

## VISUAL FIELD TOPOGRAPHY IN THE FROG'S NUCLEUS ISTHMI

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Responses to visual stimulation were extracellularly recorded with micropipettes from 125 neurons of the left nucleus isthmi in frogs, *Rana nigromaculata*, and 101 electrode tip positions were marked with cobalt staining. The present study indicates that: (1) the entire contralateral hemifield and the nasal 40° of the ipsilateral hemifield project on the nucleus isthmi topographically, and (2) there exist binocular units in this nucleus.

The nucleus isthmi (NI) in anuran amphibians is a prominent paired midbrain structure, located at the border between mesencephalic tectum and cerebellum, consisting of a cell-dense cortex (peripherally) and a cell-sparse medulla (internally) [9]. In recent years several anatomical studies [6-9, 11, 17] have shown that NI in frogs receives connections from the ipsilateral optic tectum and projects bilaterally to the tectum (Fig. 1). These reciprocal projections are topographically arranged [8, 9, 14]. Furthermore, responses of the frog isthmic units to electrical stimulation of the optic nerve and to visual stimuli have been recorded [1, 3, 7, 8, 15, 16]. Ablation studies [4, 6] supported the suggestion of Gruberg and Udin [8] that information from the eye reaches the ipsilateral tectum by way of NI. Glasser and Ingle [4] called NI a 'relay station in the ipsilateral visuo-tectal projection system of the frog', although in the light of comparative studies it seems equally appropriate to emphasize its role as a 'tectal satellite system' [5].

We made extracellular recordings of responses of 125 isthmic units to visual stimuli and marked 101 electrode tip positions with cobalt to reconstruct a visual map in the nucleus isthmi. All experiments were performed on adult frogs, *Rana nigromaculata*. The animals were immobilized with 2% gallamine triethiodide (0.15-0.25 ml) and anesthetized with 2% procaine hydrochloride (0.05 ml). After surgical operation, the frog was kept in a stereotaxic apparatus. A perimeter was centered upon the right eye of the frog. Visual stimuli were a 2° spot of light, as well as 3° and 8° black or white discs, moved automatically by a motor or manually against a grayish background, with an angular velocity of 12°/sec. Black hemispherical occluders were employed to examine binocular units. For

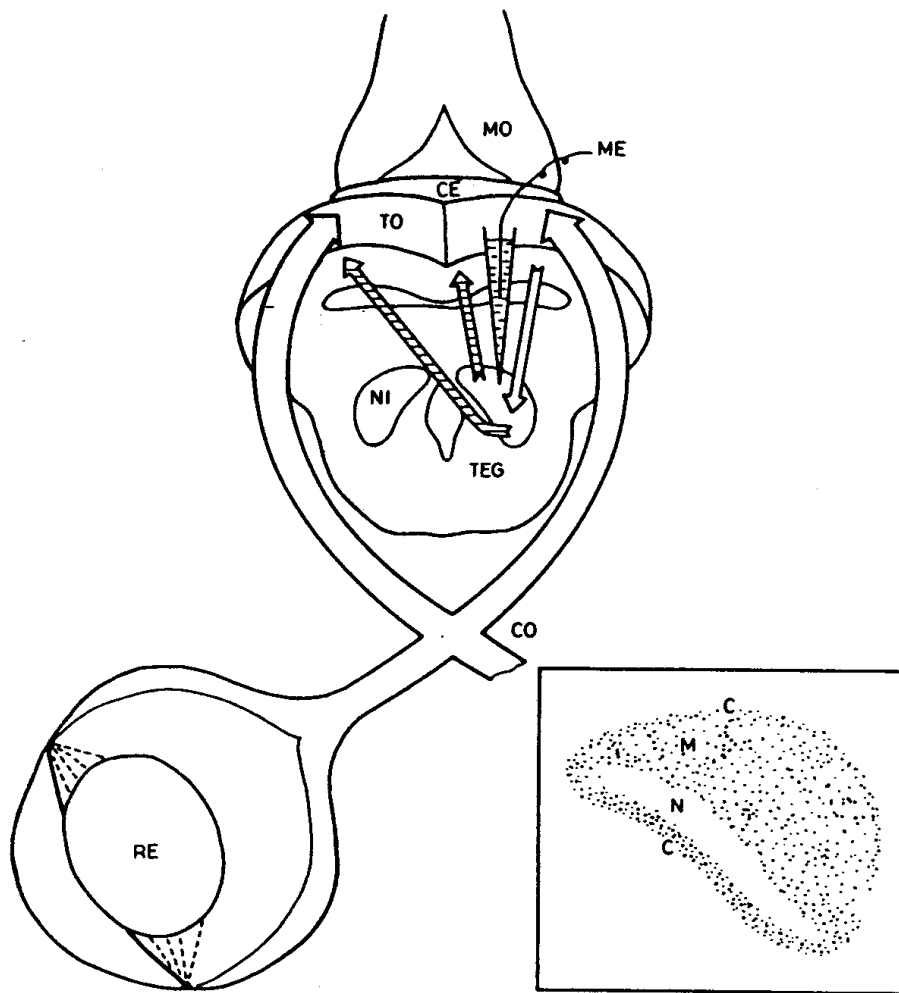


Fig. 1. Location of the nucleus isthmi in the frog brain and neuronal connections of the left isthmic nucleus with the optic tectum. The nucleus receives an ipsilateral input from the tectum and projects bilaterally to the tectum. Inset at right represents cross section of left nucleus isthmi. Abbreviations: CE, cerebellum; CO, optic chiasm; ME, recording electrode; MO, medulla oblongata; NI, nucleus isthmi; RE, right eye; TEG, tegmentum mesencephali; TO, tectum opticum. Divisions of nucleus isthmi (see inset): C, cortex; M, medulla; N, cell-free band.

extracellular recordings, micropipettes (2–4  $\mu\text{m}$  in diameter) filled with a solution containing 2.5 M NaCl and 50 mM  $\text{CoCl}_2$  were inserted into NI according to its stereotaxic coordinates. At the end of an experiment, cobalt ions were ejected by passing positive current pulses [13]. The brain was prepared for histological verification of the recording sites. Camera lucida drawings of the sections were made to reconstruct a visual map in NI.

All of 101 cobalt-stained positions of visual units recorded from the isthmic nucleus area were located within the nucleus, but not beyond its boundaries, indicating that NI proper is a well-defined part of the frog visual system. This finding seems to differ from the results obtained by Vinogradova and Manteifel [15] from their experiments on *Rana temporaria*, applying electrical stimulation to the

optic nerve. In their work, 3 out of 7 recording sites were localized outside the nucleus isthmi, suggesting that both the nucleus and its surrounding region make up a visually responsive area, called the isthmic nucleus area. The discrepancy between these findings and our results may be explained by interspecific differences, although it is more likely due to differences in stimulation, e.g. natural and artificial, respectively.

There is a visual field map in the nucleus isthmi. In general, most of the visual field, including the entire contralateral hemifield and the nasal 40° of the ipsilateral hemifield project on NI topographically. A cell-free band internal to the medial and ventral cortex represents the boundary between the contralateral and the ipsilateral hemifields. Dorsal to it is the contralateral hemifield representation. The median plane, which divides NI into rostral and caudal halves, represents the horizontal meridian of the visual field. The upper field projects upon the rostral half of NI, and upon the central and medioventral portions of the caudal half. The lower field is represented in the dorsal and lateral parts of the caudal half (Fig. 2). This topographic map generally agrees with anatomical findings by Gruberg and Udin [8], but differs in some particulars. Our results indicate that the boundary

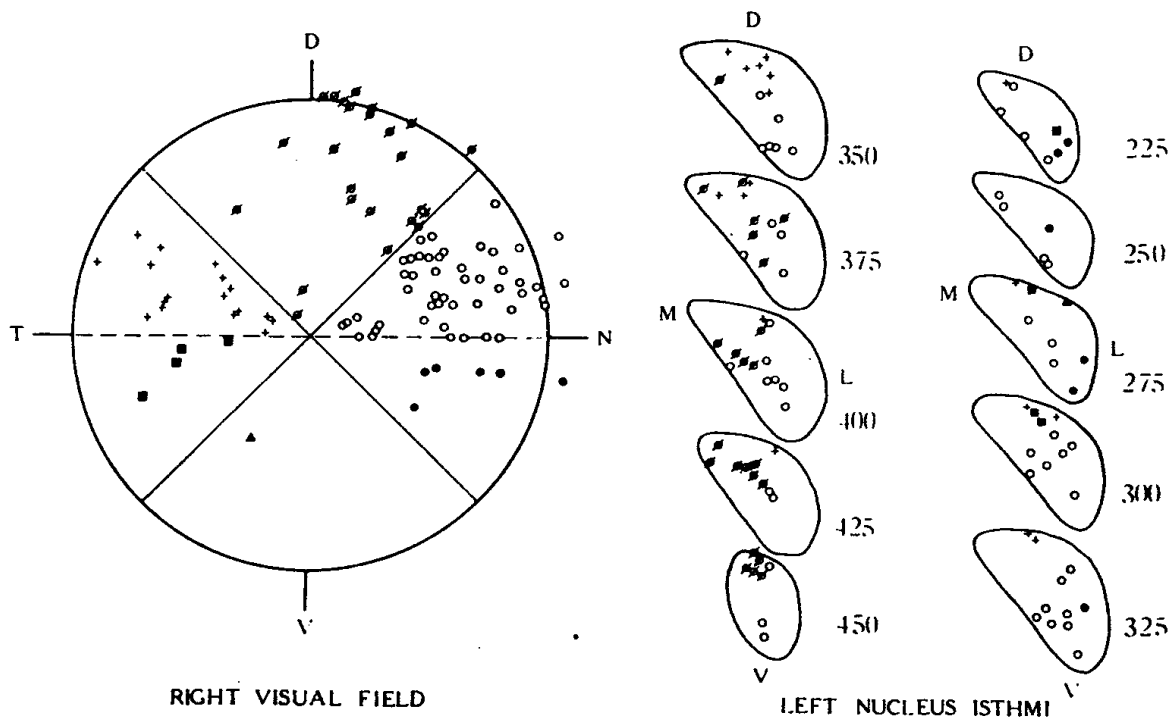


Fig. 2. Distribution of visual units in the left nucleus isthmi (right) and of their corresponding receptive fields in the right visual field (left). The latter extends outwards 100° from the center. Two oblique diameters perpendicular to each other and rotated 45° from the horizontal and vertical meridians define nasal (N), temporal (T), dorsal (D) and ventral (V) quadrants. Symbols marking electrode positions in the cross-sections of nucleus isthmi correspond to the ones representing loci of the receptive fields. The cross-sections are numbered according to the distance in  $\mu\text{m}$  from the caudal pole of the ipsilateral tectum.

separating the contralateral field from the ipsilateral field is the cell-free band, not a horizontal band of cells. Moreover, the medioventral cortex just beneath the cell-free band represents part of the ipsilateral field in front of the frog, whereas the units whose receptive fields are located in the ipsilateral field above the animal lie within the medulla dorsal to the cell-free band.

Responses to visual stimulation of 15 binocular units were recorded from the left NI. Binocular space in front of the frog includes the nasal 40° of the contralateral hemifield and 30° ipsilateral; above the frog's head, it occupies at least the central 10° of the contralateral field and 20° ipsilateral. Fourteen successfully marked binocular units were mainly distributed in the medullary part of rostral NI. The binocular isthmic units were characterized by large receptive fields, averaging 43° along the longest diameter with a range from 17° to 85°. They responded vigorously to movement of black targets and to ON and OFF of a light spot, with OFF responses being stronger than ON responses. Two of 15 units were almost equally driven by the two eyes, the remainder were predominantly activated by the contralateral eye. As far as we are aware this is the first time that binocular units have been found in NI. Based on the anatomical evidence mentioned, and considering the observations, it seems likely that the binocular convergent visual input to these units is mediated by binocular units of the tectum [2, 12] rather than via separate retino-tectal connections.

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- 1 Ansoerge, K. and Grüsser-Cornehls, U., Visual and visual-vestibular responses of frog cerebellar neurons, *Exp. Brain Res.*, 29 (1977) 445-465.
- 2 Fite, K.V., Single-unit analysis of binocular neurons in the frog optic tectum, *Exp. Neurol.*, 24 (1969) 475-486.
- 3 Glasser, S. and Ingle, D.J., The role of the nucleus isthmi in the ipsilateral visual projection to the frog's optic tectum, *Neurosci. Abstr.*, 4 (1978) 630.
- 4 Glasser, S. and Ingle, D.J., The nucleus isthmus as a relay station in the ipsilateral visual projection to the frog's optic tectum, *Brain Res.*, 159 (1978) 214-218.
- 5 Graybiel, A.M., A satellite system of the superior colliculus: the parabigeminal nucleus and its projections to the superficial collicular layers, *Brain Res.*, 145 (1978) 365-374.
- 6 Grobstein, P., Comer, C., Hollyday, M. and Archer, S.M., A crossed isthmo-tectal projection in *Rana pipiens* and its involvement in the ipsilateral visuotectal projection, *Brain Res.*, 156 (1978) 117-123.
- 7 Gruberg, E.R. and Lettvin, J.Y., Anatomy and physiology of a binocular system in the frog *Rana pipiens*, *Brain Res.*, 192 (1980) 313-325.
- 8 Gruberg, E.R. and Udin, S.B., Topographic projections between the nucleus isthmi and the tectum of the frog *Rana pipiens*, *J. comp. Neurol.*, 179 (1978) 487-500.
- 9 Khalil, S.H. and Lázár, G., Nucleus isthmi of the frog: structure and tecto-isthmic projection, *Acta. morph. Acad. Sci. hung.*, 25 (1977) 51-59.

- 10 Larsell, O., The nucleus isthmi of the frog, *J. comp. Neurol.*, 36 (1924) 309–322.
- 11 Lázár, G., Transneuronal transport in the frog visual system, *Brain Res.*, 109 (1976) 623–627.
- 12 Liege, B. and Galand, G., Single-unit visual responses in the frog's brain, *Vision Res.* 12 (1972) 609–622.
- 13 Pitman, R.M., Tweedle, C.D. and Cohen, M.J., Branching of central neurons: intracellular cobalt injection for light and electron microscopy, *Science*, 176 (1972) 412–414.
- 14 Scalia, F., The optic pathway of the frog: nuclear organization and connections. In R. Llinas and W. Precht (Eds.), *Frog Neurobiology*, Springer, Berlin, 1976, pp. 386–460.
- 15 Vinogradova, V.M. and Manteifel, Yu.B., Neuronal responses in the nucleus isthmi area of the frog to optic nerve stimulation, *Neirofiziologiya (Neurophysiology)*, 9 (1977) 33–40 (in Russian).
- 16 Vinogradova, V.M. and Manteifel, Yu.B., Neuronal reactions of the isthmal nucleus area of the frog *Rana temporaria* to visual stimulation, *ZH. Evol. Biokhim. Fiziol. (J. Evol. Biochem. Physiol.)*, 15 (1979) 172–178 (in Russian).
- 17 Wilczynski, W. and Northcutt, G., Afferents to the optic tectum of the leopard frog: an HRP study, *J. comp. Neurol.*, 173 (1977) 219–230.