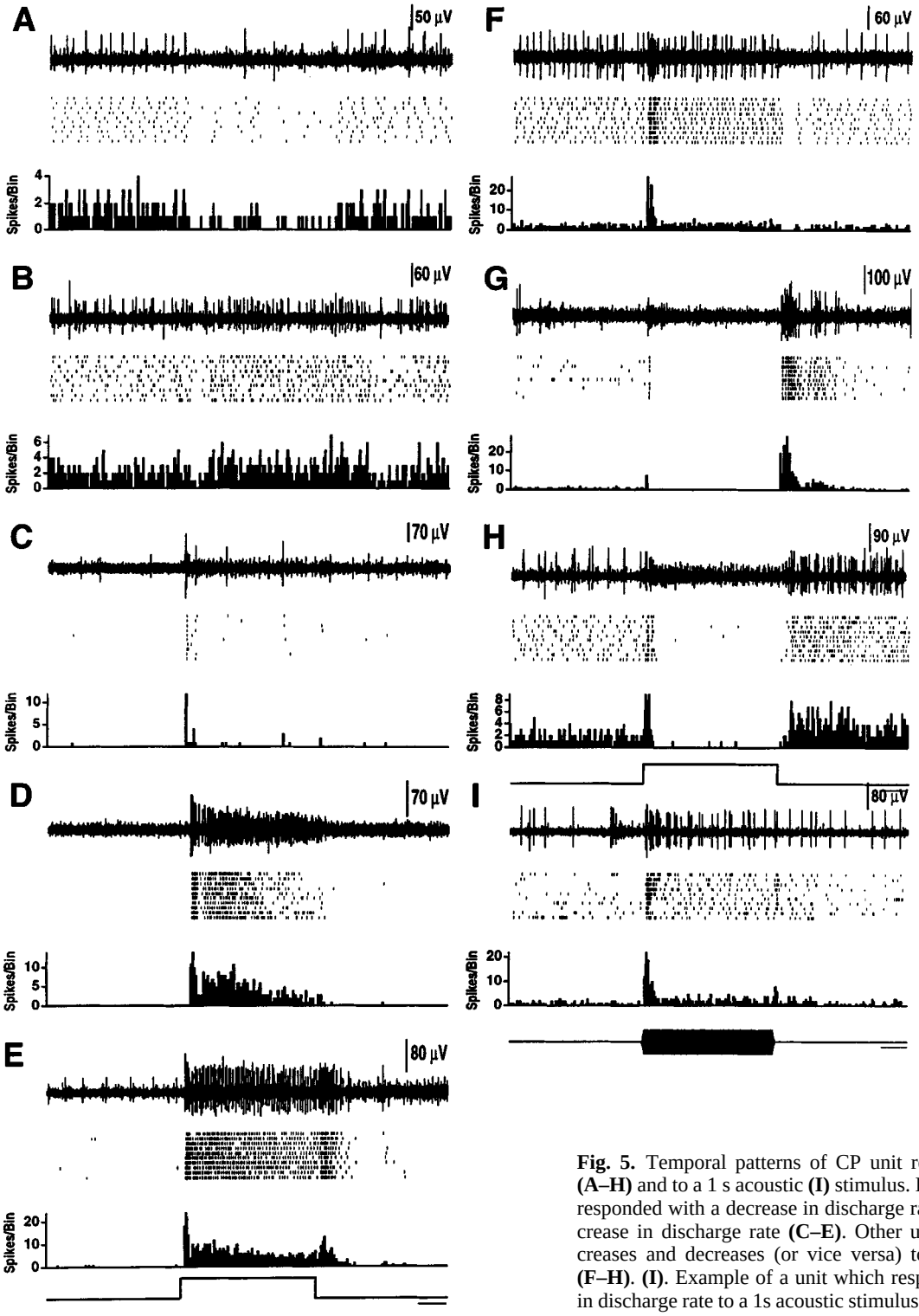

Fig. 5. Temporal patterns of CP unit responses to a 1s visual **(A–H)** and to a 1 s acoustic **(I)** stimulus. Examples of units which responded with a decrease in discharge rate **(A, B)** or with an increase in discharge rate **(C–E)**. Other units responded with increases and decreases (or vice versa) to a 1 s visual stimulus **(F–H)**. **(I)**. Example of a unit which responded with an increase in discharge rate to a 1s acoustic stimulus.

(Fig. 5C, D), four units with an increase in discharge rate to both stimulus on and off (Fig. 5E). One unit responded with a short increase in discharge rate after stimulus onset, maintained an elevated firing level during stimulation and exhibited a suppression of neural activity after stimulus end (Fig. 5F). Another unit responded weakly to stimulus on, was completely suppressed for the duration of the stimulus and responded with an increase in discharge rate at the end of the stimulus (Fig. 5G). A third unit had a similar pattern which consisted of an increase in discharge rate at stimulus on, a suppression during the stimulus and an increase in discharge rate at the end of the stimulus (Fig. 5H). Responses to acoustic stimuli of 1 s duration were recorded from one CP unit. The responses of this unit were phasic-tonic (Fig. 5I).

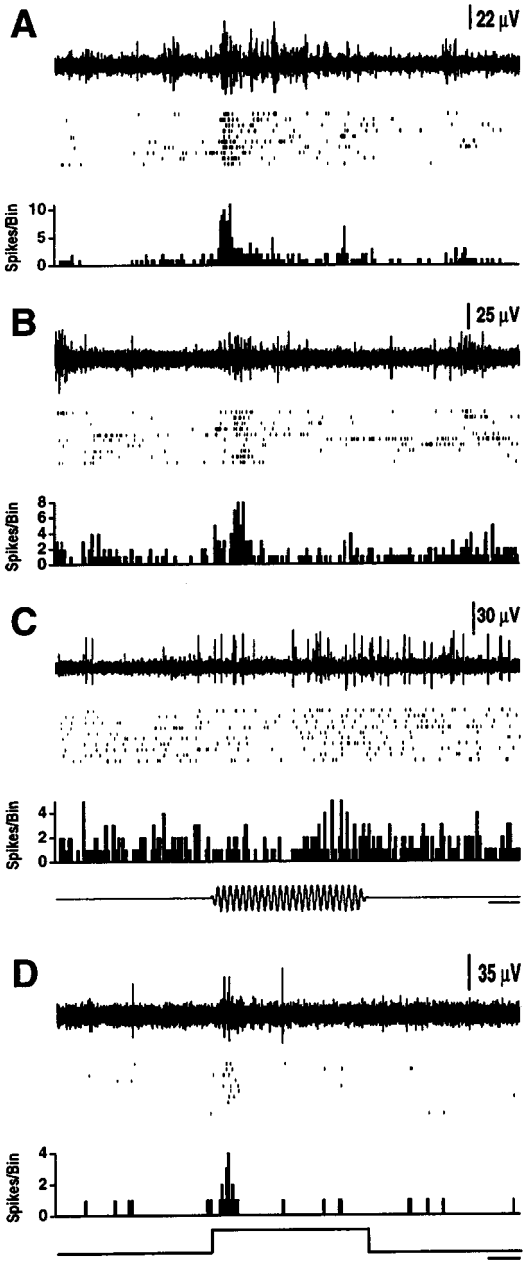

Fig. 6. Responses of TA units to sensory stimuli. Examples of units which responded to a hydrodynamic stimulus **(A–C)**. Example of one unit which responded to a visual stimulus **(D)**.

In contrast to CP units, TA units always responded to a 1 s stimulus with an increase in discharge rate independent of stimulus modality. Nine of the 12 TA units were responsive to a 1s hydrodynamic stimulus. Two units had phasic-tonic (Fig. 6A) and five units had phasic responses (Fig. 6B). Two units reached maximum discharge rate in the second half of the 1 s stimulus (Fig. 6C). The two TA units which were tested with a 1s visual stimulus responded with a phasic increase in discharge rate (Fig. 6D).

Response decrement to paired stimuli

Response decrement was investigated in 18 CP and 7 TA units by presenting two successive stimuli with time intervals between 100 and 2500 ms. Figure 7 shows data from a CP unit and a TA unit which were tested with visual stimuli. In the CP unit, response to the second stimulus was barely reduced even at stimulus intervals of 150 ms (compare Fig. 7A, B), whereas in the TA unit, response to the second stimulus was already reduced at intervals of 1300 ms (compare Fig. 7C, D). Fig. 8 summarizes the results from all units tested with paired stimuli. When tested with paired visual stimuli, 13 of the 15 CP units responded about equally well to the second stimulus even at a stimulus interval of 300 ms (Fig. 8A). In two units a response decrement already was apparent at a stimulus interval of 2300 ms. The 4 TA units tested with paired visual stimuli also showed a response decrement at stimulus intervals = 2300 ms (Fig. 8B). Three CP units were tested with paired acoustic stimuli, all three units showed an increase in response decrement with decreasing stimulus intervals (Fig. 8C). Three TA units were tested with paired hydrodynamic stimuli. One of these units showed a clear response decrement (Fig. 8D).

Discussion

According to anatomical studies, both the TA and the CP of catfish receive acoustic and mechanosensory lateral line input (Striedter, 1991). In addition ascending spinal (somatosensory) axons reach the CP of teleost fish (Murakami et al., 1986a; Ito et al., 1986). As expected, EPs and unit responses to acoustic and/or lateral line stimuli were obtained from the CP and TA. Both the CP and the TA of goldfish do not receive primary visual projections (Wullimann, 1998). Nevertheless we

encountered visual responses in these two nuclei. According to anatomical studies (Striedter, 1991; Wullimann, 1998), the PG of teleosts is another target of ascending sensory (toral) information. However, despite intensive attempts we only recorded weak EPs to lateral line and/or acoustic stimuli in the PG. PG units responding to the sensory stimuli we applied were not encountered. In light of the anatomical studies cited above the absence of robust octavolateralis responses in the PG is hard to understand but is in agreement with a study done by Echteler (1985), who found acoustic responses in the CP but not in the ventral or ventrolateral

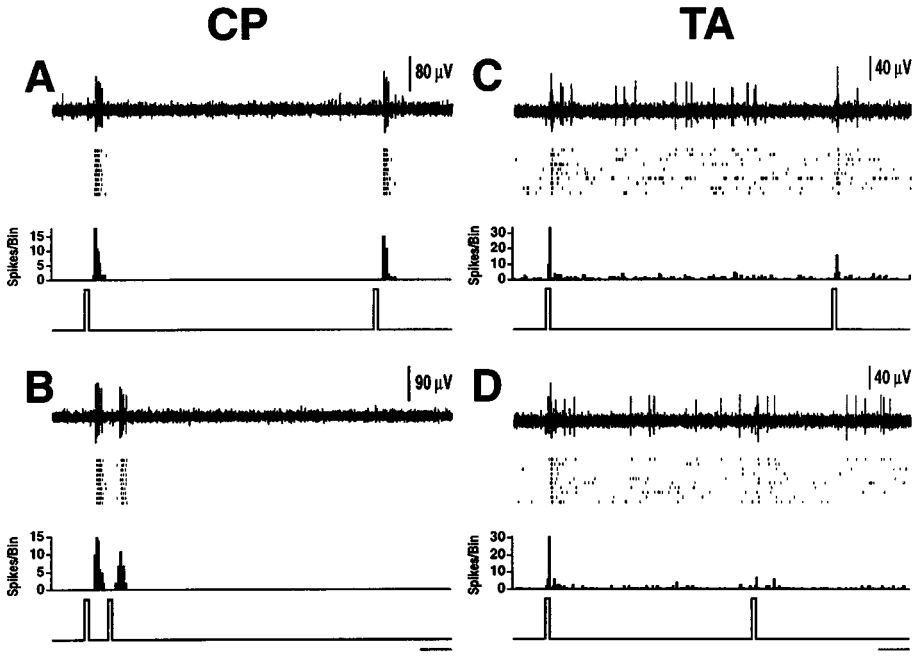

Fig. 7. Responses of a CP (left) and a TA unit (right) to paired visual stimuli. Stimulus interval was 1800 ms **(A, C)**, 150 ms **(B)** and 1300 ms **(D)**.

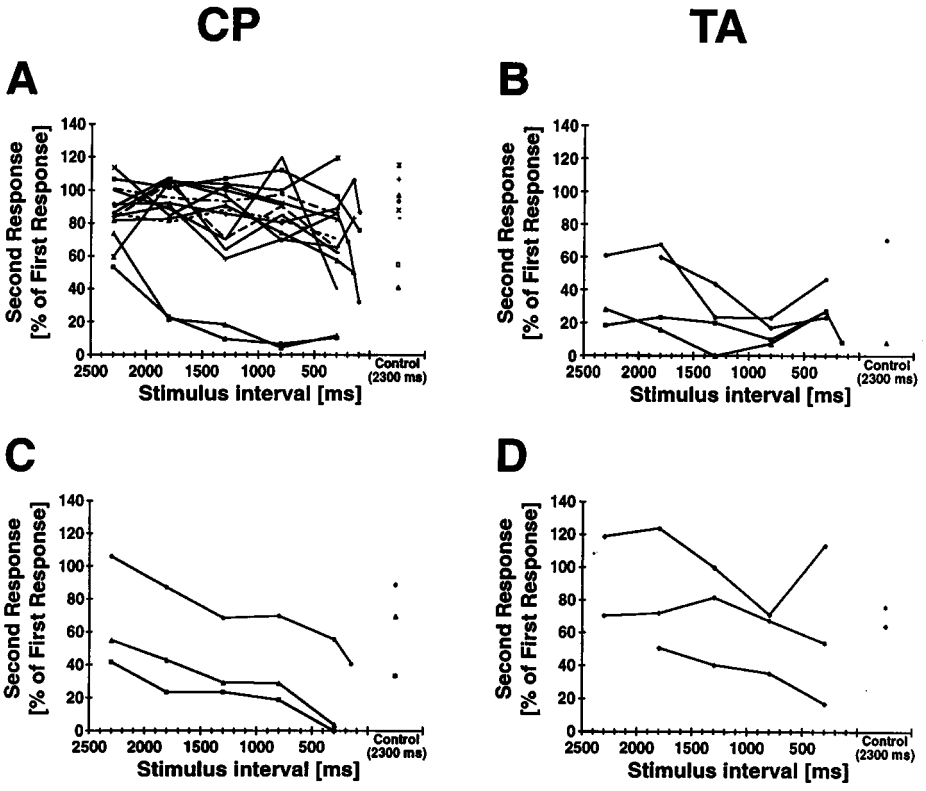

Fig. 8. Response decrement of CP units (left) and TA units (right) to paired stimuli. Response magnitude to the second stimulus as percent of the response to the first stimulus is plotted for all stimulus intervals applied. Response decrement to paired visual **(A, B)**, acoustic **(C)**, and hydrodynamic **(D)** stimuli.

diencephalon. There may be several explanations for the lack of robust EPs and unit responses in the PG: 1. The amount of sensory information which reaches the PG may be fairly small. According to anatomical studies which show massive mechanosensory projections to the PG (Striedter, 1991) this is unlikely. 2. The PG may only respond to certain distinct and complex stimuli but not to the simple sensory stimuli we used. Although this is possible, we got fairly good lateral line responses to a simple sine wave stimulus in one case. This argues against such an explanation. 3. Sensory areas within the PG may be small, i.e., even though electrode tracks were spaced at 100 µm medio-lateral and 100 µm rostro-caudal intervals we might have missed all of them. Further studies are needed to learn more about the physiology of the PG.

Many units in the ventrolateral CP responded to visual input. This again was unexpected because anatomical studies have not yet demonstrated direct visual input to the CP (Wullimann, 1998). Tectal projections to the CP of teleosts have been found, however (Northcutt and Butler, 1991). Visual and lateral line responses have been recorded from the CP of cartilaginous fishes (Bleckmann et al., 1987). Friedlander (1983) recorded visual responses from the dorsomedial thalamus of the largemouth black bass, *Micropterus salmoides*, but did not attribute these responses to a particular nucleus. Visual units we recorded from the CP showed a variety of temporal response patterns. This may reflect convergence of excitatory and inhibitory inputs having different time courses.

Only few CP units responded to our acoustic and/or hydrodynamic stimulus. This was unexpected because in previous studies strong acoustic (Echteler, 1985; Lu and Fay, 1995) responses were recorded from the CP. Lu and Fay (1995) used tone bursts (155, 417 and 833 Hz) and clicks as search stimuli and finally analyzed the responses of the acoustic units in the frequency range 75 to 1250 Hz. They found that most acoustic CP units were broadly tuned and that stimulus levels of minus10 to minus 20 dB (rel. 0.1 Pa) were sufficient to drive these units. Therefore the stimulus we used (500 Hz, 1.27 Pa or clicks, 1.7 Pa) should have been sufficient to stimulate acoustic CP units. We have no good explanation for the lack of acoustic responses in the CP.

The vibrating sphere stimulus we used (25 Hz, 360 µm p-p displacement) was clearly sufficient to drive primary lateral line afferents (Münz, 1989). Therefore the small number of CP units which responded to our lateral line stimulus may reflect the lack of direct toral lateral line input to the CP (Wullimann, 1998).

It is striking that all lesions of CP recording sites which responded to our visual stimulus were in the ventrolateral region of the CP. This region consists of large cells in contrast to the paraventricular part of the CP, which contains only small cells (Striedter, 1990a). It is possible that these anatomical differences reflect physiological differences. Perhaps the paraventricular part of the CP mainly receives auditory input while the lateroventral part mainly receives visual input. Unfortunately, in repeated experiments the number of paraventricular CP units which responded to our acoustic stimuli was small. Although unlikely we cannot rule out that our electrodes were not suitable to record from the small paraventricular cells.

In contrast to CP units, most TA units were multimodal (Fig. 3). If tested with paired visual stimuli, TA units showed a stronger response decrement than CP units. These physiological differences suggest different functions for the CP and the TA. Whereas the CP appears to be mainly involved in the unimodal processing of both visual (this study) and acoustic (previous studies) information, the TA may integrate information across sensory modalities. Both the CP and the TA have anatomical connections with the telencephalon (Striedter, 1990b; 1991). Further studies are needed to reveal whether the sensory information present in the CP and TA is passed on to the telencephalon and/or to which degree these brain nuclei are parts of descending modulatory systems.

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