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BRAIN RESEARCH

Research Report

Tectorotundal connections in turtles: An electron microscopic tracing and GABA-immunocytochemical study

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ABSTRACT

The *nucleus rotundus* of the turtles *Emys orbicularis* and *Testudo horsfieldi* was analysed by axonal tracing methods and post-embedding GABA immunocytochemistry. After injections of horseradish peroxidase or biotinylated dextran amine into the optic tectum, electron microscopic observations showed that the vast majority of ipsilateral tectorotundal axon terminals were small in size, had smooth contours and contained small, round, densely packed synaptic vesicles. These terminals were GABA-immunonegative, often gathered in clusters, and established asymmetrical synaptic contacts with either small- or medium-sized GABA-negative dendritic profiles and with GABA-immunoreactive (GABA-ir) dendrites, which did not contain synaptic vesicles. Occasional GABA-ir-labelled axon terminals were observed; these may arise from the rare GABAergic neurons in the central tectal layer, or from neurons in the ventral pretectal nucleus, which projects both to the optic tectum and *nucleus rotundus*. In addition to tracer-labelled axon terminals, we observed both GABA-negative and GABA-ir cell bodies and dendrites also labelled by the tracer. No GABA-ir presynaptic dendritic profiles containing synaptic vesicles were observed. The existence in reptiles of reciprocal connections between the *nucleus rotundus* and the optic tectum as a phylogenetically ancient feedback system is discussed.

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Abbreviations: BDA, biotinylated dextran amine; DLa, *nucleus dorsolateralis anterior*; DMa, *nucleus dorsomedialis anterior*; d, dendrite; (d–), GABA-immunonegative dendrite; (d+), GABA-immunoreactive (ir) dendrite; (d–/+), GABA-immunonegative/HRP-labelled dendrite; (d+/+), GABA-ir/HRP-labelled dendrite; GABA, gamma-aminobutyric acid; GAD, glutamic acid decarboxylase; GLd, *nucleus geniculatus lateralis*, *pars dorsalis*; HRP, horseradish peroxidase; Lp–Pulv, lateral posterior nucleus/pulvinar complex; N, nucleus; Pedd, dorsal peduncle of the lateral forebrain bundle; Pt, axon terminal containing pleomorphic synaptic vesicles; Ptv, *nucleus pretectalis ventralis*; Rot, *nucleus rotundus*; S, soma; (S–/+), GABA-immunonegative/tracer-labelled cell body; (S+/+), GABA-ir/tracer-labelled cell body; SGC, *stratum griseum centrale* of the optic tectum; SGFS, *stratum griseum et fibrosum superficiale* of the optic tectum; SGP, *stratum griseum periventriculare* of the optic tectum; TrO, *tractus opticus*; TRp, tracer-labelled axon terminal containing pleomorphic synaptic vesicles; TRr, tracer-labelled axon terminal containing round synaptic vesicles; Trtth, *tractus tectothalamicus*

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1. Introduction

The *nucleus rotundus* (Rot), a relay of the retino-tecto-thalamo-telencephalic (tectofugal) visual pathway, has been extensively studied by light microscopy in a variety of reptilian species (turtles: Hall and Ebner, 1970; Belekhova and Kosareva, 1971; Kosareva et al., 1973; Tumanova and Ozirskaia, 1974; Parent, 1976; Rainey, 1979; Balaban and Ulinski, 1981a,b; Rainey and Ulinski, 1982a,b; Reiner, 1994; Belekhova et al., 2003; crocodiles: Braford, 1972; Pritz, 1975, 1995, 1997; Pritz and Stritzel, 1986; lizards: Foster and Hall, 1975; Butler, 1978; Ebbesson, 1981; Hoogland, 1982; Bruce and Butler, 1984; Martinez-Marcos et al., 1998; Guirado et al., 2000; Davila et al., 2002; snakes: Ulinski, 1977; Gruberg et al., 1979; Schroeder, 1981; Dacey and Ulinski, 1983; Welker et al., 1983; Berson and Hartline, 1988; Ulinski et al., 1992). The wide variety of different anterograde and retrograde degeneration and axonal tracing methods used in these studies show consistently that the optic tectum massively innervates the ipsilateral Rot and, to a lesser extent, the contralateral Rot. These afferent fibres arise from cells located in the central tectal layer (*stratum griseum centrale*, SGC; Foster and Hall, 1975; Northcutt, 1984; Ulinski et al., 1992; Reiner, 1994; Martinez-Marcos et al., 1998; Guirado et al., 2000; Davila et al., 2002; Belekhova et al., 2003), and also from some neurons located in the deep tectal layers (Reiner, 1994; Martinez-Marcos et al., 1998; Belekhova et al., 2003). Several morphologically distinct types of tectorotundal projection neurons receive a retinal input onto their dendrites, which extend into the superficial retinorecipient tectal layers.

Studies of the synaptic organisation of the reptilian Rot are considerably fewer in number. In normal material from *Emys orbicularis* (Ozirskaia and Tumanova, 1976), *Pseudemys scripta* and *Chrysemys picta* (Rainey and Ulinski, 1982a), and *Caiman crocodilus* (Schroeder and Pritz, 1996), rotundal cell bodies and dendrites are postsynaptic to two types of axon terminals. The former type contains round synaptic vesicles and makes asymmetrical synaptic contacts with the dendrites of rotundal neurons. These may be organised into clusters, and are more common on the distal two-thirds of the dendrites. The latter type contains small flattened or pleomorphic vesicles and makes symmetrical synaptic contacts with the somata and dendrites of rotundal projection neurons (Tumanova and Ozirskaia, 1974; Rainey and Ulinski, 1982a). Degeneration studies (Tumanova and Ozirskaia, 1974; Rainey and Ulinski, 1982b) show that the terminals of the tectorotundal projection correspond to those of the first type observed in normal material. Comparable findings have been described in the lizard *Psammodromus algirus* (Davila et al., 2002) after unilateral injection of biotinylated dextran amine (BDA) into the Rot and electron microscopic analysis of the contralateral

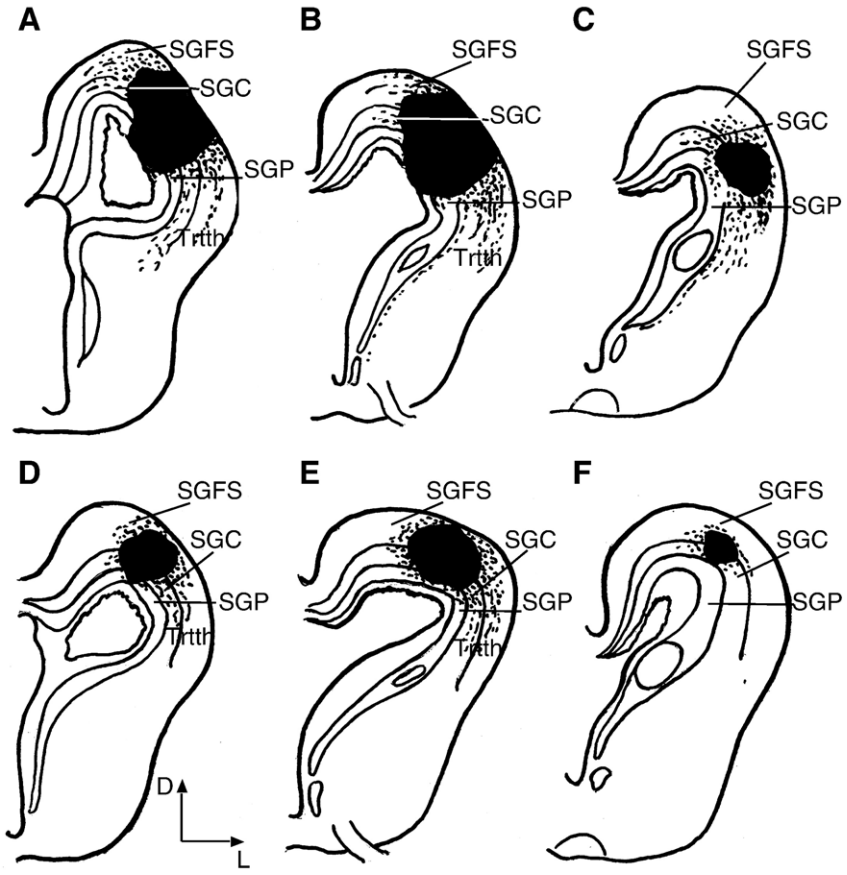

Fig. 1 – Schematic drawings of three rostro-caudal transverse sections of the optic tectum showing the localisation of the BDA injection in *Emys* (A–C) and HRP injection in *Testudo* (D–F). Black areas represent the injection site, dots the spreading areas of the tracer diffusion, and the dashed lines represent the labelled fibres. (D) and (L), respectively, represent the dorsal and lateral axes of the brain. For other abbreviations, see list.

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