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Responses of diencephalic neurons to sensory stimulation in the goldfish, *Carassius auratus*

Janina A. Kirsch,* Michael H. Hofmann, Joachim Mogdans and Horst Bleckmann

Institut fur Zoologie, Universitat Bonn, Bonn, Germany

ABSTRACT: We studied the responses to sensory stimulation in two diencephalic areas, the central posterior nucleus of the dorsal thalamus (CP) and the anterior tuberal nucleus of the hypothalamus (TA). In both the CP and the TA, units sensitive to acoustic (500-Hz sound), hydrodynamic (25-Hz dipole stimulus), and visual (640-nm light flash) stimuli were found. In the CP, most units were unimodal and responded exclusively to visual stimulation. In contrast, in the TA, most units responded to more than one modality. The data suggest that the CP is primarily involved in the unimodal processing of sensory information, whereas the TA may be involved in multisensory integration. © 2002 Elsevier Science Inc.

KEY WORDS: Teleost fish, Thalamus, Hypothalamus, Sensory processing.

INTRODUCTION

In fishes, the diencephalon can be subdivided into four zones: the epithalamus, the thalamus, the posterior tubercle, and the hypothalamus. The anatomical organization and connectivity of these areas are well described [13]. Also, some physiological studies exist of diencephalic electrosensory [6], acoustic [2,4,7], and visual [5] areas. However, it is not known to which degree the information of different modalities converges at the unit level in the diencephalon. For this reason, we investigated the responses to hydrodynamic, acoustic, and visual stimulation of two diencephalic areas: the central posterior nucleus of the dorsal thalamus (CP) and the anterior tuberal nucleus of the hypothalamus (TA).

The CP consists of a heterogenuous population of neurons [8]. It borders the ventricle dorsomedially and extends ventrolaterally into the tuberal diencephalic region [10]. Reciprocal connections between the CP and the midbrain torus semicircularis [1,12], the lateral preglomerular nucleus [9], and the TA [12] already suggest that the CP is involved in the processing of acousticolateralis information.

The TA is located ventrally in the hypothalamus and borders the periventricular hypothalamus [12]. Reciprocal connections between the TA and the anterior thalamic nucleus suggest that visual information reaches the TA [14]. The TA also receives input from the torus semicircularis [1,3,12], which suggests that the TA, like the CP, is involved in the processing of acousticolateralis information.

Here, we show that unit responses to acoustic, hydrodynamic, and visual stimuli can be recorded in both the CP and the TA. Most units in the CP responded exclusively to visual stimulation, whereas in the TA, responses were found to all three modalities.

MATERIALS AND METHODS

Single- and multi-unit recordings were made in the left diencephalon of 29 goldfish, *Carassius auratus,* using metal electrodes (impedances <2 MO). Unit responses were recorded to a series of three stimuli, which were separated by 700-ms intervals (see stimulus trace in Fig. 1). This sequence was repeated at least 10 times every 40 s. The first stimulus was a sinusoidal water motion generated by a stationary vibrating sphere (8 mm diameter, 6 mm distance to the right side of the fish). The sphere was driven by a computer-generated sine wave signal (25 Hz, 200-ms duration, 50-ms rise/fall), and peak-to-peak sphere displacement was 360 µm. The second stimulus was a sound (500 Hz, 140-ms duration, 20-ms rise/fall, 1.27 Pa at the site of the fish) generated by a loudspeaker placed in air about 40 cm behind the aquarium. The third stimulus was a light flash (20 ms, 640 nm, 2 mcd) emitted from a photo diode placed 1 to 2 mm in front of the right eye.

Units were defined as unimodal lateral line, auditory, or visual if responses were repeatedly and unambiguously elicited only by the vibrating sphere, the airborne sound, or the light flash, respectively. Units were described as bimodal or trimodal if responses were elicited by two or three of the applied stimuli, respectively.

The locations of 25 recording sites, which were marked with a small electrolytic lesion by passing a DC current through the electrode tip, were verified in 20-µm brain sections cut in a transverse plane parallel to the electrode penetration.

RESULTS

A total of 141 units was recorded, 83 in the CP and 58 in the TA. Figure 1 shows a section through the diencephalon of goldfish with a lesioned recording site in the CP. Of the 141 units recorded, 92 responded to one or to a combination of the applied stimuli. Forty-nine units did not respond to the test stimuli.

Responses to sensory stimuli were recorded in both the CP (58 units) and the TA (34 units). Figure 2A shows data from a unimodal visual unit that was recorded in the CP. The unit responded with a distinct short increase in discharge rate to a 20-ms light flash but not to acoustic or hydrodynamic stimuli. Data from a bimodal unit that was recorded in the TA are shown in Fig. 2B. This unit responded to both the hydrodynamic and the visual stimulus with a transient increase in discharge rate. It did not respond to the acoustic stimulus. Figure 2C shows data from a

* Address for correspondence: Janina A. Kirsch, Institut fur Zoologie, Universitat Bonn, Poppelsdorfer Schloss, D-53115 Bonn, Germany. Fax: +49 228 735458; E-mail: J.Kirsch@uni-bonn.de

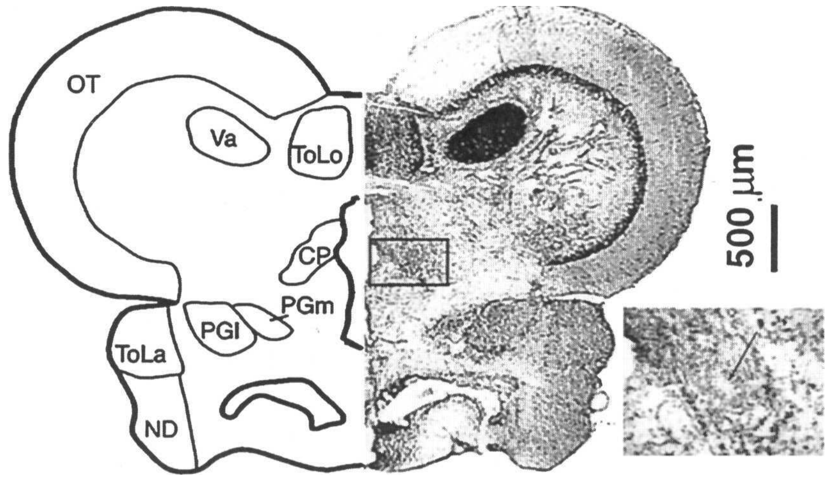

FIG. 1. Electrolytical lesion of a recording site in the brain of a goldfish. The site was defined by physiological criteria as receiving unimodal visual input. On the right, a cresyl-violet-stained transverse hemisection through the goldfish diencephalon is shown. The corresponding left hemisection is shown as a line drawing. The brain area containing the left central posterior nucleus of the dorsal thalamus (CP) (black frame) is enlarged in the inset. The black arrow in the inset points to the location of the electrolytic lesion. Abbreviations: ND, nucleus diffuses; OT, optic tectum; PO1, lateral preglomerular nucleus; PGm, medial preglomerular nucleus; ToLa, torus lateralis; ToLo, torus longitudinalis; Va, valvula cerebelli.

trimodal unit that responded to each of the three test stimuli with an increase in discharge rate. This unit was recorded in the TA.

The frequency of unimodal, bimodal, and trimodal units in the CP differed from that in the TA (Fig. 3). Most units (90%) in the CP were unimodal. Moreover, these units responded only to visual stimuli. Unimodal acoustic or unimodal lateral line units were not found. Ten percent of the CP units were bimodal and responded either to the visual and the acoustic stimuli or to the acoustic and the hydrodynamic stimuli. Trimodal units were not found.

In the TA, 36% of the units were unimodal visual, acoustic, or lateral line. Most units (64%) in the TA were multimodal (36% bimodal and 28% trimodal). Bimodal units responded to all combinations of visual, acoustic, and hydrodynamic stimuli.

DISCUSSION

The data show that unit responses to acoustic, hydrodynamic, and visual stimuli can be recorded in both the CP and the TA. However, CP and TA responses differed in that most units in the CP were unimodal visual, whereas in the TA, unimodal, bimodal, and trimodal units were found in about equal numbers.

Our data from the TA agree with previous anatomical and physiological reports that suggest that the TA receives both visual and acousticolateralis information [1,3,4,12],

To our surprise, we found that 90% of the CP units were unimodal visual. Visual CP units have not been documented before, and no anatomical data indicate sources of visual input to the CP. That physiological data have not shown visual input to the CP may be because in previous studies, only acoustic or lateral line stimuli were applied while recording from the CP [2,7]. Anatomical [1,12] and physiological [2,7] data have shown that acousticolateralis information reaches the CP. Consequently, we also found CP units that responded to acoustic or hydrodynamic stimulation. However, the percentage of these units was small, even though the frequency and intensity of our acoustic stimulus were adequate to elicit CP unit responses [7].

In any case, our findings suggests different functions for the CP and the TA. Whereas the CP appears to be involved in the unimodal processing of visual (this study) and acoustic (previous studies) information, the TA appears to be integrating across sensory modalities. Both the CP and the TA have anatomical connections with the telencephalon [11,12]. Further studies are needed to reveal whether the sensory information present in the CP and TA is passed on to the telencephalon or to which degree these brain nuclei are parts of descending modulatory systems.

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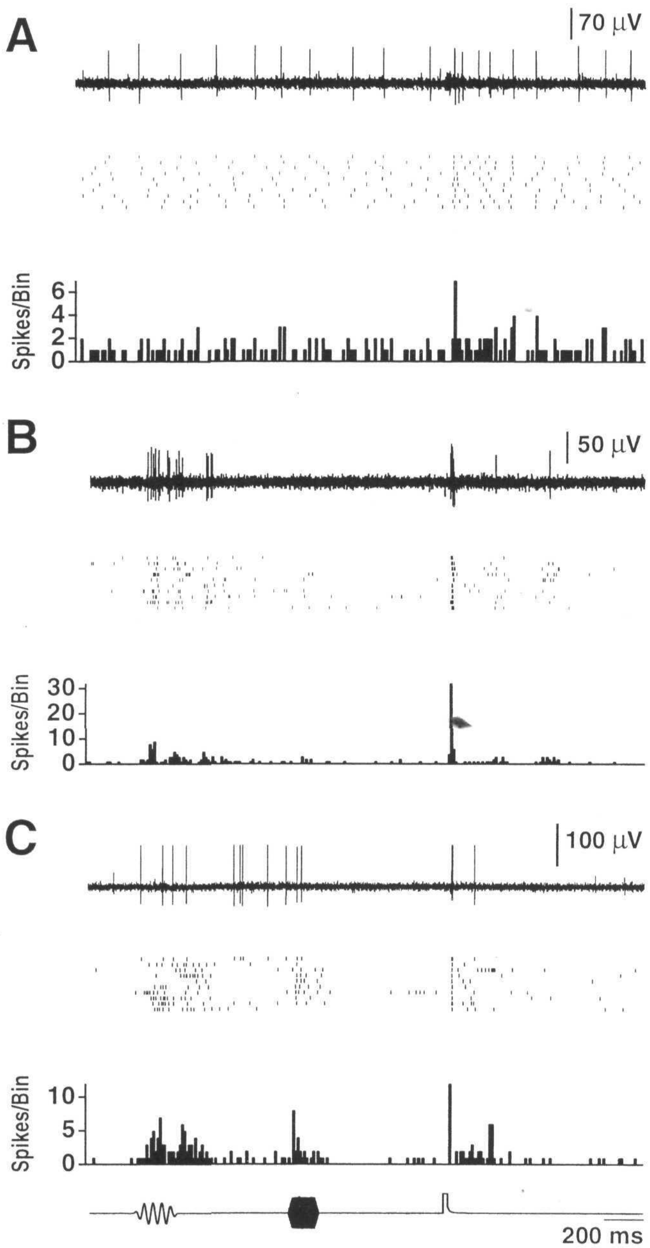

FIG. 2. Unimodal, bimodal and trimodal units in the goldfish diencephalon. (A) Example of a unimodal visual unit recorded in the CP. (B) Example of a bimodal hydrodynamic and visual unit recorded in the anterior tuberal nucleus of the hypothalamus (TA). (C) Example of a trimodal unit recorded in the TA. For each example, an original recording, a raster diagram of the responses to ten repetitions of a sequence of three stimuli (see Materials and Methods), and a peri-stimulus-time histogram (binwidth 10 ms) are shown. The bottom-most trace represents the stimulus trace.

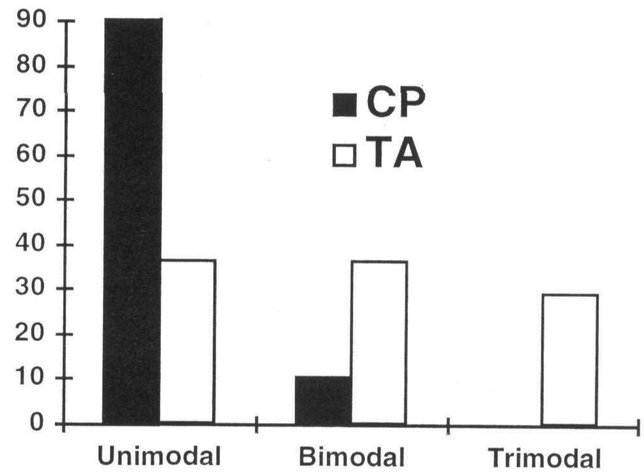

FIG. 3. Frequency of unimodal, bimodal, and trimodal units in the goldfish diencephalon. Filled bars represent data from the CP, and open bars represent data from the TA.

central posterior nucleus of the thalamus of the goldfish, *Carassiu* auratus.* J. Comp. Physiol. A 176:747-760; 1995.
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