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# Excitatory and Inhibitory Transmission from the Optic Tectum to Nucleus Isthmi and Its Vicinity in Amphibians

## Key Words

Intracellular recording  
Postsynaptic potential  
Nucleus isthmi  
Tegmentum  
Optic tectum  
Lucifer yellow  
Amphibians

## Abstract

Intracellular recordings were made from nucleus isthmi (NI) and its vicinity in toads (*Bufo bufo gargarizans*) in response to electrical stimulation of the bilateral optic tract. The results suggest that NI mainly receives its excitatory input from the ipsilateral tectum and its inhibitory input from the contralateral tectum. Tegmental cells in a region medioventral to NI were usually characterized by strong spontaneous activity and an excitatory-inhibitory sequence of postsynaptic potentials in response to stimulation of either side of the bilateral optic tract. Sixty of the recorded cells were stained with Lucifer yellow to show their morphological features and anatomical positions within NI and its vicinity.

## Introduction

Nucleus isthmi (NI) is a prominent mesencephalic visual structure found in all classes of non-mammalian vertebrates, except cyclostomes, and it is considered to be homologous to nucleus parabigeminalis of mammals [for review see S.R. Wang, 1988]. It receives its input from the ipsilateral tectum and projects back to the tectum ipsilaterally in teleosts [Ebbesson and Vanegas, 1976; Ito et al., 1981, 1982; Sakamoto et al., 1981] (although Sas and Maler [1986] reported a bilateral projection in a fish), ipsilaterally in birds [Hunt and Kunzle, 1976; Hunt et al., 1977; Kunzle and Schnyder, 1984], and bilaterally in amphibians [Glasser and Ingle, 1978; Gruberg and Udin, 1978; Grobstein et al., 1978; Gruberg and Lettvin, 1980; Grobstein and Comer, 1983; Y.T. Wang et al., 1983; Wiggers and Roth, 1991] and in reptiles [S.R. Wang et al., 1983; Kunzle and Schnyder, 1984; Sereno and Ulinski, 1987], as does nucleus parabigeminalis in mammals [Graybiel, 1978; Baley-

dier and Magnin, 1979; Sherk, 1979; Watanabe and Kawana, 1979; Mendez-Otero et al., 1980; Linden and Perry, 1983; Roldan et al., 1983; Jen et al., 1984; Kunzle and Schnyder, 1984]. Nucleus isthmi also has neural connections with nucleus pretectalis [Ito et al., 1981, 1982; Sakamoto et al., 1981; Striedter and Northcutt, 1989] and torus semicircularis [Sas and Maler, 1986] in teleosts, with nucleus anterodorsalis tegmenti in amphibians [Udin, 1987], and with nucleus profundus mesencephali or the rostral isthmal magnocellular nucleus (Imr) in reptiles [S.R. Wang et al., 1983; Sereno and Ulinski, 1987], as does nucleus parabigeminalis with the dorsal lateral geniculate and pulvinar nuclei in mammals [Graybiel, 1978; Harting et al., 1986; Hashikawa et al., 1986; Diamond et al., 1992].

Several electrophysiological studies have indicated that nucleus isthmi receives visual excitation from the ipsilateral tectum [Vinogradova and Manteifel, 1977, 1979; Gruberg and Lettvin, 1980; S.R. Wang et al., 1981, 1982, 1983; Williams et al., 1983; Yan and Wang, 1986; Wang and

## Materials and Methods

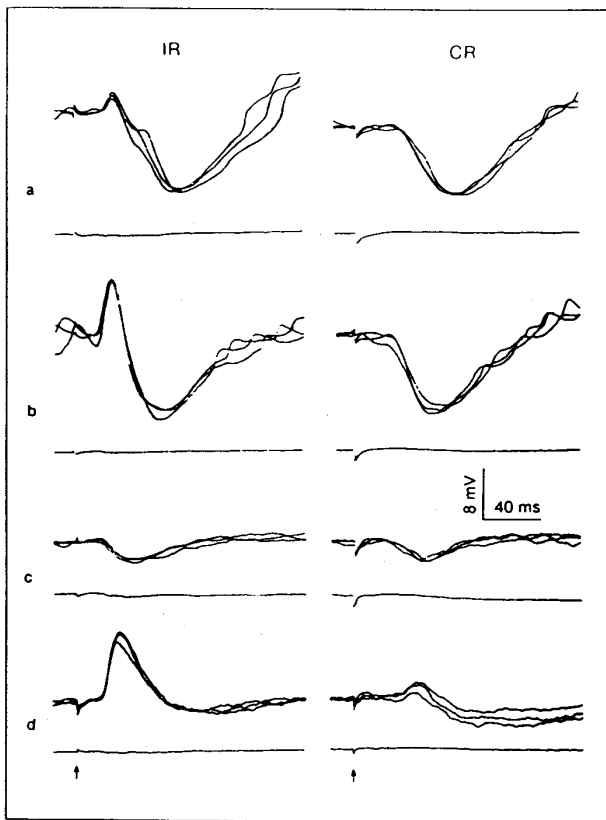
The experiments were performed on adult toads, *Bufo bufo gargarizans* (7.5–10 cm from snout to vent), and under guidelines established by the American Physiological Society and by the Society for Neuroscience. The conventional surgical and stereotaxic procedures used have already been described [S.R. Wang et al., 1982]. Briefly, the animal was immobilized with gallamine triethiodide. The optic tectum was surgically exposed as widely as possible, and a local anesthetic (procaine) was periodically applied to the transected skin and muscle surrounding the surgical area during surgery and throughout the recording sessions. Bipolar metal electrodes were bilaterally placed on the dorsal optic tract. Electrical stimuli were delivered with rectangular pulses of 30–400  $\mu\text{A}$  in intensity and 100  $\mu\text{s}$  in duration, with a frequency of 1 Hz. Usually, the threshold for postsynaptic potentials was 30–50  $\mu\text{A}$ . However, a maximal response with shortest latency often required an intensity of 100–200  $\mu\text{A}$ . The stimulus threshold was not significantly different between the ipsilateral (IR) and contralateral (CR) optic tract. Electrodes for intracellular recordings were micropipettes filled with 3 M potassium acetate, whose tips had been broken to a diameter of approximately 0.5–1.0  $\mu\text{m}$ , with impedance of 20–60 M $\Omega$ . A brief positive current pulse of about 20 nA was routinely used to facilitate impaling cells. Intracellular responses were fed into a preamplifier (WPI M-707), whose output was monitored on the screen of a Tektronix 5115 storage oscilloscope and stored with a magnetic tape recorder (Sony KW-609). The responses were played back into a signal averager (EG & G Model 4202), and then into an X-Y Plotter for display and superposition or averaging three to six times to measure their latencies. Depolarizing or hyperpolarizing current was injected intracellularly through the recording microelectrode, using a bridge circuit to identify the excitatory postsynaptic potentials (EPSPs) and inhibitory postsynaptic potentials (IPSPs), and facilitate measurement of the response latencies. In the second part of the experiments, micropipettes filled with 5% Lucifer yellow (CH, Dilithium salt, Sigma, St. Louis, Mo., USA) were used. Following intracellular recordings, the recorded neurons were injected by passing negative current of 2–5 nA through the electrodes for 2–5 min. After a survival period (up to 7 h), the brain was removed and fixed in a mixture of 3% formaldehyde and 3% glutaraldehyde, and then immersed in 30% sucrose in phosphate buffer solution overnight. Frozen sections were cut at 100  $\mu\text{m}$ , mounted, and dehydrated. Serial sections containing the marked neurons were observed and photographed with a fluorescence microscope (Olympus, B filler). The location and morphology of the neurons were reconstructed.

## Results

A total of 158 cells from the area of NI and 13 tegmental cells were intracellularly recorded in 40 toads.

### *Postsynaptic Potentials and Morphology of Isthmic Cells*

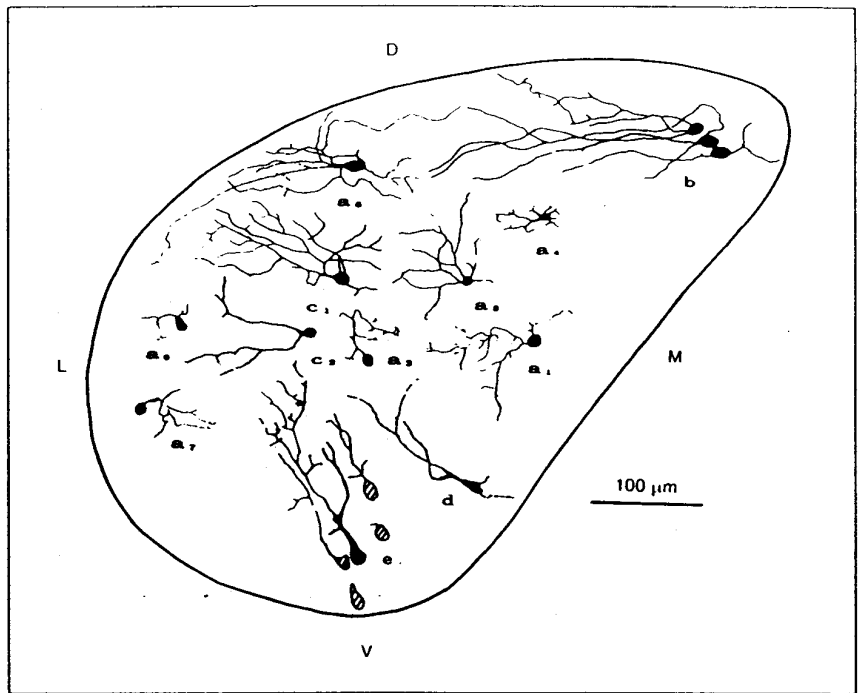
Lucifer yellow (LY) markings confirmed that of 65 labelled cells, 60 cells (92%) were localized within NI and 5 (8%) outside. These 5 tegmental cells were mainly distributed within the posterodorsal nucleus and the posteroventral nucleus ventromedial to NI. They usually had



**Fig. 1.** Postsynaptic potentials of four isthmic cells (a–d) responding to ipsilateral optic tract stimulation (IR) and to contralateral optic tract stimulation (CR). All four were labelled with Lucifer yellow and corresponded to a, b, c, and d, respectively, in figure 2. Cells a and b produced the same type of postsynaptic responses, i.e., an EPSP followed by an IPSP to IR, and an IPSP to CR. However, injection of cell b resulted in multilabelling. Cell c responded with an IPSP to either IR or CR stimulation. Cell d produced an EPSP following stimulation of either IR or CR. Arrows indicate stimulation artifacts.

Frost, 1991]. There is also some evidence suggesting that nucleus pretectalis in teleosts and nucleus profundus mesencephali in lizards may supply an inhibitory input to NI [Ito et al., 1982; S.R. Wang et al., 1983; Northmore, 1991]. In order to further reveal the functional significance of isthmic afferents, we made intracellular recordings from NI in toads following electrical stimulation of the optic tract bilaterally. We also studied the effects of optic tract stimulation on the tegmental cells outside NI. It was revealed that nearly all of the NI cells receive a possibly indirect inhibition from both tecta, besides a direct excitation from the ipsilateral tectum, and that tegmental cells mainly receive their excitatory input from both tecta.

**Fig. 2.** The distribution and morphology of some isthmic cells intracellularly stained with Lucifer yellow. The recorded cells were scattered throughout nucleus isthmi and could be grouped into five classes: a ( $a_1$ - $a_7$ ), b, c ( $c_1$ - $c_2$ ), d, and e. The postsynaptic potentials of the first four classes are shown in figure 1 with the corresponding letters. Class e produced an EPSP-IPSP sequence to IR and no responses to CR. The recorded and injected cell (solid) was surrounded by 'dye-coupled' cells, which were lightly stained (hatched). D, L, M and V represent dorsal, lateral, medial and ventral, respectively. Scale = 100  $\mu$ m.



strong spontaneous activity and were often excited by stimulation of both optic tracts; they were located deeper and more medial than the isthmic cells.

The isthmic cells usually showed no spontaneous activity and had resting potentials larger than  $-25$  mV. Many cells gave rather stable recordings and often could be maintained for a period ranging from several minutes to tens of minutes. Following ipsilateral optic tract stimulation, excitatory postsynaptic potentials followed by inhibitory postsynaptic potentials (EI type) were elicited in 117 (74%) of 158 isthmic cells, 24 cells (15%) produced I-type responses, and the remaining 17 cells (11%) showed E or EE type responses. If the first postsynaptic potential is considered, ipsilateral stimulation excited 134 cells (85%) of 158 isthmic cells recorded. Some typical examples are shown in figure 1.

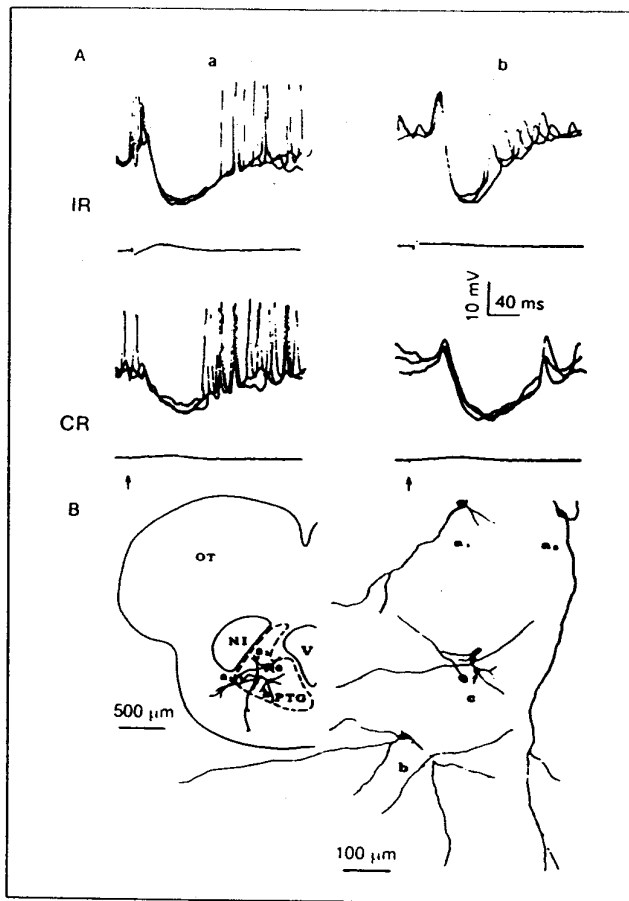
Following contralateral optic tract stimulation, 145 (92%) of 158 impaled NI cells produced I-type responses (fig. 1a-c), 9 cells (6%) were excited by optic tract stimulation bilaterally (fig. 1d), and 4 cells (2%) did not respond to contralateral optic tract stimulation. However, these 4 cells produced an EPSP-IPSP sequence to the ipsilateral stimulation.

Taken together, both ipsilateral optic tract (IR) and contralateral optic tract (CR) produced excitation in 9 cells (6%) (fig. 1d), and inhibition in 24 cells (15%) (fig. 1c);

both IR-excitation and CR-inhibition occurred in 121 cells (77%) (fig. 1a, b). The other 4 cells (2%) produced excitatory responses to IR stimulation and no response at all to CR stimulation. Therefore, nucleus isthmi receives its excitatory input mainly from the ipsilateral tectum and inhibitory input from the contralateral tectum indirectly.

In 9 isthmic cells responding to stimulation of both optic tracts with EPSPs, the latency of an EPSP to ipsilateral stimulation was shorter than that to contralateral stimulation (mean  $\pm$ SD:  $15.9 \pm 7.3$  ms vs.  $33.7 \pm 5.4$  ms). The amplitude of postsynaptic potentials produced by ipsilateral stimulation was larger than that produced by contralateral stimulation ( $7.5 \pm 3.3$  mV vs.  $2.7 \pm 1.5$  mV) in 7 cells (fig. 1d), and equal to it in 2 cells, which had amplitude of 2.4 mV and 6.0 mV, respectively. All these cells could be considered as binocular neurons. They might receive visual information from both eyes either through binocular cells or via 2 monocular cells in the tectum.

The morphologies of some Lucifer yellow-stained cells are shown in figure 2. Cells  $a_1$ - $a_7$  had various shapes but produced the same type of postsynaptic responses. An EPSP-IPSP sequence was evoked by ipsilateral stimulation and an IPSP by contralateral stimulation. These cells were distributed in the medulla of nucleus isthmi and were classified as unipolar, bipolar or multipolar cells. Some of them had large dendritic fields. A group of 3 cells (fig. 2b) was



**Fig. 3.** Tegmental cells. **A** Intracellular recordings of tegmental cells (a, b) responding to ipsilateral optic tract stimulation (IR) and to contralateral optic tract stimulation (CR). Note that these cells responded with an EPSP followed by an IPSP to either stimulation. Cell a was spontaneously active. Their morphologies correspond to a<sub>1</sub> and b in **B**. **B** Localization and morphology of some tegmental cells labelled with Lucifer yellow. Cell a<sub>1</sub> produced the same type of responses as cell a<sub>2</sub>. An exception is cell c, which responded with IPSPs to both types of stimulation. Injection of this cell also labelled three other cells, which were lightly and incompletely stained. Abbreviations: NI = Nucleus isthmi; OT = optic tectum; PTG = posterodorsal and posteroventral tegmental nuclei; V = ventricle. Scale: 500  $\mu$ m for cross-section, 100  $\mu$ m for cellular morphology.

one of several multilabelled cases. One of the cells was impaled and responded with an EPSP ipsilaterally and IPSP contralaterally. These 'dye-coupled' cells spread their dendrites together dorsolaterally. Cells c<sub>1</sub> and c<sub>2</sub> responded with an IPSP to either ipsilateral or contralateral stimulation. They had pear-shaped somata, which gave off two or more primary dendrites. Cell d, localized ventromedially, was a binocular neuron and produced an EPSP to stimulation of

either optic tract. The EPSP evoked by ipsilateral stimulation was much larger in amplitude and shorter in latency than that evoked by contralateral stimulation. Its pyramidal soma issued 2 basal dendrites and an apical dendrite, which gave off branches with varicosities. Cell e was 1 of 4 cells with an EPSP-IPSP sequence responding to ipsilateral stimulation but not contralateral stimulation. It had a pyramidal soma and thicker dendrites with a few varicosities. Lucifer yellow injection of this cell also labelled 4 other cells in its vicinity. Two of them had a few, thinner dendrites; in the other two, only the somata were stained.

#### *Postsynaptic Potentials and Morphology of Tegmental Cells*

The 13 tegmental cells intracellularly recorded were in an area deeper and more ventromedial than nucleus isthmi, and 4 of them were stained with Lucifer yellow. The tegmental cells were usually characterized by strong spontaneous activity and responded with an EPSP-IPSP sequence to either ipsilateral or contralateral stimulation (fig. 3A). In figure 3B, cells a<sub>1</sub> and a<sub>2</sub> were strongly discharging and silent only during IPSP. These 2 cells had multiangular or fusiform somata that issued long main dendrites (up to 750  $\mu$ m) ventrolaterally or ventrally. Cell b had an EPSP-IPSP sequence with rebound excitation to either ipsilateral or contralateral stimulation. It had a fusiform soma that gave off thin branching dendrites laterally, ventrolaterally, or ventromedially for a distance of up to 480  $\mu$ m. Injection of cell c also labelled 3 other cells. This cell was an exception, in that it responded with an IPSP to either ipsilateral or contralateral stimulation. It had a few thin dendrites spreading roughly mediolaterally. The other 3 'dye-coupled' cells had shorter, thin dendrites. The labelled cells were of variable shape and size (10–30  $\times$  10–15  $\mu$ m) and were localized within the posterodorsal tegmental nucleus and the posteroventral tegmental nucleus medioventral to nucleus isthmi.

#### **Discussion**

A large number of studies indicate that nucleus isthmi receives its excitatory afference from the ipsilateral optic tectum [for review see S.R. Wang, 1988], and the tecto-isthmic pathway may use acetylcholine [Hunt et al., 1977; Felix et al., 1985; S.R. Wang et al., 1985, 1986; Li et al., 1987a, b] as one of its physiological neurotransmitters. However, this study indicates that NI cells in toads also receive inhibitory input from the optic tectum bilaterally. It has been reported in various vertebrates that NI receives its

input from tegmental and pretectal areas, which receive tectal afference. In teleosts, a tectal recipient nucleus, nucleus pretectalis, projects strongly to nucleus isthmi, and pretecto-isthmic terminals have flattened vesicles and make symmetric synapses onto neurons in every part of NI, suggesting its inhibitory characteristics [Ito et al., 1981; Sakamoto et al., 1981]. In addition, the dorsal torus semicircularis in a gymnotid fish sends projection to the ipsilateral NI [Sas and Maler, 1986]. In anuran amphibians *Rana* and *Acris*, Udin [1987] demonstrated a projection to both contralateral and ipsilateral nucleus isthmi from a scattered group of large cells, nucleus anterodorsalis tegmenti, located in the mesencephalic tegmentum just rostral to nucleus isthmi. This region also receives bilateral input from the optic tectum [Lazar et al., 1983; Masino and Grobstein, 1990] and is mainly related to visual information processing [Yan et al., 1983]. In reptiles, nucleus profundus mesencephali in lizards [S.R. Wang et al., 1983] and the rostral magnocellular nucleus isthmi in turtles [Serenio and Ulinski, 1987] project to and may inhibit nucleus isthmi.

There is some other evidence for inhibitory inputs to nucleus isthmi. In teleosts, glutamic acid decarboxylase (GAD) immunohistochemistry shows a dense plexus of GABAergic terminals in nucleus isthmi [Sas and Maler, 1986]. In birds, it is suggested that the magnocellular nucleus isthmi (Imc) might send GABAergic axons to the parvocellular nucleus isthmi (Ipc) [Serenio and Ulinski, 1987], which is further supported by the finding that microiontophoretic application of GABA inhibits NI cells [Stoop et al., 1989]. In an electrophysiological study, S.R. Wang et al. [1983] found so-called 'in-out' responses in reptiles and assumed that inhibition of isthmic responses might come from nucleus profundus mesencephali. More recently, Northmore [1991] reported 2 different amplitude spikes in NI in teleosts and suggested that the monocularly excited large spikes come from direct inputs of the ipsilateral tectum, and the small, binocularly excited spikes might represent an inhibitory projection from nucleus pretectalis, which also receives bilateral projections from optic tectum [Striedter and Northcutt, 1989]. This case is very similar to the situation found by the present study in toads. Of course, it does not exclude the possibility that some inhibitory potentials were elicited by an inhibitory circuit intrinsic to nucleus isthmi or by tectal inputs directly.

The present findings also have some discrepancies with anatomical results. It has been reported that nucleus anterodorsalis tegmenti projects bilaterally to the caudal region of nucleus isthmi, and only a small number of cells per brain were labelled by horseradish peroxidase (HRP) [Udin,

1987]. However, we found that nearly all the recorded cells received bilateral inhibitory inputs. There are several possible explanations for this discrepancy: (1) nucleus anterodorsalis tegmenti may project to the whole nucleus rather than to the caudal region only. It has been observed that very large midbrain injections of HRP label a non-tectal input that fills the whole contralateral NI [Udin, 1987]; (2) the tegmento-isthmic axons arborise widely and make a large number of synaptic contacts [Udin, 1987]; or (3) there may be electrotonic coupling among NI neurons, as shown in teleosts [Williams et al., 1983]. Support for the third possibility also comes from our intracellular labelling with Lucifer yellow. In our study, about 10% of NI cells displayed multiple labelling. Up to 6 neurons were found to be coupled together after injections of fluorescent dye into one of the neurons. However, there was no evidence showing that NI cells in toads fire synchronously, as demonstrated in teleosts. On the other hand, intracellular recordings in bullfrogs and pigeons have indicated that the isthmotectal pathway mainly exerts inhibition on tectal cells, although it also excites a small number of tectal cells [S.R. Wang and Matsumoto, 1990; Wu et al., 1993]. Interestingly, a more recent investigation [S.R. Wang, Y.C. Wang, and B.J. Frost, unpubl. observ.] has indicated that the Ipc exerts a powerful inhibition on tectal cells, and the Imc might keep the excitability of the postsynaptic tectal cells at a certain excitatory level. Therefore, the optic tectum and nucleus isthmi may work together to construct a 'winner-take-all' network [Serenio and Ulinski, 1987; Y.C. Wang and Frost, 1991]. It may make animals orient towards to the most interesting object in the visual field.

The second result of the present study is that the tegmental cells could be mainly excited by stimulation of either the ipsilateral or contralateral optic tract. This is supported by neuroanatomical findings that the tectum also projects to much of the midbrain tegmentum, probably including the posterodorsal nucleus and the posteroventral nucleus [Masino and Grobstein, 1990], where we made intracellular recordings. Extracellular recordings made by Smeraski and Grobstein [1991] from the ventral midbrain tegmentum in frogs have shown that tegmental cells in this region exhibit distinctive spontaneous activity and can be activated by stimulating either of the tecta. It has been suggested that the tectotegmental projections may be related to visually elicited orienting behaviours in amphibians [Masino and Grobstein, 1990; Smeraski and Grobstein, 1991]. Therefore, nucleus isthmi and its surrounding tegmentum might be functionally distinct but might work cooperatively to mediate visually guided behaviours of animals.

## Acknowledgments

This research was supported by National Natural Science Foundation of China. We are grateful to Miss Wei S.Y. for her excellent secretarial assistance.

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