Original Paper

Brain, Behavior and Evolution

Brain Behav Evol 1998;52:55–60

# Glutamatergic Neurotransmission from the Optic Tectum to the Contralateral Nucleus Rotundus in Pigeons

*Li-Hua Huang*
*Jian-Li Li*
*Shu-Rong Wang*

Laboratory for Visual Information
Processing, Institute of Biophysics,
Academia Sinica, Beijing, China

**Key Words**
Transmitter
Receptor
Glutamatergic transmission
Antagonists
Optic tectum
Nucleus rotundus
Pigeon

**Abstract**

Neuronal responses of 114 cells to electrical stimulation of the optic tectum were extracellularly recorded from the contralateral nucleus rotundus (nRt) in pigeons *(Columba livia)*, and the effects of two glutamatergic antagonists CNQX and CPP, as well as those of GABA, were examined on rotundal cells. The results show that tectal stimulation evokes excitation in neurons of the contralateral nRt and that the excitatory responses are blocked by microiontophoretically applied CNQX, CPP and GABA. It is suggested that the contralateral tectorotundal transmission is excitatory in nature and mediated by both glutamatergic AMPA and NMDA receptors and that GABA is an inhibitory transmitter within the nucleus as well. We also review our previous findings in discussing transmitters participating in the tectofugal pathway.

## Introduction

It is accepted that there are two main visual pathways in avian brains: the tectofugal pathway and the thalamofugal pathway. The former connects the retina, optic tectum (OT), nucleus rotundus and ectostriatum, and the latter consists of the retina, thalamic dorsolateral complex and visual Wulst. Nucleus rotundus (nRt) is the most prominent structure of the diencephalon and relays signals from the stratum griseum centrale (SGC) of the optic tectum to the ectostriatum of the telencephalon [Benowitz and Karten, 1976; Engelage and Bischof, 1993]. It also receives input from the contralateral OT [Hunt and Künzle, 1976; Bischof and Niemann, 1990; Güntürkün et al., 1993; Ngo et al., 1994; Mpodozis et al., 1996]. Electrophysiological studies have shown that this nucleus is involved in the analysis of geometric pattern, brightness, color, and fine spatial detail [Hodos and Karten, 1966; Macko and Hodos, 1984] and is organized into several functionally distinct subdivisions for processing different types of visual information such as color, luminance and Z-axis motion [Wang and Frost, 1992; Wang et al., 1993].

Histochemically, the nRt subdivisions stain differentially for acetylcholinesterase (AChE) [Martinez-de-la-Torre et al., 1990] but fail to label for choline acetyltransferase (ChAT) [Güntürkün and Karten, 1991]. It appears that the nRt lacks both muscarinic and nicotinic cholinergic receptors [Dietl et al., 1988a; Watson et al., 1988; Güntürkün and Karten, 1991; Bagnoli et al., 1992]. However, this nucleus has an apparently homogenous distribution of $\gamma$-aminobutyric acid (GABA)-like terminals, which may stem from the GABAergic neurons of the subpretectal and ventral

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0006–8977/98/0521–0055$15.00/0

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Shu-Rong Wang
Institute of Biophysics, Academia Sinica
15 Datun Road, Beijing 100101 (P.R. China)
Tel. +86 10-62022010, Fax +86 10-64871293
E-Mail wangsr@mimi.cnc.ac.cn

posterior thalamic nuclei [Domenici et al., 1988; Ngo et al., 1992; Tömböl et al., 1994; Veenman and Reiner, 1994; Mpodozis et al., 1996]. There also exist binding sites of GABA-benzodiazepine receptors and $GABA_B$ receptors in the nRt [Dietl et al., 1988b; Veenman et al., 1994]. Therefore, GABA may be an inhibitory transmitter in this nucleus. On the other hand, intermediate levels of tritiated L-glutamate binding were detected in nucleus rotundus in chicks [Mitsacos et al., 1990], suggesting that glutamate is probably an excitatory transmitter in this nucleus. Recently, we have provided electrophysiological evidence that glutamate is an excitatory transmitter acting predominantly through AMPA (α-amino-3-hydroxy-5-methyl-4-isoxazole propionic acid) receptors in the ipsilateral tectorotundal transmission. Meanwhile, GABA plays a role of inhibitory transmitter in the nRt in pigeons [Gao et al., 1995].

With the aim of investigating neurotransmission from the tectum to the contralateral nRt, and of identifying transmitters in this transmission, we used microiontophoresis and electrical stimulation techniques to study electrophysiological responses of the nRt neurons to electrical stimulation applied to the contralateral tectum and the effect of glutamate antagonists on these responses.

## Materials and Methods

The experiments were performed on adult homing pigeons (*Columba livia*), both sexes, weighing 250–400 g. Pigeons were anesthetized by an i.m. injection of urethane (20%, 1 ml/100 g b.w.) and then placed in a stereotaxic apparatus. The tecta and the left telencephalon overlying the nRt were surgically exposed, and the dura was opened. For electrical stimulation, tungsten bipolar electrodes were bilaterally positioned in the SGC of the tectum, where the tectorotundal projection neurons are located. The stimulating sites in the exposed dorsolateral OT were adjusted from site to site and from depth to depth to evoke the maximal field potential in the nRt [Gao et al., 1995]. Rectangular pulses of 50–100 μs in duration, and 0.1–0.5 mA in intensity, were delivered at a frequency of 0.2–1 Hz. Nucleus rotundus was approached according to its stereotaxic coordinates [Karten and Hodos, 1967]. Rotundal neurons were isolated by their spontaneous activity and visual responses to a 5° black disk manually moved against a white screen 40 cm distant from the right eye [Wang et al., 1995]. Extracellular recordings of neuronal responses were obtained with one barrel of a five-barreled micropipette (3–5 μm diameter, 5–15 $M\Omega$ impedance) filled with 2 $M$ NaCl and 100 m$M$ $CoCl_2$. Three barrels contained the following compounds to be microiontophoretically ejected by appropriate ionic currents: CPP (3-rs-2-carboxy piperazin-4-yl-propyl-1-phosphonic acid, Tocris Neuramin, 0.01 $M$, pH 7.5), CNQX(6-cyano-7-nitro-quinoxaline-2,3-dione, Tocris Neuramin, 0.01 $M$, pH 8.3), GABA(γ-aminobutyric acid, Fluka, Switzerland, 0.5 $M$, pH 3.3). The fifth barrel, filled with 0.165 $M$ NaCl, was used for minimizing current effects by current neutralization [Salmoiraghi and Weight, 1967] or for drug control. No apparent current effects were observed in this study.

At the end of experiments, recording sites were marked with cobalt chloride [Wang et al., 1981]. The brain was removed from the skull and immersed in a saline solution containing ammonium sulfide to form a black precipitate of cobalt sulfide. The brain block was conventionally processed for histological observation.

Original research reported herein was conducted according to guidelines for the use of vertebrate animals established by the American Physiological Society and the Society for Neuroscience.

## Results

Electrical stimulation of the stratum griseum centrale of the ipsilateral tectum evoked a large field potential characteristic in the nRt, which is a good indication of the position of a recording electrode in the right place [Revzin and Karten, 1966; Gao et al., 1995]. The field potential produced by the contralateral stimulation was also characteristic and simpler than that evoked by the ipsilateral stimulation (fig. 1). Another criterion for identifying rotundal neurons is their large visual receptive fields and strong responses to a moving target [Gao et al., 1995]. Apart from the stereotaxic coordinates of neurons recorded, our cobalt-sulfide markings of 15 recording sites also confirmed that extracellular responses were convincingly recorded from the nRt (fig. 2).

### *Electrophysiology:*
### *Crossed Tectorotundal Projection Is Excitatory*

One hundred and fourteen rotundal neurons were isolated by their spontaneous activity or visual responses from the nRt. They were spontaneously active (8–12 spikes/sec) and produced strong responses to a 5° moving target. Among them, 67 neurons (59%) responded to electrical stimulation of the contralateral tectum with spikes riding on the characteristic field potential (fig. 1A). The ratio of stimulation to spikes evoked by it was usually one to one. These responses had shorter latencies ranging from 10 to 20 ms with an average of 15 ms and could follow repetitive electrical stimulation at frequencies of 50–100 Hz. It appeared that the contralateral stimulation evoked monosynaptic excitation in rotundal neurons. No apparent effects of electrical stimulation on spontaneous activity and visual responses of these cells were observed. In one cell (1%), spontaneous activity (10 spikes/sec) was inhibited by the contralateral stimulation, and this inhibition lasted for 50 ms. Forty-six other cells (40%) did not show obvious responses to electrical stimulation, even applied with current intensity of 0.5 mA and 500 μs in duration.

The effect of electrical stimulation applied to the ipsilateral tectum was also examined in 40 out of 67 cells excited

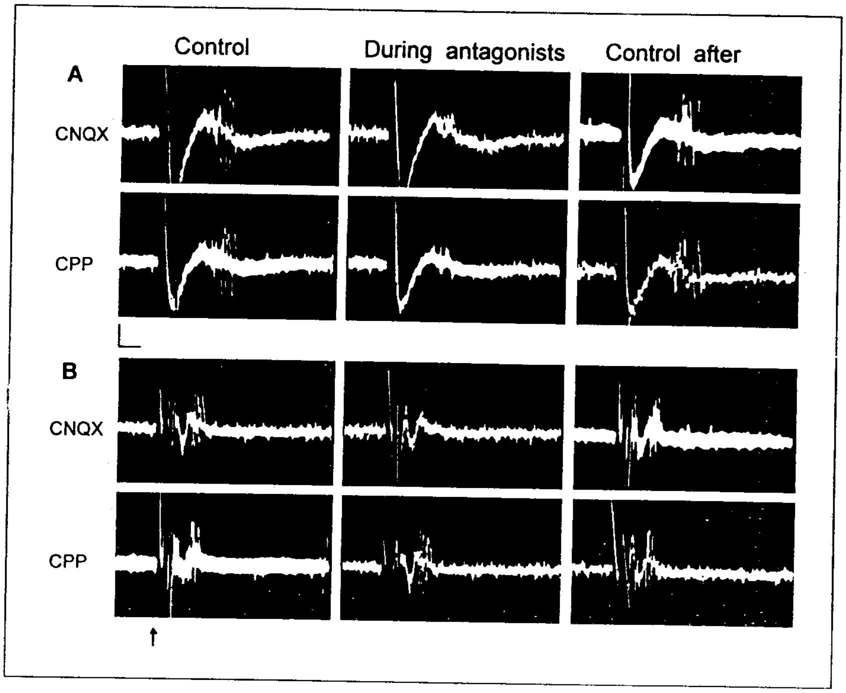

**Fig. 1.** Effects of glutamatergic antagonists CNQX and CPP on excitatory responses evoked in a rotundal neuron by electrical stimulation applied to the contralateral (**A**) and ipsilateral (**B**) tectum. Note differences in effects of CPP on neuronal responses between **A** and **B**. Three sweeps were superimposed in each trace. Arrow points to electrical stimulation artifacts. Scales: 0.05 mV and 5 msec.

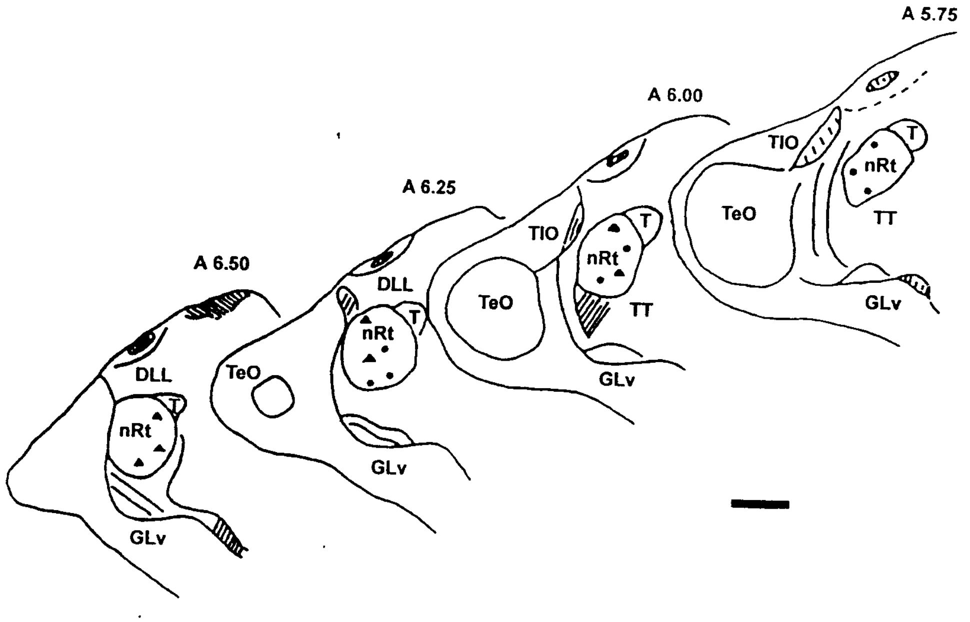

**Fig. 2.** Distribution of recording sites histologically identified with cobalt sulfide in the nucleus rotundus (nRt), where contralateral tectorotundal transmission was found. Anterior-posterior levels are according to the Atlas by Karten and Hodos [1967]. Filled circles represent electrophysiological recording sites, and filled triangles signify neuropharmacological recording sites where typical drug effects were observed. DLL = Nucleus dorsolateralis anterior thalami, pars lateralis; GLv = nucleus geniculatus lateralis, pars ventralis; T = nucleus triangularis; TeO = tectum; TIO = tractus isthmo-opticus; and TT = tractus tectothalamicus. Scale bar = 1.0 mm.

by the contralateral stimulation (fig. 1B). Of these, 33 cells (82%) were bilaterally excited. In these cases, simultaneous stimulation of both tecta produced two spikes, with a contralateral spike being preceded about 8–9 ms by an ipsilateral one. If the tecta were stimulated separately, only one spike was evoked, either a contralateral or an ipsilateral one. Two cells (5%) were excited by the contralateral stimulation and inhibited by the ipsilateral one. The onset of bilateral stimulation could be so adjusted that contralateral and ipsilateral stimulation arrived at a rotundal neuron at the same time; the excitation and inhibition produced separately by dual stimulation would cancel each other. Five other cells (13%) had no responses to the ipsilateral stimulation. On the other hand, 49 cells excited by the ipsilateral stimulation (67%) were also mostly excited by the contralateral stimulation, with 1 cell (2%) being inhibited by and 15 others (31%) producing no responses to the stimulation. Overall, it appeared that the ipsilateral stimulation was more effective in exciting rotundal neurons (table 1).

**Table 1.** Effect of bilateral tectum stimulation on 114 rotundal neurons in pigeons

| Contra/Ipsi | Excitation | Inhibition | No effect |
|---|---|---|---|
| Excitation | 33 | 1 | 15 |
| Inhibition | 2 | 0 | 0 |
| No effect | 5 | 0 | 18 |
| Not tested | 27 | 0 | 13 |

*Neuropharmacology:*
*Crossed Tectorotundal Transmission Is Glutamatergic*

Effects of glutamate antagonists CNQX and CPP were examined on 33 of 67 rotundal neurons excited by contralateral tectal stimulation. Spikes evoked in these cells were all completely blocked by microiontophoretically applied CNQX, a glutamatergic AMPA receptor antagonist, and those in 27 of 33 cells (82%) were also blocked by CPP, a specific NMDA (N-methyl-D-aspartate) receptor antagonist. These data implied that both AMPA receptors and NMDA receptors may coexist on most of rotundal neurons and that they are involved in neurotransmission from the tectum to the contralateral nRt in birds. However, these two antagonists were different in blocking the crossed tectorotundal transmission. Current intensity needed for CNQX (50–100 nA) to completely block the excitation evoked by the contralateral stimulation was much smaller than that needed for CPP (200–400 nA), and the onset of blockage by CNQX (0.5–1 min) was also much more rapid than that for CPP (1–2 min). On the other hand, complete recovery of a neuron from CNQX (5–10 min) required a much longer time than that from CPP (3–5 min). These differences in potency of the two antagonists indicated that AMPA receptors may contribute more to the crossed tectorotundal transmission than NMDA receptors.

In comparing ipsilateral tectorotundal transmission with contralateral transmission, 4 of the 33 neurons excited by both ipsilateral and contralateral stimulation were examined for the effects of antagonists on both forms of excitation (fig. 1). The former was blocked by CNQX but not by CPP, whereas the latter was blocked by either CNQX or CPP. Moreover, neuronal recovery from the contralateral blockage by CNQX took much longer time than that from the ipsilateral blockage (5–10 min vs. 3 min). In view of our previous finding that GABA can inhibit excitation evoked by ipsilaterally electrical and contralaterally visual stimulation [Gao et al., 1995], the effect of GABA was also examined on excitation produced by contralaterally electrical stimulation in additional three cells. They were all inhibited by GABA microiontophoretically applied with current intensity of 100 nA for 30 sec and recovered 3–5 min after stopping GABA application. The neuropharmacological responses of rotundal cells examined and tectal sites electrically activated in this study were not observed to be topologically related (fig. 2).

## Discussion

This is the first paper to describe electrophysiologically neurotransmission from the optic tectum to the contralateral nucleus rotundus in birds. Electrical stimulation of the OT can evoke spikes in the majority of neurons in the contralateral nRt, indicating the presence of a crossed tectorotundal pathway that is excitatory in nature. This finding is consistent with several neuroanatomical studies showing that the nRt receives its afferents from bilateral tecta and that the contralateral tectorotundal projection crosses the midline at the supraoptic decussation [Hunt and Künzle, 1976; Bischof and Niemann, 1990; Güntürkün et al., 1993; Ngo et al., 1994; Mpodozis et al., 1996]. It also lends considerable support to the notion that the decussating tectorotundal pathway may be excitatory [Ngo et al., 1994; Mpodozis et al., 1996]. Combined with our previous finding that electrical stimulation of the ipsilateral tectum and visual stimulation of the contralateral eye excite rotundal neurons [Gao et al., 1995], it is clear that both tecta project excitatory output to the nRt and that signals coming from the ipsilateral tectum and the contralateral tectum converge on most rotundal neurons. However, both signals are unlikely to arrive at the same time, because the contralateral signal travels along a longer and thinner route than the ipsilateral one [Ngo et al., 1994]. In addition, nRt also receives its extratectal inputs from the subpretectal and the ventral posterior thalamic nuclei, which in turn, receive ipsilateral as well as contralateral tectal inputs [Bischof and Niemann, 1990; Ngo et al., 1994; Mpodozis et al., 1996]. Studies of GABA-immunohistochemistry have suggested that afferents to the nRt from these nuclei may be inhibitory [Domenici et al., 1988; Ngo et al., 1992; Tömböl et al., 1994; Mpodozis et al., 1996]. Therefore, bilateral tecta could transmit excitatory signals directly and inhibitory signals indirectly to the nRt.

The second main finding of the present study is that the crossed tectorotundal transmission is glutamatergic and mediated by both AMPA and NMDA receptors. Two subtypes of glutamatergic receptors appear to coexist on the majority of rotundal neurons recorded, in agreement with the results obtained from our previous study [Gao et al., 1995], and the crossed tectorotundal transmissions are mediated by AMPA receptors. There is a noteworthy difference in the roles played by NMDA receptors in ipsilateral and contralateral tectorotundal transmissions. In the former, the contribution of NMDA receptors to the transmission is quite small or negligible [Gao et al., 1995], closely resembling monosynaptic transmission in the spinal cord [Peet et al., 1983]; whereas in the latter, NMDA receptors, together with AMPA receptors, also contribute greatly to the tectorotundal transmission. These are reminiscent of the findings by Feldman and Knudsen (1994) on the inferior colliculus in owls: that AMPA receptors are involved in auditory responses in its two subdivisions, the external nucleus and the lateral shell of the central nucleus, while NMDA receptors make a major contribution to auditory responses in the external nucleus and only a small contribution to the lateral shell. Taken together, it is suggested that AMPA receptors are responsible for fast transmission at tectorotundal synapses, while NMDA receptors may trigger synaptic modification responding to intense or convergent stimulation [Collingridge and Bliss, 1987] or mediate sensory information processing [Feldman and Knudsen, 1994].

Our previous study [Gao et al., 1995] suggested that GABA is a major inhibitory transmitter in nRt. The present paper also provides some evidence for the mediation of GABA in controlling the excitability of rotundal neurons. The fact that GABA can eliminate excitation evoked by ipsilateral and contralateral tectal stimulation, as well as visual responses of the nRt neurons, indicates that GABA is a strong 'off' transmitter in this nucleus. This is supported by several immunostaining studies showing that nRt has homogeneously distributed GABA-like terminals which may stem from the subpretectal and ventral posterior thalamic nuclei [Domenici et al., 1988; Ngo et al., 1992; Tömböl et al., 1994; Mpodozis et al., 1996]. The GABA-like terminals contain flattened vesicles and make synapses with the nRt cells [Ngo et al., 1992; Tömböl et al., 1994]. Furthermore, binding sites of GABA-benzodiazepine receptors and $GABA_B$ receptors have also been observed in the nRt of birds [Dietl et al., 1988b; Veenman et al., 1994].

In summary, the data reported here indicate that neurotransmission from the optic tectum to the contralateral nucleus rotundus in birds is excitatory and mediated by both glutamatergic AMPA and NMDA receptors. Together with our previous studies on the tectofugal pathway [Gao et al., 1995; Jiang et al., 1997], these findings suggest that glutamate is a major excitatory transmitter in the retino-tecto-rotundal pathway in birds, playing its role predominantly through AMPA receptors. However, NMDA receptors are also largely mediated in the contralateral tectorotundal projection. It will be interesting to study further the functional significance of NMDA receptors in this system. In addition, evidence is provided that GABA is a strong inhibitory transmitter within the nucleus rotundus of birds.

## Acknowledgments

This work was supported by National Natural Science Foundation of China. We are grateful to Ms Wei Shun-Yi for her excellent secretarial assistance.

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